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LONG-RANGE EFFECTS OF THE SUN'S VARIATION ON THE TEMPERATURE OF WASHINGTON, D. C.

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In a closely knit series of four recent papers [1] I have shown (1) that the sun's output of radiation varies regularly in 23 periods, all integrally submultiples of $22\frac{3}{4}$ years; (2) that customary methods of tabulating weather records, giving normal values therewith, are faulty for computations of periodic terms because the normals are taken as a whole, without segregation of times of high and of low sunspot frequency; (3) that with proper normal values and attention paid to phase changes, depending on the seasons of the year and on the sunspot frequency, the precipitation at Peoria, Ill., shows plainly control by the regular periodic variations of the sun; (4) that similar control by solar variation is to be found in the precipitation at Albany, N. Y.

Since the variation of the sun operates primarily and directly on the temperature of the atmosphere, and only indirectly on precipitation, it seemed probable that a study of temperature might show even more perfect control by solar variation than does precipitation. I therefore take up in the present paper the temperature of Washington in relation to the 23 known regular periodic variations of the sun's output of radiation. As in the Peoria and Albany papers, I employ, for the most part, the monthly mean values published in the three volumes of "World Weather Records," but supplement these by U. S. Weather Bureau publications since 1940.

As I have shown, in Smithsonian Publication No. 4090, that the normals customarily published are misleading for my purpose, I computed new normals as follows, suited to high and low sunspot activity. I chose as the dividing line a Wolf sunspot number of 20. The temperatures which follow are in degrees Fahrenheit.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
S. P.<20....	33.7	34.6	42.7	53.9	64.0	72.5	77.2	74.1	68.1	56.9	46.0	36.4
S. P.>20....	33.8	35.6	43.1	53.3	63.9	72.4	76.5	74.9	68.3	56.4	45.5	35.3

[1] Smithsonian Misc. Coll., vol. 117, No. 10 (Publ. 4088); No. 11 (Publ. 4090); No. 16 (Publ. 4095), 1952; vol. 121, No. 5 (Publ. 4103), 1953.

From these normal temperature values I computed departures, expressed in tenths of degrees, for all months available from 1854 to 1939. There is a gap in "World Weather Records" of Washington temperatures through 1860 and 1861. To avoid embarrassment by large jumps of temperature from month to month, I computed 5-month running means of the departures. That is, for March use $\dfrac{\text{Jan.–Feb.–Mar.–Apr.–May}}{5}$, and similarly for all months.

From these smoothed temperature departures I computed the effects of the 23 regular periodic variations of the sun's output of radiation, employing only the interval from 1854 to 1939. For I wished to use these results to forecast the behavior of Washington temperature from 1940 to 1951, and to compare such forecast with the actual event. Obviously it is not to be hoped to find in such a manner very close agreement between forecast and event, because of the complexity of the earth's surface and the turbulence of the atmosphere. But if it can be shown that a general forecast of seasons, whether they are to be on the whole warm or cold, wet or dry, can be made with reasonable success for 10 years in advance, it would be of inestimable value to people in many walks of life.

As was shown in the studies of precipitation at Peoria and Albany, changed atmospheric conditions at different seasons of the year and at different activity of sunspots displace the phases of the terrestrial responses to solar variations. The same holds true for the temperature of Washington. In short, the amplitudes and forms of the marches of terrestrial responses to the regular periodic solar variations do not alter greatly, though of course affected by interference of all other periodicities. But the phases of the terrestrial curves shift from season to season and alter with sunspot activity. It is not possible to subdivide the data sufficiently to follow all these phase changes accurately. I have contented myself with separate tabulations for three seasons, viz: January to April—May to August—September to December; and with two states of sunspot activity, viz: S. P.<20, S. P.>20 Wolf numbers.

The method of tabulation follows closely that used in the study of precipitation at Albany. Readers are referred to Smithsonian Publications No. 4095 and No. 4103 for information as to this method. I have gone still farther in the direction of the modifications of Peoria procedure as used at Albany, so as to strengthen the mean values in the Washington temperature tabulations. For, before taking means, I have shifted to a common phase the phases of all six mean tabula-

tions for the three seasons, and for the two intervals, 1854-1899, and 1900-1939, with all 13 periods up to $15\frac{1}{8}$ months. At Albany only seven periods were thus treated. I have also cleared every long period from $22\frac{4}{5}$ months to 91 months of overriding shorter periods, which are integral submultiples of these long periods. In this way it was found unnecessary to use periods longer than $45\frac{1}{2}$ months, for all the amplitudes of still longer periods were produced by overriding shorter ones. The 20 periods actually used for Washington temperatures were as follows, expressed in months:

$4\frac{1}{3}$, $5\frac{1}{8}$, 6-1/15, 7, $8\frac{1}{8}$, $9\frac{1}{6}$, $9\frac{3}{4}$, 10-1/10, 10-6/10, $11\frac{1}{3}$, 13-1/10, 13-6/10, $15\frac{1}{8}$, $22\frac{4}{5}$, $24\frac{2}{3}$, $27\frac{1}{4}$, $30\frac{1}{3}$, $34\frac{1}{5}$, $38\frac{2}{3}$, $45\frac{1}{2}$.

To illustrate the points brought out above I give several figures.

Figures 1 and 2 relate to the period of 13.6 months, as tabulated in tables 1 and 2. Figure 1 and table 1 cover the times when Wolf sunspot numbers exceeded 20, and figure 2 and table 2, the times when these were below 20. As usual, for periods of less than $22\frac{4}{5}$ months tables 1 and 2 each comprise six independent subordinate tables, which I am accustomed to designate as A_1, A_2; B_1, B_2; C_1, C_2. Subscripts 1 and 2 relate, respectively, to times before and after 1900 in the span of years 1854 to 1939. Letters A, B, C, relate, respectively, to the months January to April, May to August and September to December. Symbols ok, $\uparrow$, $\downarrow$ indicate whether curves were unchanged, moved earlier, or moved later in their phases before taking means marked M.

In the 13.6-month tabulation for sunspots>20, the subordinate tables have the following numbers of columns:

Designation:	A_1	A_2	B_1	B_2	C_1	C_2
No. of columns:	6	5	7	8	5	6

Without giving dates of beginnings of columns or the temperatures found in the individual columns, and recalling to the reader that, in order to keep average lengths exactly 13.6 months, certain temperatures are duplicated so that the columns as tabulated are 14 months long, I now give in table 1 the mean values for A_1, A_2; B_1, B_2; C_1 C_2 and their departures from the averages of these mean columns. The means and the departures are stated in hundredths of a degree Fahrenheit.

The columns of departures from table 1 are plotted in figure 1 with the appropriate letters. Along with their letters are given symbols ok, $\uparrow$, or $\downarrow$, to show what shifts of phases were required to bring the six curves to a common phase. In table 3 these changes of phase are made, and the mean of the departures is taken as thus arranged. This mean of departures is always employed, but reduced back to its proper
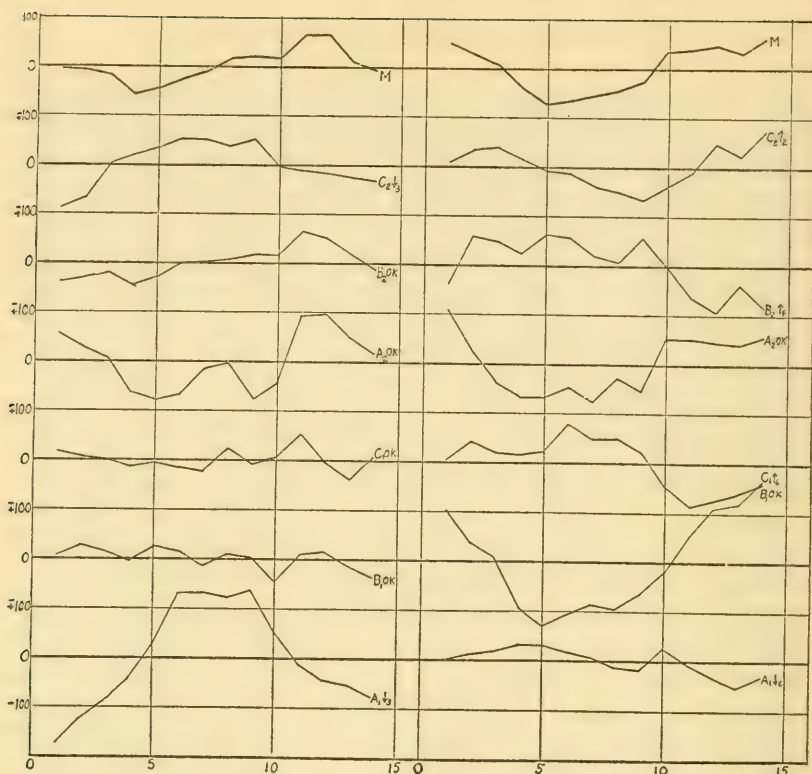
FIG. 1.—Sunspots>20 numbers.   FIG. 2.—Sunspots<20 numbers.

Six determinations of the periodicity of 13.6 months and their mean at uniform phases in each figure. Ordinates, hundredths degree Fahrenheit. Abscissae, months. Other symbols explained in the text.

TABLE I.—*Illustrating tabulation for 13.6 months. S.P.>20*

	A_1		B_1		C_1		A_2		B_2		C_2	
	Mean	Dep.	Mean	Dep.	Mean	Dep.	Mean	Dep.	Mean	Dep.	Mean	Dep.
	−173	−173	− 41	+ 5	−16	+17	+ 38	+ 57	−30	−39	− 20	−87
	−123	−123	− 17	+ 29	−28	+ 5	+ 8	+ 25	−21	−30	0	−67
	− 87	− 87	− 31	+ 15	−34	− 1	− 12	+ 7	−11	−20	+ 70	+ 3
	− 43	− 43	− 49	− 3	−44	−11	− 84	− 65	−36	−45	+ 90	+23
	+ 32	+ 32	− 21	+ 25	−42	− 8	− 96	− 77	−17	−26	+100	+33
	+135	+135	− 31	+ 15	−50	−17	− 88	− 69	+9	0	+120	+53
	+135	+135	− 59	− 13	−54	−21	− 32	− 13	+11	+ 2	+117	+50
	+125	+125	− 39	+ 7	−10	+23	− 20	− 1	+16	+ 7	+105	+38
	+137	+137	− 44	+ 2	−42	− 9	− 94	− 75	+25	+16	+118	+51
	+ 52	+ 52	− 93	− 47	−28	+ 5	− 64	− 45	+24	+15	+ 62	− 5
	− 13	− 13	− 36	+ 10	+20	+53	+ 74	+ 93	+72	+63	+ 55	−12
	− 45	− 45	− 31	+ 15	−36	− 3	+ 78	+ 97	+59	+50	+ 50	−17
	− 53	− 53	− 61	− 15	−72	−39	+ 30	+ 49	+27	+18	+ 42	−25
	− 78	− 78	− 81	− 35	−26	+ 7	− 2	+ 17	− 5	−14	+ 35	−32
Means	00		− 46		−33		− 19		+ 9		+ 67	

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phase status in the syntheses to be described below. It is used instead of the individual columns of departures given in table 1, because it rests on 37 columns of temperatures, instead of on 5, 6, 7, or 8 columns, like the individual sets of departures in table 1. The reader should recall that nearly 20 other periodicities have their effects upon the columns of temperatures used to determine the periodicity of 13.6 months. Hence it is highly desirable to screen out these interferences by numerous repetitions of the temperature columns.

The final mean of departures is graphed in the heavy line, M, of figure 1.

With this explanation of figure 1 and tables 1 and 3, it will not be necessary to explain in detail figure 2 and tables 2 and 4. But it is interesting to point out that the two heavy curves, M, of final columns of mean departures, plotted in figures 1 and 2, are very similar in form and amplitude but differ in phase, and that they are derived from wholly independent groups of temperatures, one group coming solely from times when Wolf sunspot numbers exceed 20, and the other when these were below 20.

In the 13.6-month tabulation, table 2, for sunspots<20 the subordinate tables have the following numbers of columns:

Designation:	A_1	A_2	B_1	B_2	C_1	C_2
No. of columns:	8	6	4	5	6	6

The mean of departures shown in table 4 therefore rests on the temperatures contained in 35 columns summarized in table 2.

TABLE 2.—*Illustrating tabulation for 13.6 months. S.P.<20*

A_1		B_1		C_1		A_2		B_2		C_2	
Mean	Dep.	Mean	Dep.	Mean	Dep.	Mean	Dep.	Mean	Dep.	Mean	Dep.
— 40	+ 3	+ 7	+101	+ 2	+ 2	+163	+109	—14	—37	+123	+ 6
— 31	+ 12	— 57	+ 37	+40	+40	+ 80	+ 26	+80	+57	+148	+31
— 26	+ 19	— 87	+ 7	+20	+20	+ 12	— 42	+72	+49	+155	+38
— 11	+ 32	—182	— 88	+15	+15	— 13	— 67	+48	+25	+132	+15
— 12	+ 31	—225	—131	+23	+23	— 13	— 67	+84	+61	+110	— 7
— 24	+ 19	—202	—108	+78	+78	+ 7	— 47	+80	+57	+105	—12
— 36	+ 7	—180	— 86	+50	+50	— 22	— 76	+42	+19	+ 78	—39
— 56	— 13	—190	— 96	+50	+50	+ 28	— 26	+28	+ 5	+ 67	—50
— 60	— 17	—157	— 63	+23	+23	0	— 54	+78	+55	+ 48	—69
— 15	+ 28	—110	— 16	—47	—47	+105	+ 51	+18	— 5	+ 78	—39
— 51	— 8	— 50	+ 54	—87	—87	+105	+ 51	—44	—67	+103	—14
— 74	— 31	+ 15	+109	—72	—72	+100	+ 46	—72	—95	+165	+48
— 95	— 52	+ 25	+119	—60	—60	+ 94	+ 40	—16	—39	+138	+21
— 74	— 31	+ 70	+164	—40	—40	+110	+ 56	—62	—85	+187	+70
Means — 43		— 94		00		+ 54		+23		+117	

In tables 5 and 6, and figure 3 I give the evidence which shows that it is unnecessary to employ the periodicity of $54\frac{1}{2}$ months in Washington temperature. As usual, I employ the symbols A_1 and A_2 to indi-

TABLE 3.—*Combined table for 13.6 months. S.P.$>$20*

$A_1\downarrow_3$	A_2ok	B_1ok	B_2ok	C_1ok	$C_2\downarrow_3$	Mean
− 45	+57	+ 5	−39	+17	−17	− 5
− 53	+25	+29	−30	+ 5	−25	− 8
− 78	+ 7	+15	−20	− 1	−32	−18
−173	−65	− 3	−45	−11	−87	−59
−123	−77	+25	−26	− 8	−67	−46
− 87	−69	+15	0	−17	+ 3	−26
− 43	−13	−13	+ 2	−21	+23	−11
+ 32	+ 1	+ 7	+ 7	+23	+33	+17
+135	−75	+ 2	+16	− 9	+53	+20
+135	−45	−47	+15	+ 5	+50	+18
+125	+93	+10	+63	+53	+38	+64
+127	+97	+15	+50	− 3	+51	+64
+ 52	+47	−25	+18	−39	− 5	+ 8
− 13	+17	−35	−14	+ 7	−12	− 8

TABLE 4.—*Combined table for 13.6 months. S.P.$<$20*

$A_1\downarrow_6$	A_2ok	B_1ok	$B_2\uparrow_6$	$C_1\uparrow_6$	$C_2\uparrow_2$	Mean
−17	+109	+101	+19	+60	+38	+50
+28	+ 26	+ 37	+ 5	+50	+15	+27
− 8	− 42	+ 7	+55	+23	− 7	+ 5
−31	− 67	− 88	− 5	−47	−12	−42
−52	− 67	−131	−67	−87	−39	−74
−31	− 47	−108	−95	−72	−50	−67
+ 3	− 76	− 86	−39	−60	−69	−55
+12	− 26	− 96	−85	−40	−39	−46
+19	− 54	− 63	−37	+ 2	−14	−25
+32	+ 51	− 16	+57	+40	+48	+35
+31	+ 51	+ 54	+49	+20	+21	+38
+19	+ 46	+109	+25	+15	+70	+47
+ 7	+ 40	+ 49	+61	+23	+ 6	+31
−13	+ 56	+164	+57	+78	+31	+62

cate results from temperatures recorded before and after 1900, during the interval of years 1854 to 1939. In table 5 the column A_1 is the mean of eight columns and the column A_2 of nine columns. The departures shown in these tabulations having been plotted in figure 3, the tabulation of A_2 discloses the presence of the overriding periodicity of $9\frac{1}{6}$ months, approximately one-sixth of the $54\frac{1}{2}$-month period.

To eliminate it, the departure values in column A_2, table 5, were arranged in six columns and their mean taken as shown in table 6.

These mean departures, repeated six times, are given in table 5, and, being subtracted from column A_2, give the departure column A^1_2. The values A^1_2 are plotted in figure 3, and show great similarity in form and phase relations to the departures A_1. So the mean of A_1 and A^1_2 is taken in table 5, and plotted in figure 3. It is now obvious that the
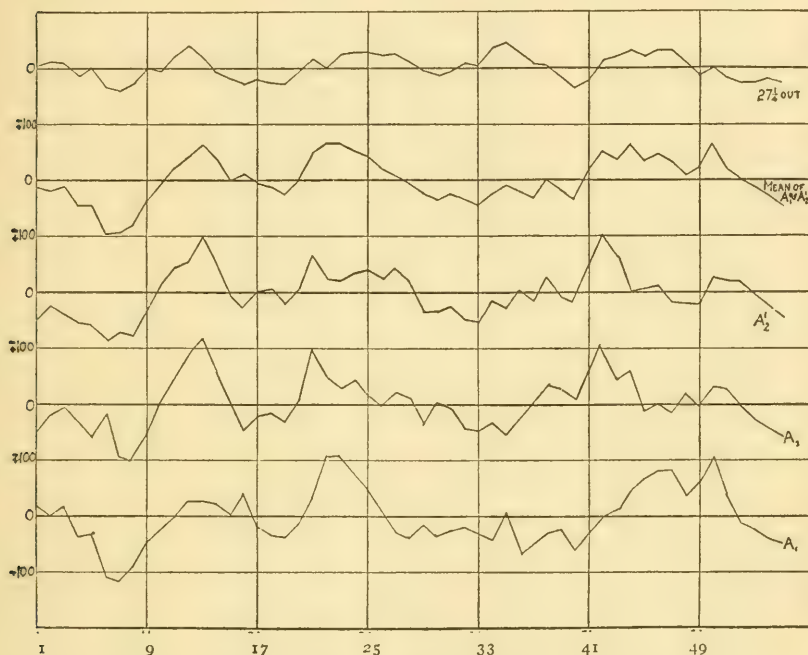

FIG. 3.—The $54\frac{1}{2}$-month periodicity, cleared of superriding periodicities, as explained in the text.

curve has an overriding periodicity of half its length. Hence the mean of departures of columns A_1 and A^1_2 is analyzed for a periodicity of $(54\frac{1}{2} \div 2)$ months, yielding the results shown in table 6 and repeated end to end in table 5. Subtracting from the values given in the next preceding column, and plotting the remainder in figure 3, it is now obvious that only the effect of the overriding periodicity of $11\frac{1}{5}$, or approximately one-fifth of $54\frac{1}{2}$ months, remains. Hence it proves unnecessary to employ the periodicity of $54\frac{1}{2}$ months at all in the synthesis of Washington temperatures. Similar steps eliminate the periodicities of $68\frac{1}{2}$ months and 91 months from consideration.

We are now prepared to test the usefulness of the 20 periodic terms which have been worked out in the Washington departures from

TABLE 5.—*Clearing the periodicity of 54½ months of overrides*

Mean of 8	Dep. A₁	Mean of 9	Dep. A₂	The 9½M.	Δ A¹₂	Mean A₁ & A¹₂	The 27½M.	Δ
— 9	+ 15	— 7	— 49	—10	—39	—12	—19	+ 7
— 24	0	+ 19	— 23	+ 3	—26	—13	—24	+11
— 6	+ 18	+ 38	— 4	+36	—40	—11	—19	+ 8
— 59	— 35	+ 9	— 33	+22	—55	—45	—40	—15
— 57	— 33	— 8	— 50	+ 8	—58	—45	—44	— 1
—134	—110	— 36	— 78	+ 8	—86	—98	—63	—35
—141	— 17	— 51	— 93	—19	—74	—95	—53	—42
—114	— 90	— 60	—102	—24	—78	—84	—56	—28
— 70	— 46	— 11	— 53	—22	—31	—38	—35	— 3
— 50	— 26	+ 44	+ 2	—10	+12	— 7	— 3	— 4
— 26	— 2	+ 89	+ 47	+ 3	+44	+21	0	+21
+ 4	+ 28	+131	+ 89	+36	+53	+40	0	+40
+ 4	+ 28	+160	+118	+22	+96	+62	+38	+24
0	+ 24	+101	+ 59	+ 8	+51	+37	+42	— 5
— 22	+ 2	+ 44	+ 2	+ 8	— 6	— 2	+18	—20
+ 14	+ 38	— 2	— 44	—19	—25	+ 6	+34	—28
— 40	— 16	+ 19	— 23	—24	+ 1	— 8	+ 5	—23
— 56	— 32	+ 23	— 19	—22	+ 3	—14	+15	—29
— 60	— 36	+ 10	— 32	—10	—22	—29	+ 1	—30
— 37	— 13	+ 50	+ 8	+ 3	+ 5	— 4	+ 2	— 6
+ 7	+ 31	+143	+101	+36	+65	+48	+33	+15
+ 80	+104	+ 88	+ 46	+22	+24	+64	+63	+ 1
+ 84	+108	+ 71	+ 29	+ 8	+21	+64	+42	+22
+ 51	+ 75	+ 83	+ 41	+ 8	+33	+54	+28	+26
+ 27	+ 51	+ 59	+ 17	—19	+36	+43	+16	+27
— 12	+ 12	+ 41	— 1	—24	+23	+17	— 6	+23
— 51	— 27	+ 60	+ 18	—22	+40	+ 6	—19	+25
— 62	— 38	+ 53	+ 11	—10	+21	— 8	—18	+10
— 42	— 18	+ 10	— 32	+ 3	—35	—26	—18	— 8
— 81	— 37	+ 43	+ 1	+36	—35	—36	—24	—12
— 52	— 28	+ 37	— 5	+22	—27	—28	—19	— 9
— 44	— 20	— 1	— 43	+ 8	—51	—35	—40	+ 5
— 54	— 30	— 6	— 48	+ 8	—56	—43	—44	+ 1
— 66	— 42	+ 7	— 35	—19	—16	—29	—63	+34
— 20	+ 4	— 11	— 53	—24	—29	—12	—53	+41
— 85	— 61	+ 16	— 26	—22	— 4	—28	—56	+28
— 70	— 46	+ 48	+ 6	—10	—16	—31	—35	+ 4
— 54	— 30	+ 74	+ 32	+ 3	+19	0	— 3	+ 3
— 60	— 36	+ 71	+ 29	+36	— 7	—21	0	—21
— 86	— 62	+ 48	+ 6	+22	—16	—39	0	—39
— 41	— 17	+ 97	+ 55	+ 8	+47	+15	+38	—23
— 27	— 3	+148	+106	+ 8	+98	+47	+42	+ 7
— 14	+ 10	+ 87	+ 45	—19	+64	+37	+18	+19
+ 19	+ 43	+100	+ 58	—24	+82	+62	+34	+28
+ 45	+ 69	+ 28	— 14	—22	+ 8	+38	+15	+23
+ 57	+ 81	+ 42	0	—10	+10	+45	+15	+30
+ 57	+ 81	+ 28	— 14	+ 3	—17	+32	+ 1	+31
+ 14	+ 38	+ 57	+ 15	+36	—21	+ 8	+ 2	+ 6
+ 37	+ 61	+ 41	— 1	+22	—23	+19	+33	—14
+ 81	+105	+ 72	+ 30	+ 8	+22	+63	+63	0
+ 1	+ 25	+ 67	+ 25	+ 8	+17	+21	+42	—21
— 36	— 12	+ 40	— 2	—19	+17	+ 2	+28	—26
— 47	— 23	+ 16	— 26	—24	— 2	—12	+16	—28
— 65	— 41	+ 2	— 40	—22	—18	—29	— 6	—25
— 72	— 48	— 16	— 58	—10	—42	—45	—19	—26
Means... — 24		+ 42						

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TABLE 6.—*Periodicities 9⅙ and 27¼M*

The 9⅙-month periodicity from departures A_2

						Mean
— 49	+ 2	— 32	+11	+ 6	0	—10
— 23	+ 47	+ 8	—32	+ 32	—14	+ 3
— 4	+ 89	+101	+ 1	+ 29	+15	+36
— 33	+118	+ 46	— 5	+ 6	— 1	+22
— 50	+ 59	+ 29	—43	+ 55	+30	+ 8
— 78	+ 2	+ 41	—48	+106	+25	+ 8
— 93	— 44	+ 17	—35	+ 45	— 2	—19
—102	— 23	— 1	—53	+ 58	—26	—24
— 53	— 19	+ 18	—26	— 14	—40	—22

The 27¼-month periodicity from mean A_1 and A^1_2

		Mean
—12	—26	—19
—13	—36	—24
—11	—28	—19
—45	—35	—40
—45	—43	—44
—98	—29	—63
—95	—12	—53
—84	—28	—56
—38	—31	—35
— 7	0	— 3
+21	—21	0
+40	—39	0
+62	+15	+38
+37	+47	+42
— 2	+37	+18
+ 6	+62	+34
— 8	+38	+ 5
—14	+45	+15
—29	+32	+ 1
— 4	+ 8	+ 2
+48	+19	+33
+64	+63	+63
+64	+21	+42
+54	+ 2	+28
+43	—12	+16
+17	—29	— 6
+ 6	—45	—19

normal temperatures for the interval from 1854 to 1939. It is proposed to synthesize the results in such a manner as to forecast the march of temperatures from 1940 to 1951, 12 years, and to compare this synthetic forecast with the event. As the departures in monthly records used for the interval 1854 to 1939 were smoothed by 5-month running means, it is proper to compute the monthly departures from

the same normals over the period 1940 to 1951, and to smooth these departures also by 5-month running means.

As it is common knowledge that the temperature of eastern United States has been gradually rising for the past century, it is highly probable that we shall find that the departures from our normals, which I computed from records of 1854 to 1939, will be prevailingly plus during the interval 1940 to 1951. On another account it is also unlikely that the scale of the synthetic summation of the effects of 20 periodicities will be exactly the scale of our normal values. For the accumulation of such inaccuracies as have resulted from computing departures from averages of 20 means, such as are shown in tables 1 and 2, must almost infallibly result in a plus or a minus departure in the synthesis. Hence, on both accounts, just mentioned, we can expect that there may be a systematic difference in level between the synthesis and the event for the years 1940 to 1951.

Furthermore, as appeared in the study of the precipitation at Peoria and Albany and, indeed, in the tabulation of Washington temperatures, in comparing results before and after 1900, there are encountered brief, as yet unpredictable, shifts of phase between synthesis and event in the study of the control of weather by periodic solar variations. Therefore we are to expect not only some systematic difference in scale level between the synthesized forecast and the event in Washington temperatures from 1940 to 1951, but we may also expect occasional brief unpredictable shifts of phase between the predicted and observed results. With these remarks we preface the results obtained.

In table 7 I give a sample of the synthesis covering only part of the year 1940. Figure 4 shows in the thin full line the synthesis, and in the thick full line the event, for the years 1940 to 1951. The systematic difference in scale referred to above amounts to 3.0 degrees Fahrenheit, the synthesis being lower than the event. It has been removed in the thick dotted line by a flat addition of 3.0 degrees to the synthesis, in order that attention might not be diverted from the comparative marches of the two curves. That is the real test of the method. In figure 4 the lighter line represents the synthetic forecast, as computed after the manner of table 7. It is apparent that the principal features are found in the curves both of forecast and event. But throughout the 12 years the event runs behind the forecast by several months. From 1940 to May 1941 the lag is 4 months. Thence, in the long interval to July 1948 the lag holds steadily at 3 months. Thence to October 1951 it is only 2 months. In the dotted line I have made these indicated shifts of phase, retreating the features of the

45½	Σ
0	+165
+10	+ 57
+17	− 42
+16	−321
+14	−431
+11	−501
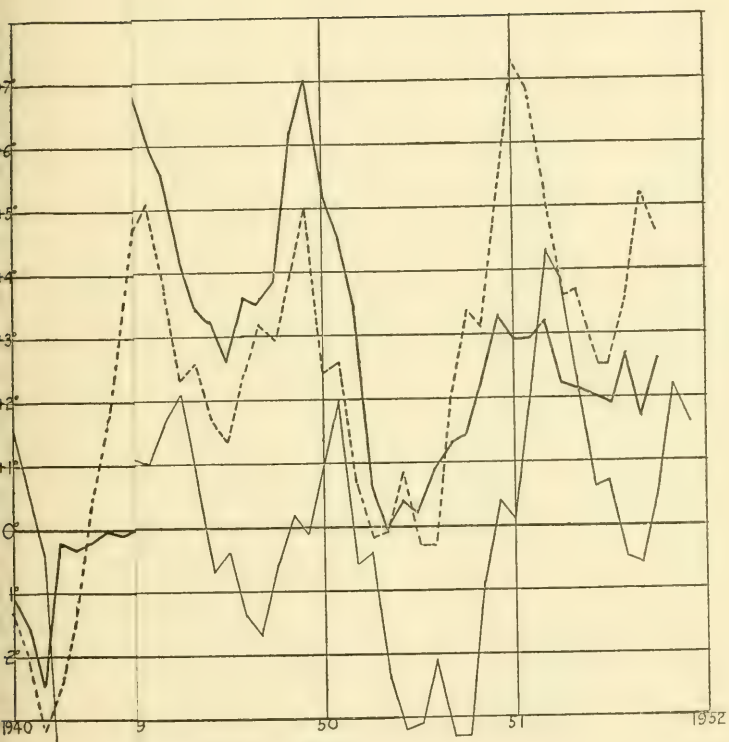
20 periodicities deter-
ed; dotted curve, pre-

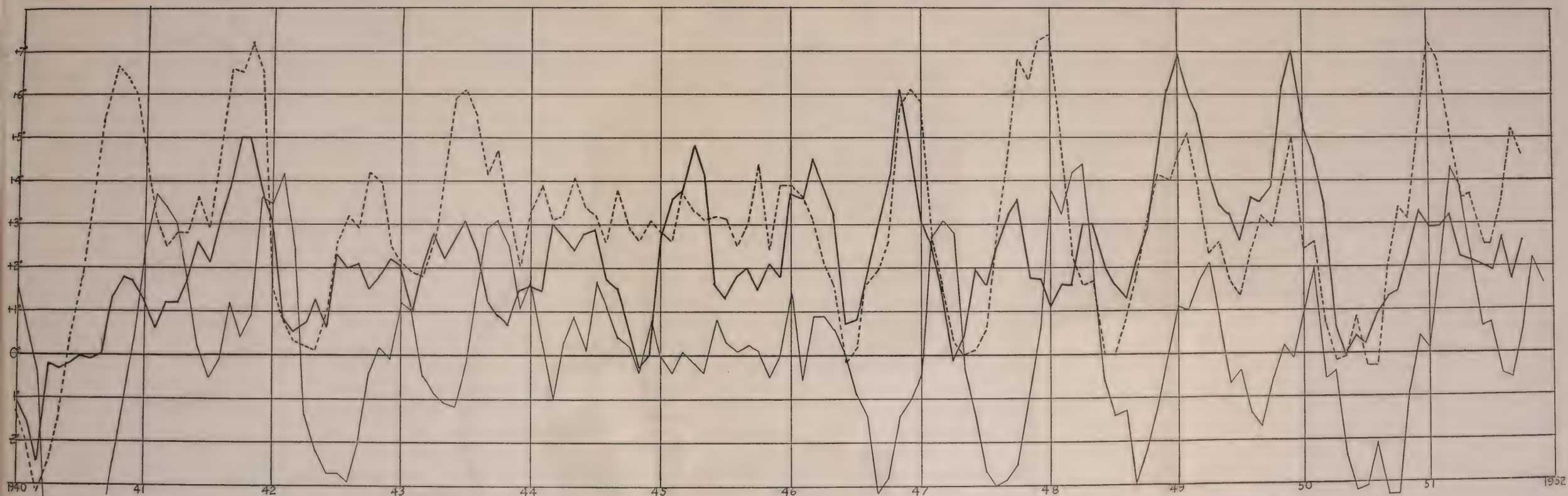| 1940	4½
Jan. ..	+24
Feb. ..	−11
Mar. ..	− 1
Apr. ..	−11
May ..	−11
June ..	− 1

Fig. 4.—Predicted and observed temperature departures for Washington, D. C., years 1940 to 1951. Prediction, synthesis from 20 periodicities determined from records, 1854 to 1939. Ordinates, degrees Fahrenheit. Abscissae, years. Heavy curve, observed; full light curve, predicted; dotted curve, predicted, altered in phases and scale as described in the text. All temperatures smoothed by 5-month running means before used.

TABLE 7.—*A sample of synthesis of periodic Washington temperature departures. Periods in months. Temperature departures in hundredths of a degree Fahr.*

1940	4⅓	5½	6₁₅	7	8⅓	9¼	9¾	10₁₀	10⁶₁₀	11⅔	13¹⁰₁₆	13⁷₁₆	15⅝	22⅔	24⅝	27¼	30⅔	34⅓	38⅔	45⅓	Σ
Jan.	+24	+31	+ 6	+23	+32	−35	+26	+43	+61	+44	+17	− 5	−18	+ 6	+ 1	−18	− 75	+48	−40	0	+165
Feb.	−11	+ 9	+27	+25	+56	−36	+65	+17	+31	+48	+24	− 8	−26	+ 1	+ 9	−24	−113	0	−47	+10	+ 57
Mar.	− 1	−10	+16	+ 2	+35	− 1	+47	+ 8	+22	+15	+30	−18	−32	− 5	+ 1	−19	− 90	− 7	−52	+17	− 42
Apr.	−11	−19	−29	−26	−14	− 7	+23	−15	− 2	−10	+21	−59	−30	−10	+ 1	−30	− 90	+28	−58	+16	−321
May	−11	−12	−24	+ 4	−28	+ 6	+ 9	−71	−21	−44	+22	−46	−23	−13	−21	−44	− 82	+ 8	−66	+14	−431
June	− 1	+ 9	+ 3	−21	−25	+16	−23	−44	−42	−52	− 8	−26	−24	−16	−77	−63	− 41	− 6	−71	+11	−501

11

heavy dotted curve of the forecast, as just indicated. Thus the forecast in the dotted line can readily be compared with the heavy full curve of the event.

To gather more data on the sporadic changes of phase, as yet unpredictable, I synthesized the periodicities from 1934 to 1939 and compared the synthesis with the event. I was surprised to find that in this interval, when, as one might say, the synthesis should be tailored to fit the event, there was less satisfactory accordance than in the forecasted interval, 1940 to 1951.

From September 1936 to September 1938 synthesis and event are exactly in the same phase. From September 1938 to January 1940 immediately preceding my forecast, the synthesis goes ahead of the event by 3 months, as it does in most of my forecasted interval, but is not yet 4 months, as immediately followed in the interval January 1940 to May 1941.

The scale level of the synthesis from 1934 to 1939 lies about 3 degrees below that of the event, as it did later, through most of the interval from 1934 to 1939, but less in the months nearer 1934. If the causes of the changes of level and of phase in these comparisons could be unraveled and such changes predicted, a very great advance in meteorology would ensue.

I think it can hardly be denied that there is a similarity between the main features of the 12-year forecast and of the event. This similarity is especially strongly marked in the rise of temperature from 1940 through 1941, though marred by the excessive rise of forecasted temperature at the end of 1940. The similarity is even more striking from May 1948 to December 1950, 8 to 11 years after the forecast began. But here an additional systematic difference of about 1 degree in level is seen.

There are many who are so impressed by the elegance of the method of correlation coefficients as an index of the worth of a forecast, that they are contemptuous of curve comparisons as a test. To me this seems unfair and misleading. For instance, old water mills used to employ tooth and pin gears, irregularly made by ordinary carpenters and having large and variable amounts of backlash. There was really 100 percent correlation in the running of a pair of these gears. But they were often out of step, owing to the combined effects of imperfect spacing and wide backlash. Computed coefficients of correlation would fall far short of 100 percent.

In the control of weather by solar variation, obvious and certain though it is, the complexity of the earth's surface and atmosphere

causes variations in the lag of response to regular periodic variations. Consequently, when it is quite obvious that a pair of curves of forecast and event are related, a rapid rise or decline may be found in one curve slightly in advance of the other. This causes large departures between the two curves and may bring down the computed correlation coefficient to apparent meaninglessness. Mere obstacles to the free opera-

TABLE 8.—*Forecast of Washington 5-month running mean Fahrenheit temperatures, 1952 to 1959*

1952	Jan.	39°.1	1954	Jan.	34°.4	1956	Jan.	37°.7	1958	Jan.	38°.8
	Feb.	40.4		Feb.	35.7		Feb.	37.3		Feb.	41.0
	Mar.	47.3		Mar.	43.4		Mar.	43.7		Mar.	47.1
	Apr.	56.9		Apr.	54.5		Apr.	55.2		Apr.	55.8
	May	66.2		May	64.8		May	64.1		May	64.7
	June	72.6		June	73.1		June	70.6		June	71.2
	July	75.7		July	78.4		July	75.7		July	76.0
	Aug.	73.9		Aug.	76.8		Aug.	74.2		Aug.	75.3
	Sept.	66.2		Sept.	72.6		Sept.	68.8		Sept.	70.1
	Oct.	55.8		Oct.	63.3		Oct.	58.7		Oct.	58.8
	Nov.	44.2		Nov.	51.7		Nov.	49.1		Nov.	48.6
	Dec.	35.2		Dec.	40.8		Dec.	40.5		Dec.	37.8
1953	Jan.	35.3	1955	Jan.	37.4	1957	Jan.	37.6	1959	Jan.	35.6
	Feb.	35.9		Feb.	37.4		Feb.	38.4		Feb.	36.6
	Mar.	43.1		Mar.	45.1		Mar.	45.0		Mar.	43.3
	Apr.	54.2		Apr.	54.3		Apr.	54.5		Apr.	54.6
	May	63.7		May	61.8		May	63.7		May	65.6
	June	72.4		June	70.3		June	70.8		June	74.3
	July	78.9		July	75.9		July	75.5		July	77.8
	Aug.	76.9		Aug.	74.3		Aug.	76.0		Aug.	76.2
	Sept.	71.6		Sept.	71.4		Sept.	68.1		Sept.	70.4
	Oct.	61.8		Oct.	62.3		Oct.	57.1		Oct.	59.1
	Nov.	49.8		Nov.	51.7		Nov.	47.7		Nov.	48.1
	Dec.	38.9		Dec.	40.4		Dec.	38.2		Dec.	40.0

tion of a cause may, in the correlation method, so far obscure the cause that it fails altogether of recognition as the cause. Yet, for practical purposes, the forecast may tell the interested agriculturalist quite nearly enough, in time and amount, the change which he wishes to know in advance.

I regard the results of this test of forecasting Washington temperature as so promising that I have ventured to synthesize the expected Washington temperatures from 1952 to 1959. This forecast is given in table 8. These forecasted 8 years of Washington temperatures I have reduced from the status of departures from normal to actual temperatures Fahrenheit. In making the forecast I have assumed that the lag between synthesis and event will be reduced to zero, and that

the scale of mean temperatures will remain 2 degrees above synthesis, as now prevailing. The comparison of forecast is to be with Weather Bureau Records, means between averages of monthly maxima and monthly minima, at the main Weather Bureau Office, 26th and M Streets, NW., Washington, D. C. Obviously, to check the accuracy of the forecast, the observed temperatures of future years must first be smoothed by 5-month running means.
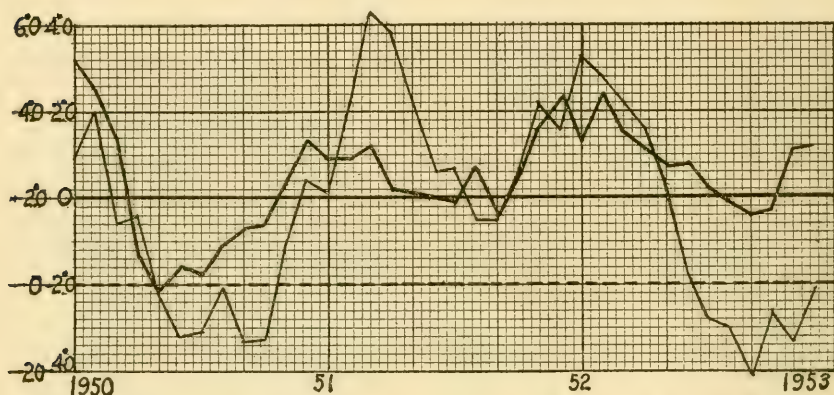

FIG. 5.—Washington temperature departures, 1950 to 1952, predicted (light curve) and observed (heavy curve). Correlation, 50.4 ± 9.7 percent. Temperatures, degrees Fahrenheit. All temperatures smoothed by 5-month running means before used.

To fix upon the probable scale difference and lag, I prepared figure 5, in which departures from normal in the synthesis are plotted from the upper zero line and the right-hand scale of ordinates. The departures observed are plotted from the lower zero line and the left-hand scale of ordinates. The plot begins with 1950 and extends through 1952. A lag of one to two months is seen, as stated above, in the years 1950 and 1951, but seems to vanish in 1952. As for the scale, the synthetic values seem to run about 2° Fahrenheit below the observed values in these three years. So I have assumed that the same scale difference and zero lag will continue till 1959, as stated above.

In view of unpredictable changes of scale and lag heretofore noted, one hardly hopes that such changes will not occur before the end of this forecast. I can hardly hope to live to see it verified to the end. It is really a forecast for 20 years in advance, beginning with the year 1940. Considering that the basis of my forecast lies in records of 1854 to 1939, centering about 1900, one may even justly say that the forecast, 1952 to 1959, is over a half century in advance.

For those who prefer correlation coefficients to graphs, figure 5 gives a correlation coefficient of 50.4 ± 9.7 percent with the scale difference of 2° Fahrenheit removed.

NEW AND INADEQUATELY KNOWN NORTH AMERICAN SPECIES OF THE COPEPOD GENUS DIAPTOMUS

BY

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Anchorage, Alaska

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INTRODUCTION

In the preparation of a new key to the calanoid Copepoda for the revised edition of Ward and Whipple's "Fresh-Water Biology," some new species of *Diaptomus* have been recognized and the status and distribution of other species have been clarified. In order that these new forms may be included in the key, the following diagnostic descriptions and notes are presented. More detailed treatment is reserved for the future monographic review of the North American species.

A considerable part of the present report deals with the species that have in one way or another been confused with *Diaptomus shoshone* Forbes. It became apparent early in the study of the subgenus *Hesperodiaptomus* that it would be necessary to establish the typical form of *D. shoshone* before it and several closely related species could be correctly separated from one another. All that remains of the original collection, which is in the Illinois State Natural History Survey, are slides consisting mostly of dissected appendages. These have been found adequate to determine both the important and unknown diagnostic characters of the type. Study of literature and other collections, particularly the Marsh and Light accessions in the U. S. National Museum, has shown that several definable forms can be unqualifiedly separated from the typical. Two of these (*D. caducus* and *D. nevadensis*) have already been distinguished by Light (1938), though he was unaware that they had been included in published records of *D. shoshone*. The others are herein described as new species.

The confusion of these species with *Diaptomus shoshone* has been largely due to the fact that certain fundamental characters of the genus have been neglected in the descriptions of North American diaptomids. Two of the most important of these are the setation of the antennules of the female, and that of the left side of the male, and the exact form of the left exopod of the male fifth leg. Both of these

characters are significant in the taxonomy of the subgenus *Hesperodiaptomus,* and particularly so in the case of *D. shoshone* and its allies.

The setation of the antennule was recognized as a fundamental specific character by Schmeil (1896) in his comprehensive analysis of the genus, and its invariability has been emphasized by Gurney (1931, p. 114). The exception mentioned by Gurney has been clarified by Kiefer (1932, p. 512). I have noted, in examination of numerous American specimens, that anomalies sometimes occur in the setation, but these are very rare and are recognizable as such because they occur in isolated individuals of a sample and on only one antennule of a pair in the female. Since the subgenus *Hesperodiaptomus*

TABLE 1.—*Antennule setation in the subgenus Hesperodiaptomus* ♀ and left side ♂

Species and sex	Segment										
	2	6	10	11	13	14	15	16	17	18	19
caducus .... ♀ ♂	4	2	2	2	2	2	2	2	2	2	2
hirsutus .... ♀	3	1	2	2	2	2	2	2	2	2	2
" .... ♂	3	1	1	2	1	2	2	2	2	2	2
shoshone .... ♀ ♂	3	1	1	2	1	2	1	2	1	2	1
novemdecimus ..... ♀ ♂	3	1	1	2	1	2	1	2	1	2	2
kenai .... ♀ ♂	3	1	1	2	1	1	1	1	1	1	1
schefferi * .... ♀ ♂	3	1	1	2	1	1	1	1	1	1	1
wardi .... ♀ ♂	3	1	1	2	1	1	1	1	1	1	1
nevadensis .... ♀ ♂	3	1	1	2	1	1	1	1	1	1	1
eiseni .... ♀ ♂	3	1	1	2	1	1	1	1	1	1	1
arcticus .... ♀ ♂	3	1	1	2	1	1	1	1	1	1	1

* *schefferi*—♂ left may occasionally have 2 on 6, as it always has on the right.

belongs to what has been termed the "multisetaceous" group, in which the number of setae on segment 11 is 2, and on segments 13-19 is either 1 or 2, it is highly desirable that the setation of all the species be known. It is therefore presented in table 1. The subgenus differs from any group that has been recorded in literature in having a species in which 4 setae are present on segment 2. In addition, some of the proximal segments may have 2 setae rather than the customary single seta.

The preliminary consideration that has been given in this study to the structure and distribution of *Diaptomus shoshone* and the forms closely allied to it suggests that the group as a whole may be valuable material for studies in variation and distribution. Such studies not only might contribute to the zoogeography of this group but also might have wider application in the much-needed evaluation of structural characters. Since the knowledge of variation and distribution is so

incomplete, no reliable analysis can be made as to the systematic status of these forms. It is therefore not superfluous to emphasize that it is of much importance that published records of *Diaptomus shoshone* and related forms be based upon accurate identification.

SYSTEMATIC DESCRIPTIONS

DIAPTOMUS (HESPERODIAPTOMUS) SHOSHONE Forbes

Figures 1-8

Diaptomus shoshone FORBES, 1893, p. 251, pl. 42, figs. 23-25.—SCHACHT, 1897 (in part), p. 141, pl. 26, fig. 3.—MARSH, 1907, p. 431, pl. 28, figs. 2-5; 1920 (in part), p. 8j; 1929 (in part), p. 17.—DODDS, 1915a, p. 102, fig. 9; 1915b, p. 290, fig. 65; 1917, p. 76; 1924, p. 4.
Diaptomus (Hesperodiaptomus) shoshone, LIGHT, 1938, p. 67.

Specimens examined.—The material studied consisted of slides in the type (Forbes) and Schacht collections in the Illinois Natural History Survey; specimens from all the localities reported by Marsh for which slides are available in the National Museum; unpublished records in the S. F. Light accession in the National Museum; and a recent alcoholic collection, consisting of 57 females and 31 males, collected by J. S. Stanford, Dry Lake, Cache County, Utah. This latter collection agrees with the type material in the basic characters, which have been checked on all the specimens.

The descriptive diagnosis and illustrations given here are based upon the Forbes slides, except for the habitus, which has been made from the Utah specimens inasmuch as it is desirable that study of whole specimens be made whenever possible from those that have been undistorted by cover-glass pressure. In all cases the term *typical form* refers to the type lot (Forbes did not designate an individual type specimen), or to individuals from other samples that agree with the type in the basic characters. The common variations that have been found are given in parentheses.

Diagnosis (emended).—Length (after Forbes) : Female, 3.1 mm.; male 2.59 mm. (Utah specimens, female, 3.7-4.4 mm.; male, 3.0-3.5 mm.). Greatest width in both sexes in the mandibular-maxillary region, the metasome tapering sharply so that the posterior portion is noticeably narrower than the anterior. Metasomal wings of female not produced outwardly, directed posteriorly, reaching to near the end of the swollen portion of the genital segment (not bifid as stated by Forbes). Urosome of female 3-segmented. Genital segment asymmetrical, the lateral areas bearing the minute sensilla produced into prominent lobes, that of the right side larger and directed backward. Caudal rami subequal to segment 3, both margins ciliate. (The illus-
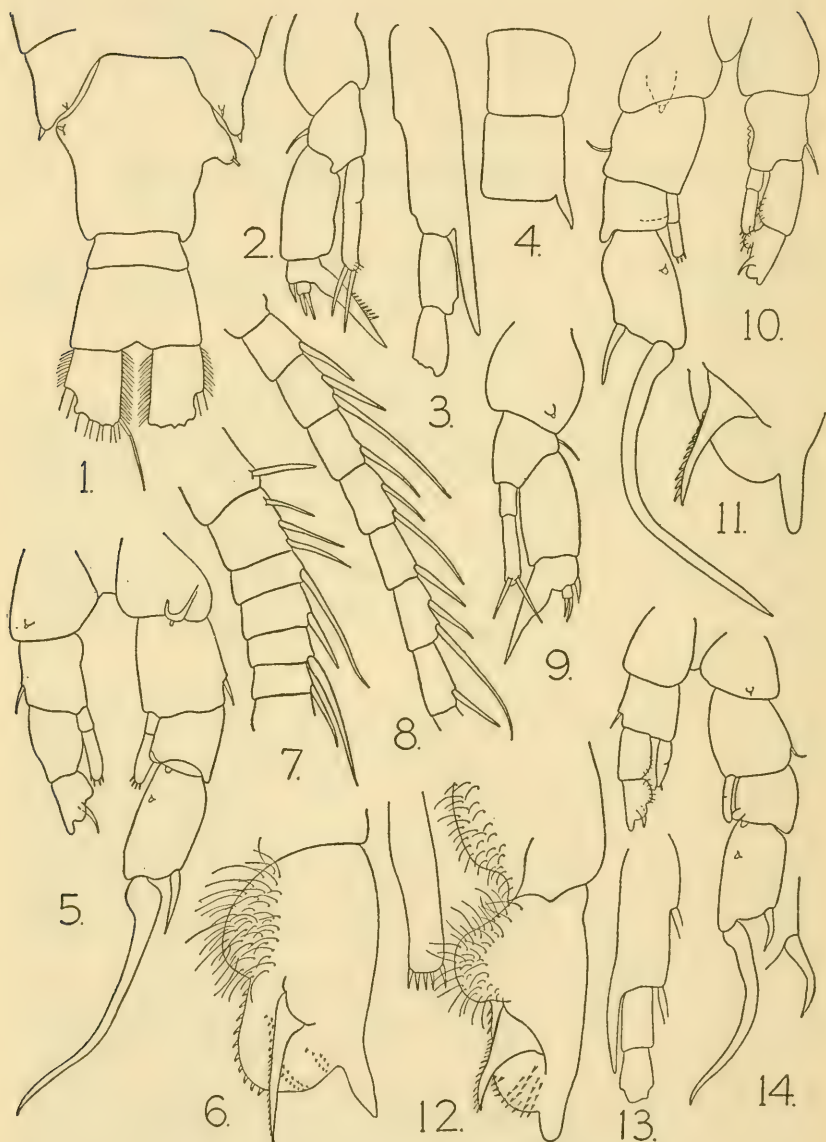
FIGS. 1-14.—(See legend on opposite page.)

trations of the female urosome given by Marsh, 1907, and by Dodds, 1915a and 1915b, agree with Forbes's description and slides and are correct. That of Schacht, 1897, pl. 26, fig. 1, is not of *D. shoshone.* It was found in checking slides in the Schacht collection that those labeled *shoshone* female were of a leptodiaptomid.)

Antennules reaching to near end of metasome, setation of female and left side of male identical, having 3 setae on segment 2, 1 seta on 6 and 10. Segments 11 and 13-19:

11	13	14	15	16	17	18	19
2	1	2	1	2	1	2	1

Right antennule of male with spines of segments 10, 11, and 13 not grossly developed; that of 10 less than width of segment, those of 11 and 13 hardly longer; that of 13 a little longer than that of 11. (These spines show considerable individual variation.) Segment 15 without spinous process. Segment 16 with a long, distally placed process (usually varying from about 30-42 percent of the length of the margin of the segment; 1 specimen examined has the extreme of 61 percent). The process of segment 23 reaching to the middle of the last segment (rarely beyond), its apex pointed (frequently rounded).

Maxilliped of both sexes grossly developed, with greatly enlarged clawlike setae on the inner side of the endopod, the terminal and outer setae much reduced in size. Leg 1 with the spine of exopod 1 long and setiform, reaching to near the end of segment 2. Leg 2 lacking Schmeil's organ.

Leg 5 of female slender. Relative lengths of the exopod and endopod of Forbes's slide 507 (fig. 2):

Exopod 1	Exopod 2 (outer)	Endopod	Endopod setae
40	36	35	19 : 22

The endopod indistinctly segmented (or distinctly so), armed apically with large, flat spinules; the setae unornamented (only a few specimens show, at high magnification, scattered hairs on these setae; Schacht's figure is undoubtedly of *shoshone,* but the dense plumosity

Figs. 1-8.—*Diaptomus (Hesperodiaptomus) shoshone* Forbes: 1, Female, metasome segments 5-6 and urosome, dorsal; 2, female, leg 5; 3, male, right antennule, apical segments; 4, male, right antennule, segments 15-16; 5, male, leg 5, posterior view; 6, male, leg 5, left exopod, segment 2, anterior view; 7, female, antennule, setae of segments 1-6; 8, female, antennule, setae of segments 13-19.

Figs. 9-11.—*Diaptomus (H.) novemdecimus,* new species: 9, Female, leg 5; 10, male, leg 5, anterior view; 11, male, leg 5, processes of left exopod, anterior view.

Figs. 12-14.—*Diaptomus (H.) kenai,* new species: 12, Male, leg 5, left exopod and endopod, anterior view; 13, male, right antennule, apical segments; 14, male, leg 5, posterior view, with detail of lateral spine.

of the endopod setae is an exaggeration). Length of the second exopod segment three times its greatest width, the whole of the claw very slender, evenly tapered from the area of the third exopod segment. Setae of the third exopod short, the inner the longer.

Leg 5 of male, right: Claw swollen at its base (not divided as shown by Forbes); shorter than the rest of the leg, about 25:33. Basipod 1 without inner lamella, sensillum on well-developed cuticular prominence. Basipod 2 without prominent raised ridge or protrusion. Exopod 2 nearly parallel-sided, with small spinule on inner posterior face; lateral spine straight, shorter (or a little longer) than the width of the segment. Endoped a little longer than the inner margin of exopod 1 (1- or 2-segmented).

Left leg reaching to about the middle of the right second exopod segment. Basipod 2 with the proximal inner half of the anterior face hardly protuberant (individually variable). Segment 1 of the exopod considerably longer than segment 2 (about 3:2). Inner process of distal segment a long, slender, tapering, distally directed spine whose basal portion is hardly widened and which reaches to the end of the outer process (or farther); its length more than half that of the outer margin of exopod 2 (measured to the base of distal process). The medial spinules of the distal pad very gross, those of the posterior and anterior faces very small, arranged in groups. Endopod 1-(or 2-) segmented.

Distribution.—The type locality is Lake Shoshone, Yellowstone National Park, Wyo. Other Yellowstone Park records given by Forbes are: Lewis Lake, Yellowstone Lake, Swan Lake, and an alkaline pond.

It has been determined from examination of the Marsh slide collection in the National Museum that only the following records published by Marsh (1920, 1929) are of typical *shoshone:* Yellowstone Lake, Wyo.; Corona, Irwin, and Pikes Peak, Colo.; Nioche Valley and Salinas, Wasatch Mountains, Utah. The Toronto, Canada, record is questionable; the only slide available is of a cyclopoid. All the other Marsh records and also those of Carl (1940) are referable to one or another of the species discussed below.

The Light accession contains three unpublished records of typical *shoshone.* One is an additional Rocky Mountain locality: A pond 28 miles east of Cooke, Mont., 9,000 feet, A. G. Rempel, collector. The others are from the Sierra Nevadas of California: Iceberg Lake, Madera County, 10,100 feet, P. R. Needham; Helen Lake, Fresno County, 10,896 feet, H. J. Rayner.

Dodds, whose illustrations agree with the typical form, has pointed out that in regions of the Rocky Mountains studied by him, *Diaptomus*

shoshone was found only in lakes at very high altitudes (around 9,000-12,000 feet). The elevation given for the type locality, Lake Shoshone, was 7,740 feet (Forbes, 1893, p. 214).

On the basis of present knowledge the distribution of typical *shoshone* appears to be restricted. All the authentic records are from high altitudes (6,000-12,000 feet) in the Rocky Mountains or Sierra Nevadas. It is not intended to suggest here that this is proof of the altitudinal distribution of the species. It should be pointed out, however, that a trend is apparent which is worthy of investigation and which may have bearing on the zoogeography of this and some of the species discussed below.

DIAPTOMUS (HESPERODIAPTOMUS) NOVEMDECIMUS, new species

Figures 9-11

Type lot.—Slides from the Light collection consisting of mounted appendages of both sexes. Temporary pond, 2 miles south of Charlo, Flathead Reservation, Mont., elevation about 3,000 feet, Gordon B. Castle, April 28, 1940. Occurring with *D. wardi.* Type slide, U.S.N.M. No. 94624.

Since only mounted appendages are available, no measurements or description of the habitus can be given. The size of the appendages indicates that the body size of both sexes is similar to that of *D. shoshone.*

Diagnosis.—Antennule setation of female and left side of male: 3 setae on segment 2, 1 on segments 6 and 10. Segments 11 and 13-19:

11	13	14	15	16	17	18	19
2	1	2	1	2	1	2	2

Right antennule of male: Spines of segments 10, 11, and 13 not long, that of 13 of irregular shape, longer than that of 11. Segment 15 lacking a process; 16 with a distally placed process, its length about 20 percent of that of the segment. Process of segment 23 stout, straight, the apex pointed, reaching to near the end of segment 25.

Leg 5 of female: Exopod 1 (outer margin) a little longer than exopod 2, 47:45. Exopod 2 wider at base than in typical *shoshone,* the width to total length, 20:45; the claw not so slender as in *shoshone,* gradually tapered beyond the middle. Endopod 2-segmented (or indistinctly so), longer than the inner margin of exopod 1. The inner seta of exopod 3 subequal to, or not as stout or long as, the outer.

Leg 5 of male: Claw not swollen at base, nearly as long as the rest of the leg, 37:35. Right basipod without modification or armature. Right exopod 2 somewhat enlarged, with a blunt spinule on inner posterior face. Right endopod 2-segmented, longer than exopod 1. Left

basipod 2 with prominent inner proximal protrusion; serrate cuticle particularly conspicuous on inner anterior face (such a serration is a rudimentary structure which may be present or absent in hesperodiaptomids). Exopod 1 longer than exopod 2 (about 37 : 25). Inner process a stout spine with a slightly widened base, reaching to near the end of the distal process, its length a little less than one-half that of the outer margin of exopod 1 (to base of distal process).

The trivial name of this species refers to segment 19 of the antennule, which differs from that of *shoshone* in the presence of 2 setae rather than 1 seta. The question of whether *D. novemdecimus* is a subspecies of *D. shoshone* should be considered in future studies. The status of species has been given here because of the antennular setation, which has long been considered by competent authorities to be a stable specific character. In the several samples of typical *shoshone* that have been examined no individuals of either sex have been found to have 2 setae on segment 19. In addition, the two can be separated by two definable characters of the male fifth leg which also differ in other species of *Hesperodiaptomus*—that is, the length and shape of the claw and the size and shape of the inner process of the left exopod. This combination of a pattern of close structural similarity and definable differences in seemingly basic characters appears to make these two species valuable for studies in the interrelationships of the hesperodiaptomid group and the problem of evaluation of characters. Until adequate knowledge of variation and distribution is available, it is my opinion that any attempt at subspeciation is both arbitrary and premature.

DIAPTOMUS (HESPERODIAPTOMUS) KENAI, new species

Figures 12-17

Diaptomus shoshone, MARSH, 1920 (in part), p. 8j; 1929, p. 17.—CARL, 1940, p. 81; ? 1944, p. 30.
? *Diaptomus shoshone*, THACKER, 1923, p. 88.

Type lot.—100 specimens of both sexes. Shallow mountain pond on Palmer Creek Road, about 12.6 miles southeast of Hope, Kenai Peninsula, Alaska, Charles S. Wilson, August 24, 1949. Occurring with *D. tyrrelli*. Holotype female, U.S.N.M. No. 94632; allotype male, U.S.N.M. No. 94633.

Diagnosis.—Length (dorsal view): Female, 2.03-2.08 mm.; male, 1.87-2.04 mm.

The wings of the last metasomal segment of female a little asymmetrical, the lateral tip of each side drawn out, that of the right side larger than the left. Urosome of female 3-segmented. Genital seg-

ment symmetrical, without lateral protrusions. Third segment and caudal rami subequal in length; the greatest width of the rami a little more than one-half their length (21 : 35), ciliate on inner margin.

Antennules of female reaching to near the middle of the genital segment. Numerical setation: 3 on 2, 1 on 6 and 10, 2 on 11, and 1 on 13-19. The seta of segment 1 short, not reaching to the end of segment 2; all setae comparatively short, none reaching beyond the middle of the succeeding three segments. Left antennule of male with same setation as female.

Right antennule of male with the spines of 10, 11, and 13 thick, none longer than the width of their segments, proportions to one another, 11 : 16 : 21. Segment 15 without a process; segment 16 with a distally placed process reaching beyond the end of the segment, its length about 28 percent of the length of the segment. The process of segment 23 reaching to about the middle of the last segment, straight or outcurved.

Maxilliped not so grossly developed as in *shoshone*. Setiform spine of exopod segment 1 of leg 1 only about half the length of segment 2. Leg 2 lacking Schmeil's organ.

Leg 5 of female: Exopod 1 (outer margin) a little longer than exopod 2 (35 : 33). Proportion of greatest width to length of exopod 2, about 15 : 33; this great width gradually decreased throughout the length of the "claw" to near its apex where it may be abruptly narrowed. The outer seta of exopod 3 always stouter and usually much longer than the inner. Endopod 2-segmented, as long as, or longer than, the inner margin of exopod 1. The apex more or less prolonged on the inner side, armed with a few short spinules, the length of the subterminally placed setae about half that of the endopod.

Leg 5 of male, right: Claw short, only a little longer than the exopod; its base hardly swollen. Exopod 2 with spinule on the posterior inner face; the lateral spine short, characteristically incurved on the inner side. Endopod about as long as exopod 1, 1- or 2-segmented. Left leg reaching to a little beyond the right exopod 1. First segment of exopod a little longer than the second. The inner process a broad-based spine, not reaching to the end of the distal process.

This species is the only one of the *shoshone* group that has the setation of the antennule reduced to one on segments 13-19. This character distinguishes it from all the others, and particularly from *D. caducus*, to which it would appear to be most closely allied. The female fifth leg has a distinctive shape given to it by the widening of the second exopod segment. The inner process of the left exopod of the male fifth leg is distinguished by the broadened base from which it tapers to a slender spine.
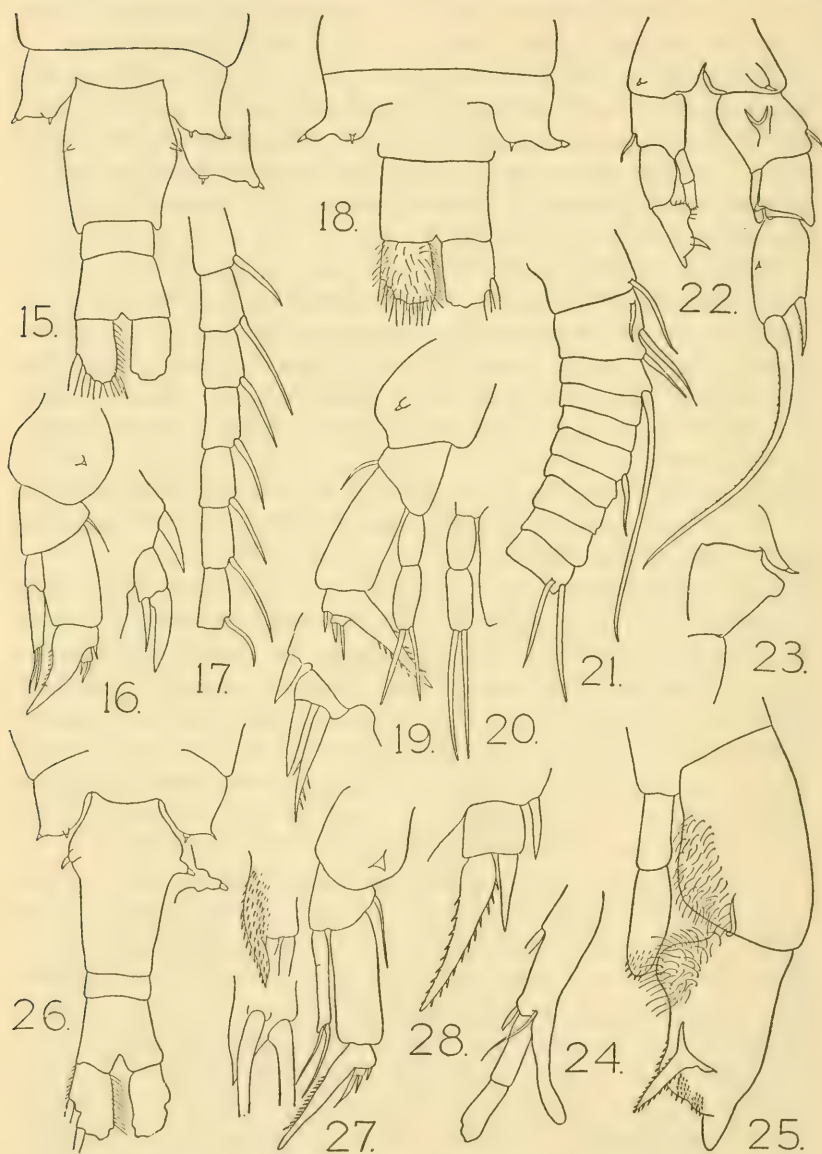
Figs. 15-28.—(See legend on opposite page.)

Distribution.—The specimens reported as *shoshone* by Marsh from the Pribilof Islands, Alaska, and from Wheat Meadows, Calif., are referred to this species. Marsh is supposed to have identified the specimens reported by the Thackers, but slides from their British Columbia localities have not been found in the National Museum collections. They have here been questionably referred to *D. kenai* because the record falls within the distribution pattern of this species. Slides labeled *D. shoshone* by Carl and reported in the British Columbia records of his 1940 paper are in the Light accession and have been identified by me with *D. kenai*. In addition to these collections and the type lot from Alaska, a large number of collections from Oregon and California have also been examined and referred to this species. These records are extensive enough to show that the species is not altitudinally restricted. In Oregon and California it is rare on the coast but of frequent occurrence in the Cascade and Sierra Nevada mountain ranges, where it has been collected to an elevation of 9,000 feet. The species also occurs in the Cascades of Washington, having been found in a collection from Lake George, Mount Rainier National Park, referred to me by C. C. Davis.

DIAPTOMUS (HESPERODIAPTOMUS) CADUCUS Light

Diaptomus caducus LIGHT, 1938, p. 67, figs. 1-5, 23.
Diaptomus shoshone, MARSH, 1929 (in part), p. 17.
Diaptomus sicilis, CARL, 1940 (in part), p. 81.

Specimens reported by Marsh from Vancouver Island, British Columbia, are referable to this species. A slide labeled *D. sicilis* by Carl is present in the Light collection; the locality given is: Pond, Victoria, British Columbia. This specimen is clearly identifiable from the antennular setation as *caducus*.

Diaptomus caducus has been adequately described by Light, and if proper attention is given to the highly important setation of the anten-

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FIGS. 15-17.—*Diaptomus (Hesperodiaptomus) kenai,* new species: 15, Female, metasome segments 5-6 and urosome, dorsal, with detail of right "wing"; 16, female, leg 5, with detail of lateral setae of exopod; 17, female, antennule, setae of segments 13-19.

FIGS. 18-25.—*Diaptomus (H.) hirsutus,* new species: 18, Female, metasomal wings and distal portion of urosome, dorsal; 19, female, leg 5, with detail of lateral setae of exopod (type lot); 20, female, leg 5, endopod with elongate setae (lot from Eldorado County, Calif.); 21, female, antennule, segments 1-10, showing setae of segments 1, 2, 3, 6, and 10; 22, male, leg 5, posterior view; 23, male, leg 5, profile of protrusions of right basipod segments; 24, male, right antennule, apical segments; 25, male, leg 5, detail left exopod and endopod, anterior view.

FIGS. 26-28.—*Diaptomus (H.) nevadensis* Light: 26, Female, metasome segments 5-6 and urosome, dorsal; 27, female, leg 5, with detail of apex of endopod, 2 different views; 28, female, leg 5, detail of lateral setae of exopod.

nules (table 1) there should be no confusion of this species with any other known hesperodiaptomid. The species is unique among known diaptomids in having 4 setae rather than the usual 3 on the second segment in both sexes, including the right antennule of the male. Occasional specimens have been found in which 2 setae are also present on segments 4-7 on one antennule of a pair, apparently an anomaly rather than a variation of the species.

Present knowledge of distribution confines this species to the Pacific coast areas from central California to British Columbia, where it characteristically occurs in temporary ponds and roadside ditches. The one mountain record given by Light is referable to the new species described below.

DIAPTOMUS (HESPERODIAPTOMUS) HIRSUTUS, new species

Figures 18-25

Diaptomus caducus LIGHT, 1938 (in part), p. 69.

A single female from Granite Lake, Amador County, Calif., was incorrectly assigned to *caducus* by Light. Another collection made at a later date from the same locality yielded numerous specimens and has been made the type lot of the new species.

Type lot.—100 specimens of both sexes. Granite Lake, Amador County, Calif., 6,800 feet, June 22, 1937, R. E. Smith. From Light collection in the U. S. National Museum. Holotype female, U.S.N.M. No. 94628; allotype male, U.S.N.M. No. 94629.

Other California mountain collections in the Light accession referable to this species are: Several ponds in Lassen National Park; pond at Columbia, Sierra County; pond near Summit Lake, Shasta County; Silver Ford, Eldorado County.

Diagnosis.—Length: Female, about 1.88 mm.; male, about 1.79 mm. Greatest width in both sexes in the middle of the cephalic segment, that of the female about 28 percent of the length. Posterior margin of metasomal wings of female slightly bifid, the outer portion produced laterally. Urosome of female 3-segmented. Genital segment symmetrical, not swollen laterally. Caudal rami shorter than segment 3 (about 29:35); their width about 71-76 percent of the length; both margins and entire dorsal surface hairy. Urosome of male symmetrical, length of caudal rami subequal to segment 5, with hairs on the inner margins only.

Antennules reaching nearly to end of metasome. Those of female having 3 setae on segment 2, 1 on 6, 2 on 10, 11, and 13-19; seta of 3 unusually long, reaching about to end of segment 10. Left antennule

of male differing from that of female in having 1 seta on segments 10 and 13 (2 on 11 and 14-19), seta of 3 reaching about to segment 8. (This sexual difference found in all the lots of specimens examined.) Right antennule of male: Length of spines of segments 10 and 11 less than the width of their segments and shorter than that of 13, which is exceedingly slender and reaches about to the middle of segment 14; segment 16 with a short, distally placed process not reaching beyond the end of the segment. Process of segment 23 spatulate, its tip always rounded, reaching to the end of 24 or to the middle of 25. Leg 2 lacking Schmeil's organ.

Leg 5 of female: Endopod 2-segmented, as long as, or longer than, exopod 1; apex truncate, with few spinules; setae subequal in length to endopod or longer.

Leg 5 of male, right: Claw subequal to (or a little longer than) the rest of the leg. Basipod 1 without prominent inner lamella. Basipod 2 with raised ridge on posterior surface, produced proximally into a rounded lobe (fig. 23 shows profile of ridge, without pressure); this structure reduced to indefinite shape by cover-glass pressure (fig. 22). Exopod 2 with small spinule on inner posterior face, lateral spine a little shorter (or longer) than width of segment. Left exopod: Segment 1 a little longer than segment 2, 19 : 15. Inner process a tapered spine with a narrowly expanded base. Distal pad with minute spinules arranged in groups on the anterior side; those of the posterior side larger and thickly set, extending far up on the face of the segment.

The trivial name of this species refers to the presence of hairs on the dorsal surface of the caudal rami of the female, a condition unusual in *Diaptomus*. *D. caducus* has been found to have hairs on both surfaces of the caudal rami, but they are few in number and scattered, in contrast to the numerous thickly set hairs of *hirsutus*. The two species appear to be related. They are the only ones known in which the segments of the female antennule proximal to segment 11 have some of the setae multiplied. *D. hirsutus* is clearly defined in its characters and the male is strikingly different from that of *caducus* not only in the setation of the left antennule (table 1) but in several of the characters of the fifth leg (greater length of the claw, modification of the right basipod 2, and the elongate form of the inner process of the left exopod). These characters, as well as those of the female, have been found in all the several collections examined. Present knowledge of distribution confines *caducus* to the Pacific coast area and *hirsutus* to the mountains of northeastern and north-central California.

DIAPTOMUS (HESPERODIAPTOMUS) NEVADENSIS Light

Figures 26-28

Diaptomus nevadensis LIGHT, 1938, p. 69, figs. 6-7.
Diaptomus shoshone, MARSH, 1929 (in part), p. 17.

The specimens reported by Marsh as *shoshone* from Devils Lake, N. D., are referable to this species.[1]

Only males were present in the type lot from Nevada. Since publication, Light collected and identified the species from another Nevada and several California localities, as listed: An alkaline lake, Washoe County, Nev., 5,000 feet; Honey Lake and Horse Lake, Lassen County, Calif.; Middle Lake, Cedarville, Modoc County, Calif.

The above collections contained females, from which an allotype specimen has been selected for description.

The male in the new Nevada and California collections shows no significant differences from that described by Light from the type lot, except that the lateral spine of the right second exopod of the fifth leg is noticeably longer, equaling at least the width of the segment (in the type specimen, which has been examined, it is considerably less). The typical male is characterized by:

Large size (about 3.5 mm.).

Left antennule: 2 setae on 11, 1 on 13-19.

Right antennule: Spines of 10 and 11 exceptionally slender, that of 11 longer than that of 13. Short spinous processes on both segments 15 and 16. Process of segment 23 long and curving.

Leg 5: Claw comparatively short, only a little longer than the exopod; its base swollen. Right basipod 1 with prominent inner lamellar expansion. Second exopod segment of right leg greatly enlarged, with a very small spinule on inner posterior face. Left exopod: Segment 1 a little longer than segment 2; the inner process a very short, but broad-based, toothlike spine, not reaching beyond the base of the distal process. Distal pad having the spinules closely set, not arranged in groups.

The North Dakota specimens differ from the Nevada and California males in having the second exopod segment of the right leg not conspicuously enlarged, and in the absence of the short spinous process on the 15th segment of the right antennule. The female shows no differences.

Diagnosis of female.—Allotype female: U.S.N.M. No. 94627.

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[1] Specimens recently reported as *D. shoshone* by J. E. Moore (Can. Journ. Zool., vol. 30, p. 422, 1952) from saline lakes in Saskatchewan have also been examined and found to be *D. nevadensis*.

Honey Lake, Lassen County, Calif., June 1938, collected and identified by S. F. Light.

The female is large but comparatively slender. Length 3.85-4.05 mm. Greatest width only 23.6 percent of length. Metasomal wings not expanded or produced laterally, symmetrical. Urosome 30 percent of total length, 3-segmented. Genital segment widened proximally with slight lateral protrusions, the sensillum of the right side borne on a larger protrusion than that of the left. Caudal rami subequal in length to segment 3, proportions of length to width about 3:2; ciliate on both margins.

Antennules reaching to the middle of the genital segment. Numerical setation: 3 on segment 2, 1 on 6 and 10, 2 on 11, and 1 on 13-19. The seta of segment 1 not elongate, hardly reaching to the middle of segment 2; that of 3 reaching to end of segment 6. All the segments extremely slender, the length of segments 17-19 are 4 to 5 times their width. Setae of segments 7, 9, and 14 exceptionally long, that of 7 the longest, reaching to middle of segment 13. Relative proportions of these setae: Segment 7:265; segment 9:210; segment 14:175.

Maxilliped very gross, as in *shoshone*, the endopod shorter than the preceding basipod segment, and armed with very stout clawlike setae. Leg 2 lacking Schmeil's organ.

Leg 5 elongate and slender, the total exopod almost twice the length of the basipod. Relative lengths:

Basipod 1 + 2	Exopod 1	Exopod 2
90	90	85

The inner spine of exopod 3 much stouter and longer than the outer spine, armed with stout marginal spinules. Endopod shorter than inner margin of exopod (61:85), indistinctly 2-segmented, the inner apex produced into a sharp prolongation which is armed with coarse hairs; the terminal setae about two-thirds the length of the endopod.

Although it lacks any striking modification of the second basipod segment in the male right fifth leg, *D. nevadensis* appears to be referable to the *eiseni* rather than to the *shoshone* group of *Hesperodiaptomus*. This is evident in the male fifth leg in the regular arrangement of the spinules of the distal pad of the left exopod and the prominent inner lamellar expansion of the first basipod segment; and in the right antennule by the presence of a spinule on the fifteenth segment, which though not always present in members of the *eiseni* group, has not yet been found in those of the *shoshone* group. The fifth leg of the female is strikingly similar to that of typical *eiseni* from which it can be distinguished by the prominent prolongation of the apex of the endopod; in *eiseni* the endopod has only a minute production of the apex.

DIAPTOMUS (HESPERODIAPTOMUS) SCHEFFERI, new species

Figures 33-42

Diaptomus shoshone var. *wardi*, JUDAY AND MUTTKOWSKI, 1915, p. 23, fig. 1, A-E.
Diaptomus wardi, MARSH, 1920, p. 8j, pl. 3, fig. 10; 1929 (in part), p. 23.

This interesting Pribilof Island species was erroneously identified by Juday and Muttkowski as *wardi* Pearse, which they considered to be a variety of *shoshone*. Marsh (1920, 1929) accepted this incorrect identification but did not refer the species to *shoshone*. Study of Montana specimens which are referable to typical *wardi* (see below) show several distinctive differences between the two forms. The most striking and the one that has hitherto been misinterpreted is the structure of the protrusion of the second basipod segment of the male right fifth leg.

There has been available for study some of the original material examined by Juday and Muttkowski, now in the Marsh collection in the National Museum, and additional specimens also from the Pribilof Islands, referred to Dr. Light by Dr. Victor B. Scheffer, chief of Pribilof Fur Seal Investigations, U. S. Fish and Wildlife Service. The species is named for Dr. Scheffer.

Type locality.—Upper Ice House Lake, St. Paul Island, Pribilof Islands, Alaska. Holotype female, U.S.N.M. No. 94625; allotype male, U.S.N.M. No. 94626.

Diagnosis.—Length: Female, about 2.66 mm.; male, about 2.5 mm. Urosome of female 3-segmented, symmetrical, the sensilla borne on very slight lateral protrusions. The caudal rami longer than the third segment (15:11) with hairs only on the inner margin.

Antennules of female reaching about to the middle of the genital segment. Numerical setation: 3 on 2, 1 on 6 and 10, 2 on 11, 1 on 13-19. The seta of segment 1 reaching to the middle of segment 4; that of 3 subequal in length to that of 1, reaching to near the end of segment 6. Left antennule of male usually armed as in the female, the seta of segment 1 not so long, reaching to the middle of 2, that of 3 to the middle of 7. The right antennule differing from the left in having 2 setae on segment 6 (occasional specimens have 2 setae on the left, but this is not usual); spines of segments 10, 11, and 13 only moderately developed, the length of all less than the width of their segments, that of 11 longer than that of 13. The midportion of the antennule only moderately swollen, segment 15 lacking a process, that on 16 short, distally placed, its length about 15 percent of the length of the segment. The process of segment 23 usually long, slim, always pointed, reaching to near the end of, or beyond, the last segment, the

inner edge usually smooth, but it may have one to several rounded notches.

Leg 5 of female slender throughout. Exopod segments subequal to one another, claw of exopod 2 very slim. Lateral seta of exopod 2 shorter than third exopod segment. Outer seta of exopod 3 very short and narrow, about one-half the length of the inner which is usually stout (slim in some specimens), armed with spinules. Endopod a little shorter than the inner margin of exopod 1, indistinctly 2-segmented, or distinctly so; the apex truncated, without apical production, armed with a few stout spinules and hairs. The setae set terminally, the outer the longer; proportions of endopod to outer seta to inner seta, 38 : 28 : 17. The setae always armed with short stout hairs, often plainly visible at low power.

Leg 5 of male, right: Claw about as long as the rest of the leg, slender, curving, symmetrical throughout. Basipod 1 with moderately expanded inner protrusion. Basipod 2 with long heavy ridge on posterior face, and a rectangular lamella placed just above the middle of the inner margin; this lamella clearly not a mere continuous protrusion of the segmental body but a cuticular outgrowth consisting of a heavy medial portion and an outer membrane. Exopod 2 lacking the usual spine of the inner posterior face. Left leg: Basipod 2 with the proximal inner portion protruding. Second exopod segment a little longer than the first. Both pads large; the distal with its spinelets thickly set and not arranged in groups. The inner process a short slender spine swollen at its base, reaching a little beyond the edge of the pad.

DIAPTOMUS (HESPERODIAPTOMUS) WARDI Pearse

Figures 29-32

Diaptomus wardi PEARSE, 1905, p. 148, pl. 13, figs. 1-4.

The type locality of *D. wardi* is Spokane, Wash. So far as is known, types do not exist in any available collection, although Juday and Muttkowski (1915) mentioned that they examined specimens referred to them by Pearse. Marsh's (1920) figure of *D. wardi* from Pribilof Island material is *D. schefferi*.

The confusion of these two species would be difficult to clarify without specimens of *D. wardi*. Fortunately the Light collection contains slides on which are appendages of two unidentified females (leg 5) and two males (leg 5 and antennules) which are so like Pearse's illustrations of *D. wardi* that there can be no doubt of their identity. These specimens occurred in the Montana collection with
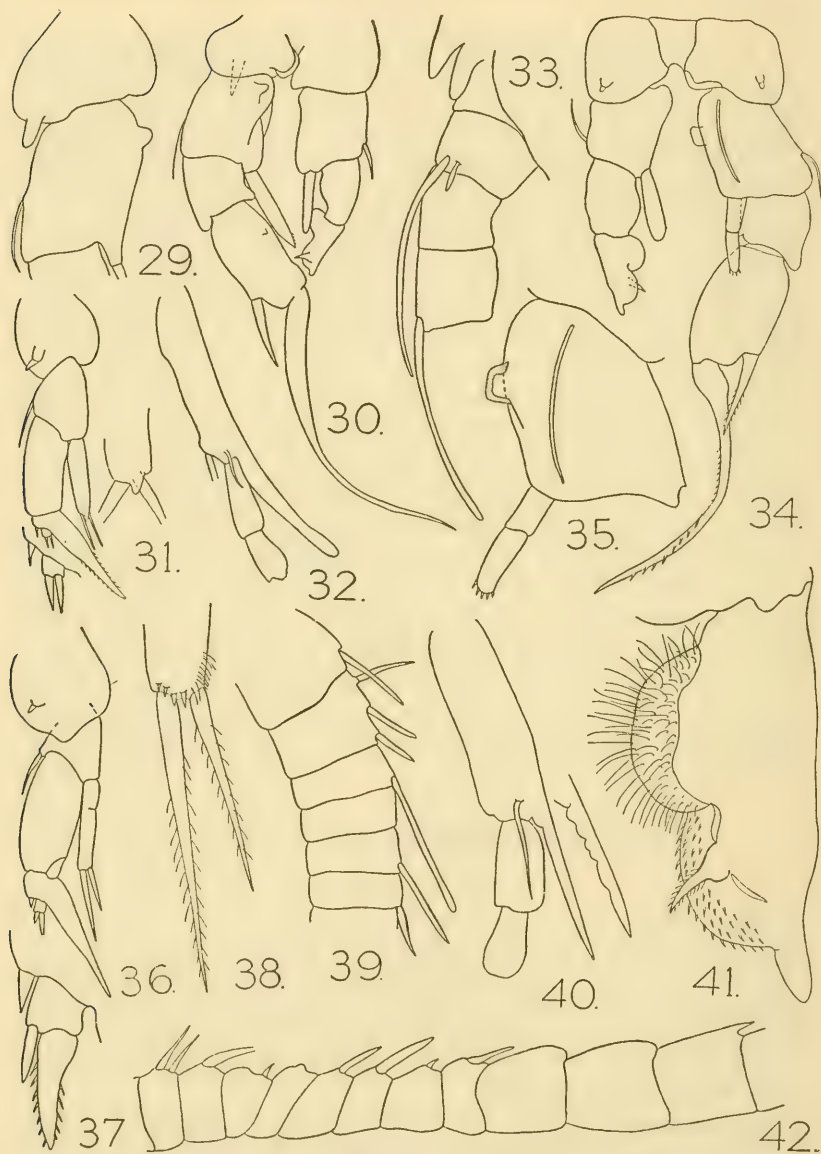
FIGS. 29-42.—(See legend on opposite page.)

Diaptomus novemdecimus, described above. This apparently constitutes the first valid record of the species since its description.

The protrusion of the second basipod segment of the male right fifth leg is not at all like the lamella on the medial margin of *D. schefferi,* which is definitely of cuticular origin. That of *wardi* appears instead to be an outwardly projecting lobed protrusion of the proximal inner portion of the segment itself. Until unmounted appendages not distorted by cover-glass pressure can be examined, its exact structure may not be determinable, but one of the slides contained a profile view which appears to be quite natural (fig. 29). In the other mount, the outline of the protrusion is clearly visible, though flattened (fig. 30). It appears to be of the nature of that described above for *D. hirsutus.*

The Montana specimens agree with Pearse's description in other characters of the male fifth leg: The elongate cuticular prominence of the right basipod 1 which bears the minute sensillum; the very long endopod of the right leg; the extremely slender claw subequal to the rest of the leg; and the structure of the left exopod and the inner process, similar to *D. schefferi.* These characters preclude possibility of identity with *D. shoshone.* Pearse did not indicate a minute spinule on the posterior face of the second exopod, which is present in the Montana specimens. The process of segment 23 of the right antennule agrees exactly with that shown by Pearse; it reaches beyond the apex and is rounded at the tip. Segment 6 has only 1 seta, and the spines of segments 10, 11, and 13 are all longer than the width of their segments, that of segment 11 longer than that of 13; both segments 15 and 16 have minute processes, that of segment 16 is at the middle of the segment, thus differing from the usual distally placed lamelliform process of other hesperodiaptomids. The left antennule has 2 setae on segment 11 and 1 on 13-19. Unfortunately, the antennule of the female had not been dissected, and it can only be assumed for the present that its setation is like that of the male.[2]

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[2] Whole specimens of *D. wardi* have been examined since this report was first written. The number of setae on these segments of the female antennule is the

FIGS. 29-32.—*Diaptomus (Hesperodiaptomus) wardi* Pearse (Montana): 29, Male, leg 5, right basipod (profile view of inner protrusion of basipod 2); 30, male, leg 5, anterior view; 31, female, leg 5, with details of endopod apex and exopod setae; 32, male, right antennule, apical segments.

FIGS. 33-42.—*Diaptomus (H.) schefferi,* new species: 33, Female, rostral filaments and segments 1-3 of antennule (with detail of setae of segments 1 and 3); 34, male, leg 5, posterior view; 35, male, leg 5, right basipod 2 and endopod; 36, female, leg 5; 37, female, leg 5, detail of lateral setae of exopod; 38, female, leg 5, detail of endopod apex and setae; 39, male, left antennule, setae of segments 1-6; 40, male, right antennule, apical segments, with variation of process of segment 23; 41, male, leg 5, detail of left exopod segment 2, anterior view; 42, male, right antennule, segments 6-16, showing setae of 6, and spines and processes of other segments.

The female fifth leg is exactly like that illustrated by Pearse, though it appears to be more slender. The endopod has two well-developed, equal, nonplumose setae, about half the length of the endopod which is very slightly produced between them. The setae of exopod 3 are very short and subequal, that of exopod 2 is very minute.

DIAPTOMUS (ARCTODIAPTOMUS) ARAPAHOENSIS Dodds

Diaptomus arapahoensis DODDS, 1915a, p. 99, figs. 3-6.
Diaptomus bacillifer, MARSH, 1924 (in part), p. 485; 1929, p. 8.

Marsh (1920) reported the occurrence of the Eurasian species *Diaptomus bacillifer* on the Arctic coast of Canada and on St. Paul, Pribilof Islands. In 1924 he supposedly extended its range in North America by placing in synonymy with it the species *arapahoensis,* described by Dodds from the Rocky Mountains of Colorado. I have examined Marsh's specimens of *bacillifer* and find his identification to be correct. Further examination of cotypes of *arapahoensis,* which are in the U. S. National Museum, and a new collection in the Light accession, from the Rocky Mountains of Montana (Hidden Lake, G. B. Castle collector), indicates that Dodds's species is not referable to *D. bacillifer* as Marsh had supposed.

The fifth leg of the male in most groups of *Arctodiaptomus* shows, as in many species of *Hesperodiaptomus,* very close structural similarity, and it is necessary to take into consideration all the characters of the copepod when making identifications. The male fifth leg of *arapahoensis* is built on the same general plan as that of *bacillifer.* The most noticeable difference is the presence of a large, cuticular, spinelike structure on the midposterior face of the right second exopod segment. This is absent in *bacillifer* but is similar to that found in other species (*salinus, acutilobatus*). This process is much larger than depicted by Dodds.

The setation of the female antennules and the left male antennule of the Canadian and Alaskan specimens of *bacillifer* agrees with that given by several authors for Eurasian specimens. There are 2 setae on segments 11 and 13 and 1 on segments 14-19, and the seta of segment 1 in the female is very long. *Diaptomus arapahoensis* has been found to have the following setation in the female:

11	13	14	15	16	17	18	19
2	2	1	2	1	2	1	1

The seta of segment 1 reaches to near the end of segment 5 and is sparsely plumose, being similar in this to *bacillifer.* The male left

same as in the male. The seta of segment 1 is very long, reaching about to segment 12.

antennule differs from the female in having 1 seta on all segments 13-19. This difference exists in both the type (Colorado) and Montana collections.

D. arapahoensis bears unmistakable resemblance to the Asiatic species *D. acutilobatus* Sars (1903). The antennule setation of the female agrees with that given for this species by Gurney (1931, table, p. 115). In order that its exact identity may be known, and particularly since there is a difference in the antennule setation of the two sexes, a fact not known for *acutilobatus,* it appears best to await comparison of actual specimens of the two forms, before a decision as to their conspecificity is made.

DIAPTOMUS (LEPTODIAPTOMUS) PRIBILOFENSIS Juday and Muttkowski

Diaptomus pribilofensis JUDAY AND MUTTKOWSKI, 1915, p. 25, figs. 1-6.
Diaptomus tyrelli, MARSH, 1915 (in part), p. 459; 1929, p. 23.—HOOPER, 1947, p. 80.

This is a form widely spread in Alaska and western Canada and has for years been considered synonymous with *D. tyrrelli* (corrected spelling). It is closely allied to *D. coloradensis* from the Rocky Mountains and forms with it and the Asiatic species *Diaptomus angustilobus* Sars (1898) a group of seemingly allopatric species. Its supposed synonymy with *tyrrelli* has been unfortunate in obscuring the pattern of its distribution and its closer relationship to the other species of the group. Specimens reported by Hooper as *tyrrelli* from western Canada have been examined and identified as *pribilofensis*.

DIAPTOMUS (EUDIAPTOMUS) GRACILIS Sars

Diaptomus gracilis is a well-known Eurasian species new to North American fauna. It has been found recently in several of my Alaskan collections. It appears to be common in the Arctic regions of Alaska, having been found on the western coast (lakes of the lower Yukon River and Bristol Bay areas) and on the Arctic slope at Umiat. In south-central Alaska it occurred in collections of the Kuskokwim River area at McGrath and in Wonder Lake, Mount McKinley National Park.

DIAPTOMUS (AGLAODIAPTOMUS) MARSHIANUS, new species

Figures 43-51

Type lot.—13 females, 45 males. Lake Jackson, Leon County, Fla., April 3, 1950, Murray H. Voth collector. Holotype female, U.S.N.M.
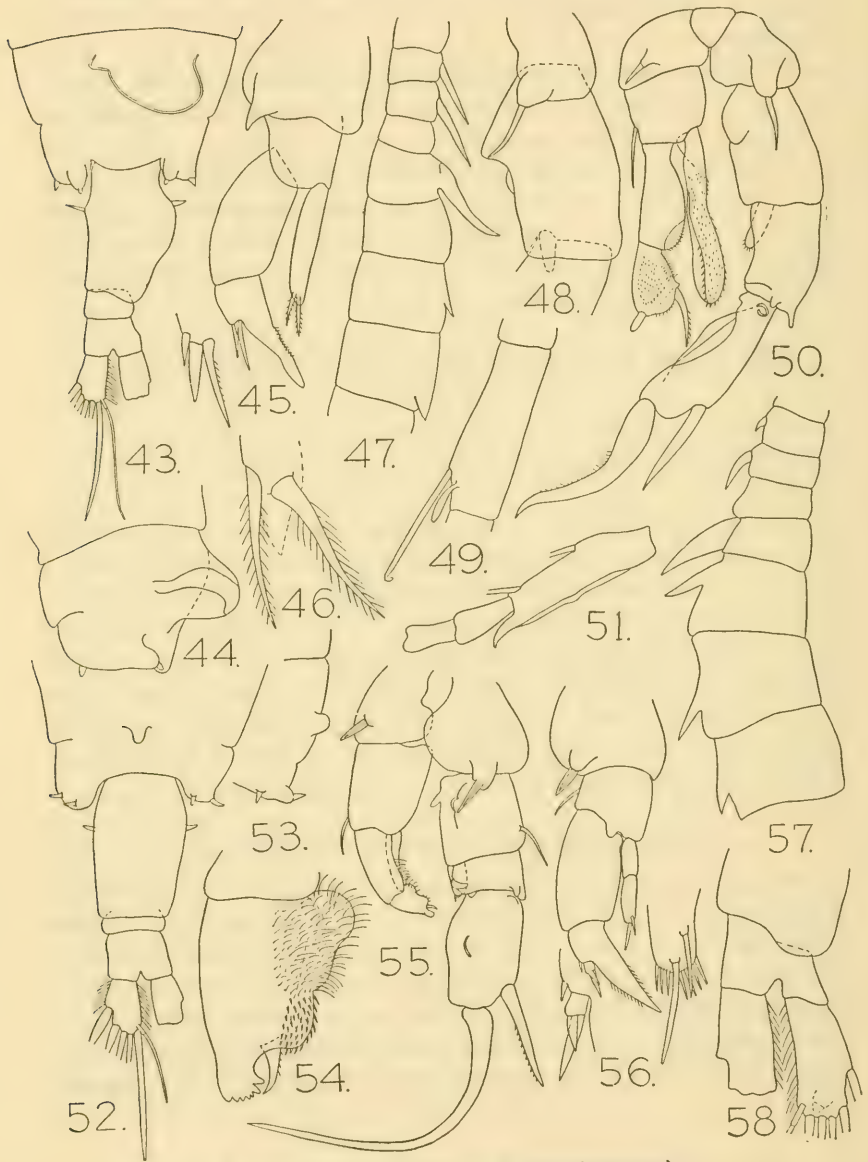
FIGS. 43-58.—(See legend on opposite page.)

No. 94634; allotype male, U.S.N.M. No. 94635. Occurring with *D.* (*Arctodiaptomus*) *floridanus* Marsh and *D.* (*Skistodiaptomus*) *mississippiensis* Marsh.

Diagnosis.—Length, dorsal view: Female, 1.55-1.89 mm.; male, 1.3-1.58 mm. Greatest width of female in segments 2 and 3, equaling about 28 percent of the length. Metasomal segment 5 with an unusual dorsal protuberance consisting of an erect cuticular frill, placed mostly on the right side. The wings of the last segment not produced laterally, the inner portion rounded so as to form a lobe in dorsal view.

Urosome of female 3-segmented. Genital segment noticeably asymmetrical, the right side being very tumid. Caudal rami longer than segment 3, 25:20, their width 64 percent of their length, ciliate on inner margin only; the inner dorsal seta as long as the inner caudal seta.

Antennules reaching beyond the caudal rami by the last 2-3 segments. Numerical setation: 2 on segment 11, 1 on segments 13-19. The seta of segment 1 short, reaching to the middle of segment 2, that on 3 reaching to segment 6. Setae of segments 17, 19, 20, and 22 stiff and uncinate, their length less than, or equal to, that of the segment. Setation of left antennule of male like that of the female, including the uncinate setae. Right antennule of male having spines of 10 and 11 longer than the width of their segments, that on segment 13 longer than that of 11, strongly outcurved; segments 15 and 16 with spinous processes. The process of segment 23 reaching to about the middle of 24, outcurved, accompanied by a narrow membrane.

Maxilliped not grossly developed, the distal lobe of the basal segment with 3 setae in both sexes. Schmeil's organ present on the endopod of leg 2.

Leg 5 of female: Basal segment with large sensillum on broad base. Exopod 1 and 2 subequal in length, exopod 3 not separated. Seta of exopod 2 present, set closely with the setae of exopod 3; the inner seta with marginal serrations. Endopod longer than inner margin of

Figs. 43-51.—*Diaptomus* (*Aglaodiaptomus*) *marshianus,* new species: 43, Female, metasome segments 5-6 and urosome, dorsal; 44, female, metasome segments 5-6, lateral view; 45, female, leg 5, with detail of lateral setae of exopod; 46, female, leg 5, detail of endopod setae; 47, male, right antennule, spines and processes of segments 10-16; 48, male, leg 5, right basipod (with profile of inner protrusion) and outline of endopod; 49, female, antennule, detail of uncinate seta of segment 19; 50, male, leg 5, posterior view; 51, male, right antennule, apical segments.

Figs. 52-58.—*Diaptomus* (*Mastigodiaptomus*) *texensis,* new species: 52, Female, metasome segments 5-6 and urosome, dorsal; 53, female, metasome segments 5-6, lateral view; 54, male, leg 5, left exopod, apical segment, posterior view; 55, male, leg 5, posterior view; 56, female, leg 5, with details of exopod setae and apex of endopod; 57, male, right antennule, spines and processes of segments 10-16; 58, male, distal segments of urosome, dorsal.

exopod 1, its setae not longer than half its length, both with enlarged bases and thickly plumose.

Leg 5 of male, right: Basipod 1 with a long spinelike sensillum reaching to near the middle of the next segment. The inner proximal portion of basipod 2 with a prominent lobed protrusion accompanied distally by a small narrow hyaline lamella (fig. 48) ; the distal portion of the segment lacking the cuticular process present in many species of *Aglaodiaptomus*. The first exopod segment about as long as basipod 2, the outer distal portion produced. Proportions of exopod 1 to exopod 2, 25 : 40. Inner portion of exopod 2 deeply grooved, the anterior side with a protruding flange ; relative length of lateral spine to exopod 2, 26 : 40. Claw subequal to exopod 2, very stout and curving. Endopod a little less than one-half the length of exopod 1.

Left leg : Sensillum of basipod 1 a stout spine. Exopod 1 noticeably longer than exopod 2, 24 : 16. Exopod 2 broadened distally, the distal process digitiform, nearly one-third the length of the outer margin of the segment ; the inner process a long, curving, setiform spine, nearly 3 times the length of the distal (14 : 5), spinulose on its inner margin ; the sclerotized marginal area of the segment produced to a point at its base. The proximal pad consisting of a hairy region on the upper inner margin ; the distal pad of spinulose areas on the posterior face. The endopod very large, reaching to near the end of exopod 2, the inner portion grooved, the entire surface thickly spinulose from above the middle to the end.

Taxonomic position.—The subgenus *Aglaodiaptomus* was proposed by Light in 1938. The original list of included species should be revised as follows :

D. piscinae Forbes (1893) should be recognized as a synonym of *D. leptopus* Forbes (1882). The type collections of Forbes (Illinois Natural History Survey) as well as those of Schacht and Marsh have been examined, and no definable structural difference has been found. (The details of this study are reserved for future publication.) In the synonymy of *leptopus* should also be placed *D. manitobensis* Arnason (1950). I wish to acknowledge Dr. Arnason's courtesy in permitting me to examine type material of his proposed species.

Diaptomus spatulocrenatus Pearse (1906) was omitted from Light's list.

The species *Diaptomus pseudosanguineus* Turner (1921), which was omitted by Marsh (1929), should be recognized, although there are certain inadequacies in the description. The species was described from the St. Louis, Mo., area, and on the basis of the description it is not referable to any of the known species of *Aglaodiaptomus*. The

female of *pseudosanguineus* is described as having a pair of long, curved spines on the ventral portion of the genital segment, and the photographic illustrations show a process distad to the genital protuberance in 2 lateral views of what appear to be two separate individuals (Turner, 1921, pl. 1, fig. 3; pl. 2, figs. 1 and 2). Such a process does not occur on the genital segment of any of the species of *Aglaodiaptomus,* all of which have been examined. The male fifth leg is most comparable to that of *spatulocrenatus,* resembling it in the proportions of the segments of the left exopod which are subequal, and the endopod which is described as having a crenate inner margin. The right first exopod segment differs from *spatulocrenatus* in having the distal outer portion produced as in *conipedatus* and *marshianus.* No detail can be made out, from the illustration, of the right second basipod segment, adequate knowledge of which is extremely important in the taxonomy of this group. No type material of Turner's species is known to be in existence.

Diaptomus marshianus is distinguished in the female by the peculiar dorsal protuberance of the metasome. There is no evidence in any of the other species of *Aglaodiaptomus* of such cuticular development. There can be no question, however, of the reference of this female to *Aglaodiaptomus* and hence to the male described from this collection, because the female shows unmistakable aglaodiaptomid characters in the uncinate setae of the antennule, the presence of three rather than four setae on the distal lobe of the basal segment of the maxilliped, and the dense plumosity of the endopod setae of the fifth leg. The male fifth leg most closely resembles that of *spatulocrenatus* and *conipedatus,* from which it can be distinguished by the lack of a distal cuticular process of the right second basipod segment and by the grosser development of the left endopod. It appears to differ from *pseudosanguineus* in having the first left exopod segment considerably longer than the second.

It is a personal pleasure to give the name of Dr. C. Dwight Marsh to a distinctive American species of *Diaptomus.* In this connection, attention should be drawn to the fact that Kiefer (1936, p. 309) has shown that the species named *D. marshi* by Juday (1914) should be known as *D. colombiensis* Thiebaud. Kiefer has stated that Thiebaud's paper was actually published as a separate in 1912 instead of 1914.

DIAPTOMUS (MASTIGODIAPTOMUS) TEXENSIS, new species

Figures 52-58

Type lot.—200 specimens of both sexes. Temporary roadside pond, county road to Bayside, about 1.5 miles west of Rockport, Aransas County, Tex., "spring" of 1945, Joel W. Hedgpeth collector. Holotype female, U.S.N.M. No. 94630; allotype male, U.S.N.M. No. 94631.

Diagnosis.—Length, dorsal view: Female, 1.5-1.6 mm. Greatest width of female in segment 3, 26-28 percent of length. Distal part of fifth metasomal segment of female usually with a small, medially placed, rounded dorsal protuberance (not always present). Wings not expanded, the left larger than that of the right side, both with spinelike sensilla, that on the inner portion of the left side usually directed outward. Urosome of female 3-segmented. Genital segment symmetrical, without lateral protrusions, lateral sensilla stout. Caudal rami longer than segment 3 (26:20) ; their width about 61 percent of their length; both margins ciliate; the dorsal seta about one-half to three-fourths the length of the inner caudal seta. Urosome of male asymmetrical; segment 4 produced backward on the right side; caudal rami asymmetrical, the right longer than the left, with a cuticular process on its ventral side near the base of the inner setae.

Antennules of female reaching beyond caudal rami by last two segments. Setation: 2 on segment 11, 1 on segments 13-19; seta of segment 1 short. Left antennule of male like that of female. Right antennule of male: Spine on segment 8 not enlarged, that of segment 10 hardly larger than that of 8, that of 11 nearly as long as width of its segment, that of 13 not much longer than the width of its segment, but exceedingly stout. Segments 14, 15, and 16 with stout spinous processes. Proportions of spines and processes to one another:

8	10	11	13	14	15	16
3	5	14	20	13	14	5

Segment 23 with a short, outcurved process, reaching about to the middle of segment 24.

Maxilliped slender, setation of basal segment normal ; the inner setae of the endopod not clawlike, all shorter than the endopod; the outer and terminal setae longer than the endopod (40: 37). Schmeil's organ present on endopod of leg 2.

Leg 5 of female stout, width of exopod 1 about half its length. Sensillum of basipod 1 a long, stout, flat spine. Exopod 1 a little longer than exopod 2 (27: 25). Exopod 3 separated, its outer seta short and spinelike, closely set with and usually overlying the inner seta ;

lateral seta of exopod 2 present, shorter than exopod 3. Claw with spinules on both margins. Endopod nearly as long as inner margin of exopod 1, 2-segmented, bearing 2 setae, the outer longer than the inner, which is set considerably above the tip of the endopod; tip of endopod with double row of stout hairs.

Leg 5 of male, right: Sensillum of basipod 1 a stout spine, in posterior view overlying the second basipod segment and directed toward a protrusion of the segment whose central portion consists of a crescent-shaped sclerotized lamella. The inner proximal portion with an inwardly and sometimes distally directed small marginal lamella. Exopod 1 with small lamellae on both inner and outer distal portions. Exopod 2 bulging medially, with a crescent-shaped sclerotization on the midposterior face; the lateral spine distally placed, stout and straight, its length less than that of the segment. Claw strongly curved at middle, as long as the rest of the leg.

Left leg: Sensillum of basipod 1 stout as on the right side. Inner part of basipod 2 produced proximally. Exopod 1 more than three times longer than exopod 2 (50:15). The distal process short and broad, its margins strongly serrate; the inner process spiniform, reaching to the end of the distal. Pads medial in position, the proximal the larger.

Taxonomic position.—This new species is allied to the southwestern species *D. albuquerquensis* Herrick, the known distribution of which extends through the Rocky Mountain States from Utah to Guatemala in Central America. The only other species of the subgenus on the continent, *D. amatitlanensis* M. S. Wilson (1941), is also known from Guatemala. There are no authentic records of the group from southeastern United States. Florida specimens identified by Schacht (1897) as *D. albuquerquensis* are undoubtedly referable to *D. floridanus* Marsh (1926). Such is also true of the specimens from Georgia listed by Humes (1950). Specimens to which Humes referred have been sent to me by Dr. M. S. Ferguson, of the United States Public Health Service, and have been found to be *D. floridanus*.

Diaptomus saltillinus Brewer, which is closely allied to *D. floridanus,* is found in Texas and some other areas where the *albuquerquensis* group occurs. *D. saltillinus* and *D. floridanus* belong to the subgenus *Arctodiaptomus* Kiefer (1932) and the *albuquerquensis* group to the subgenus *Mastigodiaptomus* Light (1939). There are superficial resemblances between these two groups of species, but they should not be confused with each other if careful attention is given to basic subgeneric characters such as are found in the left exopod of the male fifth leg, the armature of the endopod of the female fifth leg, and the

presence in *Mastigodiaptomus* of 2 setae on segment 11 of the female and left male antennules, as contrasted to the single seta of this segment in *saltillinus* and *floridanus*.

D. texensis is distinguished from *albuquerquensis* by several easily recognized differences in the male right fifth leg. In *albuquerquensis* the lateral spine of exopod 2 is longer than the segment, the second basipod segment has the inner proximal portion bulging upward as does also the marginal lamella, and the distal posterior face has a characteristic sculpturing of the cuticle that is lacking in *texensis*. The females are very similar but can be separated by the lateral protrusions of the genital segment and the usual shortness of the endopod of the fifth leg of *albuquerquensis*.

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THE METAMORPHOSIS OF A FLY'S HEAD

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A legless, almost headless, wormlike maggot hatches from the egg of a fly; but the maggot is not a young fly in the sense that a kitten is a young cat, or even in the sense that the nymph of a grasshopper is a young grasshopper. The maggot does not grow up into a fly, and neither does it literally transform into a fly. It is a highly specialized larval form of its species, which, though developed directly from the fly's egg, becomes a creature self-sufficient in all respects except that of procreation. Structurally the fly larva is so different from its parents that it cannot itself go over into the next fly generation. Consequently nearly all the larval tissues finally go into a state of dissolution, and the fly is then newly generated from groups of undifferentiated cells that are carried by the larva but which form no essential part of the larval organization.

This potentiality of dual development from a single egg becomes most accentuated among the Diptera in the cyclorrhaphous families. It affects not only the internal organs, but also the body wall, which is almost entirely replaced during the pupal stage from groups of cells, known as imaginal discs, that remain undeveloped from an early period, and at the end of the larval life begin an active growth that forms the integument and appendages of the pupa. The cells of the larval integument degenerate before the advancing new epidermis and are cast into the body cavity where they become food for the developing imaginal tissues. During larval life the regenerative discs of the thorax and head are contained in narrow-necked pouches of the epidermis, closed at their outer ends beneath the cuticle. Within these pouches the appendage rudiments may develop continuously through the larval instars without being exposed at the larval moults. Finally, however, during the prepupal or early pupal stage the pouches are everted and the appendages quickly grow to the state of development they have when the pupa is exposed by the shedding of the last larval cuticle, while the everted pouches themselves expand by cell proliferation and construct the pupal integument.

All this has been known for nearly a century. Weismann (1864) said that the thorax and head of the fly, together with their appendages, the halteres, the wings, legs, antennae, eyes, and mouth parts develop within the body of the larva, and the truth of this statement has been verified by numerous subsequent workers. Most of the earlier students of the structure and metamorphosis of the cyclorrhaphous larva, however, did not understand the morphology of the larval head. Though they correctly described facts, their identification of anatomical parts is often entirely erroneous, and later writers, taking their statements literally, either criticize them as false, or perpetuate their errors. In the following pages an attempt will be made first to understand the nature of the head of a cyclorrhaphous larva, and then to put together the story of the formation of the adult head as far as it can be compiled from our present information on the subject.

In the lower nematocerous flies the metamorphic changes between larva and adult are less intense than in the cyclorrhaphous families, and larval tissues may go over directly into adult tissues. In the larva of *Corethra,* for example, as described by Weismann (1866), the imaginal discs of the thorax are mere groups of cells in the larval epidermis, which begin development in the prepupal period and then form only the pupal appendages. The general integument of the pupal thorax in this case is a product of renewed growth activity in the cells of the larval epidermis, which simply remodel the thorax into the form of the pupal thorax. The same applies to changes of the head, the pupal head being formed by alterations in shape and size of the larval head within the unshed cuticle of the last larval instar. The imaginal mouth parts of Nematocera have been shown by Kellogg (1902) to be formed directly within the larval mouth parts; the adult antennae, however, which are generally much longer than the larval organs, develop with only their distal ends in the larval antennae. In some of the lower flies, as will be shown later, the imaginal antennae grow within pockets of the integument, and the pockets may include also the rudiments of the compound eyes.

The structural disparity between the larva and the adult in the Cyclorrhapha is due to the specialized form that the larva has acquired, rather than to that of the adult fly. The larval head of these flies in particular has become so highly modified in a specific way that it is difficult to understand how it has been evolved from a head of more usual structure. Only a small part of the adult head is derived directly from the larval head.

The apparent, or functional, head of a muscoid maggot is a small, rounded lobe at the anterior end of the body (fig. 2 A, *LH*) more or less sunken into the thorax. Apically this larval head bears a pair of

large papillae, on each of which are situated two small sense organs, but there are no eyes of any kind. The under surface of the head (A) presents a median depression from which projects a pair of strongly
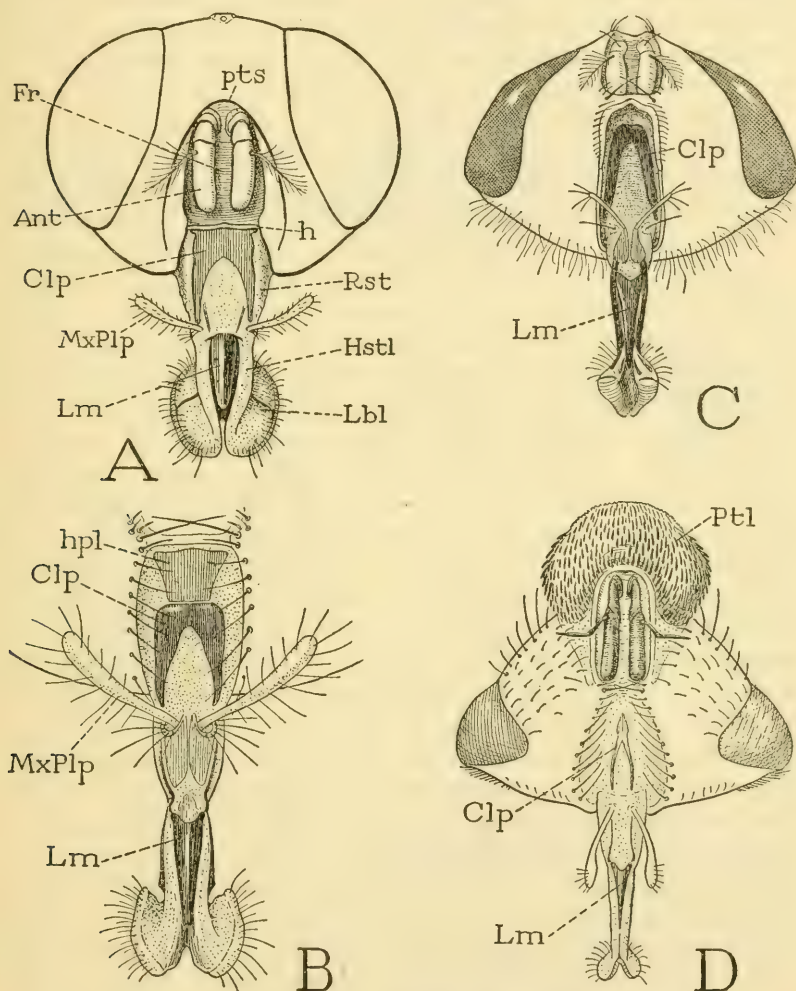

FIG. 1.—Head and proboscis of adult muscoid flies.

A, *Musca domestica* L., anterior. B, *Calliphora vicina* R.-D. (*erythrocephala* Meigen), clypeus and proboscis. C, *Callitroga macellaria* (F.), ventral. D, *Gonia* sp., with ptilinum everted.

sclerotized, decurved hooks (*mh*) partly covered by lateral folds of the integument. Below the bases of the hooks is a soft median lobe (*Lb*), which at least serves the larva as an under lip, and appears to be a true larval labium. Above the labium, between the bases of the

hooks, is the food-intake orifice of the larva (*Atr*), but it leads immediately into an atrial chamber before the mouth of the larval sucking apparatus.

The larval organ of ingestion is a suction pump lying within the thorax, supported by a strongly sclerotized structure commonly called by students of cyclorrhaphous larvae the "buccopharyngeal skeleton" or the "cephalopharyngeal apparatus" (fig. 2 B). By whatever name this complex structure is known, it is an important part of the larval head retracted into the thorax. In details of shape it differs characteristically in different species, but the general form and structure of the organ is that shown here for the mature larva of *Callitroga macellaria*.

The dorsal part of the sucking apparatus (fig. 2 F) is a long, thin, hyaline plate having a strongly contrasting, dark U-shaped sclerotization around its anterior end with the arms extending posteriorly along the lateral margins. From the edges of this sclerotized part of the dorsal plate a strong lateral plate descends on each side (B) and expands below into a broad posterior extension. Supported between the lower edges of the lateral plates is the sucking pump of the larva (*CbP*), which is continuous anteriorly from the atrium above the labium (*Lb*) and posteriorly into the oesophagus (*Oe*). The lumen of the pump when contracted is crescent-shaped in cross section (D, *Cb*), but on its concave upper wall are attached two rows of large dilator muscles (*dlcb*) arising on the arms (*Clp*) of the U-shaped sclerotization of the dorsal plate. Anterior to the lateral plates is a smaller, independent, median, ventral plate (B, *e*) on which the mouth hooks (*mh*) are articulated. This plate, which lies on the base of the dorsal wall of the larval labium (C, *e*), is H-shaped in ventral view (E, *e*). In front of its crossbar are two small sclerites bearing minute sense organs, and a narrow anterior V-shaped sclerite. Just behind the crossbar is the opening of the salivary duct (B, E, *SlDct*), which discharges on the base of the labium.

The dorsal plate of the larval sucking apparatus is covered by a very delicate, closely adherent membrane (fig. 2 B, *a*). Anteriorly, however, the membrane becomes free, forming the dorsal wall of the atrium (*Atr*), and is then continued into the wall of the ventral depression of the external larval head (A). When the atrium is exposed by cutting away the covering membrane (C) there is seen projecting into it from the anterior end of the dorsal plate of the sucking apparatus a small conical lobe (*Lm*) with a minute sclerotic tip. This lobe is clearly the larval labrum; in a first instar larva the sclerotized tip is larger and forms a conspicuous tooth.

The "buccopharyngeal skeleton" of the cyclorrhaphous larva is

perhaps generally regarded as a structure distinctive of the larva, since most entomologists do not seem to have observed that it is almost a replica of the supporting skeleton of the sucking pump of the adult fly, which is commonly known as the "fulcrum" of the proboscis. This structure in the fly (fig. 3 F) consists of the clypeus (*Clp*) and a pair of lateral plates (*f*), called the paraclypeal phragmata, inflected
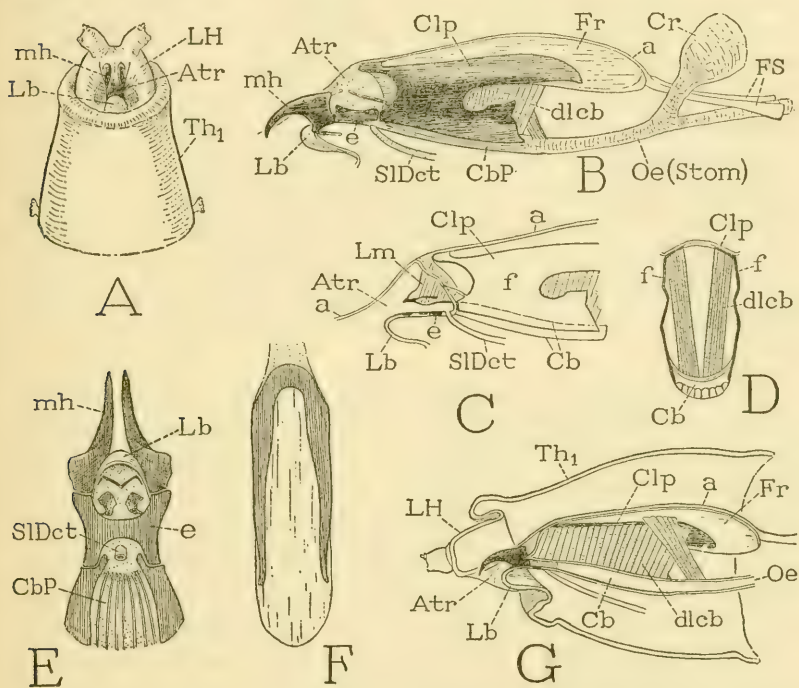

FIG. 2.—Larval head structures of *Calliroga macellaria* (F.).

A, head lobe of larva (*LH*), partly retracted into prothorax, ventral. B, feeding apparatus ("buccopharyngeal skeleton") of a mature larva, lateral. C, diagram of anterior end of sucking apparatus, with lateral wall of atrium (*Atr*) cut away, exposing the labrum (*Lm*). D, cross section of sucking apparatus, showing inflection of paraclypeal phragmata (*f, f*) from edges of clypeus, supporting the cibarial pump (*Cb*). E, ventral surface of anterior part of cibarial pump and H-shaped sclerite (*e*) supporting the mouth hooks (*mh*) and the labium (*Lb*). F, frontoclypeal plate of sucking apparatus, dorsal. G, diagrammatic lengthwise section of head and prothorax, mesal view of right half.

from the clypeal margins, which support between their lower edges the sucking pump (*CbP*) of the food tract. The dilator muscles of the pump (G, *dlcb*) arise on the clypeus and are enclosed between the paraclypeal phragmata. The cross section of the "fulcrum" of the fly (E), therefore, is an exact duplicate of a similar section of the "buccopharyngeal" apparatus of the larva (fig. 2 D), and there can scarcely

be any question that the two structures are merely imaginal and larval forms of the same thing.

The clypeus of a muscoid fly is generally U-shaped or V-shaped with the closed end dorsal. In *Musca* and *Calliphora* (fig. 1 A, B) the clypeus (*Clp*) is fully exposed on the base of the proboscis; in *Callitroga* (C) it is deeply sunken in a cavity on the under side of the head; in *Gonia* (D) it is relatively very small. In *Musca* (A) the broad base of the clypeus is closely hinged to the lower margin of the frons (*Fr*); in *Calliphora* (B) a hinge plate (*hpl*) intervenes between the frons and the muscle-bearing plate of the clypeus; in *Callitroga* (C) the sunken clypeus is separated by membrane from the epistomal ridge beneath the frons; in *Gonia* (D) the diminutive clypeus is well removed from the frons. In any case, the proboscis, with the clypeus and the sucking apparatus, swings back and forth below the frons in the ample membranous connection of the clypeus with the head by muscles attached on the supporting skeleton of the sucking pump. The latter and the clypeus are, therefore, known as the "fulcrum" of the proboscis.

Finally, to understand the nature of the parts that compose the "fulcrum" of the adult muscoid fly, we must go back to the more primitive condition in the orthopteroid insects. A median section through the distal part of the head of a cockroach (fig. 3 A) shows that there is a specific preoral food pocket, the *cibarium* (*Cb*), between the epipharyngeal wall of the clypeus (*Clp*) and the sloping basal part of the hypopharynx (*Hphy*). Two suspensory rods on the cibarial floor extend up through the angles of the mouth (*y*) and give attachment to muscles from the frons. On the anterior or upper wall of the cibarium are attached thick bundles of muscle fibers (*dlcb*) arising on the external clypeal area of the head. These muscles are compressors of the clypeus, but their contraction expands the cibarium. If, then, the movable lobe of the hypopharynx is brought against the inner surface of the labrum (*Lm*), the cibarium will become practically a closed chamber opening anteriorly from the food meatus (*fm*) between the labrum and the free lobe of the hypopharynx, and proximally into the stomodaeum (*Stom*). It is very probable that the cibarium thus serves the cockroach as an organ for the ingestion of liquids. On its dorsal wall are transverse compressor muscles not shown in the figure. The true mouth of the cockroach is the opening of the cibarium (*Mth'*) into the stomodaeum. An important point to bear in mind is that the cibarial muscles of the clypeus are separated from muscles of the stomodaeum arising on the frons by the frontal ganglion and its brain connectives.

The homology of the sucking pump of the fly with the cibarium of the cockroach has been amply illustrated by Gouin (1949).

In various insects the cibarium becomes a permanently more or less closed chamber by a lateral union of the epipharyngeal wall with the base of the hypopharynx, so that the functional mouth opening may come to lie beneath the base of the labrum. The cibarium thus becomes more efficient as a sucking organ. Among the Diptera this condition is fully developed in the lower families, and is well illustrated in the mosquito (fig. 3 B). The cibarial pump of the mosquito (*CbP*) has a strongly sclerotized basinlike floor; the intake orifice lies beneath the base of the labrum and thus constitutes a *secondary mouth* (*Mth″*). Since the floor of the pump in the mosquito corresponds with the hypopharyngeal floor of the cibarium in the cockroach, the hypopharyngeal stylet of the mosquito (B, *Hphy*) represents only the free lingual lobe of the cockroach hypopharynx (A, *Hphy*). A section of the sucking pump of the mosquito (indicated by the arrow at B) shows two sets of strong dilator muscles (*dlcb*) from the clypeus to the concave upper wall of the pump.

The cibarial pump of the mosquito projects freely into the head (fig. 3 B), and, though it is strongly sclerotized and is suspended from the frons by muscles attached on a pair of proximal processes (*y*), it is still not braced against the pull of the dilator muscles. This condition has been remedied in the higher flies. In some of them, as in the mydas fly (C), a strong ridge is inflected from a groove on each side of the clypeus, and the distal ends of the ridges (*f*) are fused with the lateral walls of the pump, thus serving to hold the latter firmly in place. From this simple condition it is only a step to that in the muscoid flies in which the clypeal ridges have been enlarged into broad paraclypeal phragmata (F, *f*) supporting the full length of the pump. The dilator muscles of the pump (E, *dlcb*) are thus boxed in between lateral plates (*f, f*), and the pump is securely braced against the clypeus. As in the cockroach and the mosquito, the primary mouth of the muscoid fly is the opening of the cibarium into the stomodaeal oesophagus (F, *Mth′*), but the functional mouth (*Mth″*) is the entrance into the cibarium from the food meatus (*fm*) between the labrum and the hypopharyngeal stylet. However, in those flies in which the labellar lobes of the labium form a broad, food-collecting disc (D), the deep notch between the lobes (*Mth‴*) is the real intake aperture for liquid food, and has been termed the *prestomum*.

The paraclypeal phragmata are not primarily inflections from the extreme edges of the clypeus. In the adult male of *Tabanus*, as has been shown also by Bonhag (1951), the clypeus is divided longitudi-

nally into three areas by a groove on each side well within the epistomal sulcus. These clypeal grooves in *Tabanus* form merely a pair of internal ridges, but it is clear that the ridges represent the beginning of paraclypeal phragmata in other flies. Developmentally the phragmata are first formed in the larva, and they may be well developed in brachycerous as well as in cyclorrhaphous larvae. Theoretically, however, it seems probable that the complex sucking apparatus must have been first evolved in the adult fly, since the larvae of lower dipterous families have biting and chewing mouth parts.

On returning now to the larva, it is clear that the sucking pump (fig. 2 B, *CbP*) is the cibarium, as it is in the fly. The dilator muscles of the larval cibarium lying in front of the frontal ganglion, therefore, should identify the part of the dorsal plate on which they take their origin as the clypeus (*Clp*), since these muscles entirely conform with the cibarial muscles of the adult. In the larva, however, there is an oblique posterior group of fibers just behind the frontal ganglion, attached below on the stomodaeal oesophagus (G) and arising on the posterior part of the dorsal plate of the sucking apparatus mesad of the cibarial muscles. In the cyclorrhaphous flies the stomodaeum proceeds from the cibarial pump as a simple tubular oesophagus (figs. 2 B, 3 F, *Oe*), but in adult Brachycera it is differentiated immediately behind the cibarium into a second, smaller pharyngeal pump, with its dilator muscles arising on the frons, and these muscles are those represented in the cyclorrhaphous larva by the oesophageal muscles arising on the posterior part of the dorsal plate of the sucking apparatus. The structure and mechanism of the pharyngeal pump in the adult of *Tabanus* are well described and illustrated by Bonhag (1951).

In the larvae of Stratiomydiae the pharyngeal pump has been converted into a crushing organ by the transformation of its dorsal wall into a thick plate with a convex, sometimes strongly ridged, under surface that fits like a broad pestle into the concave, mortarlike ventral wall. This pharyngeal organ is sclerotically continuous with the long, slender cibarial pump, from the end of which it turns upward like the bowl of a pipe from the stem (fig. 6 B, *Phy*). It is the *Schlundkopf* of Jusbaschjanz (1910), who calls the cibarium the "pharynx"; it is described in the larva of *Odontomyia alticola* by Cook (1949), and Schremmer (1951) gives a fully detailed account of its structure and probable use in the larva of *Stratiomys chamaeleon*. The organ is operated by dorsal muscles arising on the frontoclypeal area of the head. A large anterior muscle inserted at the junction with the cibarium is shown by Cook to lie before the frontal ganglion and its brain connectives. This muscle, therefore, is a cibarial muscle; the other, posterior muscles are true frontal pharyngeal muscles.

The attachment of both frontal muscles and clypeal muscles on the dorsal plate of the larval sucking apparatus should identify this plate as a *frontoclypeal* element of the head skeleton, which is a well-defined,
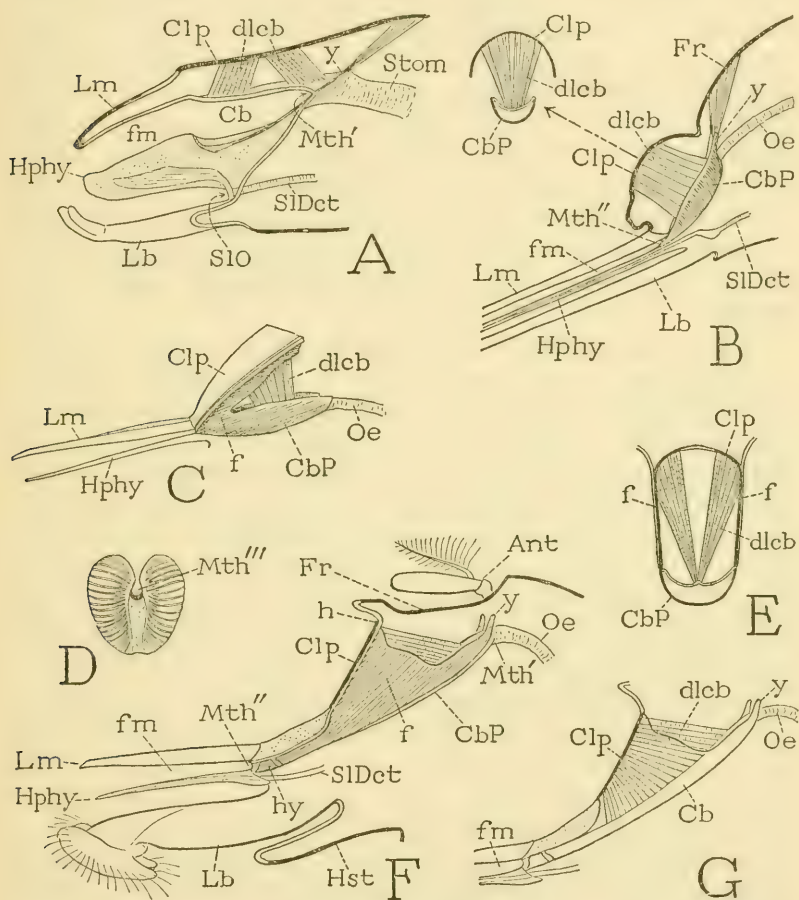

FIG. 3.—The sucking apparatus of adult Diptera, and comparison with the cibarium of a cockroach.

A, diagrammatic lengthwise section of head of a cockroach. B, diagram of sucking apparatus of a mosquito. C, same of a mydas fly. D, labellar disc of a muscoid fly. E, cross section of sucking apparatus of adult *Callitroga macellaria.* F, sucking apparatus and mouth parts of adult *Callitroga macellaria,* lateral. G, lengthwise section of sucking apparatus of same, showing clypeal dilator muscles of cibarium.

median dorsal area of the head in most nematocerous and brachycerous fly larvae (fig. 6 A). Cook (1949) has called this entire area the "clypeus," but in so doing he disregards the evidence from muscle attachments in insects having the clypeus separated from the frons, in

which the cibarial muscles arise on the clypeus and the postcibarial muscles on the frons. The frontal and clypeal areas, however, are often continuous. Ludwig (1949) says merely that this area of the head in the larva of *Calliphora* "includes the clypeus and some additional part of the cranium." The sucking apparatus of the cyclorrhaphous larva, therefore, is a more complex structure than that of the adult fly in so far as it includes not only the clypeus and the cibarium, but also the frons and frontal muscles of the stomodaeum. The frontoclypeal plate and the sucking apparatus of the larva lie entirely within the thorax, a position they have acquired either by retraction or by the overgrowth of a fold from the thorax, or by both means. The frontoclypeal plate is connected with the external larval head (fig. 4 D, *LH*) by the membrane (*a*) extending back from the latter over the atrium.

The H-shaped plate of the larva that lies on the base of the labium and supports the mouth hooks (fig. 2 B, E, *e*) suggests by its position the hyoid sclerite of the adult (fig. 3 F, *hy*), but in the larva the salivary duct (*SlDct*) opens behind the H-shaped plate, while in the adult it enters the hypopharyngeal stylet anterior to the hyoid. The hypopharynx in the larva is represented only by the floor of the cibarium, a free hypopharyngeal lobe corresponding with that of the cockroach (fig. 3 A) or with the hypopharyngeal stylet of the fly (F, *Hphy*), being absent in the larva. The larval labium (fig. 2 A, C, *Lb*) does not become the labium of the adult; the labium of the fly is developed from a pair of histoblastic pouches formed inside the larval labium.

The nature of the mouth hooks of the cyclorrhaphous larva has been a subject of much discussion, some writers contending that the hooks are mandibles, others that they are not. The latest advocate of their mandibular nature is Ludwig (1949). If the larval mouth hooks are not mandibles, the question is, what are they? In the first place, it is curious that mandibles should have their only articulations on a plate on the base of the labium, and secondly, since the muscles of the hooks are attached on the paraclypeal phragmata of the sucking apparatus, it is an unusual thing for mandibular muscles to arise on any part of the clypeus. However, since the parietal walls of a typical insect cranium are obliterated in the fly larva, the phragmata offer the only available solid support for the muscles, and muscles do change their points of origin where efficiency demands a change. On the other hand, if the hooks are not mandibles, they cannot be homologized with any other structure of other insects, and it is hardly to be supposed that such highly developed feeding organs should be developed *de novo* for the express use of the larva. However, since the hooks disappear at

the end of larval life and the adult fly has no mandibles, the larval hooks cannot be put to the crucial test of finding what they become in the imago, and for this same reason we may leave the matter without further discussion, inasmuch as the mouth hooks are not involved in the metamorphosis of the larva into the fly.

In most nematocerous and brachycerous families the head of the larva is more or less retracted into the thorax, so that it is at least partly ensheathed in a fold of the prothorax. In the cyclorrhaphous larva, however, the head appears to consist of an external part bearing the apical sense organs of the larva, and of a retracted part that includes only the frontoclypeal area, which carries the labrum and supports the cibarial sucking apparatus. The cyclorrhaphous larva thus presents a cephalic condition that is difficult to understand, and even the known facts of embryonic development do not make the condition entirely clear.

The head of the embryo at an early stage of its development is a simple structure. As shown by Pratt (1901) in *Melophagus ovinus* (fig. 4 A) the embryonic head presents a dorsal lobe above the entrance into the food tract (*Cb*) and a ventral lobe below it. The dorsal lobe, which contains a group of compressor muscles (*dlcb*), Pratt calls the "muscular sucking tongue," but we can easily recognize this lobe as the labrum and clypeus (*Lm, Clp*), and the muscles as the dilators of the future cibarial pump (*Cb*). The ventral lobe is clearly the larval labium. This stage of the embryo may be diagrammatically presented in a more conventional form as at C of the figure. The short dorsal wall of the embryonic head represents at least the clypeus of the larva (D, *Clp*) bearing the labrum and giving attachment to the dilator muscles of the cibarium.

The primary embryonic head now becomes covered by the forward growth of an integumental fold (fig. 4 A, C, *hf*) from behind it, which goes over the labrum (B) and forms the roof of an antechamber, the head *atrium* (*Atr*), before the mouth of the cibarium (*Cb*), while the fold itself becomes at least a part of the external head lobe of the larva (D, *LH*) bearing the larval sense organs. The overgrowth of the primitive head by this secondary dorsal head fold is well illustrated also in *Calliphora* by Ludwig (1949, fig. 58). According to Pratt (1901) there is a dorsal and a ventral fold in *Melophagus* (A, B, C, *hf, vf*). Unfortunately Pratt's terminology is confusing because he calls the newly formed atrium the "pharynx," and the cibarium the "stomodaeum." With the completion of the dorsal head fold the embryo acquires the essential head structure of the larva, represented diagrammatically at D of the figure. The frontoclypeal plate and the

cibarial apparatus thus become enclosed within the thorax, and the major part of the external larval head lobe (*LH*) bearing the larval sense organs appears to be a secondary structure formed by the dorsal head fold extended from *c* to *d*. The original space (*b*) beneath the fold later becomes obliterated by the close apposition of the inner wall of the fold (*a*) on the frontoclypeal plate, but the labrum (*Lm*) is left projecting freely into the atrium (*Atr*).

Of the two sense organs on each of the apical papillae of the larva, the dorsal one, according to Ludwig (1949), represents the larval antenna, the ventral one the maxillary palpus. This opinion was also that of Weismann (1864), but other authors have considered the interpretation doubtful. The alleged antennal organ is shown by Ludwig to be innervated by a long branch from the labrofrontal nerve—a most unusual association for an antennal nerve, and neither the nerve nor the sense organ can have any relation to the antenna of the adult. The ventral sense organ, Ludwig says, "is the maxillary palp sense organ," but apparently the only basis for this statement is that the organ in question is innervated by a branch from the "mandibular-maxillary-labial nerve." A sense organ wherever located must have a nerve. The origin of the papillar sense-organ nerves from head ganglia is not proof that the organs are either antennal or maxillary, but it is convincing evidence that, whatever they are, they belong to the head, and Ludwig shows, moreover, that the organs originate in the epidermis of the lateral walls of the embryonic head. It becomes a problem, therefore, to understand how these sense organs in the larva come to be situated on the external head lobe formed by the head fold, and their position on this lobe raises the question as to whether the fold pertains to the thorax or to the head.

As seen in longitudinal sections the head fold of the cyclorrhaphous embryo (fig. 4 A, B, *hf*) suggests the prothoracic fold that partly ensheaths the head of many nematocerous and brachycerous larvae (fig. 6 A, B, *thf*). Schremmer (1951) asserts that there appears to be no remnant of a head in the cyclorrhaphous larva, and that as a result of the forward growth of the dorsal fold the larval sense organs come to be on the anterior end of the thorax. Holmgren (1904) apparently regarded the larval head lobe as a derivative of the thorax, but he says nothing of the sense organs. Pantel (1898) called the larval head lobe a "pseudocephalon." Ludwig (1949) also attributes at least a part of the head fold to the thorax because it contains a pair of muscles innervated from the prothoracic ganglion that "insert on a sclerotized area between the mandibles." In the *Callitroga* larva, however, these muscles do not arise in the head lobe itself but on the overhanging

anterior part of the prothorax, so, if the larval head lobe is a part of the head, the muscles in question are merely prothoracic head muscles.

In a cross section of the embryonic head of *Calliphora* it is shown by Ludwig that the head fold (fig. 6 C, *hf*) covers only a narrow space (*b*) above the frontoclypeal surface (*Clp*). The inner lamella of the fold (*a*) arches immediately over the frontoclypeus, while the outer lamella has become continuous with the parietal walls of the head. If
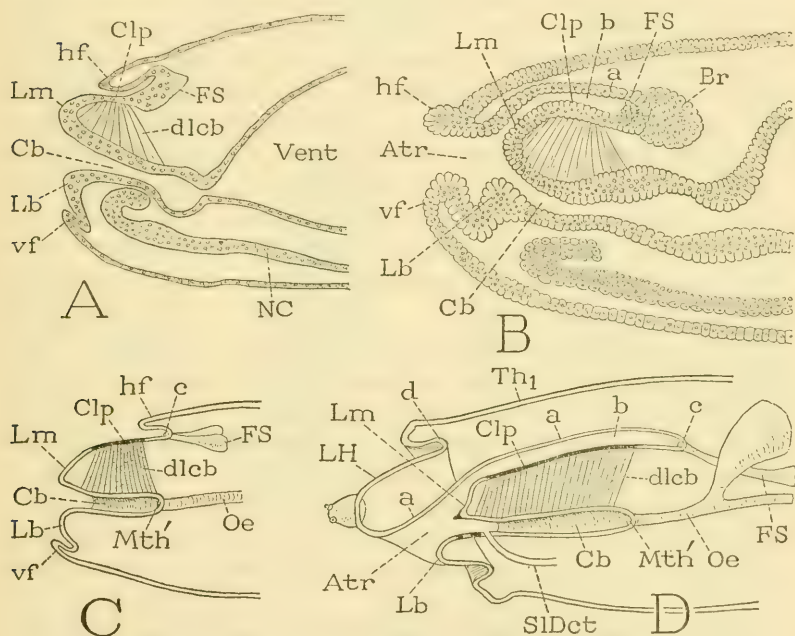

FIG. 4.—Development of the larval head of a cyclorrhaphous fly.

A, lengthwise section of embryonic head of *Melophagus ovinus* (from Pratt, 1901), showing beginning of head fold (*hf*). B, later stage of same (from Pratt, 1901), in which the head fold has grown forward over the labrum and labium, which are now enclosed in a secondary preoral atrial chamber (*Atr*). C, diagrammatic expression of A. D, diagrammatic analysis of the anterior larval structure based on B.

the fold proceeds over the head as a narrow median growth from the thorax alone, it is difficult to understand how it becomes so intimately a part of the head wall. In any case, it is evident that this head fold of the cyclorrhaphous larva is something quite different from the prothoracic fold that ensheaths the base of the head in a brachycerous larva.

The head fold of *Calliphora*, Ludwig (1949) says, appears at about the thirteenth hour of the developing embryo, and "is in the shape of a

U, with the open end pointed anteriorly." Its lateral margins lie mesad of the developing larval sense organs. If, therefore, the head fold grows forward in this manner with its arms extending along the edges of the frontoclypeal area, it would seem that, whatever its origin, the extension of the fold must be at the expense of the head wall itself, and that the arms of the fold close medially from the sides as the fold advances. If this is the manner of growth of the fold, the condition seen in cross sections of the embryonic head (fig. 6 C) becomes understandable. Furthermore, only by some such process of growth from the head wall could the lateral sense organs on the embryonic head be carried up over the labrum and finally come to be situated on the anterior end of the fold, which forms at least the dorsal part of the head lobe of the larva. It is, then, certainly more rational to regard the larval head lobe as a part of the head itself than as a derivative of the thorax. Clearly there is need for further study of the nature of the head fold and the manner of its growth, and Schremmer (1951, p. 362) has promised a new investigation "über die Enstehung des Cyclorrhaphenlarvenkopfes."

When a young insect in its development takes a path widely divergent from that of its parents, and acquires a head structure as extraordinarily specialized as that of the cyclorrhaphous larva, it is evident that the larval structure cannot be "transformed" into that of the adult. The head of the fly, therefore, is practically a new structure developed without reference to the larval head. In the evolution of the Diptera, however, the cyclorrhaphous way of forming the adult head has been derived from a more simple method retained in some of the lower flies.

Among the nematocerous Diptera, as has been shown by Kellogg (1902) in *Simulium* and *Bibiocephala,* the imaginal (pupal) head may be formed simply and entirely within the loosened cuticle of the larval head, and the imaginal mouth parts are formed inside the cuticle of the larval mouth parts. The antennae of the pupa, because they are much longer than those of the larva, find space for their growth between the pupal head and the cuticle of the larval head, but their tips are retained in the corresponding larval organs. In *Corethra,* as described by Weismann (1866), the long slender antennae of the pupa become sunken into pouches of the pupal head, from which they are everted when the larval cuticle is shed. In *Corethra* the compound eyes are formed on the surface of the pupal head beneath the larval cuticle. In *Tendipes* (*Chironomus*) Miall and Hammond (1900) showed that both the antennae and the compound eyes of the pupa are developed within longitudinal infoldings of the epidermis of the dorsal wall of the pupal

head inside the larval cuticle. Dissection of a mature *Tendipes* larva reveals a pair of long pockets converging from the larval antennae to the posterior end of the head (fig. 5 A), each of which contains an axial tubular antenna (*Ant*) and, in the wall of its basal part, the developing rudiment of a compound eye (*E*). These elongate pockets
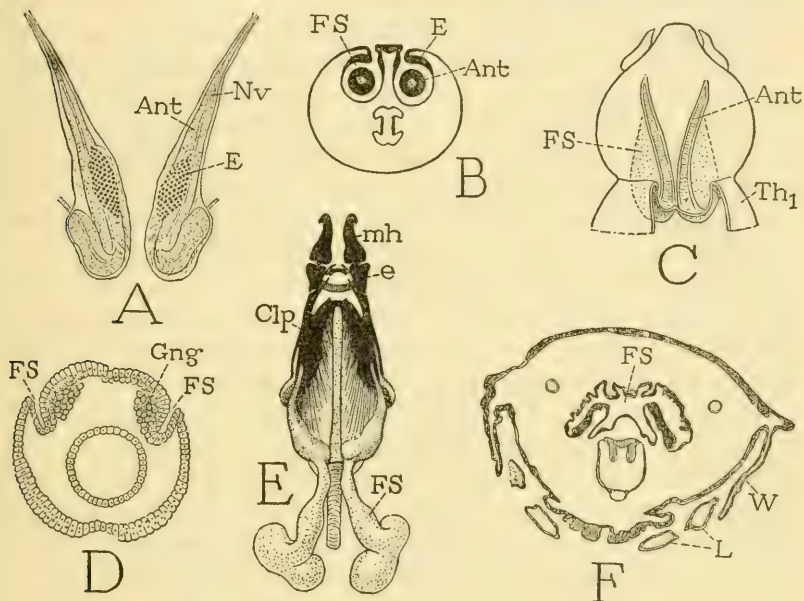

FIG. 5.—Development of the frontal sacs.

A, oculoantennal pockets from head of a mature tendipedid (chironomid) larva, *Tendipes plumosus* (L.), extending posteriorly from larval antennae. B, diagrammatic cross section of pupal head of *Psychoda alternata* showing open grooves (*FS*) containing imaginal antennae and rudiments of compound eyes (outline from Feuerborn, 1927). C, diagrammatic dorsal view of head of young pupa of same, showing oculoantennal grooves extended into pockets of prothorax (outline from Feuerborn, 1927). D, cross section of head of embryo of *Melophagus ovinus* showing origin of frontal sacs (*FS*) on sides of head (from Pratt, 1901). E, dorsal view of feeding apparatus of mature larva of *Rhagoletis pomonella*, with fully developed frontal sacs (*FS*) extending posteriorly from frontoclypeal plate (from Snodgrass, 1935). F, cross section of 7-hour prepupa of *Drosophila melanogaster* showing united frontal sacs produced into lateral pouches with folded walls (from Robertson, 1936).

lie immediately beneath the ecdysial cleavage grooves of the larval head. Very similar groovelike pockets of *Psychoda* are described and figured by Feuerborn (1927) as infoldings of the pupal head (B, *FS*) open by narrow slits on the surface, and containing the developing antennae (*Ant*) and compound eyes (*E*). In *Psychoda* the grooves extend into the front part of the thorax (C) as pockets, which deepen as the pupa develops.

It is probable that similar developmental processes occur in other Nematocera, though little attention has been given to the details of metamorphosis in these flies. The oculoantennal pockets of the head very clearly are equivalent to the peripodal pouches of the thorax in which the imaginal legs are developed and to the pouches that contain the wing rudiments.

In the higher Diptera the oculoantennal pockets, known as the *frontal sacs,* are present in the larvae as long-necked pouches extending from the posterior end of the frontoclypeal plate of the sucking apparatus into the thorax as far as the retracted brain, with which they are connected by ocular nerves (figs. 2 B, 5 E, 6 B, *FS*). In the stratiomyid *Odontomyia* Jusbaschjanz (1910) says the pouches contain only the histoblasts of the compound eyes (fig. 6 B, *FS*), the antennae arising from the surface of the head as in *Corethra.* In all cyclorrhaphous flies that have been described, however, the frontal sacs contain the rudiments of both the eyes and the antennae. These sacs are formed in the embryo and are present in all stages of the larva, but reach their full development only in the last larval instar. In their early origin, therefore, the frontal sacs of the head in the cyclorrhaphous flies more nearly resemble the thoracic peripodal pouches of the legs than do the oculoantennal pockets of the Nematocera, which appear only in the prepupal stage. Because in the late embryo the sacs appear to arise from the inner end of the passage between the inner lamella of the head fold and the underlying frontoclypeal plate (fig. 4 B, *FS*), this passage (*b*) has been regarded as an unpaired part of the sacs, and the latter have been erroneously said to be invaginations from the atrium (*Atr*), or from the "pharynx" if the atrium is mistaken for the pharynx. The point at which the sacs grow into the thorax (D, *c*) is simply overgrown by the head fold, and the true origin of the sacs is on the lateral parts of the embryonic head.

According to Ludwig (1949) the imaginal discs of the compound eyes in the embryo of *Calliphora* arise as ectodermal thickenings on the lateral walls of the head, but in the larva both the ocular and the antennal rudiments are contained in a pair of membranous sacs lying along the sides of the oesophagus. Ludwig does not explain how the sacs are developed, or how they come to contain the histoblasts of the eyes and antennae. In his figure 57 he shows the left sac exactly as all other writers have depicted the frontal sacs, and yet he says "embryonic studies reveal no such pouches." Furthermore, Ludwig attributes to Pratt (1901) the absurd statement that the common opening of the sacs "is drawn forward and downward, and then posteriorly through the mouth," and on this assertion he bases a criticism of Pratt's work.

However, Pratt makes no such statement, or anything like it. More concisely than does Ludwig himself, Pratt describes in *Melophagus ovinus* the origin of the frontal sacs ("dorsal head discs") as dorsolateral thickenings of the epidermis of the embryonic head. Early in their history the discs begin to invaginate in the form of crescentic slits (fig. 5 D, *FS*), and later they move dorsally to the back of the head, where their outer parts unite in a single, transverse depression, while the inner parts increase in length and extend separately into the
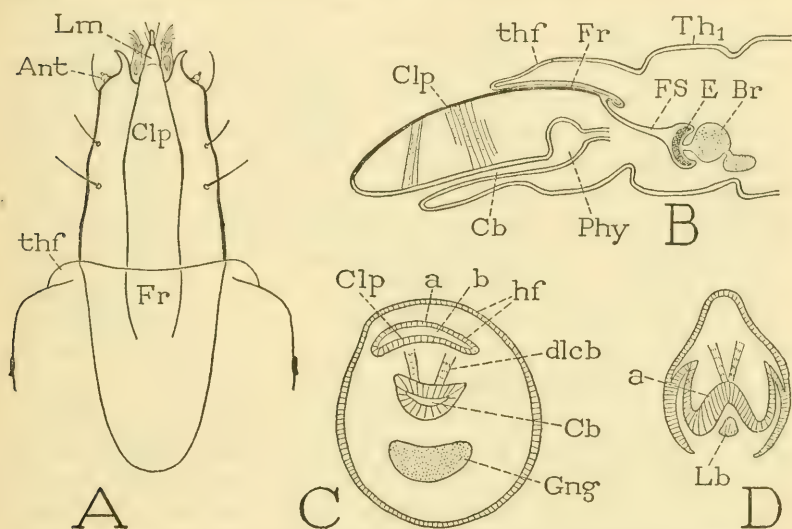
Fig. 6.—Head of stratiomyid larva and sections of embryonic head of *Calliphora*.

A, larval head of *Ptecticus trivittatus* (Say) partly ensheathed in fold of prothorax, dorsal. B, lengthwise section of larval head and prothorax of *Odontomyia* (combination diagram from Jusbaschjanz, 1910, relettered). C, cross section near base of head of 15-hour embryo of *Calliphora* (from Ludwig, 1949). D, cross section of head lobe of 16-hour embryo of *Calliphora*, overhanging the labium (from Ludwig, 1949).

body cavity as a pair of stalked sacs that lie in contact with the cerebral ganglion. Now there takes place, from behind the mouth of the sacs (fig. 4 C, *c*), the formation of the dorsal fold (*hf*), which grows forward over the head. Since the inner lamella of the fold becomes closely adherent to the frontoclypeal plate, it thus comes about that in the larva the sacs *appear* to be attached to the posterior end of the larval sucking apparatus (figs. 2 B, 5 E, *FS*). Their true opening at the posterior end of the head beneath a fold of the thorax (*thf*) is shown by Jusbaschjanz (1910) in his sectional figure of a stratiomyid larva (fig. 6 B, *FS*).

From the description of the early history of the frontal sacs given by Pratt it is clear that the frontal sacs of the cyclorrhaphous flies can be correlated in their origin with the oculoantennal grooves of the pupal head in the Nematocera. That, in the former, the sacs arise in the embryo instead of in the pupa shows that the imaginal discs of the head have followed the same course of evolution as have those of the thorax, which also in the higher flies have come to be formed in the embryo.

The further history of the frontal sacs has been followed by Wahl (1914) in *Calliphora* and by Robertson (1936) in *Drosophila*. Weismann (1864) observed that the head of the fly is formed from two "cell masses" (the frontal sacs), which at first are in contact and later become united. Jusbaschjanz (1910) noted that in a stratiomyid larva there is only one frontal sac (*Kopffalte*) at the time of pupation, from which fact he concluded that the two primary sacs must have united in a single pouch. Wahl (1914) specifically describes the formation of a single sac in the early pupa of *Calliphora* by a dissolution of the mesal walls of the original two sacs followed by a union of their outer walls. The resulting unpaired sac then increases in size by expansion of lateral pouches, and its walls become thrown into numerous irregular folds. In *Drosophila* Robertson (1936) says the closely appressed frontal sacs begin to fuse two hours after the formation of the puparium. The median walls break down and the broken edges of one sac unite with those of the other until the two sacs have completely united (fig. 5 F, *FS*) except at their posterior ends where the optic concavities are applied to the cerebral ganglia.

At pupation the cephalic fold of the larva retracts (fig. 7 B, *hf*), the passage (*b*) beneath it opens and becomes continuous with the lumen of the now single frontal sac (*FS*), so that, as Wahl (1914) shows in the early pupa of *Calliphora*, the frontal sac comes to open directly to the exterior above the mouth of the cibarium ("pharynx"). The same thing was noted by Pratt (1897) in *Melophagus*, but Pratt's language is somewhat confusing to a modern reader when he says "the lumen of the discs and that of the pharynx become completely merged and form together a single continuous space." The "discs" are the frontal sacs, the "pharynx" is the larval atrium. When now the pupa is first exposed by the shedding of the last larval cuticle within the puparium, there is to be seen at the anterior end of the body only a great hole in the front of the prothorax (fig. 7 A). This stage is the cryptocephalic phase of the pupa. Shortly thereafter the walls of the cavity are suddenly everted, and the pupa thus acquires a head (C). The pupal head is at first relatively small and not fully developed, but it takes on its

definitive size and structure (D, E) during the rest of this phanero-cephalic stage of the pupa. When the head of *Drosophila* is first everted, Robertson says, the eyes are brought to their final position, but are not yet histologically completed, and the antennae are simple thickenings of the front wall of the head. Bodenstein (1950) describes in detail the development of the compound eyes in *Drosophila*.

Ludwig (1949) emphatically denies that there is any process of in-vagination involved in the formation of the head of the fly. However,
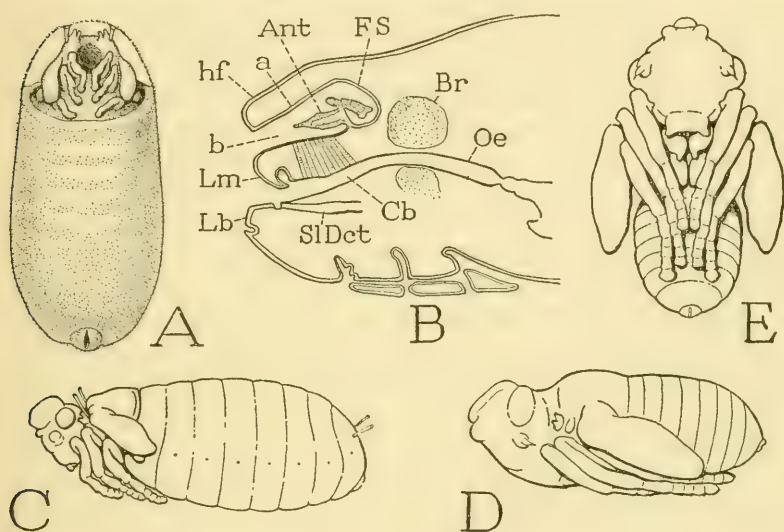
FIG. 7.—The pupa.

A, cryptocephalic pupal stage of *Rhagoletis pomonella*, ventral. B, lengthwise section of anterior end of 10-hour prepupa of *Drosophila melanogaster* showing opening of frontal sac just before pupation (from Robertson, 1936). C, early phanerocephalic pupal stage of *Rhagoletis pomonella*. D, mature pupa of *Rhagoletis*, lateral. E, same, ventral.

since the adult head is visibly everted in the pupal stage, it is not clear how it became introverted without a previous inversion. The frontal sacs are actually ingrowths of the embryonic integument, and an in-growth is usually called an "invagination," though admittedly it is more properly an introversion. Furthermore, Ludwig criticizes a former statement by the writer (1935, p. 313) that "the entire facial region of the head, including the area of the frons and that of the imaginal antennae and compound eyes, is invaginated into the thorax." This statment is in accord with the findings of other writers, since the time of Weismann (1864), and all that is needed to demonstrate its truth is a glance at a pupa in the cryptocephalic stage, whether of

Musca, Calliphora, Drosophila, or *Rhagoletis* (fig. 7 A). When the frontal sac is everted, it brings with it the eyes and the antennal rudiments, and its walls form the epidermis of all parts of the fly's head except that part derived from the sucking apparatus of the larva. The cuticular skeleton of the latter is shed at the moult to the pupa, but the matrix of the organ must remain to form the more simple sucking apparatus (or "fulcrum") of the adult, though the transformation has not been observed.

In the change from the larva to the adult the frontoclypeal plate of the larva undergoes a very considerable modification. First, it is distinctly divided, in the fly, into frontal and clypeal elements; the clypeal area retains the muscles of the cibarium, the frons now carries the attachments of the postcibarial frontal muscles of the stomodaeum. The shape of the clypeus in the adult becomes reversed from that of the larva, in that, though U-shaped or V-shaped in both, the open end is distal in the adult (fig. 1, *Clp*). The frons of the fly is a part of the head wall, including specifically the depressed area of the face (*Fr*) in which the antennae are lodged.

Again we may point out that the frontal sacs of the cyclorrhaphous fly larva from which the imaginal head is formed are cephalic equivalents of the thoracic histoblasts, which latter not only give rise to the legs and wings, but in the higher flies regenerate the thoracic integument as well. As an example we may refer to Robertson's (1936) account of the formation of the imaginal thorax in *Drosophila*. As the histoblast pouches of the legs and wings open to allow the contained appendages to evert, their edges expand by cell proliferation, while the surrounding larval cells retreat and are gradually sloughed off into the body cavity to be devoured by phagocytes. The newly generated areas spread over the thorax, unite, and finally construct the entire thorax of the fly. In describing the formation of the thorax of *Melophagus,* Pratt (1897) says: "In proportion as the larval hypodermis disappears under the attack of the phagocytes, the edges of the imaginal discs grow and take its place, forming the imaginal hypodermis." The idea that the larval cells are *first* destroyed by phagocytes, however, is not in accord with results of later investigators. The cephalic histoblasts of the fly have no opposition from larval cells because of the great reduction of the larval head; the elaborate head of the cyclorrhaphous fly is practically a new structure with no counterpart in the larva.

Likewise, the mouth parts of the fly owe little to those of the larva. The larval mouth hooks are not re-formed in the pupa, and the fly has no trace of mandibles. The adult labium is formed from a pair of his-

toblastic pouches developed inside the larval labium. According to Wahl (1914) these ventral histoblasts give rise to the entire proboscis of the fly, including the hypopharynx, the maxillary remnants, and the labrum, which statement suggests that the matter should be reinvestigated. The cyclorrhaphous larva, as already observed, has no free hypopharyngeal lobe, and the salivary duct opens on the base of the labium (fig. 2 C, *SlDct*). In the fly, on the other hand, the salivary outlet duct traverses a median stylet arising at the base of the labium, which is commonly called the hypopharynx. Because this stylet gives passage to the salivary duct, however, Ferris (1950) asserts that it is not a hypopharynx, but a secondarily developed outgrowth containing the salivary outlet. According to the same interpretation the Hemiptera and Siphonaptera also should not have a hypopharynx. While it is generally true that the salivary outlet duct of insects opens between the base of the hypopharynx and the base of the labial prementum, the opening is sometimes on the base of the hypopharynx, as in the cockroach (fig. 3 A, *SlO*), in dragonflies, and, as shown by Weber (1938), in the Psocoidea. The hypopharynx is a median, postoral outgrowth of the ventral wall of the head, principally on the maxillary segment, but it may encroach on the labial segment. If the organ includes a labial element, therefore, it is nonetheless a hypopharynx, and if the salivary duct opens into a pocket on its base it might traverse its entire length. In the larvae of nematocerous flies a hypopharynx is present, but, as in other holometabolous insects, it is united with the labium in a composite suboral lobe and the outlet duct of the salivary glands opens distally between the two component parts of the latter. The ancestors of the Diptera, therefore, must have possessed a true hypopharynx, and there would seem to be no reason why it should not be restored in the adult, just as are the legs. Weismann (1864) called the median mouth stylet of the fly "die Kieferborste," and described it as formed by the union of paired parts about a cellular strand that became the salivary duct. Again, we can say only that the pupal development of the mouth parts of the cyclorrhaphous flies needs further investigation, since the ordinary criterion of correlating the adult parts with the larval parts cannot be invoked.

A comparison of the mouth parts of the fly with those of the cockroach shows at least that the stylet containing the salivary outlet of the fly (fig. 3 F, *Hphy*) corresponds exactly in position with the free lobe of the hypopharynx in the cockroach (A, *Hphy*). Its grooved dorsal surface, moreover, is continued into the floor of the sucking pump (F, *CbP*), which represents the floor of the cibarium on the base of the hypopharynx in the cockroach. Even the oral arms of the suspensory

rods of the cockroach hypopharynx (A, y) may be retained in the flies as a pair of short cibarial processes (B, F, y) embracing the primary mouth (F, Mth').

Finally, in connection with the metamorphosis of the fly's head, we should mention the ptilinum, since it constitutes an example of exceptional development in the pupa of a special structure for the temporary use of the fly. The ptilinum is a vesicular introversion of the front of the head of the pupa in the schizophorous families of the Cyclorrhapha, which is everted by the emerging fly to open the anterior end of the enclosing puparium. After emergence, the lips of the opening come together in the long groove of the head that arches over the bases of the antennae (fig. 1 A, pts). As described by Laing (1935), in *Calliphora* the ptilinum is formed in the young pupa from the head wall just above the antennae, which on the third day of pupal life begins to introvert and soon becomes a crumpled sac inside the head with a greatly thickened cuticle. Eversion of the ptilinum in the emerging fly is brought about by blood pressure resulting from contraction of the abdomen. The surface of the organ in different flies may be smooth, covered with fine spicules, or, as in *Gonia* (fig. 1 D), thickly coated with coarse spines. After the ptilinum has served its purpose it is again retracted and remains as a large though shrunken body in the fly's head. The retraction is caused by muscles, which are fully described by Laing. Some of the muscles are special ptilinal retractors, and these muscles disappear during the first two days of the life of the fly.

Metamorphosis in the cyclorrhaphous Diptera is a "change of form" in the insect as a whole, but it is not a transformation of the maggot into a fly. The maggot represents an extreme degree to which juvenile development among the insects has diverged from the evolutionary course that produced the adult, until the young insect has become an independent creature in no way structurally related to its parents. The embryo develops directly into the form of the larva and not into that of the insect that produced it, but certain cells of the larval tissues retain the potentiality of reproducing the corresponding adult tissues, while the rest of the larval tissues, after performing their temporary function, go into dissolution and become food for the growing imaginal tissues. The maggot is in no sense a recapitulation of any stage in the evolution of the fly, except larval stages of its more recent ancestors. The larval form is determined at an early period of development in the egg, and when the larva has completed its destiny it gives way to the ancestral development of the fly, but the manner in which the modern

fly is developed has no phylogenetic significance. The larval development and the adult development are known to be under control of hormones, but the mechanism of dual inheritance has not been explained.

EXPLANATION OF LETTERING ON THE FIGURES

a, membrane over frontoclypeal plate of larva, inner wall of head fold.

Ant, antenna.

Atr, head atrium.

b, space between head fold of embryo and frontoclypeal plate.

Br, brain.

c, posterior end of frontoclypeal plate, origin of inner wall (*a*) of head fold.

Cb, cibarium.

CbP, cibarial pump.

Clp, clypeus.

Cr, crop.

d, end of dorsal wall of head fold.

dlcb, dilator muscles of cibarial pump.

e, H-shaped sclerite supporting mouth hooks.

E, rudiment of compound eye.

f, paraclypeal phragma.

fm, food meatus.

Fr, frons.

FS, frontal sac.

Gng, ganglion.

h, hinge of clypeus on frons.

hf, head fold.

Hphy, hypopharynx.

hpl, hinge plate of clypeus.

Hst, hypostome.

Hstl, haustellum.

hy, hyoid sclerite.

L, legs.

Lb, labium.

Lbl, labellum.

LH, external larval head lobe.

Lm, labrum.

mh, mouth hooks of larva.

Mth', primary mouth (entrance to stomodaeum).

Mth'', secondary mouth (entrance to cibarium).

Mth''', tertiary mouth, prestomum (aperture to food meatus between labella).

MxPlp, maxillary palpus.

NC, nerve cord.

Nv, antennal nerve.

Oe, oesophagus.

Phy, pharynx.

Ptl, ptilinum.

pts, ptilinal sulcus.

Rst, rostrum of proboscis.

SlDct, salivary duct.

SlO, salivary orifice.

Stom, stomodaeum.

Th, thorax.

thf, thoracic fold.

Vent, ventriculus.

vf, ventral head fold.

W, wing.

y, oral arm of hypopharyngeal suspensorium, or of floor of cibarium.

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SOLAR VARIATION, A LEADING WEATHER ELEMENT

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CONTENTS

INTRODUCTION

On January 28, 1953, the American Meteorological Society devoted the day to consideration of the influence of solar variation on weather. An early speaker said he acknowledged the results of conscientious studies of total solar variation, which had been made, as probably sound. But the variations found appeared to be of the order of 1 percent, or much less. No reasonable theory could show that these might have important weather influences. He distrusted statistical conclusions, unless grounded on sound theory. Statistics might show that it is dangerous to go to bed, for the great majority of decedents died in bed. The remainder of the panel appeared to agree with him that, because percentage solar-constant variations are small, it is needless to consider the possibility that variations of total solar radiation affect weather importantly. The discussion was mostly confined to matters relating to the high atmosphere, in the stratosphere and beyond. Suggestions were discussed as to whether the large effects of solar changes known to exist in the high atmosphere could be connected with weather changes in the troposphere. No positive result was reached.

One gathered the impression that meteorologists are so firmly convinced that variations of total solar radiation are of negligible weather influence, and that statistical methods of proof are to be ignored, that they probably do not read attentively any publications of the contrary tendency. I do not agree that the last word has been said. I submit several propositions.

1. Statistically derived results may be accepted, if well supported by observation, without supporting theory. Kepler's laws were accepted statistically for many years before there was any supporting theory.

2. A conclusion may be accepted as a valuable working hypothesis, without being proved in the rigid sense, e.g., that the square of the hypotenuse of a right-angle triangle equals the sum of the squares of the other two sides.

3. In lieu of theoretical support, to be supplied later, a statistically derived proposition, A, may be adequately supported as a working hypothesis, if accepted phenomena, B, C, D, E, — — — — which stem from a related source, are harmonious with proposition A. I propose to show that the proposition that the variations of solar radiation are important weather elements is thus adequately supported.

Further support comes when forecasts with high correlation compared to probable error result from such hypotheses. *I depend strongly on this paragraph in what follows.*

However, I will venture a suggestion toward a theory of the matter.

1. It is commonly observed that the temperature is responsive to the *direction* of the wind.

2. The direction of the wind depends on the orientation of the station with respect to the cyclonic structure prevailing.

3. H. H. Clayton found, by his tireless statistical work, over a quarter of a century ago, that the "centers of action," about which the cyclonic structure forms, are largely displaced in position on the earth's surface, as solar-constant measures rise and fall.[1]

4. If this Clayton effect is accepted, the mystery is no longer why large temperature and associated weather changes follow small percentage solar-constant changes, but rather why the "centers of action" shift when solar-constant changes occur.

5. If meteorologists doubt the Clayton effect, they may find 30 years of 10-day solar-constant measures in paper No. 27, cited below, which they may compare with weather maps of the period 1920 to 1950.

To provide a groundwork for reference, I first list certain pertinent publications of the past 20 years. A book would be needed if one collected all the evidence which supports the conclusion in hand. I shall give below a few of the more telling references. Those interested may find numerous others from the papers cited and from H. H. Clayton's earlier papers in the Smithsonian Miscellaneous Collections. Students of research know that early work is often found partly erroneous as later results come in. So it is here in some measure. Nevertheless, I think all the papers cited here still retain features of some value and interest. Fundamental to the whole pattern, however, is the paper "Periodicities in the Solar-constant Measures," Smithsonian Miscellaneous Collections, vol. 117, No. 10, 1952 (reference No. 27, below), to which I particularly invite attention.

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PROPOSITION I

Correlation of other solar phenomena with solar-constant measures indicates the probable reality of solar variation

Applying my criterion No. 3, above, I shall now cite evidence that variation observed in Smithsonian solar-constant measures is associated with variation (*a*) in solar faculae areas; (*b*) in sunspot numbers; (*c*) in calcium flocculi areas; (*d*) in incidence of magnetic storms; and (*e*) in ionospheric data.

Dr. H. Arctowski, of Poland, was attending a meeting in Washington when his savings and work were swept away by the invasion of his country. I suggested to John A. Roebling that it would be helpful if so eminent a European meteorologist should examine our case for the variation of the sun and its control of weather. Mr. Roebling consented to support this project. After several months Dr. Arctowski told me: "I believed in neither proposition. But I determined to give them a fair trial. When I found them unsupported, I intended to tear up my papers and resign. I could not take money under false pretenses." After a brief time, however, Dr. Arctowski came to believe in both propositions, and said: "I have become more enthusiastic about them even than Dr. Abbot himself."

a. Referring to Dr. Arctowski's paper, reference No. 14 above, I reproduce his figures 1, 3, 4, and 5 as figures 1, 2, 3, and 4 herein.

b. Referring to L. B. Aldrich's administrative report on the Astrophysical Observatory for 1952 (Rep. Secretary Smithsonian Inst., 1952, p. 131), I reproduce here as figure 5 his figure showing the correlation of solar-constant measures with sunspot numbers.

c. Referring to my paper "Weather Predetermined by Solar Variation," reference No. 18 above, I reproduce figure 6 of that paper as figure 6 here. I call attention to the similarity of the full and dotted curves of the figure. This similarity indirectly proves the correlation claimed as *c,* above. Each month the curves represent means of effects on numerous occasions.
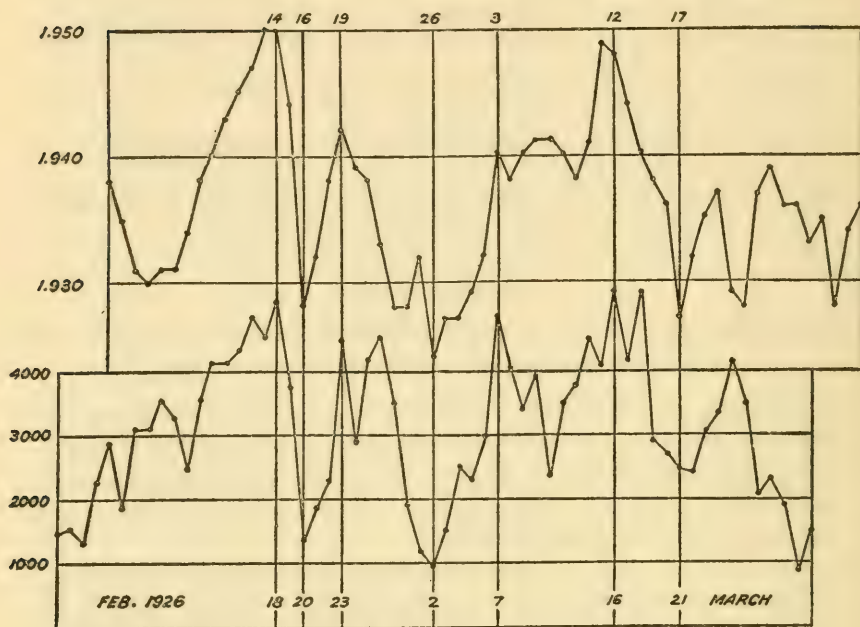
FIG. 1.—Variations of the solar constant and of areas of solar faculae. Daily solar-constant values for February and March, 1926, and areas of faculae.
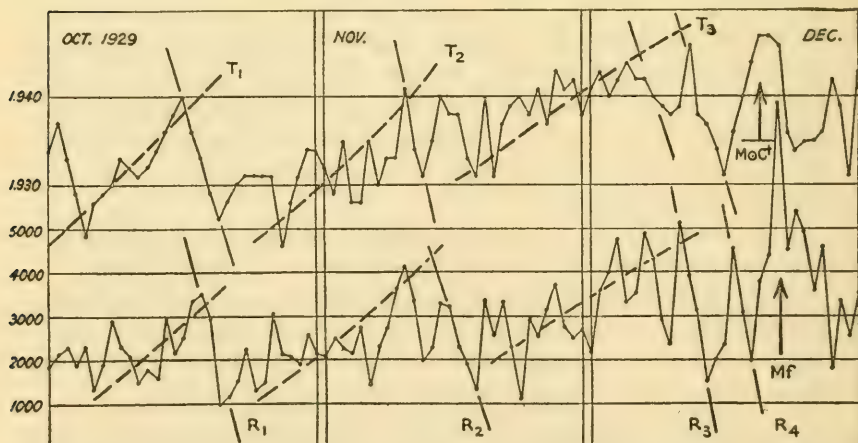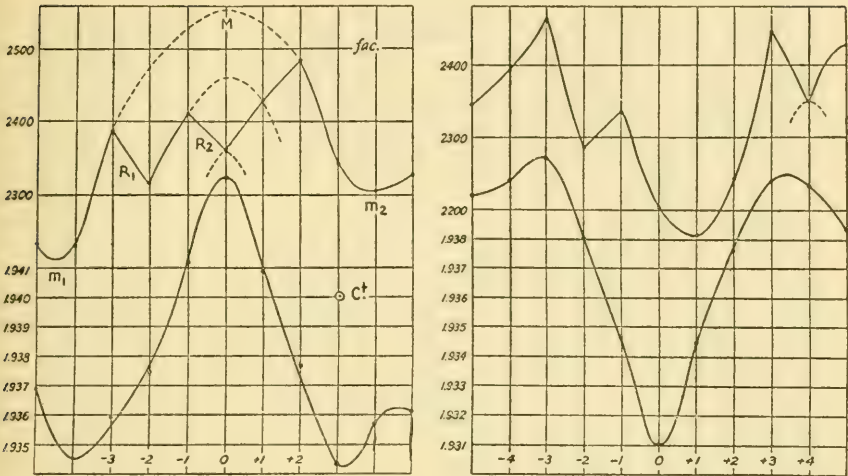

FIG. 2.—Discontinuous trends in solar constant and solar faculae. Solar constants and faculae, October, November, and December, 1929.

Figs. 3 and 4.—Time relations between maxima and minima in the solar constant and solar faculae. Means of faculae and solar constants for the 5 days before and the 5 days after the dates of 72 selected days of maxima and 82 days of minima of solar constants.
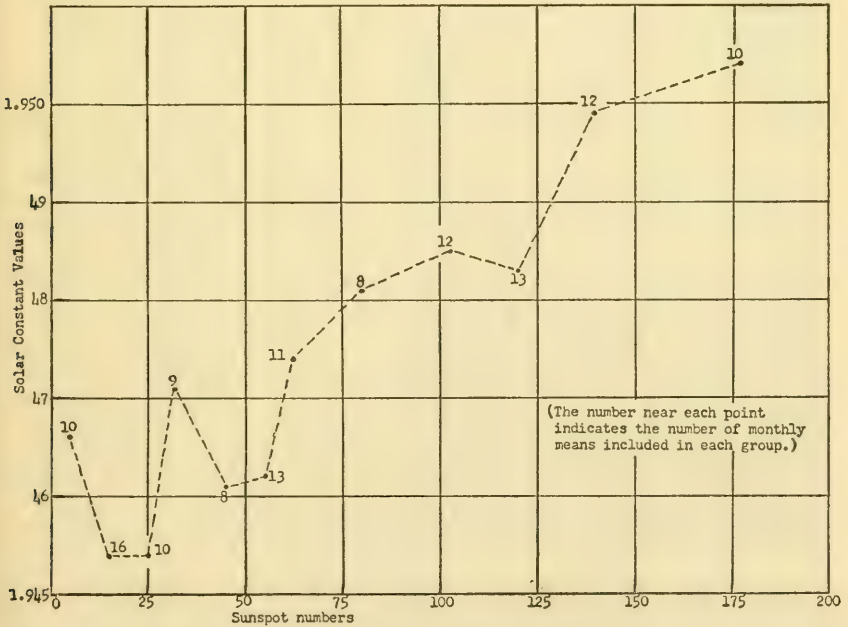

Fig. 5.—Monthly mean values of the solar constant compared with monthly means of sunspot numbers for the same days.
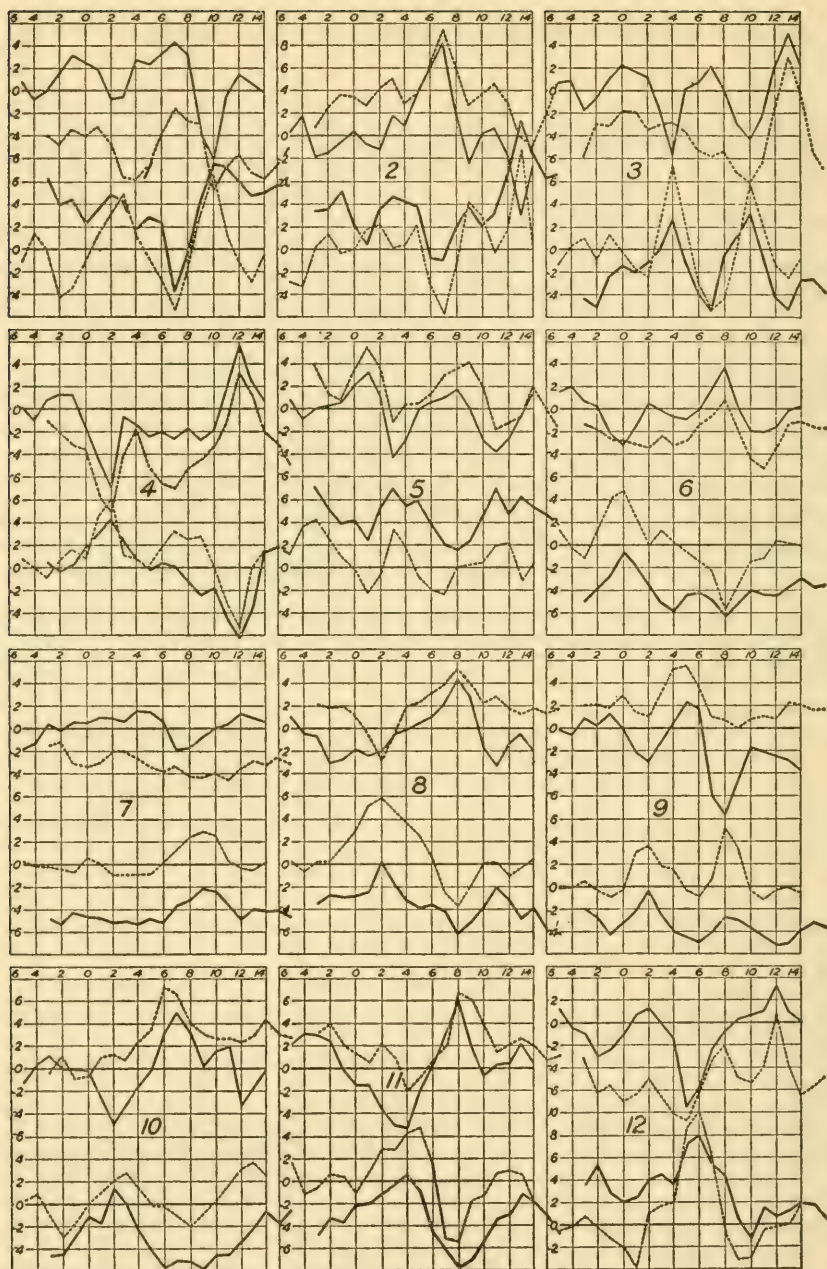
Fig. 6.—Average marches of temperature departures, Fahr., at Washington, D. C., accompanying sequences of solar change (a) of the solar constant in years 1924 to 1936; (b) of character figures for solar calcium flocculi in years 1910 to 1937, for months January to December. Ordinates are temperature departures; abscissae are days from beginning of solar-constant sequence. Flocculi band curves are displaced 2 days to right. Temperature changes following rising solar radiation above, falling radiation below.

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d. Referring to my paper "Magnetic Storms, Solar Radiation, and Washington Temperature Departures," reference No. 25 above, I reproduce figure 2 of that paper as figure 7 here. I call attention to the sharp depression of the solar-constant measures by $\frac{1}{3}$ percent on the day of the height of the magnetic storm. It is the mean result representing 53 great magnetic storms over the years 1923 to 1946.
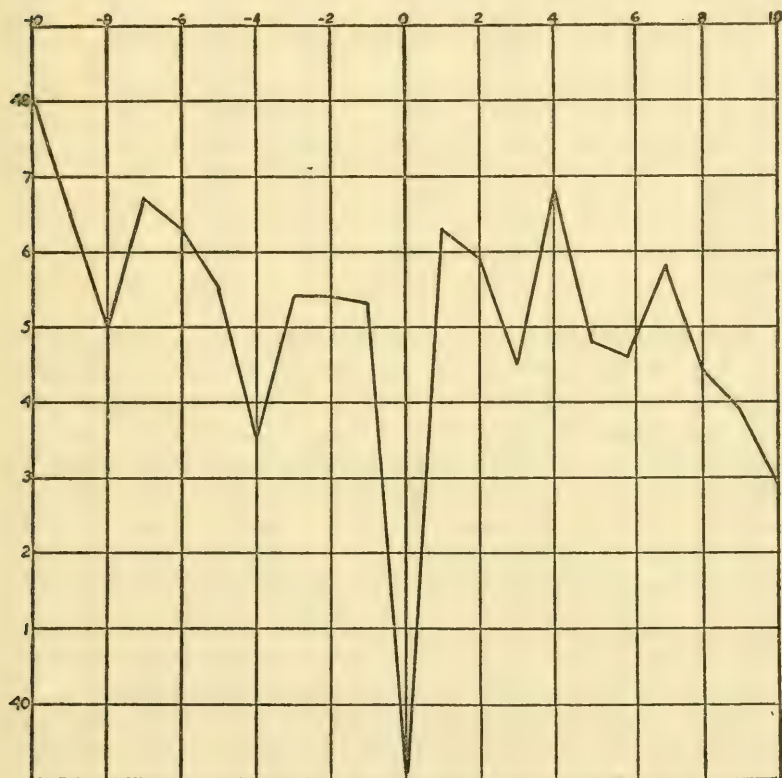

FIG. 7.—Depression of solar constant attending severe magnetic storms. Abscissae, days before and after height of storm; ordinates, solar constant (to be prefixed by 1.9).

I refer also to the note by F. E. Dixon of the Imperial College of Science and Technology, reference No. 12 above, and to H. Koppe's conclusions, reference No. 30 above.

e. Referring to my paper "The Sun's Short Regular Variation and Its Large Effect on Terrestrial Temperatures," reference No. 22 above, table 7 of that paper is from values of the ionospheric quantity, Fe, furnished me by Dr. John Fleming from records of the ionospheric

stations at Huancayo and Watheroo for the years 1938 to 1944. As given there, the records have been cleared of average monthly march and of sunspot influence, and are as follows:

TABLE 1.—*Ionospheric data, Fe. Monthly and sunspot effects removed*

Months	1938	1939	1940	1941	1942	1943
January	378	369	341	352	333	325
February	375	360	344	351	328	330
March	376	344	347	340	340	334
April	384	343	331	322	323	317
May	370	336	313	296	303	294
June	342	328	311	293	296	286
July	342	334	313	304	300	287
August	349	345	336	318	302	293
September	354	366	344	325	312	299
October	361	361	353	330	320	304
November	370	352	359	332	328	314
December	375	346	357	334	329	322

I shall show in a later section that variations in solar-constant measures, among many others, have regular periods of 6-1/30, 9-7/10, $11\frac{1}{2}$, and 13-1/10 months. I do not use longer periodicities than these here, because the ionospheric data are of too brief duration. In figure 8 [2] I show the mean curves representing these periods in the ionospheric quantity Fe, computed from the table just given. The four curves are, respectively, means of 12, 7, 6, and 5 repetitions of the periods. Their amplitudes, respectively, are 4, $4\frac{1}{2}$, 9, and $6\frac{1}{3}$ percent of mean Fe. The amplitudes of the corresponding curves of variation of the solar-constant measures (see reference No. 27 above) are, respectively, 12/100, 10/100, 17/100, and 11/100 percent, being means obtained from 16 to 28 repetitions, according to length of period.

With these correlations shown in figures 1–8, I rest my claim that criterion No. 3 is satisfied as regards the *reality* of solar variation. Other evidence could be given, but this seems sufficient to establish as a reasonable working hypothesis that there is really a variation in the output of total radiation from the sun.

PROPOSITION II

Phenomena exist harmonious with a master period of $22\frac{3}{4}$ years in the variation of solar-constant measures

I shall now show that (*a*) the features of solar-constant measures themselves of 1924 to 1927 are approximately repeated after about 23

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[2] Figure 8 will be referred to again later.

years in the years 1947 to 1950; (b) this $22\frac{3}{4}$-year period is also found in sunspot frequency; (c) also in the magnetic polarity of sunspots; (d) also in the thickness of tree rings; (e) also in terrestrial temperatures; (f) also in terrestrial precipitation.

a. To show the master period in solar variation, I reproduce here as figure 9 figure 4A from my paper "Periodicities in the Solar-constant Measures," reference No. 27 above. The amplitude is 0.9 percent.
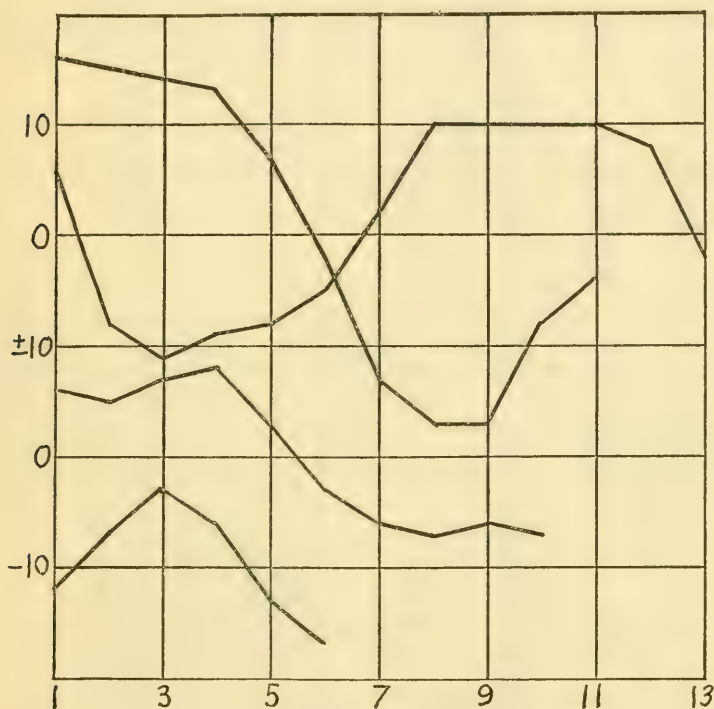

FIG. 8.—Variation of Fe in solar periods of 6-1/30, 9-7/10, $11\frac{1}{3}$ and 13-1/10 months.

b. I reproduce here as figure 10, figure 10 of my paper "Solar Radiation and Weather Studies," reference No. 3 above. It will be found that alternate sunspot-cycle areas, i. e., the right-hand curves of figure 10, are all greater in area included by the curves than the left-hand areas. So the double of the usually termed "$11\frac{1}{3}$-year cycle" in sunspot frequency is also a sunspot period. Note that a line through sunspot minima would incline to the left, as years increase, which shows that period to be less than 23 years.

c. Dr. George E. Hale discovered over 40 years ago the reversal of

polarities of sunspots with alternate recurrences of the $11\frac{1}{3}$-year cycles. That is, he discovered a period of about $22\frac{3}{4}$ years in sunspot magnetism.

d. I reproduce figure 30 from my paper just cited (No. 3 above) as figure 11 here. It shows similar features in the march of tree-ring
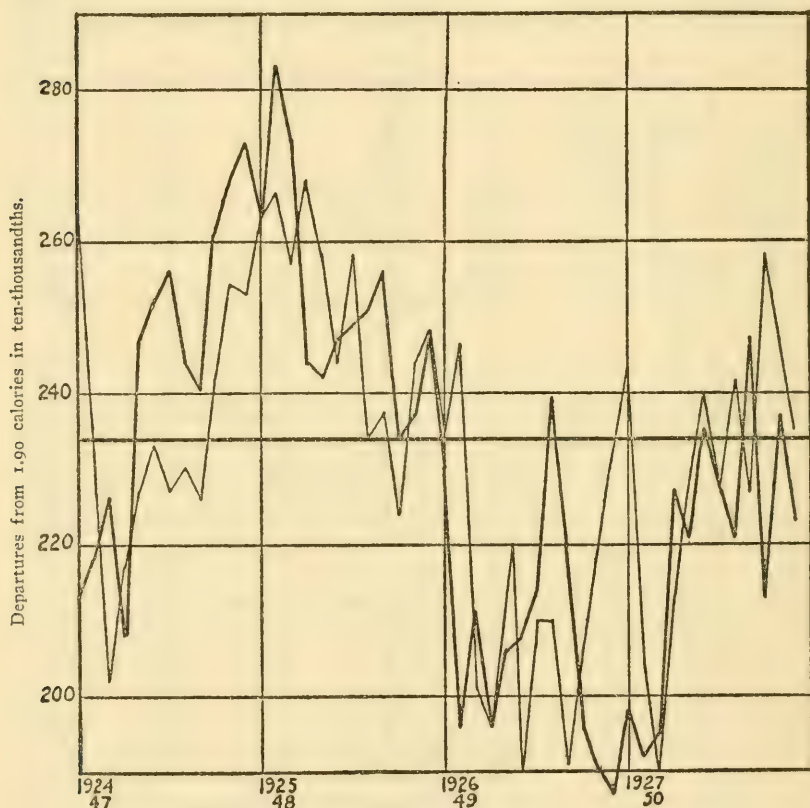

FIG. 9.—Comparison of solar constants 1924-1927 (heavy lines) and 1947-1950 (light lines).

widths in southern California for four successive cycles of 23 years each. These features stand out clearly in the mean curve at the bottom of figure 11.

e. I reproduce here as figure 12, figure 1 of my paper "Some Periodicities in Solar Physics and Terrestrial Meteorology," reference No. 9 above. The figure traces 23-year cycles in the temperature of St. Petersburg, Russia, from 1752 to 1912, and also brings out the double period of 46 years.

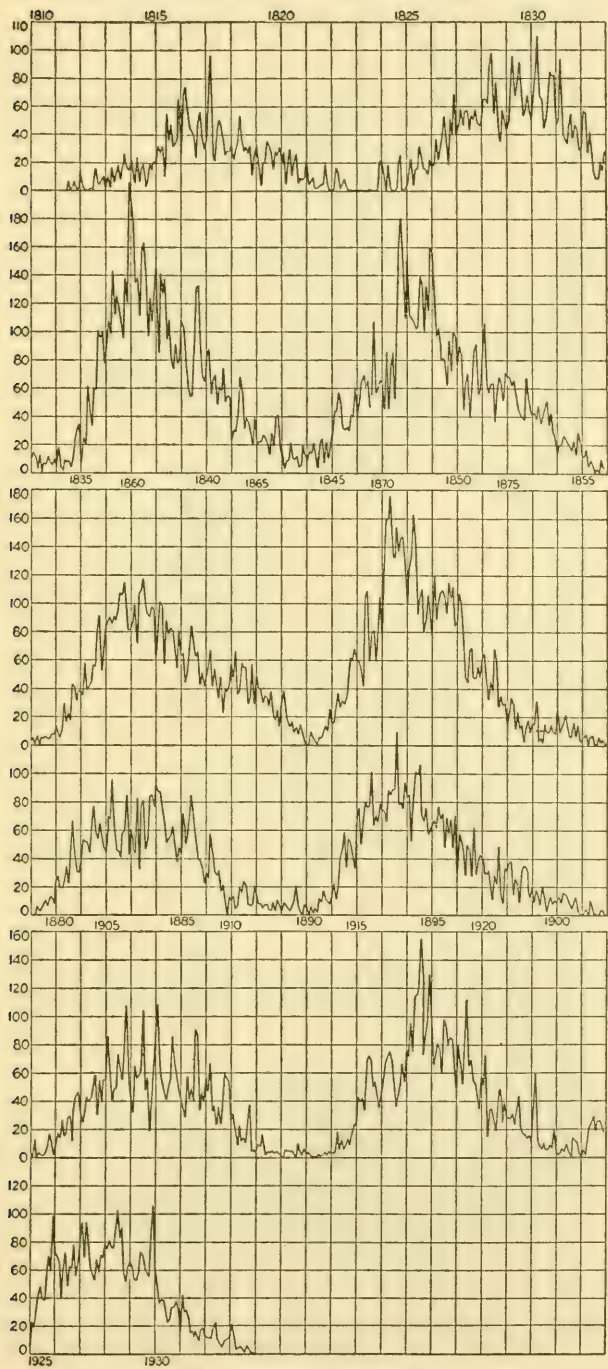*f.* I reproduce here as figure 13, figure 22 of my paper "Weather
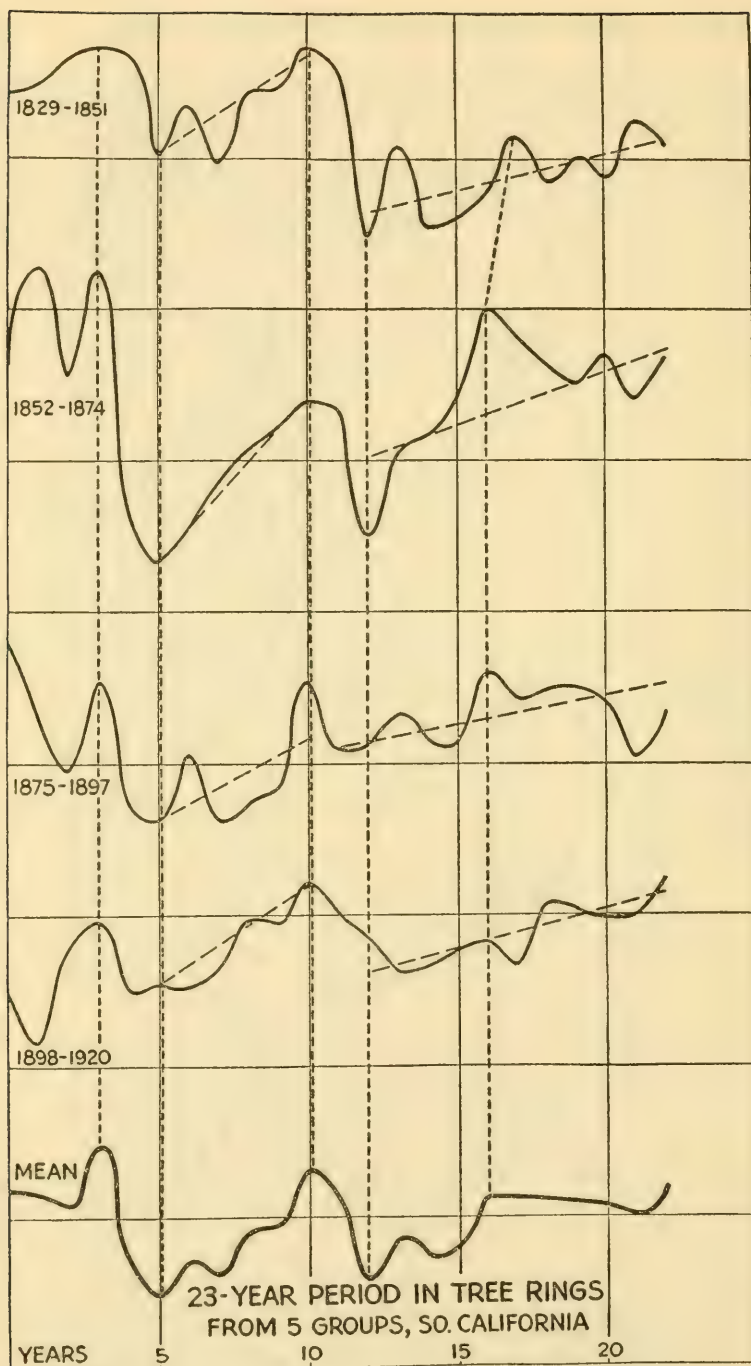
FIG. 10.—Wolf sunspot numbers, 1810-1933.

FIG. 11.—Cycles of 23 years in tree-ring widths. Individual cycles of 23 years show features which are found preserved in the mean of four cycles, or 92 years.
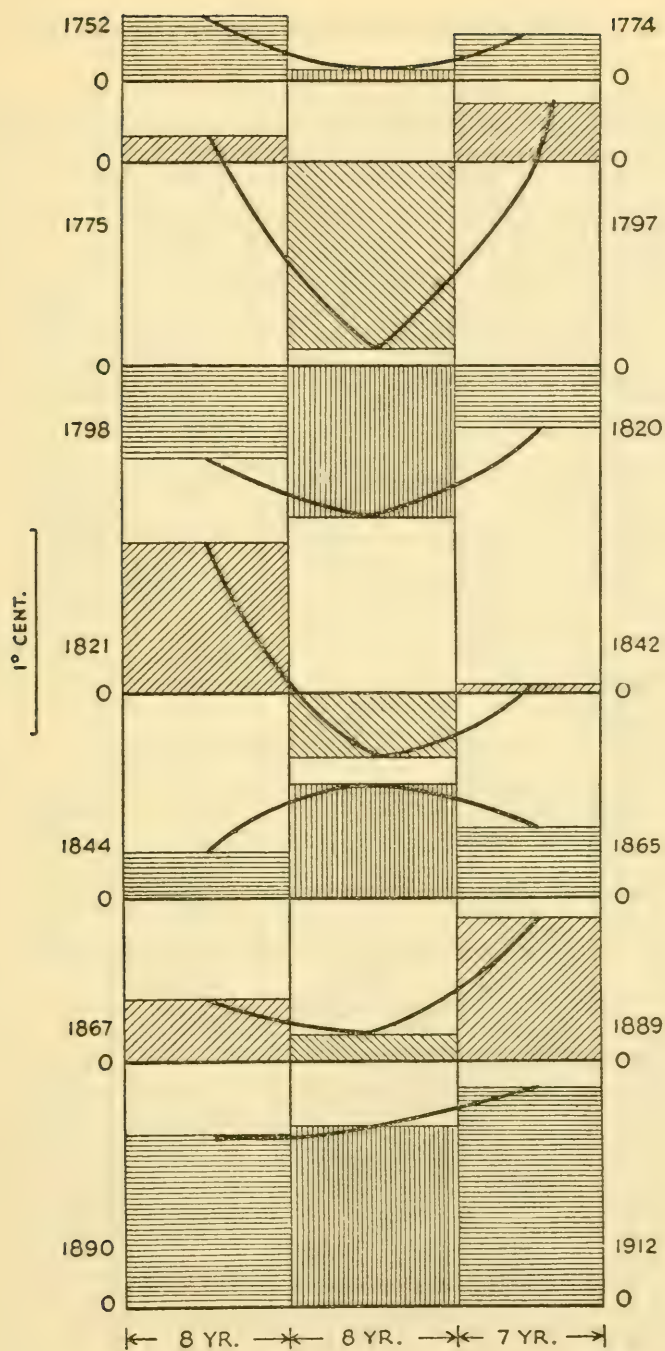
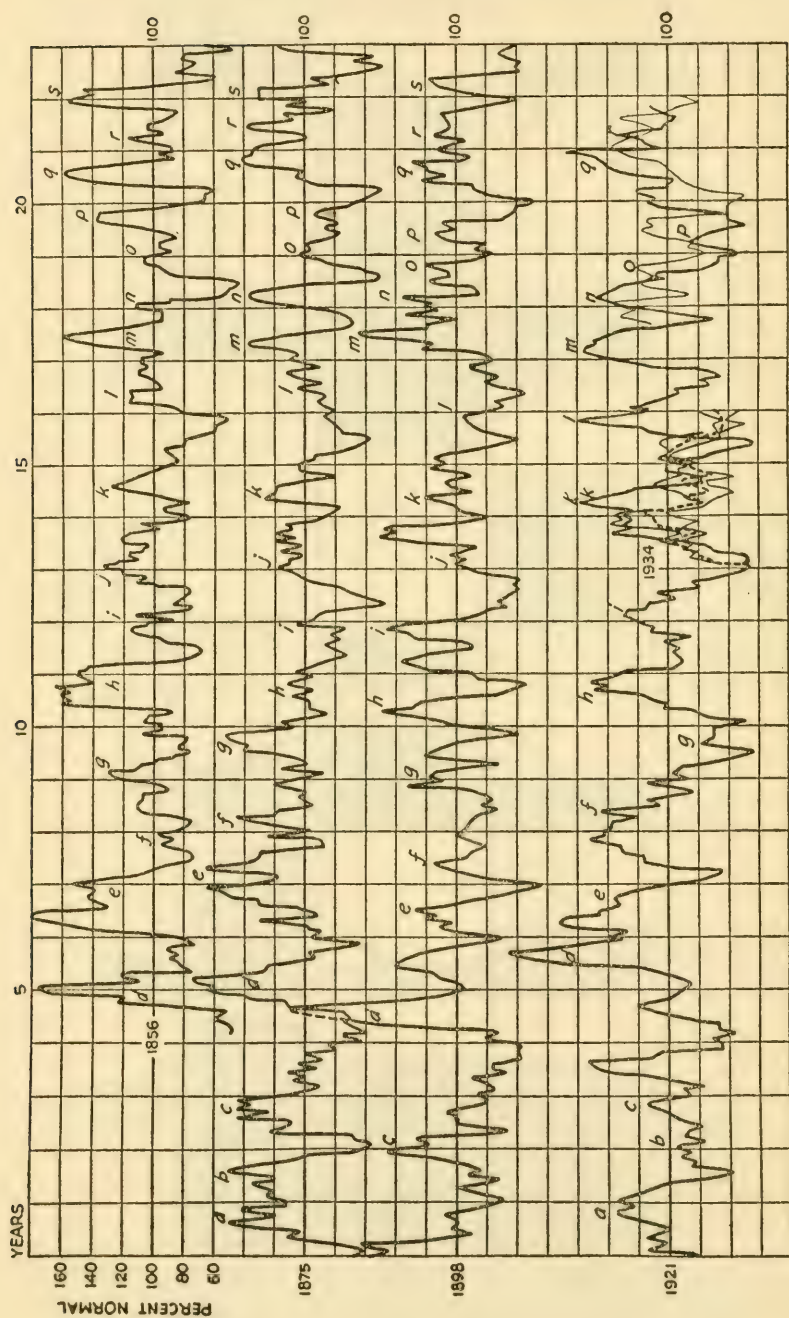FIG. 12.—23- and 46-year periodicities in St. Petersburg temperatures.

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Fig. 13.—Precipitation at Peoria, Ill., smoothed by 5-month running means, arranged in 23-year cycles. Letters represent similar features in successive cycles. Forecasts (dotted line, from 1931; thin line, from 1938) made by consideration of preceding cycles.

Predetermined by Solar Variation," reference No. 18 above. It shows how the features of precipitation at Peoria, Ill., tend to repeat themselves at intervals of slightly less than 23 years.
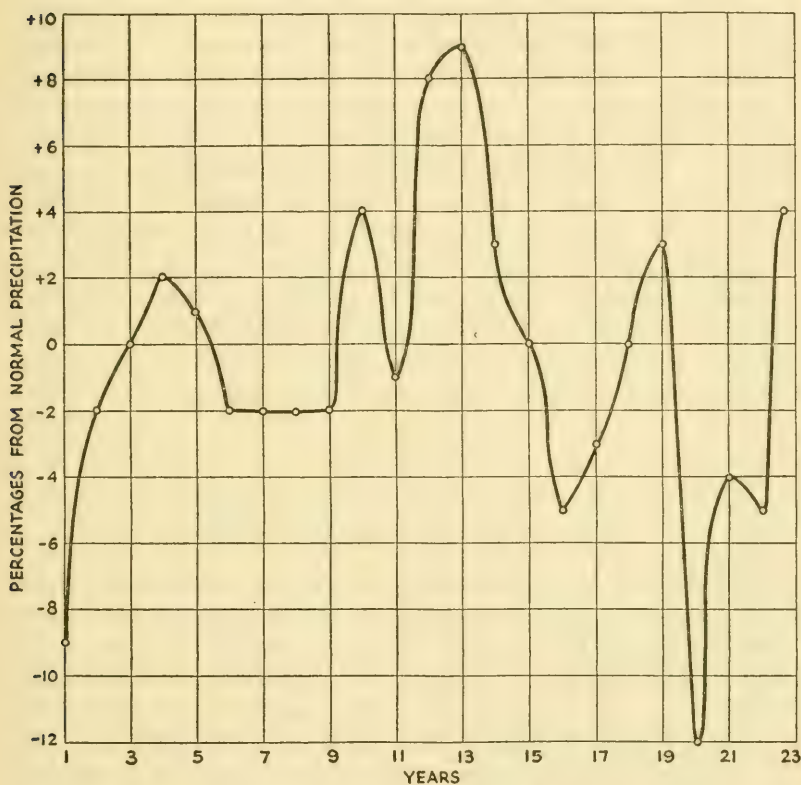
FIG. 13A.—Mean 22⅔-year cycle in Southern New England precipitation. 1750 to 1931. Mean of 8 cycles.

g. I reproduce here as figure 13A, figure 1 of my paper "Rainfall Variations," reference No. 5 above.[3]

Many other harmonious phenomena might be brought forward, but sufficient has been shown to support the working hypothesis of a 22¾-year period in solar variation.

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[3] The New England drought of 1952 falls in timely with this curve.

PROPOSITION III

Integral submultiples of $22\frac{3}{4}$ years are regular periodicities in solar variation

I shall show that (a) at least 23 such periods were found by tabulating solar-constant measures of the years 1924 to 1950; (b) in tabulations of the longer submultiple periods, integral submultiples of these long periods, which, of course, are also integral submultiples of the master period of $22\frac{3}{4}$ years, appeared plainly in the mean values; (c) several of these submultiple periodicities were sought for and found in ionospheric records; (d) by analogy to harmonics in musical sounds, since three integral submultiples of $22\frac{3}{4}$ years were discovered as supposedly isolated periods in solar variation 20 years ago, it is reasonable to expect that a large number of integral submultiples of $22\frac{3}{4}$ years will be found to occur as regular periodicities in solar variation.

Before disclosing these evidences I insert an account of the purpose and results of the Smithsonian solar-constant campaign.

INTERLUDE

On the purpose and accomplishments of the Smithsonian research on the variation of total solar radiation

Measurements of the solar constant of radiation were made by Dr. S. P. Langley at Allegheny, and then in his famous expedition to Mount Whitney, Calif., in 1881. Becoming the third Secretary of the Smithsonian Institution in 1887, one of his first acts was to found the Astrophysical Observatory. After completing its first research on the infrared line and band spectrum of solar radiation, in the year 1902 Dr. Langley directed that the measurement of the solar constant of radiation should be undertaken, not especially for fixing that constant, but rather, by a long series of measurements, to find if it is a variable. His impelling thought was that in solar variation might lie a hitherto unknown weather element of great significance.

Dr. George E. Hale cordially seconded this project, and, after the establishment of Mount Wilson Observatory, he urged Langley to undertake the research there. Accordingly I was sent out in 1905, and excepting 1907, 1917, 1918, and 1919, made measurements of the solar constant there every year up to and through 1920. L. B. Aldrich observed there in 1917, 1918, and 1919. We also, following Langley's original suggestion, erected a tower telescope with mirrors, forming a solar image 20 centimeters in diameter. This image was allowed to drift across the slit of the spectrobolometer. Every day of solar-con-

stant measurement, in the years 1913 to 1920, we made automatic drift curves, showing the distribution of energy in many wavelengths across the east-west diameter of the sun. This, too, was done expressly to discover variations useful for weather forecasting. A positive correlation was discovered between the solar constant and solar-contrast measures. (See also, in that connection, paper No. 27 cited above.)

In 1917, H. H. Clayton, then chief forecaster for Argentina, informed Dr. Walcott, then Secretary of the Smithsonian, that, by combining into large groups the Mount Wilson solar-constant measures, he had secured sufficient accuracy in mean values to show direct correlation with weather elements. This led us to establish a solar-constant station at Calama in the nitrate desert of Chile. Soon after, with John A. Roebling's aid, it was removed to Mount Montezuma, at 9,000 feet altitude. Since 1920, when possible, daily measures of the solar constant of radiation have been made there and also at other Smithsonian observing stations on high mountains in arid lands. Mr. Clayton published many papers showing the correlation of solar-constant measures with weather. After his return to Massachusetts he conducted privately for many years, till his death, a long-range weather-forecasting business, based on solar variation, and had many paying clients.

About 20 years ago, having a long series of 10-day mean values of the solar-constant measures, I made a chart of them extending the length of my office. Standing at a distance, I sought to discover repetitions of configurations in the variations. I noted a small regular variation of slightly more than 8-months period. Proceeding similarly, I discovered regular periods of variation of about $11\frac{1}{4}$ months, and of about 39 months. It then occurred to me to find the least number of months of which, within the errors of determination, these three periods would be approximately integral submultiples. The number 273, seven times 39, 24 times $11\frac{1}{4}$, and 34 times 8, seemed best. This number, 273 months, recommended itself as a solar period, because it is approximately twice the sunspot cycle and thus equal to Hale's magnetic cycle in sunspot polarities.

Having three integral submultiples of 273 months represented in the variation of solar-constant measures, I naturally sought for others. This search, as completed for the present, is described in my paper "Periodicities in the Solar-constant Measures," published in 1952, reference No. 27 cited above. *As I shall show, it would be quite impossible for meteorologists to discover these regular periodicities in weather elements had they not first been found in solar variation.*

In passing, I remark that it greatly strengthens our case for the validity of solar-constant work that the 10-day means, covering the 30-

year interval 1920 to 1950, which yielded the results published in paper No. 27 cited above, rest throughout the 30 years on two stations in opposite hemispheres. Winter in California coincides with summer in Chile. For several years the 10-day means from Mount St. Katherine, in Egypt, also contributed to the results published in paper No. 27.

I now proceed with the correlations promised above.

a. I quote, as table 2, part of table 1A from paper No. 27 cited above.

TABLE 2.—*Periodicities in solar-constant observations*

Period Months	Amplitude Percent	Period Fraction of 272	Period Months	Amplitude Percent	Period Fraction of 272
2⅐	0.05	1/127	13-1/10	0.11	1/21
3-1/20	0.05	1/90	15⅙	0.09	1/18
4⅓	0.06	1/63	22¾	0.07	1/12
5-1/18	0.05	1/54	24¾	0.12	1/11
6-1/30	0.12	1/45	30⅓	0.13	1/9
7	0.08	1/39	34½	0.15	1/8
8-1/14	0.06	1/34	39	0.20	1/7
9-1/10	0.08	1/30	45½	0.13 *	1/6
9-7/10	0.10	1/28	54½	0.13	1/5
10-6/10	0.06	1/26	68	0.25	1/4
11⅕	0.17	1/24	91	0.12	1/3
11.43	0.11	1/24	272	...	1
12.0	0.20	....			

* This figure for amplitude was fixed before extraneous periods were removed, as in figure 14.

b. I now show, as figure 14, six broken curves and one smooth curve, all relating to the period of 45½ months in solar variation. Curve A represents the direct mean of seven repetitions, from the monthly means of the solar-constant measures, of the 45½-month period. It is plain that it contains a period of $45\frac{1}{2} \div 3$ months. This period being removed, we have curve B. Now a period of $45\frac{1}{2} \div 4$ months is discovered. Removing it from curve B we have curve C. Then a period of $45\frac{1}{2} \div 2$ months seemed indicated. Removing it from curve C, we have curve D. There now appears a period of $45\frac{1}{2} \div 5$ months. Removing it we have curve E. It discovers a period of $45\frac{1}{2} \div 7$ months. Removing it, we have curve F. Curve F contains a period of $45\frac{1}{2} \div 13$ or 3½ months, but I do not remove it. For it is now easy to draw the smooth curve G, which is the real curve of the 45½-month period.

As will be seen, the researcher has no option. Once started he must follow this path. The periods discovered in solar variation by

figure 14 are $\frac{1}{6}$, 1/12, 1/18, 1/24, 1/30, 1/42, and 1/78 of $22\frac{3}{4}$ years.

c. I again invite attention to figure 8, which shows that periods observed in solar-constant variation of 6-1/30, 9-7/10, $11\frac{1}{5}$, and 33-1/10 months also occur in the ionospheric data on Fe given in table 1.

There is another aspect of this matter of Fe which adds to its evidential quality. From solar-constant measures, as set forth in the paper cited above as No. 27, the times of maxima and minima for solar radia-
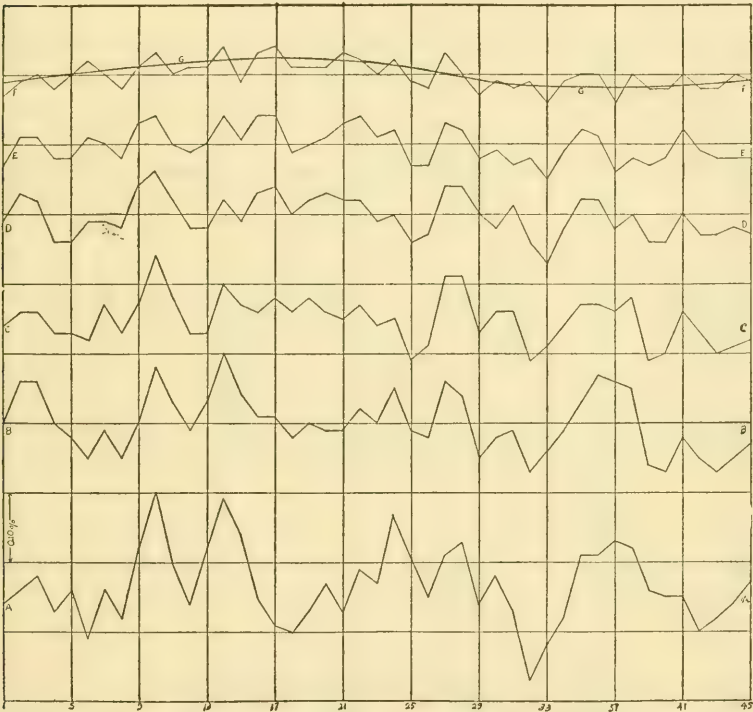
FIG. 14.—The $45\frac{1}{2}$-month period in solar variation.

tion in the year 1938 are as follows (December, when given, is December 1937) :

Period	6-1/30	9-7/10	$11\frac{1}{5}$	13-1/10
Maxima	January	December-January	September	March
Minima	March	April-June	March	June-July

From figure 8, here, the times of maxima and minima for Fe in the year 1938 are as follows:

Period	6-1/30	9-7/10	$11\frac{1}{5}$	10-1/10
Maxima	March	April	January-April	August
Minima	December	December	August-September	March

Thus we find, to within the error of determinations, that for all four subperiods maxima in radiation are simultaneous with minima in Fe, and vice versa. This is, of course, exactly the relationship which we should expect, if the supposed periodicities are real.

I have additional evidences of correlation of solar periods and ionospheric observations. From the publication of the National Bureau of Standards entitled "Ionospheric Data," I have tabulated the mean monthly values of the quantity h^1F2 for the hours 11, 12, and 13, from
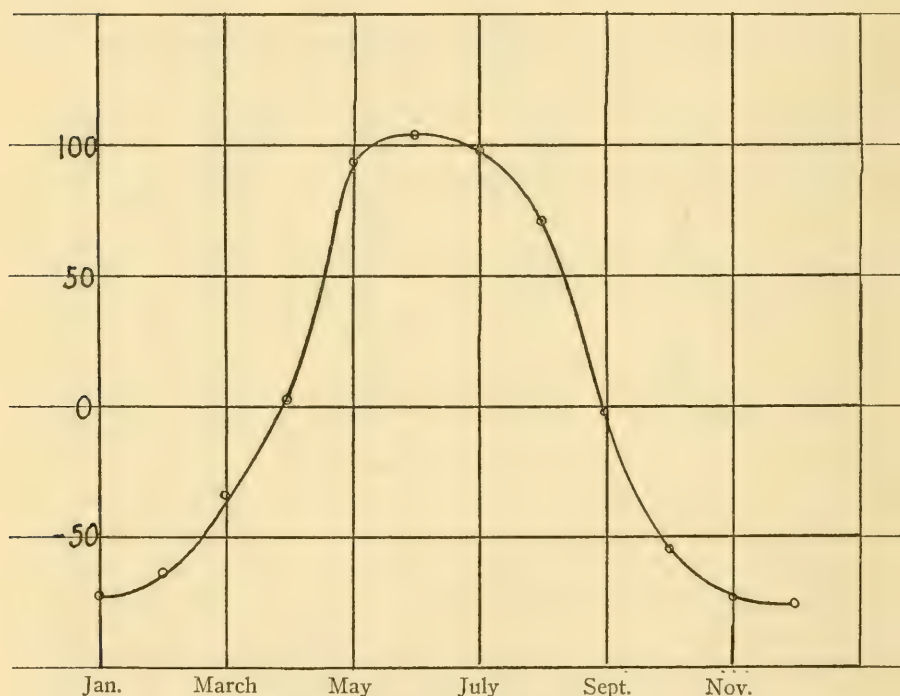

Fig. 14A.—The yearly march in the ionospheric quantity h^1F2.

September 1944 to December 1952. Taking the general mean of these 101 mean monthly values of h^1F2 for the hour of noon, it comes out 314. I computed the departures from this mean value, and arranged them by months. Taking the means of these monthly departures over 8+ years, they are as represented in figure 14A. I then removed this average annual march from the departures. Next, the corrected departures were plotted against the appropriate sunspot monthly Wolf numbers. The resulting graph (not shown here) was well represented as a straight line, yielding the sunspot correction 0.22 (Wolf No. — 100). Applying this sunspot correction, I obtained the corrected

departures of h^1F2 to be compared to the subordinate periodicities in solar variation.

In figure 14B I give graphs of 12 periodicities of the corrected ionospheric character h^1F2 and based on January 1940. These are solar-constant periods. It seemed desirable to remove from the periodicities
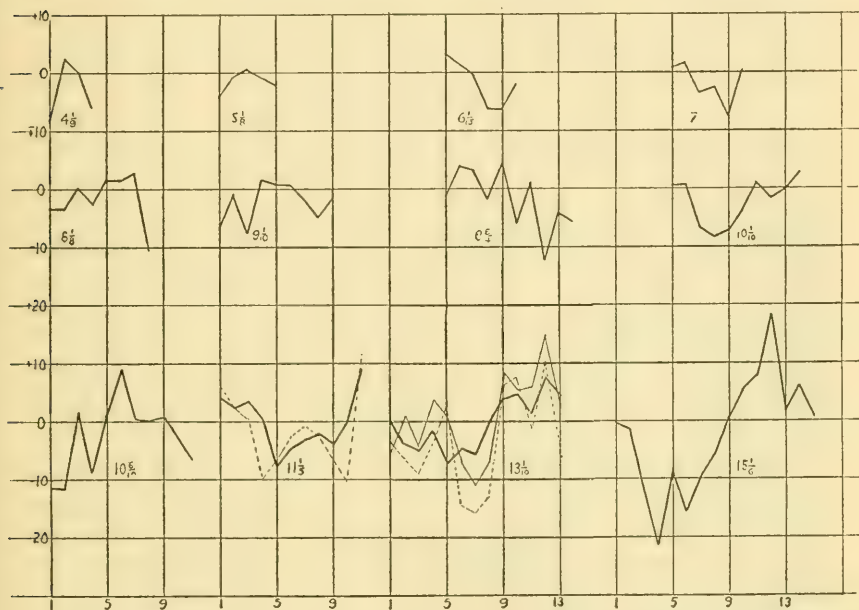

FIG. 14B—Submultiples of $22\frac{3}{4}$ years found as periods in this ionospheric quantity h^1F2. Periods in months.

TABLE 3.—*Characteristics of periodicities of h^1F2*

Periods	$4\frac{1}{3}$	$5\frac{1}{8}$	6-1/15	7	$8\frac{1}{8}$	9-1/10
Amplitudes	3.7	1.7	3.5	2.9	4.2	2.9
No. of columns	23	19	16	14	12	11

Periods	$9\frac{3}{4}$	10-1/10	10-6/10	$11\frac{1}{5}$	13-1/10	$15\frac{1}{6}$
Amplitudes	5.3	3.5	6.3	5.3	4.7	12.2
No. of columns	10	9	9	9	8	6

of $11\frac{1}{5}$ and 13-1/10 months superriding periodicities of $11\frac{1}{5} \div 2$, 13-1/10$\div 2$, and 13-1/10$\div 3$ months. In these cases the original results are shown dotted, the results cleared of superriders are shown heavy and full. Table 3 gives the characteristics of these curves of figure 14B. The periods are in months, the amplitudes in percentages of 314.

As regards the comparative phases of the periodicities in the solar radiation and in the h^1F_2 data, we should expect them to agree. For, as figure 14A shows, the higher radiation of summer months brings higher values of h^1F_2. But a comparison of phases is uncertain for several reasons. First, the periods of solar variation all start from August 1920, while the basis for h^1F_2 stems from September 1944. In the intervening 24 years there are 67 repetitions of $4\frac{1}{3}$ months. An error of 1 percent in the period would shift the phases by almost 3 months. Exactly the same percentage consideration (1 percent corresponds to 3 months) applies to all the other periods. They are none of them certain to 1 percent. Second, the plots of solar-constant and h^1F_2 periodicities show such ragged outlines that the phases of maxima and minima in both quantities are uncertain by one or several months. The 10-1/10-month period must be omitted, in comparing phases, for lack of solar-constant data. With these considerations before us, only the two periodicities, 13-1/10 and $15\frac{1}{6}$ months, are found unreasonably discrepant from the expected agreement of the phases. In these two cases the repetitions of the h^1F_2 data are so few that the mean values may not indicate the phases as they should. The other nine periodicities show phases close to agreement, as expected.

I remark that for the shorter periods, where there are many columns of repetitions from which to form the means shown as graphs in figure 14B, the curves are very satisfactorily smooth. When the number of columns becomes small, naturally the curves are ragged, for each periodicity is affected by the influences of all the others, including many not shown here, and only as the means of very large numbers of repetitions could these other periodic influences be eliminated. It was impracticable to search for longer periods than $15\frac{1}{6}$ months with so few ionospheric data, but all the solar periods given in table 2, above, from $4\frac{1}{3}$ months to $15\frac{1}{6}$ months are represented in figure 14B and table 3. Since, as I have shown, the quantities Fe and h^1F_2 are plainly responsive to the periodicities found in the solar-constant measures, it is probable that the other ionospheric quantities must be so also.

  d. All the periods given in table 2 are integral fractions of $22\frac{3}{4}$ years, to within experimental error of determining their lengths.

I conceive that criterion 3 is satisfied as regards the working hypothesis of the existence of regular periodic solar variations, with periods integrally related to $22\frac{3}{4}$ years.

Of weather aspects

Hitherto I have treated only of variations in solar-radiation measures, in correlation with other phenomena, and intercorrelations among variations of solar-radiation measures themselves.

I come now to correlations of variations in solar-radiation measures with weather changes. These are of two kinds: A, Correlations not involving periodicities; B, correlations involving periodicities.

PROPOSITION IV

Correlations exist between variations in solar-constant measures and weather, not involving periodicities

I shall cite: (*a*) West Indian hurricanes correlated with depression of solar-constant measures. (*b*) Rising and falling sequences in solar-constant measures and correlated temperature changes. There are published nearly 100 independent correlations of this sort which might be cited, all involving temperature changes of several degrees Fahrenheit, and, as far as their depending on solar-constant variations is concerned, the result is backed up by the fact that sequences of variation of the areas of calcium flocculi, observed at Ebro, are associated with marches of Washington temperature nearly identical to those correlated with solar-constant changes. (*c*) Features of precipitation repeated approximately in $22\frac{3}{4}$-year intervals.

a. I reproduce here, as figure 15, figure 1 of paper No. 24 cited above. Counting from first reports of 45 West Indian hurricanes of the years 1923 to 1946, the solar-constant measures dropped sharply by $\frac{1}{4}$ percent, on the average, on zeroth day. A solar-radiation depression appears to act as a trigger to set off a hurricane when conditions are ripe.

b. I invite attention again to figure 6, referred to above. This shows 24 independent correlations between solar-constant changes and Washington temperatures. The temperature changes shown in figure 6 are opposite for rising and falling solar-constant, or solar-flocculi, measures. The temperature changes shown, which are averages for great numbers of occasions for all 12 months of the year, range from 2° to 10° Fahrenheit. Similar correlations have been published for several other cities, making nearly 100 independent correlations of this kind.

c. I invite attention again to figure 13. The $22\frac{3}{4}$-year master period in solar variations includes many precipitation features repeated approximately from cycle to cycle.

Criterion No. 3 appears to be satisfied as a working hypothesis regarding correlations of solar-constant changes with weather, both as to temperature and precipitation, as well as with hurricanes.
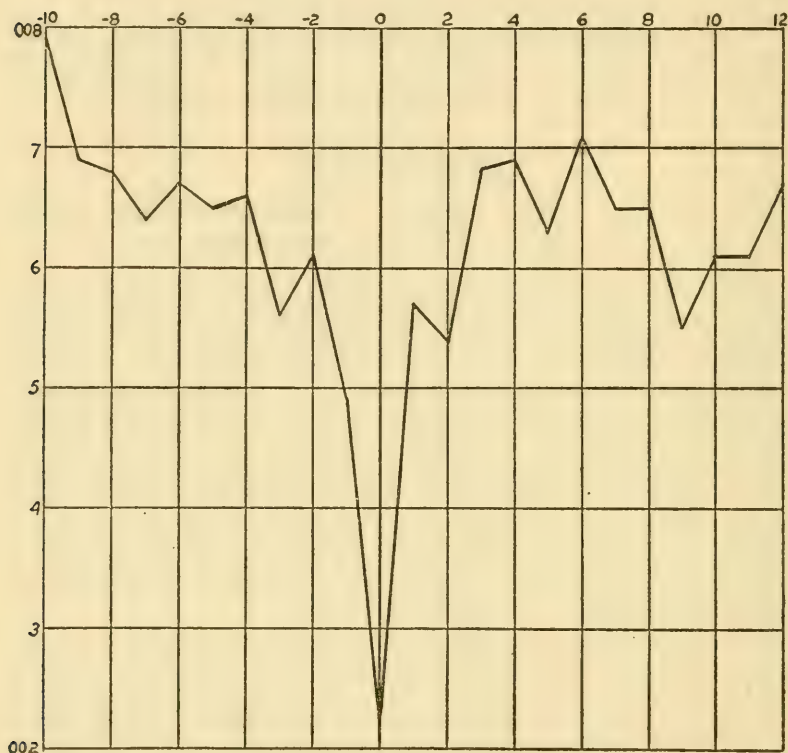
FIG. 15.—Mean solar-constant values preceding and following first reports of West Indian hurricanes. Abscissae, days before and after report dates; ordinates, solar-constant values, to be prefixed by 1.94.

PROPOSITION V [4]

Correlations exist between regular periodic changes in the solar-constant measures and weather changes

INTERLUDE ON LAGS

Before proceeding with this section, attention must be directed to *lags* in the responses of weather to changes of solar radiation. It is common knowledge that maximum temperatures, both diurnal and annual, lag behind the highest intensities of insolation. Such lags differ

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[4] This section imports a new and powerful element in meteorology.

from place to place, and from season to season. They also differ in a secular fashion. These differences in lag attend differences in configuration of the land; differences in human occupation of the land; differences in the transmissive conditions of the atmosphere to solar rays; and differences in the "greenhouse" properties of the atmosphere.

With these facts in mind, it should be expected that weather responses to other regular periodic solar-radiation changes will alter in phases from place to place; with the season of the year; with the prevalence of sunspots, since the varying intensity of solar ionic bombardment of the earth's atmosphere tends to alter its transmissibility; and, in a secular fashion, over long spans of years, because human occupation of the land differs.

It is not possible to fully anticipate and allow for these changes of phases of responses of weather to regular periodic changes in solar radiation. As a reasonable approach, I am accustomed to tabulate weather data separately in three parts of the year, viz, January to April; May to August; September to December. Also I tabulate separately for sunspot numbers $\geqq$ 20 Wolf numbers. Also I tabulate separately for years before and after 1900.

There is still another consideration. Weather records are customarily published with respect to normal values. These normal values, as published, are computed as monthly means of all values over a very long span of years. It is found, however, that normal values differ importantly when sunspot numbers are $\geqq$ 20 Wolf numbers. Hence, before using weather records to compare with regular periodic changes in solar radiation, I compute two sets of normals, for sun spots $\geqq$ 20 Wolf numbers, and compute two sets of departures, accordingly. (In this connection, see paper No. 28 cited above.)

With all these variable, and not entirely controllable, factors affecting phases of response of weather to regular periodic solar changes, *it is quite impossible for meteorologists to discover solar control by mere tabulation of weather records.* For in tabulations neglecting these variable factors, all regular periodic weather changes would be hopelessly mixed up by unknown phase changes as well as by interference between many periods. *It is indispensable to know the solar periods first, and to make an organization of the tabulations, such as I have described.*

Fortunately phase-changing effects are much less troublesome with the longer solar periods. For as the period increases, fewer and fewer numbers of repetitions of it can be found in the weather records, and so mean results are, from that point of view, less and less satisfactory.

It would, indeed, be futile to subdivide the tabulations as extensively as stated above, when tabulating long periods. Retaining only the secular subdivision, before and after 1900, I give up all the other subdivisions for periods exceeding 20 months. Still, an embarrassment remains for shorter periods, because, with a twelvefold subdivision of records, there are too few repetitions to give strong means. I therefore make the questionable assumption that, though phases change with time of the year, prevalence of sunspots, and years before and after 1900, the amplitudes and forms of responses to regular periodic solar changes will not change greatly. Hence, after computing these, I reduce the six tabular means for one sunspot condition to the same phase, and take the general mean, in a common phase, as representative of amplitude and march. Though, as remarked, open to question, this is better than using the weak individual mean values. Thus I obtain generalized means for sunspot numbers $\geqq 20$. When I apply them to forecasting, I readjust their phases to that proper to each of the 12 tabulations.

With these remarks, I am prepared to show the evidence that regular periodic solar variations control weather.

a. In a paper on the temperature of Washington, D. C. (reference No. 32), and in paper No. 31 listed above, I show that, both as to temperature and as to precipitation, over 20 regular periodicities in solar variation are also found in weather records of 86 years, 1854 to 1939, as tabulated with regard to the principles explained above. These numerous regular periodicities range separately to maximum amplitudes of 2° F. as regards temperature and from 5 to 25 percent as compared to normal precipitation.

b. When all known periodicities are synthesized with due regard to phases, so as to make up ostensibly the whole weather complex, these numerous, separately determined, regular periodicities of variation from the normal over long terms of years exhibit approximately the same amplitudes of variation in their syntheses as the observed weather.

c. Such syntheses of total weather over long terms of years show generally the same principal features, and nearly in the same phases, as observed weather.

d. Forecasts, 50 or more years in advance, from such syntheses show fair agreement with observed weather.

e. In brief support of these propositions, urgently referring to original papers for further evidence, I reproduce here as figures 16, 17, and 18, figures 1, 2, and 5 of the paper on Washington temperature,

(No. 32, referred to above), and as figures 19, 20, 21, and 22, figures 1, 2, 3, and 5 from paper No. 31 cited above.

Figures 16 and 17 show the 12 independent determinations of the Washington temperature periodicity of 13-6/10 months. Figure 16, relating to sunspot numbers > 20, gives pairs of determinations from Washington temperature records of 1854 to 1899 and 1900 to 1939,
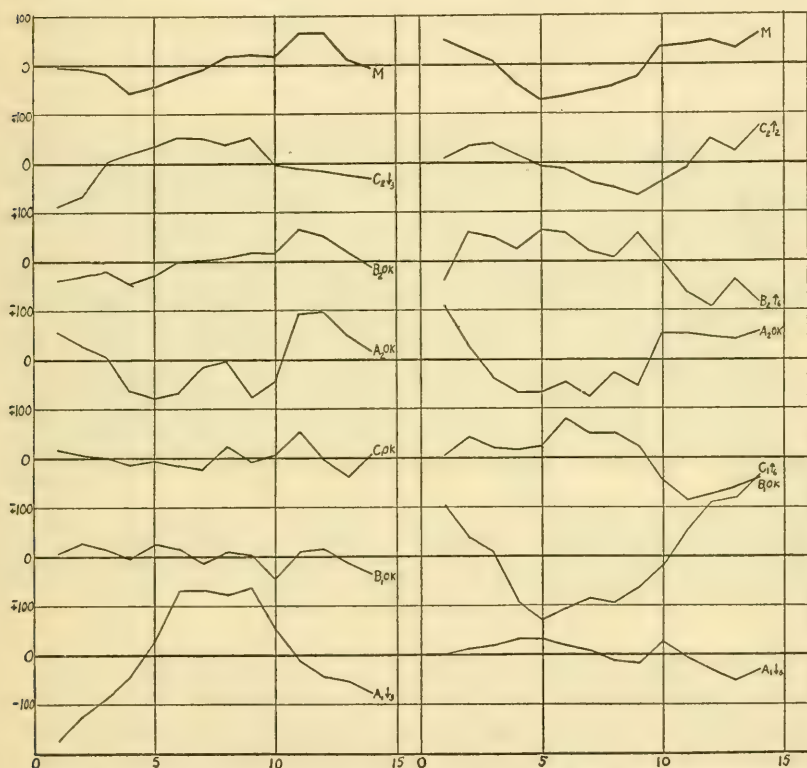
FIGS. 16 AND 17.—The periodicity of 13-6/10 months in Washington temperature departures. Ordinates in hundredths degree Fahr. The symbols O.K., ↓ and ↑ indicate phase changes in getting means.

respectively, for the three seasons January to April, May to August, and September to December, all adusted to a common phase and averaged. Figure 17 shows the same for sunspot numbers <20. It will be seen that the thick-lined mean curves for sunspot numbers ≧ 20 are similar in form, but differ in phase, and have ranges of about $1\frac{1}{2}°$ F.

Figure 18 is a synthetic prediction, 50 years in advance, of the temperature of Washington, 1950 to 1952, based on 20 regular periodici-

ties determined from monthly records of the years 1854 to 1939, centering about 1900. The prediction is in the thin line. The thick line is the event. The two scales of ordinates, separated 2° F., indicate, as expected, that Washington is now warmer than 50 years ago. I should add that all the data are smoothed by 5-month running means. The coefficient of correlation between forecast and event is 50.4 ± 9.7 percent.

Figure 19 shows the $45\frac{1}{2}$-month period, computed as a straight mean of all repetitions of that period, in precipitation records at Albany
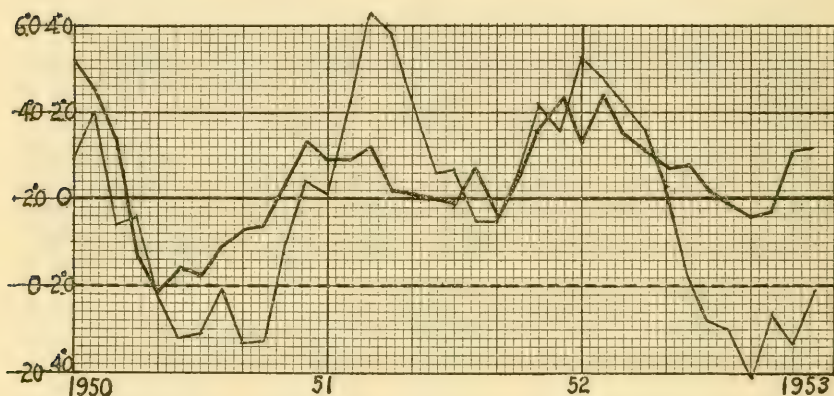

FIG. 18.—Synthetic prediction, 50 years in advance of mean basis, and verification on Washington temperature. Computed from temperature records 1854 to 1939 with 20 regular periodicities, all integral submultiples of $22\frac{3}{4}$ years. Correlation coefficient 50.4±9.7 percent. Forecast, lighter curve, right-hand scale. Event, heavy curve, left-hand scale. Temperatures Fahr., 5-month running means.

over the interval of 90 years, 1850 to 1939. It carries several integrally related shorter periods on its back. The curves a and c represent the years 1850 to 1899, and 1900 to 1939, respectively. Being similar, and in the same phase, their average, b, is used in what follows. Withdrawing the average period of $45\frac{1}{2} \div 3$ months, curve d results. Withdrawing from it the average period $45\frac{1}{2} \div 4$ months, curve e results. Withdrawing from it the average period $45\frac{1}{2} \div 5$ months, curve f results. Withdrawing from it the average period $45\frac{1}{2} \div 2$ months, curve g results. The smooth heavy curve is the $45\frac{1}{2}$-month period freed from all encumbrances. It has the amplitude 7 percent of normal precipitation at Albany.

Figures 20 and 21, relating to the periodicity of $11\frac{1}{3}$ months in Albany precipitation, will be understood from the description just given of figures 16 and 17. The heavy mean generalized curves, for sunspots $\geqq$ 20 Wolf numbers, are similar in form and amplitude, but

FIG. 19.—The 45½-month periodicity in Albany precipitation, cleared of over-riding periodicities, integral submultiples thereof.
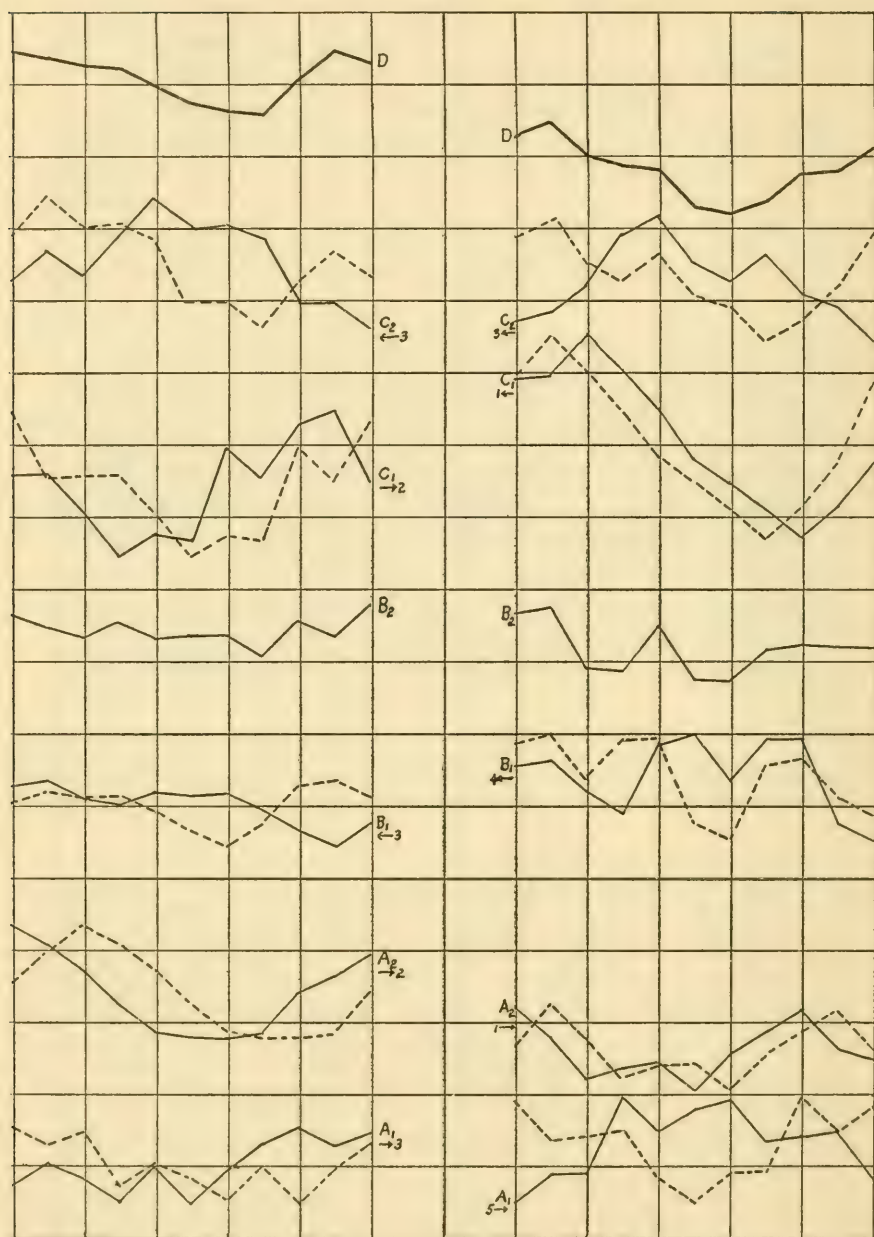
FIGS. 20 (left) and 21 (right).—Fig. 20, combination of six separate determinations of the 11½-month periodicity into one general mean, for times when Wolf sunspot numbers exceed 20. Fig. 21, same as figure 20 for Wolf sunspot numbers less than 20. Full curves are originals, dotted curves with phases shifted as per arrows.

differ in phase. Their amplitude is about 9 percent of normal precipitation at Albany.

Figure 22 shows predictions of precipitation at Albany for the years 1928 to 1931. The event is the heavy line. The dotted line is a prediction made wholly by synthesis from the forms and amplitudes of 22 regular periodicities determined from records of 1850 to 1899, centering about 1875. The correlation coefficient between this prediction and event is 44.0±9.5 percent. The light full line is synthesized from all records of 1850 to 1939, centering about 1900. I should add that in this precipitation work the monthly records are smoothed by 5-month running means. These forecasts may be claimed to be 55 and 30 years in advance, respectively, counting from the central years of their bases. I also computed the correlation coefficient for the light full line, representing synthesis of averages of 22 periodicities, 1850 to 1939. It is 75.6±6.9 percent. If it be urged that this is not evidential, because 1930 lies within the 90-year basis 1850 to 1939, I reply that only 41 months, January 1928 to May 1931, can be of direct influence, but 1,039 other months really control the prediction.

SUMMARY

I have sought to support, as a reasonable working hypothesis, the union of five propositions:

1. The sun's output of general radiation is variable.
2. Solar variation has a master period of about $22\frac{3}{4}$ years.
3. Solar variation has numerous subordinate regular periodicities, all integrally related to $22\frac{3}{4}$ years.
4. Solar variation affects weather importantly, irrespective of periodicities.
5. Weather responds importantly to most of the regular periodic solar variations. This is a new, powerful element in meteorology.

Each of these five conclusions is supported by correlations with several other classes of phenomena, as follows:

Conclusion 1:
    a. Areas of solar faculae.
    b. Prevalence of sunspots.
    c. Areas of solar flocculi.
    d. Incidence of great magnetic storms.
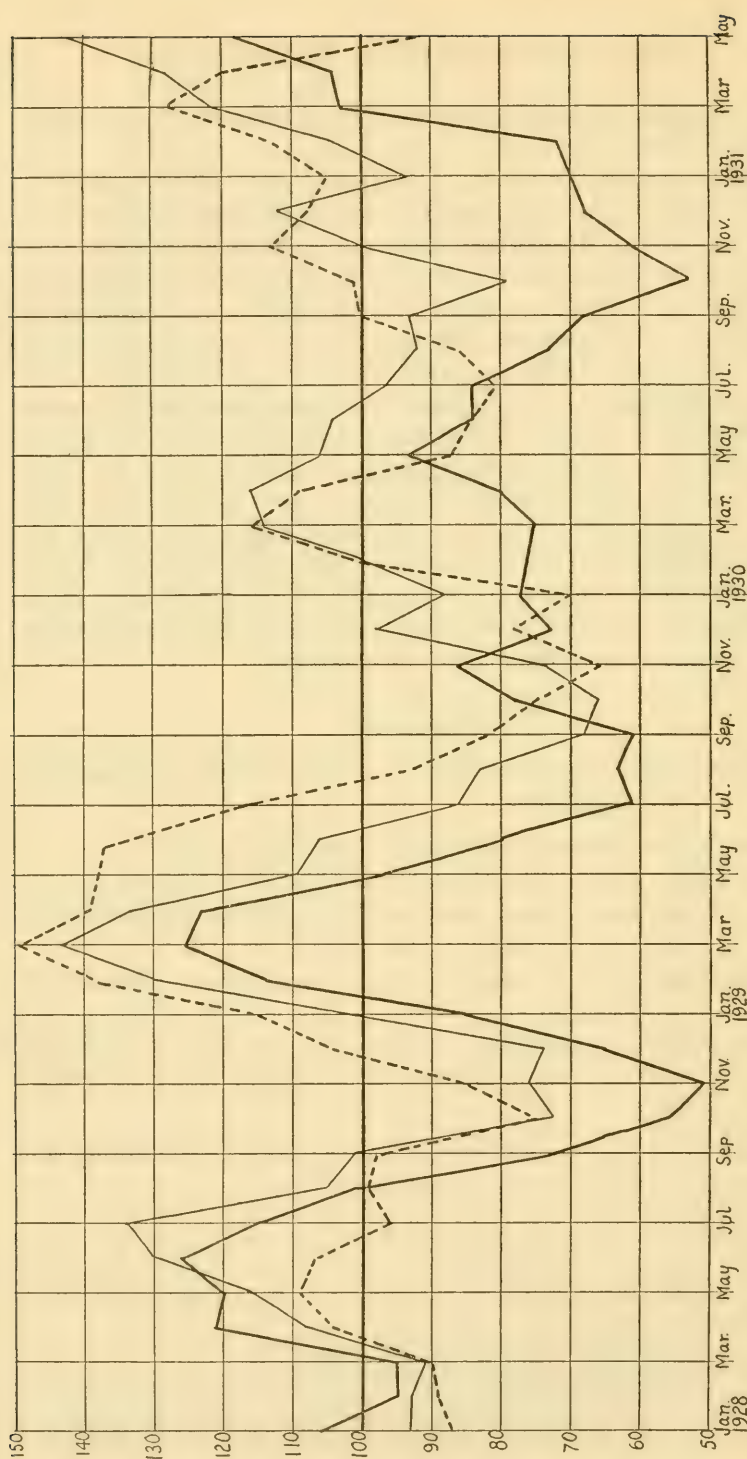   *e.* Ionospheric changes.

Fig. 22.—Precipitation observed at Albany, 1928 to 1931, compared to syntheses of periodicities based on 90 years, 1850 to 1930, and on 40 years, 1850 to 1890, respectively. Heavy full curve = observed; light full curve = synthesis from 90 years; heavy dotted curve = synthesis from 40 years.

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Conclusion 2:

a. Solar-constant measures approximately repeated in form of march of variation after about 22¾ years.

b. This period found in sunspot frequency.

c. Also in magnetic condition of sunspots.

d. Also in thickness of tree rings.

e. Also in terrestrial temperatures.

f,g. Also in terrestrial precipitation.

Conclusion 3:

a. Over 20 regular periods, submultiples of 22¾ years, found in solar-constant measures.

b. The longer of these regular subperiods carry submultiple regular periods upon themselves.

c. Many of these submultiple periods are found in ionospheric changes.

d. Analogy with sound harmonics leads us to expect many other integral subperiods, after three of them were independently discovered.

Conclusion 4:

a. West Indian hurricanes, a trigger effect of depressed solar constants.

b. Very numerous temperature changes correlated to solar variations.

c. Numerous precipitation features repeated at 23¾-year intervals.

Conclusion 5:

a. Nearly all subperiodicities found in solar-constant measures are found strongly represented in temperature and precipitation.

b. Syntheses of temperature and precipitation periodicities yield approximate march of observed weather.

c. Forecasts 50 or more years in advance of mean years of bases, from such syntheses, yield tolerable accord with observed weather, with correlation coefficients from 5 to 11 times their probable errors.

SILVER-DISK PYRHELIOMETRY

(With 1 Plate)

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(Publication 4136)

SILVER-DISK PYRHELIOMETRY

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(With 1 Plate)

In June and July 1932, Dr. C. G. Abbot and L. B. Aldrich compared silver-disk pyrheliometer S.I. 5_{bis} with an improved form of the water-flow pyrheliometer.[1]

The mean of 37 comparisons indicated the constant of S.I. 5_{bis} should be 0.3625. The original constant of S.I. 5_{bis} (0.3715) was determined by Dr. Abbot and W. H. Hoover in August 1931 by 24 comparisons with A.P.O. 8_{bis}. Eight more comparisons in September 1932 by Aldrich and Hoover indicated the constant of S.I. 5_{bis} should be 0.3718. Silver-disk pyrheliometer A.P.O. 8_{bis} has been used since 1912 solely for standardization at Washington. Thus the scale of the Smithsonian revised scale of 1913 is too high by the ratio 0.3718 to 0.3625, or 1.0256—about 2.5 percent.

The results of 42 more comparisons in July 1934 by the same observers were in close agreement with the results of 1932. The mean value of the constant of S.I. 5_{bis} in 1932 was 0.3625, and 0.3629 in 1934.[2]

No comparisons were made between 1934 and 1947. In August 1947, 18 comparisons gave 0.3626 as the constant of S.I. 5_{bis}.[3] The results of the comparisons between silver-disk pyrheliometer S.I. 5_{bis} and the standard water-flow pyrheliometer No. 5 in 1932, 1934, and 1947 are based on Dr. Abbot's habit of reading the silver-disk pyrheliometer. L. B. Aldrich made a few observations with S.I. 5_{bis} in 1932.

Since there is a small personal equation in reading the silver-disk pyrheliometer more comparisons were made in 1952 between S.I. 5_{bis} and the standard water-flow instrument No. 5. The results of

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[1] Smithsonian Misc. Coll., vol. 87, No. 15, 1932.
[2] Smithsonian Misc. Coll., vol. 92, No. 13, 1934.
[3] Smithsonian Misc. Coll., vol. 110, No. 5, 1948.

1952 are based on A. G. Froiland's habit of reading the silver-disk pyrheliometer. In order to insure comparable results with the water-flow pyrheliometer no changes were made in the instrument.

Figure 1, A, B, and C, shows the instrument in some detail. The two chambers $a\,b\,c$ and $a'\,b'\,c'$ are almost exactly the same in all details. The distilled water enters at d and divides into two streams at
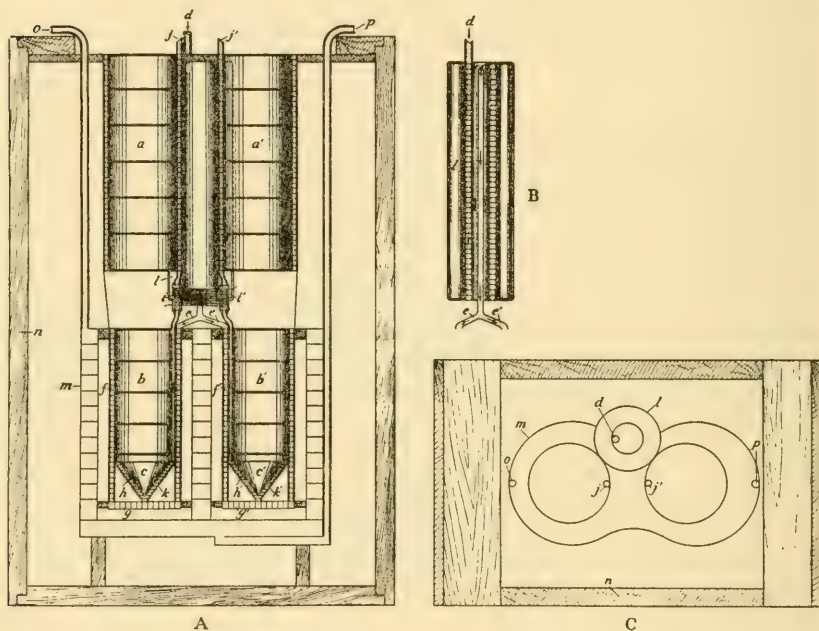
FIG. 1.—Standard water-flow pyrheliometer.

e and e'. The water flows around the receiver at d and d' and out of the instrument at j and j'. i and i' are the thermoelectric junctions used to determine the equality of temperature of the water streams outflowing from the two chambers. m is the water bath for the two receivers, water entering at p and being discharged at o. n is a wooden case surrounding the instrument. The heating coils are indicated by k and k'. Not shown is a shutter for alternating the chambers exposed to solar and electric heating. A detailed description of one of the receivers is given in volume 3 of the Annals of the Astrophysical Observatory.

In order to keep the water bath surrounding the two receivers and the distilled water entering the instrument at the same temperature, we used a 50-gallon drum of water as a source of water for the water

bath. A circulating pump continually stirred the water in the drum and a bypass on the pump circulated some of the water through the water bath. The distilled water flowed through a coil in the drum before entering the instrument. Thus the bath water and the distilled water were always at the same temperature when leaving the drum.

All the precautions that were taken in 1932, 1934, and 1937 to insure greater accuracy were again taken in the present comparisons. In addition, we found it very important to have the rate of flow of water in the two receivers as near the same as possible. The water entering the receivers may not be at exactly the same temperature as the water bath around the receivers, thus any change in the temperature difference would produce a drift of the galvanometer.

In order to get the flow of water the same in the two circuits, we exposed both receivers to solar radiation and adjusted the flow of water until the galvanometer remained at the open circuit zero. Thus the two streams of water were at the same temperature and since they were both receiving the same amount of heat the rate of flow should be the same.

Water currents of approximately 50 cubic centimeters per minute in each branch of the pyrheliometer were found to give good results, but rates as low as 35 and as high as 65 cubic centimeters per minute were used without affecting the results. Temperature of the water bath varied from 23° to 28° C. on different days.

Table 1 gives the results of the comparisons. The mean of 100 observations gives 0.3622 as the constant of S.I. 5_{bis}. The average deviation from the mean is 0.27 percent and the maximum deviation from the mean about 0.9 percent. The above value is about .13 percent lower than the mean of the previous values.

TABLE 1.—*Summary of 1952 comparisons*

Date 1952	Time	Calories by water-flow No. 5	Corrected reading of silver-disk S.I. No. 5_{bis}	Constant of silver-disk S.I. No. 5_{bis}	Deviation from mean
Sept. 28	8:38	1.368	3.775	.3624	+ 2
	44	1.376	3.790	.3630	+ 8
	50	1.380	3.796	.3636	+ 14
	56	1.388	3.847	.3609	− 13
	9:05	1.400	3.877	.3611	− 11
	11	1.411	3.889	.3627	+ 5
	17	1.413	3.895	.3628	+ 6
	23	1.412	3.906	.3616	− 6
	29	1.418	3.931	.3608	− 14
	35	1.428	3.951	.3614	− 8

(*continued*)

TABLE 1.—*Summary of 1952 comparisons* (continued)

Date 1952	Time	Calories by water-flow No. 5	Corrected reading of silver-disk S.I. No. 5_{b1s}	Constant of silver-disk S.I. No. 5_{b1s}	Deviation from mean
Sept. 29	9 : 22	1.405	3.861	.3638	+ 16
	28	1.410	3.879	.3638	+ 16
	34	1.407	3.894	.3613	− 9
	40	1.408	3.899	.3612	− 10
	46	1.415	3.918	.3611	− 11
	52	1.419	3.937	.3604	− 18
	58	1.425	3.947	.3609	− 13
	10 : 04	1.434	3.944	.3635	+ 13
	10	1.445	3.975	.3635	+ 13
	11 : 14	1.447	3.986	.3630	+ 8
	20	1.454	4.018	.3620	− 2
	26	1.462	4.015	.3641	+ 19
	32	1.461	4.011	.3642	+ 20
	38	1.458	4.022	.3624	+ 2
	44	1.466	4.027	.3640	+ 18
	50	1.454	3.996	.3639	+ 17
	56	1.464	4.025	.3637	+ 15
	12 : 02	1.454	4.005	.3629	+ 7
	08	1.464	4.013	.3649	+ 27
	14	1.457	4.004	.3639	+ 17
Sept. 30	9 : 44	1.423	3.922	.3628	+ 6
	50	1.421	3.930	.3617	− 5
	56	1.430	3.961	.3610	− 12
	10 : 02	1.431	3.949	.3624	+ 2
	08	1.426	3.945	.3613	− 9
	14	1.430	3.959	.3611	− 11
	20	1.433	3.990	.3591	− 31
	26	1.446	3.988	.3626	+ 4
	32	1.438	3.998	.3596	− 28
	38	1.454	4.013	.3623	+ 1
Oct. 1	11 : 11	1.446	3.990	.3625	+ 3
	17	1.453	4.027	.3607	− 15
	23	1.458	4.029	.3620	− 2
	29	1.458	4.020	.3628	+ 6
	35	1.458	4.029	.3619	− 3
	41	1.457	4.008	.3635	+ 13
	47	1.454	4.018	.3617	− 5
	53	1.469	4.058	.3621	− 1
	59	1.472	4.058	.3627	+ 5
	12 : 05	1.472	4.067	.3621	− 1
	13	1.463	4.054	.3610	− 12
	19	1.458	4.023	.3623	+ 1
	25	1.461	4.048	.3609	− 13
	31	1.465	4.037	.3628	+ 6
	37	1.447	3.994	.3623	+ 1
	43	1.451	4.007	.3621	− 1

(*continued*)

TABLE 1.—*Summary of 1952 comparisons* (concluded)

Date 1952	Time	Calories by water-flow No. 5	Corrected reading of silver-disk S.I. No. 5_{b1s}	Constant of silver-disk S.I. No. 5_{b1s}	Deviation from mean
	49	1.445	3.980	.3631	+ 9
	55	1.427	3.947	.3616	− 6
	1 : 01	1.418	3.878	.3657	+ 35
	07	1.427	3.918	.3642	+ 20
Oct. 9	8 : 17	1.447	3.971	.3644	+ 22
	23	1.450	3.995	.3630	+ 8
	29	1.463	4.050	.3613	− 9
	35	1.465	4.053	.3614	− 8
	41	1.478	4.065	.3635	+ 13
	47	1.479	4.087	.3619	− 3
	53	1.494	4.123	.3623	+ 1
	59	1.492	4.119	.3623	+ 1
	9 : 05	1.496	4.150	.3604	− 18
	11	1.506	4.166	.3616	− 6
	39	1.516	4.196	.3612	− 10
	45	1.526	4.235	.3604	− 18
	51	1.530	4.242	.3607	− 15
	57	1.534	4.245	.3615	− 7
	10 : 03	1.543	4.265	.3617	− 5
	09	1.550	4.276	.3625	+ 3
	15	1.548	4.276	.3620	− 2
	21	1.549	4.276	.3623	+ 1
	27	1.551	4.291	.3614	− 8
	33	1.548	4.291	.3607	− 15
	11 : 03	1.554	4.290	.3623	+ 1
	09	1.557	4.305	.3616	− 6
	15	1.558	4.311	.3613	− 9
	21	1.558	4.311	.3614	− 8
	27	1.558	4.311	.3613	− 9
	33	1.548	4.291	.3607	− 15
	39	1.553	4.297	.3614	− 8
	45	1.546	4.277	.3615	− 7
	51	1.546	4.296	.3599	− 23
	12 : 04	1.540	4.241	.3632	+ 10
Oct. 11	9 : 48	1.530	4.224	.3622	0
	54	1.535	4.226	.3632	+ 10
	10 : 00	1.537	4.218	.3645	+ 23
	06	1.541	4.240	.3635	+ 13
	12	1.545	4.250	.3636	+ 14
	18	1.549	4.276	.3623	+ 1
	24	1.548	4.276	.3619	− 3
	30	1.539	4.241	.3630	+ 8
	36	1.540	4.251	.3622	0
	42	1.543	4.261	.3621	− 1

Mean of 100 observations (6 days)........... 0.3622

Average deviation........... 0.00097

FIG. 2.—Photographic copy of Froiland's original reading of the silver-disk pyrheliometer.

STANDARD WATER-FLOW PYRHELIOMETER AS MOUNTED AT
TABLE MOUNTAIN, CALIF.

Figure 2 is a photographic copy of A. G. Froiland's original readings of the silver-disk pyrheliometer S.I. 5_{bis} on September 29, 1952.

A summary of all the comparisons between S.I. 5_{bis} and standard water-flow No. 5 is given below:

No. of values	Date	Mean constant S.I. 5_{bis}
37	1932	.3625
42	1934	.3629
18	1947	.3626
100	1952	.3622

The variations in the above results are probably within the limit of error of the observations; thus we may assume the constant of S.I. 5_{bis} has remained constant since 1932.

The constant of S.I. 5_{bis}, as detemined by 32 comparisons with the standard silver-disk pyrheliometer A.P.O. 8_{bis} in 1931 and 1932, was 0.3718. The mean of 64 comparisons with A.P.O. 8_{bis} just before S.I. 5_{bis} was carried to Table Mountain, Calif., and 64 comparisons just after its return to Washington gave exactly the same constant. The mean of all good comparisons between S.I. 5_{bis} and A.P.O. 8_{bis} from 1931 to 1953 gives 0.3719 as the constant of S.I. 5_{bis}. This would indicate that A.P.O. 8_{bis} has remained unchanged since 1932.

The mean of all the above results would indicate that the scale of Smithsonian revised pyrheliometry of 1913 is very nearly 2.5 percent too high.

SOME EXPERIMENTS WITH THE SILVER-DISK PYRHELIOMETER

In the following series of experiments with the silver-disk pyrheliometer the source of radiation was a 100-watt microscope lamp. An enlarged image of the filament was focused on the silver disk by means of a lens and the voltage on the lamp maintained constant with a voltage regulator. Silver-disk pyrheliometer S.I. 5_{bis} was used in most of the tests.

A DETERMINATION OF THE CONSTANT K

A correction is added to the reading of the silver-disk pyrheliometer which depends upon the mean bulb temperature while exposed to radiation. The correction is $[K(T\text{-}30°)]$ R where T is the mean bulb temperature, R the rise in temperature in 100 seconds plus the cooling corrections, and K is a constant. The value of K in use is 0.0011. This value was determined experimentally, using two silver-

disk pyrheliometers.[4] The present determination was made with one pyrheliometer.

In this experiment and all the following experiments the lamp was turned on about an hour before making a series of readings. The lamp was very constant during a day's observations and changed very little from day to day.

In one set of observations the following results were obtained: The mean of 18 observations at a mean bulb temperature of $34.°21$ was 3.388, and a mean of 12 observations at a mean bulb temperature of 21.66 was 3.435. The above readings represent the rise in temperature of the silver disk with all corrections applied with the exception of the one depending on the mean bulb temperature. If this correction is applied, the two values should be the same. Thus $3.388 + [4.21\ K\ (3.388)] \equiv 3.435 + [-8.34\ K\ (3.435)]$, or K is equal to 0.001095. Other determinations of K with various temperature differences gave results of K between 0.00104 and 0.00118, with a mean value approximately 0.0011. One set of observations made with pyrheliometer S.I. 89 gave 0.00109. Some of the determinations of K were made with the pyrheliometer in a water-cooled chamber with a hole in one end to admit the radiation and a slot along one side to read the thermometer. Also an automatic shutter opening and closing device was used for some of the work. In any set of observations individual values were within ± 0.3 percent of the mean.

SERIES OF OBSERVATIONS IN WHICH THE COOLING CORRECTION DURING THE FIRST 100 SECONDS IS ZERO OR NEAR ZERO

In making a series of readings it has been our practice to start readings 20 seconds after completing an observation. Thus a 4-minute shaded period occurs between each 2 minutes of exposure. Each value is independent and the total rise in temperature of the silver disk is much less than the rise in temperature of the silver disk with only a 2-minute shaded period between each 2-minute exposure.

In the following experiment sets of six readings each were taken and for each set the cooling correction for the first 100 seconds of the first reading was zero or near zero. Sets of readings were made at different temperatures and some were made with the automatic shutter opening and closing device. After the fifth reading the mean

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[4] Smithsonian Misc. Coll., vol. 95, No. 23, 1937.

bulb temperature and the cooling correction remained about constant. The mean of 30 sets is given below:

No. of reading	1	2	3	4	5	6
Corrected reading	3.202	3.206	3.208	3.210	3.211	3.212

The above indicates some increase in the reading from 1 to 6. The change is small, however, after the second reading. This fact was noted about 20 years ago, when many comparisons were being made between the silver-disk and the Ångström pyrheliometers. Since that time, when using the silver-disk pyrheliometer, we have preheated the silver disk from one to three minutes before starting a series of readings. Series of readings taken after the silver disk was preheated gave very consistent readings. Some of the discrepancy in the readings shown above may be due to a delay in opening and closing the shutter or a time lag in reading the thermometer. The rate of movement of the mercury thread is different in the first two or three readings of a set from that in later readings of the set when the rate of heating and cooling remain about constant.

EFFECT OF DELAY IN OPENING AND CLOSING SHUTTER

A set of readings were made using the regular method of opening and closing the shutter and then a set in which there was a delay of 10 seconds in opening the shutter after the end of a shaded period and a delay of 10 seconds in closing the shutter after an exposure period. The results in the latter case were about 3 percent higher. Thus a delay in opening and closing the shutter of even one second may result in an error of 0.3 percent. Variation in the time of opening and closing the shutter may explain the variation of the results with the silver-disk pyrheliometer by different observers. The pyrheliometer readings in this series of tests were made by L. B. Aldrich and W. H. Hoover. With the regular method of reading the pyrheliometer and the shutter operated by hand there was a difference of about 0.2 percent between the readings of the two observers. When the automatic shutter-opening device was used this difference was reduced to 0.1 percent or less.

EFFECT ON THE PYRHELIOMETER READINGS WHEN READINGS ARE TAKEN BEFORE THE PYRHELIOMETER CHANGES TO AMBIENT TEMPERATURE

For this test the pyrheliometer was placed in the chamber of the water bath and the automatic shutter device was used when readings

were made. With the water bath at 15° and the pyrheliometer at the same temperature, a few readings were made with the bath maintained at 15°. The temperature of the bath water was then changed to about 35° and readings made while the pyrheliometer was changing temperature. The first three readings were from 0.5 to 0.7 percent too high. When the pyrheliometer was about 5° below the temperature of the bath more readings were taken. These readings agreed with the original set of readings. These results indicate that the pyrheliometer should be near the ambient temperature before making an observation.

In a paper on the Abbot silver-disk pyrheliometer [5] L. B. Aldrich discussed in some detail the method of observing with the silver-disk pyrheliometer and listed some precautions to be taken to insure greater accuracy. One precaution should be added. The shutter should be opened immediately at the end of the first shaded period and closed immediately after the end of the exposed period. A delay of a few seconds may result in an error of 1 percent or more.

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[5] Smithsonian Misc. Coll., vol. 111, No. 14, 1949.

THE EXTERNAL MORPHOLOGY OF THE DRAGONFLY ONYCHOGOMPHUS ARDENS NEEDHAM

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THE EXTERNAL MORPHOLOGY OF THE DRAGONFLY ONYCHOGOMPHUS ARDENS NEEDHAM [1]

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In 1917 Tillyard brought together all the scattered information regarding the morphology as well as other biological studies of dragonflies in a book entitled "The Biology of Dragonflies." His discussion of morphology in this book was based on the writings of previous workers who were mainly interested in comparative studies of certain organs. Since this date some morphological characters have been further and well investigated, but other structures remain inadequately studied. Furthermore, entomologists working on dragonflies have paid little attention to the new interpretations given by Ferris and Pennebaker (1939), Ferris (1940), Snodgrass (1947), and others on the fundamental structures of certain parts of the body of insects in general. There is not a single species of dragonfly that has been studied critically in the light of the most recent morphological interpretations.

The purpose of the present study is fourfold: (1) To bring into unity all the different terminologies that have been used in morphological and taxonomic work on dragonflies; (2) to apply the knowledge of the most recent morphological interpretations; (3) to bring out some new interpretations of morphological characters that the author believes to be inadequately or erroneously treated previously; and (4) to serve as a contribution to the morphology of dragonflies, especially as a foundation for future taxonomic studies.

Onychogomphus ardens Needham (Gomphidae) has been selected for study for three reasons: (1) It belongs to the primitive family Gomphidae of the order Odonata. This family is well represented by genera and species in my own collection, which will be used for

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future taxonomic studies. (2) Specimens of this species are of large size and therefore relatively easy to study. (3) It is rather common in South China.

HEAD

(Figures 1-6)

The head of *Onychogomphus ardens* Needham is hypognathous and somewhat anteroposteriorly flattened, the anterior aspect being convex and the posterior aspect being concave. Posteriorly it is attached to a narrow neck. The female differs from the male in having a pair of *occipital horns* (fig. 2: OCCH) on the occipital margin.

The areas generally referred to as frons, vertex, and occiput by earlier workers are designated as such in this paper. No attempt has been made to change their names, although they have been interpreted differently by modern morphologists (DuPorte, 1946; Snodgrass, 1947). The old designations are used here without modification to avoid further confusion in taxonomic work.

SUTURES OF THE CRANIUM OR CAPSULE

The principal sutures of the cranium are postocellar, epistomal, subgenal, ocular, parafrontal, postoccipital, and clypeal sutures.

The POSTOCELLAR SUTURE (POS) is a transverse suture which separates the vertex from the occiput. It lies between the two compound eyes at their closest points. According to Lew (1933) this suture is secondarily developed and is not homologous with the epicranial suture (e.g., Garman, 1927) of other insects. This suture is designated by Lew as postocular suture; but unfortunately in the same paper he created another term, *postocellar suture,* evidently referring to the same structure. The latter term is probably the one he meant to use, while the former term might be a typographical error, since it is definitely not descriptive of its position. Snodgrass (1947), however, mentioned "The cleavage line on the head of larval Odonata is characteristically T-shaped rather than Y-shaped, inasmuch as the frontal arms usually go almost straight laterally." In the present species the postocellar suture represents the transverse bar of the T and therefore corresponds to the frontal arms.

The EPISTOMAL SUTURE (ESS), or frontoclypeal suture, is a distinct and almost straight line across the anterior part of the cranium. Along this suture a strong *epistomal ridge* (ESR) is produced internally.
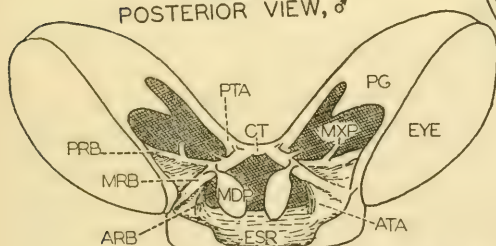
Each of the SUBGENAL SUTURES consists of two portions, the *pleurostomal* and *hypostomal sutures.* The *pleurostomal suture* (PMS)
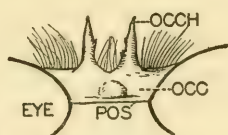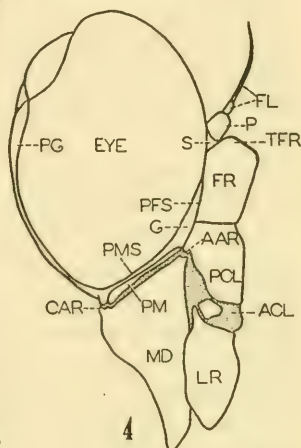
1 ANTERIOR VIEW, ♂
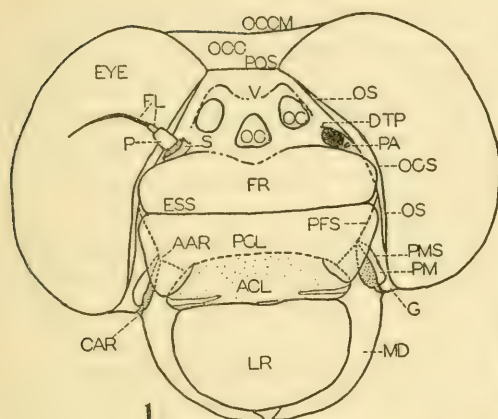
2 OCCIPUT, ♀
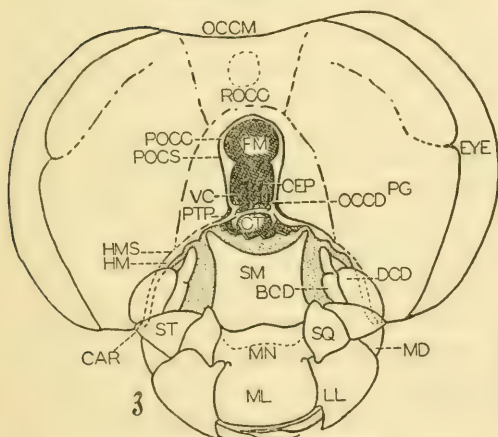
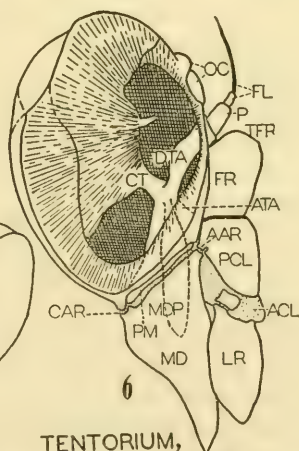3 POSTERIOR VIEW, ♂

4 LATERAL VIEW

5 TENTORIUM, VENTRAL VIEW

6 TENTORIUM, LATERAL VIEW

Figs. 1-6.—Head.

marks the lateroventral margin of the capsule above the mandibular bases and between the anterior (AAR) and posterior articulations (CAR) of each. Along this suture the anterior tentorial arm (ATA) is produced internally, and to it a narrow sclerite, the *pleurostoma* (PM), is attached. The poorly defined *hypostomal sutures* (HMS) each follows closely the posterior margin of the cranium between the posterior articulation of the mandible (CAR) and the *posterior tentorial pit* (PTP).

The OCULAR SUTURES (OS) surround the bases of each of the compound eyes except in the anterior aspect of the head where a narrow band of sclerite, the *ocular sclerite* (OCS), is interposed between them.

PARAFRONTAL SUTURES (PFS) are present, one on each side of the frons. Apparently no name has previously been given to them although they are shown in many drawings of various species of dragonflies by different authors (e.g., Tillyard, 1926; Lew, 1933). These are probably the *frontogenal sulcus* of DuPorte (1946) or *lateral grooves* of Snodgrass (1947). Each suture extends from the middle of the inner margin of the eye near the antenna to the anterior articulation of the mandible, thus separating frons from gena. Each is hidden by the lateral portion of the elevated frons and clypeus and therefore is invisible in the anterior aspect of the head. Along this suture a low ridge is produced internally.

The POSTOCCIPITAL SUTURE (POCS) closely parallels the dorsal and lateral margins of the *foramen magnum* (FM).

The CLYPEAL SUTURE is absent, but its position is indicated by a distinct line of demarcation between the sclerotized postclypeus and the mostly membranous anteclypeus.

The antennal socket is well defined but is not circumscribed by an antennal suture.

AREAS OF THE CRANIUM

The principal areas of the cranium are clypeus, frons, vertex, occiput, genae, postgenae, postocciput, pleurostomae, hypostomae, and eyes. The *gula* is absent in this species. However, it has been very vaguely indicated as being present in the order Odonata by earlier workers. Calvert (1893) said that the gula was membranous; Tillyard (1917) probably concurred with him in this matter. Marshall (1914) probably wrongly designated submentum as gula.

The CLYPEUS is a large transverse sclerite differentiated into a light-colored, mostly membranous *anteclypeus* and black-colored, sclerotized *postclypeus*. The latter areas are separated by deep indentations on

both sides. The *anteclypeus* (ACL) is light-colored, laterally produced into a lobelike structure, with a narrow sclerotized piece on each side extending mesally from the tip of the lobe a distance of one-third the width of the anteclypeus. The *postclypeus* (PCL) is black, with or without a small transverse light-colored spot on each side. It expands laterally and extends ventrally, thus overlapping a portion of the lateral lobe of the anteclypeus. A small condyle, the *anterior articulation of mandible* (AAR), is produced on each side near the base of the postclypeus. It is covered by the laterally expanded portion of the postclypeus so that it cannot be seen in the anterior aspect of the head.

The FRONS (FR) is a large, transverse, convex area which is bounded ventrally by the epistomal suture, laterally by the parafrontal sutures, and dorsally by a transverse furrow between it and the vertex. It is differentiated by a sharp fold into an upper horizontal portion and an anterior or vertical portion, but there is no sutural demarcation between these regions. The upper portion is called the *top of frons* (TFR) which is differentiated into two low prominences separated by a broad median furrow. A broad, transverse, light-colored stripe covers most of the top as well as a part of the anterior portion of the frons. This stripe is sometimes separated in the middle along the median furrow. In this light-colored area there are a few small black tubercles each of which bears a minute hair.

The VERTEX (V) is a trapezoidal area bounded ventrally by a groove between it and the frons, dorsally by the postocellar suture, and laterally by the ocular sutures. It bears a pair of antennae and three *ocelli* (OC), the latter being very large. The deeply sunken middle ocellus is a little lower in position than the lateral ocelli. Along the dorsal rim of the middle ocellus there is a very low but large knoblike tubercle which bears a group of fine and wavy long hairs. External to the tubercle and the lateral ocellus there is a subsemicircular ridge. The *dorsal tentorial pits* (DTP) are present as a pair of semicircular sutures above and lateral to the bases of the antennae (mostly obscured by the antennae in anterior view and by the eye in lateral view). It is interesting to point out here that the dorsal tentorial pits are present in the adult dragonflies (Lew, 1933) whereas they are usually represented by a pair of callosities in the dragonfly nymphs and many insects. Two peculiar *papillae* (PA), about two-thirds as long as the third antennal segment, situated one on each side very close to the external rim of the antennal socket, are present in both sexes. They are small and usually obscured from view by the antennae and therefore are easily overlooked. Apparently they have not been reported

heretofore. They occur also in *Onychogomphus micans* Needham which is very closely related to the present species, but not in *Ictinogomphus rapax* (Rambur) (Gomphidae) and *Anax nigrofasciatus* Oguma (Aeschnidae) which I have examined.

The furrow which separates the frons from the vertex is called *frontal furrow* or *frontal suture* by Tillyard (1917). These terms are confusing since the structures they define are definitely not homologous with the frontal sutures of other insects. Morphologically speaking (DuPorte, 1946; Snodgrass, 1947), the areas of the frons, vertex, and occiput described here are not homologous with those of other insects or even with these areas as designated in certain other species of dragonflies, although they are generally so considered by students of Odonata.

The OCCIPUT (OCC) is situated on the top of the head between the compound eyes. In the anterior aspect of the head it appears as a transverse area bounded ventrally by the postocellar suture, laterally by the compound eyes, and dorsally by the occipital border, or *occipital margin* (OCCM), which is almost twice as wide as the postocellar suture, and fringed with long black hairs. In the female there is a pair of *occipital horns* (OCCH) on the occipital margin. These are not to be confused with a pair of similar horns which arise on the vertex above the lateral ocelli and which are also, but erroneously, called the occipital horns. Such horns occur in a number of species of the family Gomphidae, e.g., *Gomphus flavicornis* Needham (Lew, 1933, pl. 8, fig. 9), *Gomphus cuneatus* Needham, and *Davidius bicornutus* Selys. The posterior aspect of the occipital region is called the *rear of the occiput* (ROCC). It is a subquadrate area situated above the foramen magnum, with a large, light, yellow-colored marking in the center. Laterally it is demarked with weakly defined furrows or wrinkles which indicate the dividing line between it and the postgenae.

The GENAE (G) are small sclerites. Dorsally each gena is bounded by the parafrontal and the ocular sutures, and ventrally to its evaginated margin is attached a small transverse sclerite, the *pleurostoma* (PM).

The POSTGENAE (PG) are a pair of large sclerites, one on each side of the posterior aspect of the head. The outer margin of each postgena which borders the eye is notched at about the center. Mesally and mesoventrally the postgena is bounded by the postoccipital suture and hypostomal suture respectively. Ventrally it is fused with the gena. This fused portion bears the posterior articulation of the mandible.

The POSTOCCIPUT (POOC) is a roughly horseshoe-shaped narrow

sclerite surrounding the dorsal and lateral sides of the foramen magnum, with its ends terminating at the *posterior tentorial pits* (PTP) where a pair of small transverse processes, the *occipital condyles* (OCCD), are produced toward each other. On each side of the foramen magnum the postocciput is produced mesally into a short process.

The PLEUROSTOMAE (PM) are very small transverse sclerites, one on each side, situated in the evaginated ventral margin of the gena between the anterior and the posterior mandibular articulations.

The HYPOSTOMAE (HM) are narrow bands or thickenings, one on each side bordering the lower margin of the postgena between the posterior articulation of the mandible and the posterior tentorial pit.

The COMPOUND EYES (EYE) are large, and are closest together along the postocellar suture. Each is evaginated in the middle on its posterior margin as shown in figures 4 and 5.

TENTORIUM

(Figures 4-6)

The tentorium consists of a corporotentorium and three pairs of tentorial arms, namely, dorsal, anterior, and posterior.

The CORPOROTENTORIUM (CT), or tentorial body, is a transverse bar very close to the posterior surface of the head capsule and appearing as the floor of the foramen magnum. Apparently it is often mistaken for the *gula* by some students of Odonata.

The POSTERIOR TENTORIAL ARMS (PTA) arising from distinct *posterior tentorial pits* (PTP) are very short and are not differentiated from the corporotentorium.

The ANTERIOR TENTORIAL ARMS (ATA) arise from extremely elongated tentorial pits lying along the entire lengths of the pleurostomal sutures. Each anterior tentorial arm is a fanlike structure strengthened by three heavily sclerotized ribs radiating from the corporotentorium. The *posterior rib* (PRB) extends to the posterior mandibular articulation, the *middle rib* (MRB) to the anterior mandibular articulation, and the *anterior rib* (ARB) to the lateral end of the epistomal ridge. On the ventral surface of the middle rib there are two processes: the anterior process is called the *mandibular process* (MDP) and consists of a very large, ovoid, tendonlike structure with a short, narrow stalk. The large ovoid portion is inserted in the heavy muscles of the mandible. The posterior process is called the *maxillary process* (MXP) and is a long and slender tendon supplying attachment for the maxillary abductor muscles. On the posterior rib there is also a short process.

Each of the DORSAL TENTORIAL ARMS (DTA) consists of a simple flattened structure arising from the middle rib of the anterior tentorial arm. Each narrows slightly in the middle and is apically fused firmly with the invagination of the dorsal tentorial pit.

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HEAD APPENDAGES

(Figures 7-16)

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The movable parts of the head are the antennae, labrum, mandibles, maxillae, hypopharynx, and labium.

The ANTENNAE (ANT) are short, inconspicuous, setaceous, and 4-segmented. The basal segment, or *scape* (S), is very thick. The second segment, or *pedicel* (P), is subequal in length and about half the diameter of the preceding segment. The third and the last segments are collectively called the *flagellum* (FL), or *distalia,* which is slender and bristle-like; the third segment being about two-thirds as long as the pedicel; the last segment being longer than the other three segments combined.

The LABRUM (LR), or upper lip, is a transverse subovoid sclerite, movably attached to the anteclypeus and functions as one of the mouth parts. It is generally regarded as not a true appendage. Great differences of opinion exist among entomologists as to its homology. For more detailed accounts the reader is referred to recent papers by Ferris (1947) and Henry (1948). Aborally (fig. 7) it is slightly convex, black, with two large ovoid yellow spots, and fringed with many long hairs along its distal and lateral margins. Adorally (fig. 8) it has a flat surface, is black on lateral regions, and has a large clear area called the epipharynx in middle. The *epipharynx* (EPX) consists of a round, slightly depressed, sclerotized area in the center surrounded by a group of small circular tubercles and hairs. These tubercles are probably taste organs. Some hairs are grouped together to form the *brushes* (BH) pointing mesad.

The *mandibles* (MD) are very strong unsegmented appendages bearing strong teeth which may be divided into two groups: a large basal *mola* (MO) and a distal group of three *incisors* (ICS).

The base of the mandible is triangular in shape, with one lateral and two mesal angles. The mesal angles are designated as inner and outer. The mandible is attached to the head capsule by two articulations, the ginglymoid *anterior articulation* (AAR) at the outer angle and the condylic *posterior articulation* (CAR) at the lateral angle. A strong *flexor tendon* (FT) is attached to the inner angle and a weak *retractor tendon* (RT) to the lateral angle.

The adoral side (fig. 10) of the mandible has two tuberculate and hairy areas, one at the base of the incisors and the other parallel to the margin of the mola, the former area being crescent-shaped. The aboral side (fig. 9) of the mandible has a similar crescent-shaped, tuberculate, and hairy area which is slightly depressed and joins with a ridge extending to the anterior articulation.

The three *incisors* (ICS) are of unequal length; one of them being very long, sharply pointed, slightly curved, and bearing the smaller basal one on its mesal edge and an even still smaller medial one on its adoral side. The *mola* (MO) has four cusps set on a broad base in the shape of a Z on the right mandible and inverted Z ($\diagdown$) on the left mandible. The cusps are placed one at each end and one at each angle of the Z.

The MAXILLAE are composed of several parts, namely, cardo, stipes, inner lobe, and outer lobe.

The *cardo* is an elongate structure internally strengthened by an X-shaped ridge, the mesal arms of the X being submarginal and the lateral arms marginal. It is divided into *basicardo* (BCD) and *disticardo* (DCD) by a suture which is situated along the lateral margin of the basolateral arm and the mesal margin of the distomesal arm. The concave area of the basicardo between the basal arms is about two-thirds as large as the weakly sclerotized convex area of the disticardo between the distal arms; the latter area being adorned with a few long hairs.

The *stipes* (STI) is a large elongate rectangular structure adorned laterally with many short hairs on its inflected area and apically with many long hairs. A mesal submarginal *sutural groove* (SG) (Snodgrass, 1935) sets off a narrow area called *parastipes* (SG) (Crampton, 1923b, p. 83). An isolated sclerite is present in the membrane which attaches along the margin of the lateral inflected area. Nothing is known about this sclerite although it has been shown in drawings by earlier workers (e.g., Tillyard, 1917, p. 16, fig. 4).

The *inner lobe* (IL) and the *outer lobe* (OL) are two freely movable processes, the former being generally regarded as representing the fused *lacinia* and *galea* of more typical mandibulate insects, and the latter the *palp*.

The *inner lobe* (IL) is a large process basally fused with the stipes but separated from the parastipes by a narrow strip of membrane. Basally it is expanded on its mesal portion and adorned with many long hairs. Apically it is narrowed and gently curved, ending in three teeth pointing mesad, the apical tooth being very long and the middle one the smallest. The weakly sclerotized area along the mesal margin

of the apical half of the inner lobe bears three widely spaced teeth of subequal length, also pointing mesad.
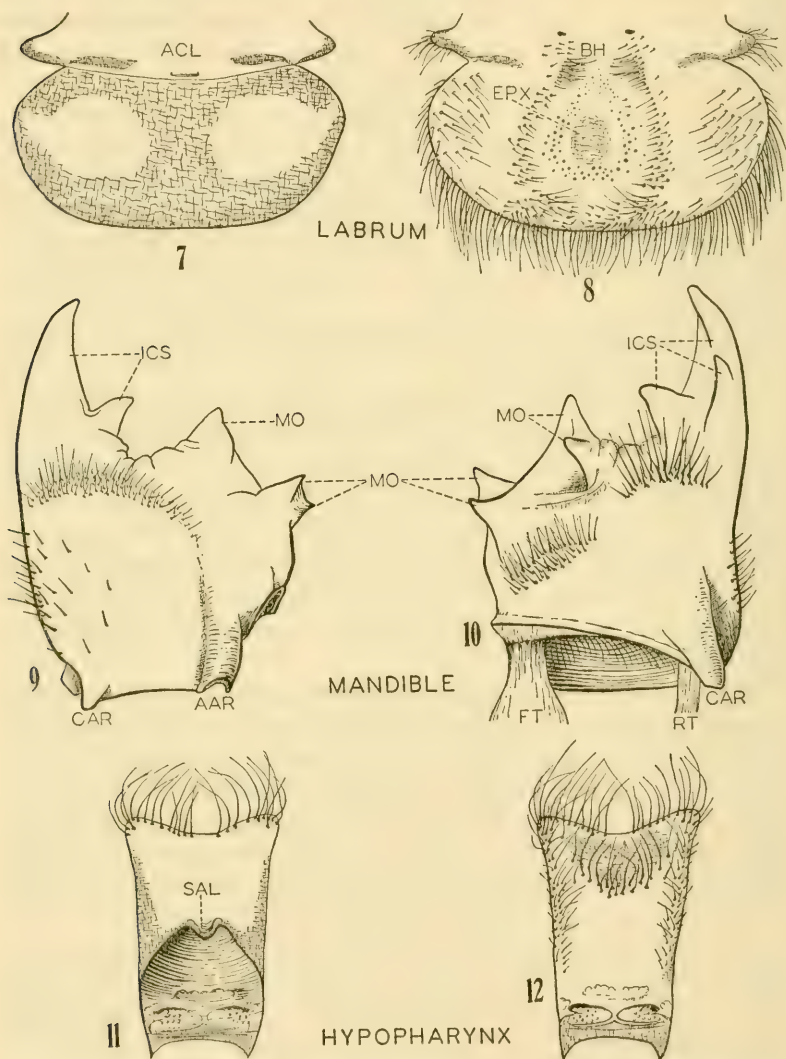
FIGS. 7-12.—Mouth parts. 7, 9, and 11, Aboral views; 8, 10, and 12, adoral views.

The *outer lobe* (OL) is a stout, slightly curved, fingerlike structure, about as long as the inner lobe, with the lateral portion of the basal half weakly sclerotized and unpigmented. Basally it is situated on a small transverse sclerite on the adoral side of the maxilla.

The HYPOPHARYNX is a large, elongate, wedge-shaped lobe in the preoral cavity, apparently consisting only of the *lingua,* with its aboral surface (fig. 11) about half as long as its adoral surface (fig. 12), its lateral sides slightly divergent, and its apical margin slightly emarginate.

Adorally (fig. 12) the hypopharynx is adorned with hairs. Those hairs along the distal margins and surrounding the subapical, depressed, sclerotized area are very long and widely spaced. Basally the hypopharynx has a heavily sclerotized transverse bar which is fused laterally with a pair of slightly raised sclerotic structures immediately distal to it; the former with a low, transverse internal ridge, and the latter with a number of small round nodules. A single transverse, raised, somewhat wrinkled, weakly sclerotized structure, and a pair of similar smaller ones are situated distal and lateral to the sclerotized structures respectively.

Aborally (fig. 11) the lateral walls of the hypopharynx contain a pair of *basal plates,* the apical ends of which are attenuate, whereas the basal ends expand and extend along the basal margin of the hypopharynx to the *salivarium* (SAL).

The LABIUM consists of the following movable parts: Submentum, mentum, middle lobe, squames, lateral lobes, and movable lobes.

The *submentum* (SM) is a quadrangular piece with its basal margin slightly evaginated and its lateral edges subparallel to each other. Basally it is bounded by membrane continuous with the neck region. Laterally and adorally it is connected with the mesal margins of the cardines and stipites of the maxillae and with the base of the hypopharynx by a large membrane.

The *mentum* (MN) is a transverse area. Adorally (fig. 16) it is partly membranous, with a pair of large transverse subrectangular sclerites imbedded in the membrane. These sclerites are adorned with long hairs on their bulging lateral portions. Apically the mentum is separated from the middle lobe by a distinct membranous fold. Aborally (fig. 15) it is sclerotized on its basal half and weakly so on its distal half, with distinct line of demarcation between these regions. The basal half is fused laterally with the squames. The distal half is unpigmented, adorned with a few scattered microscopic hairs, and fused distally with the middle lobe. Distolaterally it is evaginated into a socketlike structure on each side to which the mesobasal portion of the lateral lobe is attached.

The *middle lobe,* or *median lobe* (ML), is a large subrectangular piece which, according to Butler (1904), corresponds to the ligula of other insects. The latter term is not to be used, because a part of

the pronotum is also called the median lobe. Adorally (fig. 16) it is weakly sclerotized and pigmented on its apical third and narrowly so along its lateral portions, with long hairs on these areas: the re-
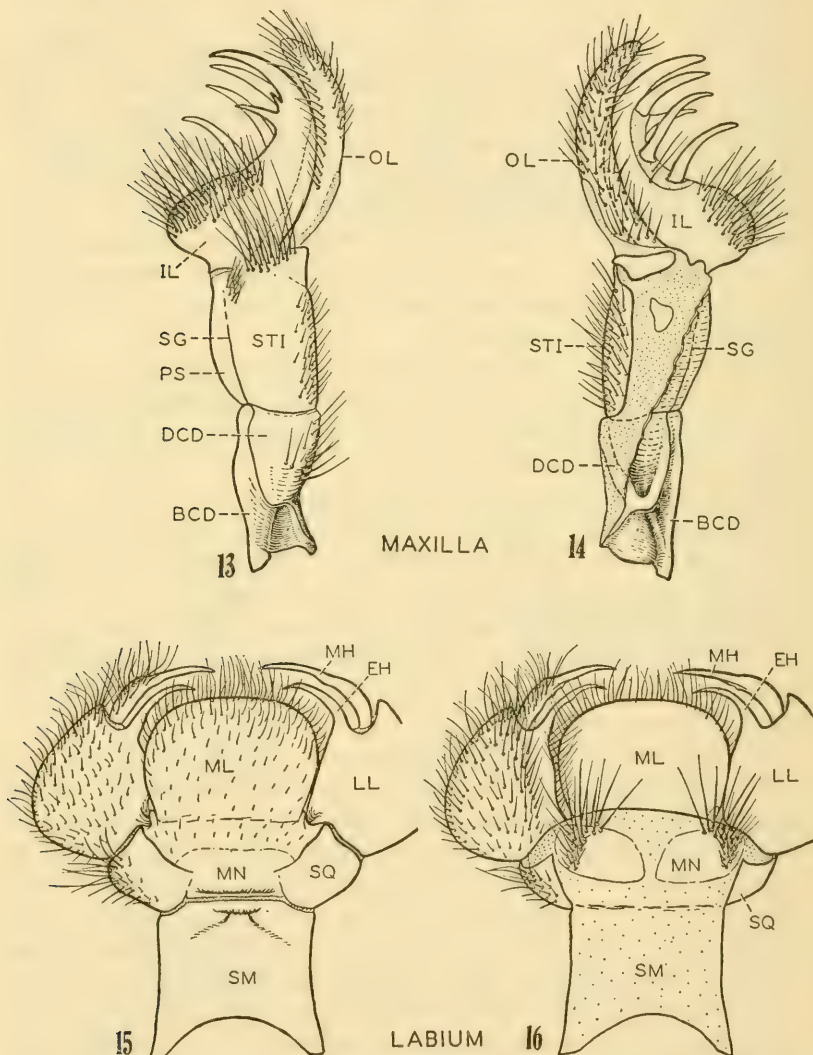
FIGS. 13-16.—Mouth parts. 13 and 15, Aboral views; 14 and 16, adoral views.

maining area is unpigmented and adorned with a few scattered microscopic hairs.

The *squames* (SQ) are a pair of convex sclerites, which, according to Tillyard (1917), correspond to the palpigers. (The term squames

is rather confusing since it has been used to designate different struc-
tures in different orders of insects.) Aborally (fig. 15) they are
subrectangular in shape, mesobasally fused with the basal portion of
the mentum, laterally deflected to approach the sclerites of the mentum
on the adoral side.

The *lateral lobes* (LL) are a pair of hairy sclerotized structures
attached to the squames and mentum, with their mesal margins straight
and their lateral margins strongly convex. Each lobe is produced
mesoapically into a very long, bare, and sharp *end hook* (EH) point-
ing meso-orally. Lateral to the end hook is an even longer hairy
movable hook (MH) with its basal half about twice as wide as its
apical half.

CERVIX

(Figures 17-20)

The cervix (sometimes called neck or microthorax) is a region
between the head and the prothorax, narrow anteriorly, mainly mem-
branous, with lateral, dorsal, and ventral cervical sclerites. The *lateral
cervical sclerites* are the largest and serve as pivots for the head while
the other sclerites are mostly small and completely surrounded by
membranes.

Each of the LATERAL CERVICAL SCLERITES consists of a basal *post-
cervicale* (PC) and a distal *eucervicale* (EC) (Crampton, 1926)
forming a hinge at their juncture. The *postcervicale* is V-shaped, fit-
ting between the pronotum and the episternum, with the arms of the
V pointing anteriorly. The *eucervicale* is incompletely divided into a
dorsal and a ventral portion by a deep and narrow incision. The
anterior half of the dorsal portion of the eucervicale is unpigmented
and whitish. The ventral portion is somewhat twisted, produced mesad
and then anteriorly into a long process called the *cephaliger* (CEP);
the latter lies freely inside the cervical membrane, with its apex con-
nected with the *occipital condyle* (fig. 3, OCCD).

There are two transverse DORSAL CERVICAL SCLERITES (DC) in the
middle of the cervix, with a pair of small and weakly sclerotized
sclerites between them; the posterior transverse sclerite also being
weakly sclerotized. Another pair of dorsal sclerites is situated on the
posterior margin of the cervix: they are fairly large in size, well
sclerotized, and partly obscured dorsally by the anterior lobe of the
pronotum.

The paired VENTRAL CERVICAL SCLERITES (VC) are roughly L-
shaped, with the transverse bars of the L's almost touching each other,
and the other ends of the L's being in contact with the occipital con-

dyles. There is a small weakly sclerotized area attached at the angle of the L, with many tiny tubercles each bearing a microscopic hair.

THORAX

The thorax is differentiated into two distinct parts, namely a small prothorax and a large synthorax (the latter also called pterothorax) representing the fused mesothorax and metathorax.
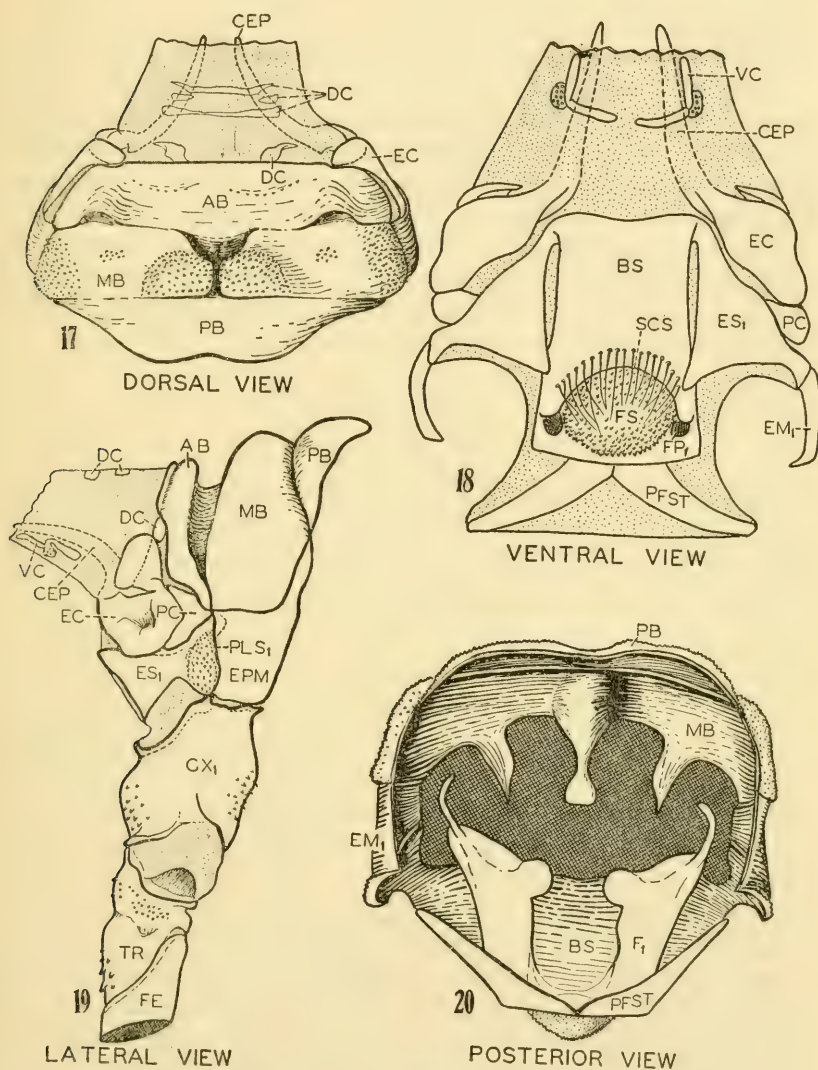
PROTHORAX

(Figures 17-20)

The prothorax is a small segment, narrow anteriorly, with its length subequal to the vertical diameter of its anterior end which is about two-thirds that of its posterior end. The *pronotum* (figs. 17, 19) covers the dorsal half of the segment, topographically differentiated into anterior, median, and posterior transverse lobes alternated with two furrows where ridges are produced internally. The *anterior lobe* (AB) has its anterior margin whitish. The anterior furrow is deep and about as broad as the anterior lobe, laterally with a depression on each side where a long, pointed apodeme is produced internally. The *median lobe* (MB) is divided into two parts by a narrow median sagittal groove. It is minutely tuberculate in the areas on both sides of the median groove and on its lateral portions and with a similar but smaller area between them. The lateral tuberculate areas are adorned with fine, long, and wavy hairs. A large semicircular depression is situated at the anterior end of the median groove and gives rise to an internal apodeme which is long, slightly curved, narrow in the middle, and expanded distally into a discoidal structure. The *posterior lobe* (PB) is somewhat like a Cupid's bow in shape on its dorsal aspect, dorsally minutely tuberculate, and with long, fine, wavy hairs all over.

Each of the PROPLEURA (fig. 19) consists of two approximately equal-sized sclerites, the episternum and the epimeron, separated by the *pleural suture* (PLS_1) which is almost perpendicular to the long axis of the body. Along the pleural suture a low ridge or *lateral apodeme* is produced internally. The *episternum* (ES_1) is a transverse piece, narrow in the middle, with its dorsoanterior angle fused with the sternum, and its posterior portion slightly bulging. It is minutely tuberculate all over, with the bulging area having larger tubercles and long wavy hairs. The *epimeron* (EM_1) is a rectangular piece, slightly higher than wide, tuberculate only on its ventroposterior portions, dorsally produced into a narrow strip along the posterior border

of the pronotum to approach closely the lateral end of the posterior lobe.

FIGS. 17-20.—Prothorax and neck.

The PROSTERNUM (fig. 18) consists of an anterior, large, elongate, rectangular piece and a posterior pair of small sclerites, the latter collectively termed the *postfurcasternum* (PFST) (Crampton, 1926). The rectangular piece is divided into two portions, an anterior *basi-*

sternum (BS) and the posterior *furcasternum* (FS), by an anteriorly arched *sternacostal suture* (SCS) which ends at the large *furcal pits* (FP), or *apophyseal pits* (Ferris, 1940). Along the sternacostal suture a ridge is produced internally.

The *basisternum* is fused on its anterior angles with the episterna. It is minutely tuberculate, with a broad, shallow, submarginal circumscribing depression; the posterior course of the depression being weakly sclerotized and unpigmented. The area between the posterior depression and the sternacostal suture is raised, with long hairs along its anterior margin. The central area of the *furcasternum* (FS) between the furcal pits and the sternacostal suture is protuberant and rather coarsely tuberculate. The *furca* (F_1) consists of a pair of large, inverted, foot-shaped apodemes widely separated from each other; each arm with a long narrow tendon at its apex.

SYNTHORAX
(Figures 21-27)

The *synthorax,* or *pterothorax,* is composed of the fused mesothorax and metathorax, ventrally carrying two pairs of legs on its anterior half, and dorsally two pairs of wings on its posterior half. The pleura are very large while the terga and the sterna are very small.

TERGA
(Figures 21, 22)

The terga are connected with the pleura only by membranes. They are not connected with the latter by prealares anteriorly or by postnotum posteriorly, such as is the case in most other winged insects. Thus, it would seem that the terga can move up and down without distortion during flight.

The anteriormost part of the mesotergum is roughly a T-shaped structure divided into the ACROTERGITE (ATG) and the PRESCUTUM (PSC_2) by the *antecostal suture* (ACS) along which a pair of small phragmata is produced internally. The ends of the transverse bar of the T are the *prealares* (PRA) which serve, in the present species, as pivots for the anterior lobes of the *humeral plates* (HP), and are connected posteriorly with the *detached plates of the scutum* (Snodgrass, 1935) to be described later.

The *scutum* (SCT_2) is a large, somewhat ovoid, convex structure, wider posteriorly, with a large, central portion weakly sclerotized and unpigmented. Anteriorly the lateral portion of the scutum is detached

into a bilobed plate which is fused with the prealare. Posteriorly the
adanal sclerite, or *posterior notal wing process* (PWP), is narrowly
separated from the scutum by an incision and is articulated with the
axillary plate. The detached plate of the scutum has been shown by
Snodgrass (1930, fig. 11 A, *a*; 1935, fig. 123 B, *a*), but its importance
in the wing mechanics has not been well investigated. It consists of
two lobes, the anterior *suralare sclerite,* or *anterior notal wing process*
(AWP), and the posterior *adnotal sclerite,* separated by the notal
incision or the lateral emargination. Near the mesal margin of the
detached plate there is a groove along which an *apodeme* (AP) is
produced internally. The latter is a large, elongate structure, apically
expanded into an irregularly elongate plate which is constricted in
the middle. This apodeme is called cap-tendon by earlier workers
(Calvert, 1893; Tillyard, 1917). To this apodeme the principal ele-
vator muscle is attached. Two more small sclerites are present. One
of these is the *first axillary* (IAX), also called notal ossicle, notale,
or notopterale. It is elongate triangular, situated along the mesal
margin of the humeral plate, and mostly obscured by the latter in
dorsal view. The other small sclerite, distinct from the adnotal sclerite
in this species, is situated between the latter and the anteromesal
margin of the axillary plate. A preliminary study of *Anax junius,* a
common American species (Aeschnidae), shows a condition in which
the detached plates are not fused with the prealares and the axillary
sclerites are not independent from the anterior notal wing processes.
The importance of the detached plates of the scutum and the axillary
sclerites morphologically and phylogenetically in the wing mechanism
will be discussed later.

   The SCUTELLUM (SCL$_2$) is a comparatively small, convex, trans-
verse, ovoid sclerite from the posterolateral angle of which the corru-
gated *axillary cords* (AXC) are produced. A small transverse sclerite
is closely applied to and partly fused with the anterior margin of the
axillary cord. Along the line of fusion a low ridge is produced in-
ternally and to it the *postscutellum* (PSCL$_2$) is articulated.

   The POSTSCUTELLUM (PSCL$_2$) (= acrotergite, Whedon, 1938) is
even larger than the scutum. It is a subrectangular sclerite, pigmented
laterally only, separated by an internal V-shaped ridge into three re-
gions which are probably inaccurately termed median postscutum and
lateral postscutella by Tillyard (1917).

   The anteriormost part of the metatergum is a narrow transverse
sclerite, the PRESCUTUM (PSC$_3$), with a submarginal suture along
which a low ridge is produced internally. It is mostly obscured by the

preceding postscutellum to which it is connected by a tiny linear sclerite on each side.

The SCUTUM (SCT$_3$) is a large transverse sclerite with rounded anterior angles. Its central portion is weakly sclerotized and unpigmented. A small spinelike apodeme is produced internally from a pit which is situated very close to its anterior margin. Laterally the suralar, adnotal, and adanal sclerites are not separated from the scutum (also true in *Anax junius*).

The SCUTELLUM (SCL$_3$) and the *axillary cords* (AXC) are similar to those of the preceding segment, except that the latter structures are divergent posteriorly in the metathorax.

The POSTSCUTELLUM (PSCL$_3$) is mainly weakly sclerotized, unpigmented, and merged with the membrane between it and the first abdominal tergite, except for a trace of sclerotized area on each side posterior to the axillary cord.

PLEURA

(Figure 21)

The pleura of the synthorax are very large and greatly modified. Laterally the synthorax has two oblique sutures, the *mesothoracic pleural* (PLS$_2$) and the *metathoracic pleural* (PLS$_3$) sutures, located between the coxae and wing base of their respective regions. On the lower portion of the synthorax between the two pleural sutures is a transverse ovoid spiracle, the *posterior spiracle,* or *metastigma* (IIISP). Just anterior to the metastigma is a short slanting suture, the *middle lateral suture* (MLS), which represents the remnant of the *intersegmental suture* (Snodgrass, 1909).

Different names have been used by various taxonomic workers to designate the above-mentioned sutures as follows:

Mesothoracic pleural suture

=Humeral suture (Calvert, 1893; Needham, 1903, 1930; Tillyard, 1917; Fraser, 1933).
=First lateral suture (Needham, 1903, 1930).

Intersegmental suture (Snodgrass, 1909)

=Interpleural suture (Tillyard, 1917).
=Middle lateral suture, or middle suture (Needham, 1930).
=First lateral suture (Rambur, 1842; Calvert, 1893; Tillyard, 1917).
=Second lateral suture (Needham, 1930).
=Anterolateral suture (Fraser, 1933).

Metathoracic pleural suture

=Second lateral suture (Calvert, 1893; Tillyard, 1917).
=Third lateral suture (Needham, 1930).
=Posterolateral suture (Fraser, 1933).

The course of the *mesothoracic pleural suture* (PLS_2) is crooked, with its lower one-fourth almost perpendicular to the longitudinal axis of the body, its upper three-fourths slightly bowed and slanting posteriorly, and with a short portion between them smoothly curved. The angle of skewness is 60° and the angle of tilt of wing bases is 32° in the present species. These angles are greater than the corresponding angles in any gomphine dragonfly measured by Needham and Anthony (1903). Needham and Anthony defined the *degree of skewness* or inclination (also called angle of humeral suture) as the acute angle between the suture and an imaginary line perpendicular to the longitudinal axis of the body, and the *angle of tilt of wing bases* as the acute angle between a line drawn through the wing bases and the longitudinal axis of the body. It must be pointed out that Tillyard (1917) used the term angle of obliquity in synonymy with skewness, both of which he defined as angle of tilt of wing bases. This must not be confused with the angle of skewness of Needham and Anthony.

The *metathoracic pleural suture* (PLS_3) has almost the same shape as the preceding one except that its lower one-fourth is a little slanting posteriorly instead of almost perpendicular to the longitudinal axis of the body, and its upper three-fourths is almost straight.

Particular attention is here given to the courses of the pleural sutures and the relative positions of the wings and the legs. The older view as to the phylogenetic origin of the orientation of these parts is well expressed by Tillyard (1917, 1926), Imms (1948), and others who maintain that the great development of the mesothoracic anepisterna "pushes" the wings backward away from the head, carrying the terga with them, and that the correlated growth of the metathoracic epimera "pushes" the sterna and the legs forward so that the latter come into position close behind the mouth. However, judging from the courses of the pleural sutures, it is believed that the vertical positions of the lower portions of the pleural sutures (a condition usually considered to be primitive) probably indicate the primitiveness of this region while the posteriorly slanting positions of their upper portions probably indicate the evolutionary enlargement of the upper portion of the synthorax. The static nature of the lower region indicates that the legs have not been "pushed" forward, while the posteriorly slanting position of the upper region indicates that the wings
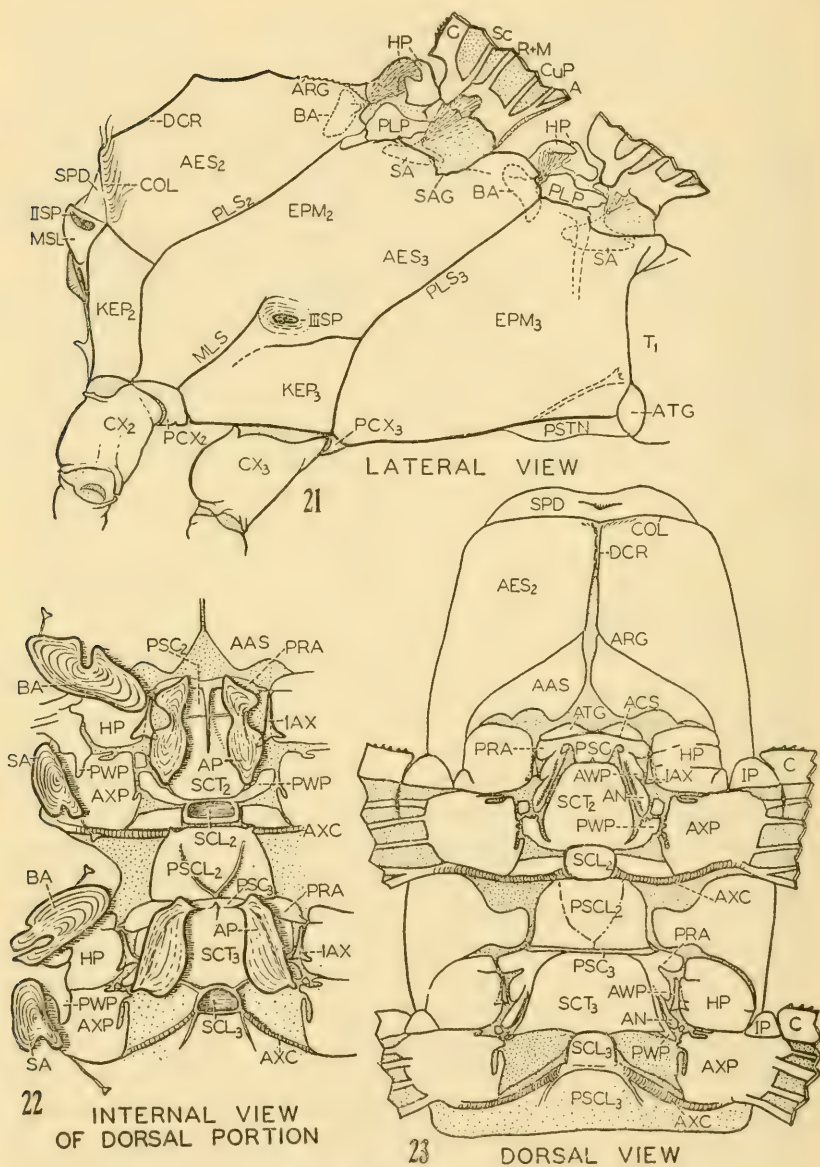
FIGS. 21-23.—Synthorax.

have moved backward away from the head, to a position at or near the center of gravity of the greatly elongated body of the insect.

Regarding the positions of the three pairs of legs, it is interesting to note that the knee joint between the femur and the tibia of the prothoracic leg is directed sideward, that of the mesothoracic leg, sideward and backward, that of the metathoracic leg, backward. The pleurocoxal articulation of the metathoracic leg indicates a rotation of its axis of about 90°. The result of the rotation of the metathoracic legs might be of definite advantage to the insect in catching prey during flight or in perching on the twig. The legs are not fitted for walking but they serve very well for climbing when that mode of progress is required.

The mesothoracic episternum is divided by an inverted V-shaped suture into anepisternum and katepisternum. The *anepisternum* (AES$_2$) is greatly expanded and meets with the corresponding part of the other side of the thorax along the middorsal line to form a ridge, the *dorsal carina* (DCR), anterior to the wing bases. At the anterior end of the dorsal carina there is a transverse ridge, the *collar* (COL), which is adorned with fine wavy hairs. On the dorsal aspect of the synthorax the area between the collar and the wing bases is called the *front of synthorax*. At about the middle of the front of synthorax the dorsal carina is raised into a sharp point. Posterior to this point the carina is divided into two low ridges which are parallel for a short distance and then widely divergent. These ridges are collectively called the *antealar ridge* (ARG), or *crest*. The area posterior to the ridge is called the *antealar sinus* (AAS). Anterior to the collar there is a transverse sclerite, the *spiracular dorsum* (SPD), which is medially invaginated to form a hornlike apodeme. The deflected portions of the spiracular dorsum are called *mesostigmatic laminae* (MSL). Each lamina bears an anterior spiracle, or *mesostigma* (IISP). A preliminary study of a few species of gomphine dragonfly nymphs shows that there are three pairs of small intersegmental sclerites: a median pair (the members of which are narrowly separated from one another), a lateral pair bearing the spiracles, and a ventrolateral pair anterior to the katepisternum. Some, if not all, of these plates are referred to as prothoracic spiracle plates by Snodgrass (1909) who states that "in the adult they unite with each other across the back, thus forming a complete spiracular dorsum which fuses with the mesothorax. . ."

The *katepisternum* (KEP$_2$) is a vertical sclerite ventrally separated from the sternum by a distinct oblique suture, the *sternopleural suture* (SPS), from which two large apodemes, the *prefurca* (PF$_2$) and the

squame (TN_2), are produced internally. Anteriorly the katepisternum is flanged by a narrow strip of sclerite which is continuous with the mesosternum and is probably a part of it.

The *mesepimeron* (EPM_2) is fused with the metathoracic anepisternum, except below the metastigma where the *middle lateral suture* (MLS) is separated from the mesepimeron. This sclerite surrounds the posterior half of the mesothoracic coxal cavity.

The metathoracic episternum is divided into two parts, the *anepisternum* (AES_3) and the *katepisternum* (KEP_3), by an incomplete and slightly undulate suture below the metastigma. Dorsally the anepisternum is produced into a hairy lobe between the two wing bases. Ventrally the katepisternum extends to a place lateral to the furcal pit, without any suture separating it from the sternum. The metathoracic *epimera* (EPM_3) are very large, fusing ventrally with each other to make a large unsutured area. This area bears a conspicuous median inverted Y-shaped pigmented area that is quite in contrast to that of the neighboring regions because of its lighter color and the direction of pigment streaking. The Y-shaped area has longitudinal streaks while the neighboring portions have transverse streaks. A pair of small apodemes at the center of the Y and a low ridge along the stem of the Y are produced internally; the latter thickening is visible externally and was often mistakenly regarded as a suture by earlier workers. The area between the arms of the Y is called *poststernum* or *pseudosternum* (PSTN) and is generally regarded as a secondary sclerite filling the gap between the metasternum and the first abdominal sternite. This interpretation seems very inadequate and a more careful study of this sclerite is very desirable. The *postcoxale* (PCX_3) is situated on the mesal edge of the metathoracic coxal cavity. The latter is elongated, with the coxal articulatory process lateroposteriorly located.

<div style="text-align:center">

STERNA

(Figure 24)

</div>

The *mesosternum* (IIST) is a clearly defined area between and in front of the two furcal pits, medially keeled, laterally separated from the katepisternum by an oblique suture, the *sternopleural suture* (SPS), anterolaterally produced into a narrow piece along the anterior margin of the katepisternum on each side. The *furcal pits* (FP_2), or *apophyseal pits* (Ferris, 1940), are close to one another, and are situated near the mesal margins of the coxal cavities. The *metasternum* (IIIST) is medially keeled, laterally deeply invaginated along both sides of the keel (fig. 26, posterior view of cross section

of metasternum posterior to furcal pits; fig. 27, anterior view of cross section of same slightly posterior to the preceding section), and partly obscured by the approximately raised *postcoxales* (PCX₃).

<div align="center">SYNTHORACIC ENDOSKELETON</div>

<div align="center">(Figure 25)</div>

The synthoracic endoskeletal projections are of different forms: (1) Ridges, (2) a complicated fusion product called the neural canal surrounding the nerve trunk, and (3) a median hornlike apodeme on the spiracular dorsum.

The ridgelike apodemes are mesopleural and metapleural, intersegmental, peristigmatic, and precostal apodemes. The *mesopleural* and *metapleural apodemes* (PLA_2, PLA_3) are strengthened by about eight short ridges projecting from their posterior sides. The lower portion of the mesopleural apodeme along the edge of the katepisternum and the apodeme between the anepisternum and katepisternum are inappropriately called (due to different interpretation of sclerites) the sternoepimeral and sternoepisternal apodemes respectively by Tillyard (1917). The *intersegmental* or *interpleural apodeme* (IPLA) is a simple ridge with a spinelike process at its upper end near the metastigma, and with a very long fine tendon projecting from it at about the middle of its course. The *peristigmatic apodeme* (PSA) lies along the suture separating the metathoracic anepisternum from the katepisternum. The *precostal apodemes* are situated along the mesothoracic sternopleural sutures. From each precostal apodeme two distinct structures are produced: the *prefurca* (PF_2) and the *squame* (TN_1). The *prefurca* is a tonguelike structure along the edge of the stigmatic lamina. The squame (which term is also used in maxilla) consists of a short stalk apically expanded into an elongate flat surface, situated anterior to the coxal cavity: this is regarded by Tillyard, probably erroneously, as a part of the furca.

The NEURAL CANAL (figs. 26, 27, NC) is a complicated fusion product of several invaginated processes. This fusion product is differentiated into two portions: an anterior portion on the mesosternum and a posterior portion on the metasternum. These two portions are connected dorsally, but are open between them on each side.

The anterior portion of the neural canal is formed into a complete ring by the apical fusion of the mesothoracic furcal arms. The dorsal portion of this ringlike structure is expanded into a flat surface which is produced anteriorly into a pair of short protuberances, a pointed process curling ventrad (fig. 24), and lateroposteriorly into a long flat
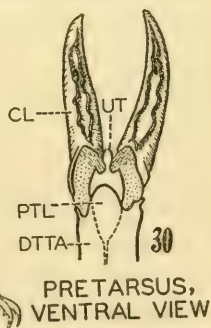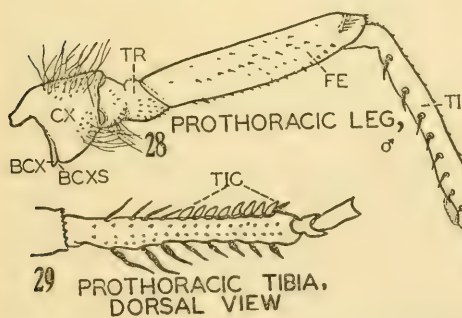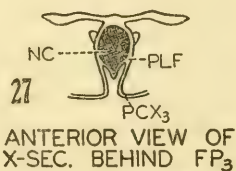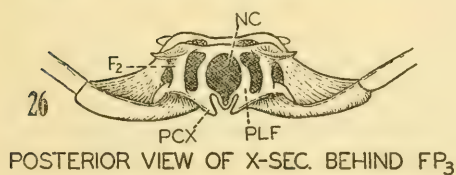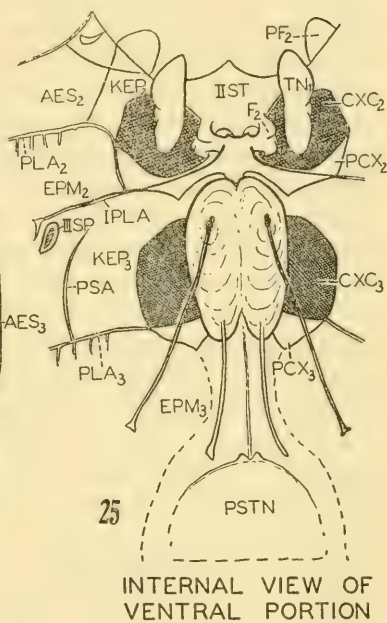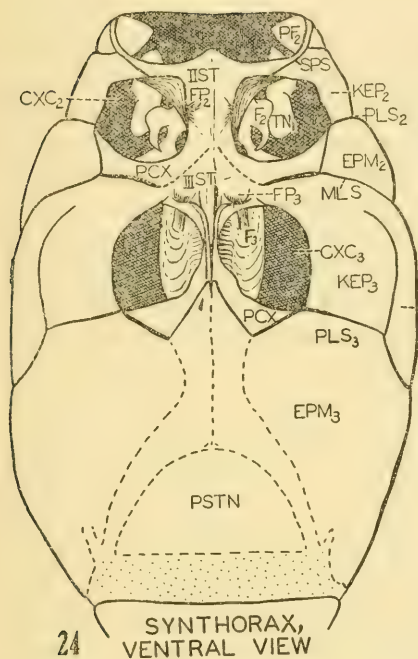
arm which is attached to the posterior margin of the postcoxale to act as a brace.

The posterior portion of the neural canal is an elongated structure formed by the apical fusion of the invaginated *sternal fold* (fig. 26, PLF). The dorsal of this fusion product is greatly expanded into a shieldlike structure which is an elongate, ovoid, flat surface, with two foci of heavy sclerotization anteriorly and posteriorly with a pair of long, narrow, ribbonlike tendons (fig. 25). The foci of sclerotization indicate the positions of the metathoracic furcal arms which are lateral to the sternal folds (fig. 25). From each focus a very long, fine tendon is produced.

WINGS

The wings are held horizontally on both sides of the body: they are unable to fold back on the top of the abdomen. This method of holding the wings is pointed out by Crampton (1924) and his contemporary workers as an important archaic characteristic of the Palaeopterygota (including as living forms the dragonflies and mayflies). It appears that this condition is accounted for by the primitive structure of the wing base. However, it is interesting to note that great confusion exists in the literature regarding the structure of the regions at the bases of the wings of dragonflies and possibly also of mayflies. Structures involved are (1) wing base, (2) axillary sclerite and lateral regions of scutum, (3) pleural wing process and epipleurites, (4) principal wing muscles, (5) articulatory points, and (6) the mechanics of flight.

The WING BASE (fused bases of wing veins) consists of two strongly sclerotized plates, the anterior *humeral plate* (HP) and the posterior *axillary plate* (AXP). Dorsally the humeral plate is divided into three lobes by transverse grooves. Ventrally the lateral edge of the humeral plate is connected by membrane to the distal margin of the pleural wing process. It does not seem to form an articulation with the anterior arm of the pleural wing process such as is mentioned by Snodgrass (1935, p. 221). The axillary plate is subquadrate in shape, slightly convex dorsally, posteriorly fused with the *axillary cord* (AXC). The costal vein (C) is articulated with a small *intermediary plate* (IP) which is in turn articulated with the posterior lobe of the humeral plate. Ventrally a short, rounded protuberance is found at the fused bases of C and Sc. The veins posterior to R+M are firmly fused with the axillary plate. The base of R+M is forked. Its dorsal branch strengthens the anterior margin of the axillary plate. Its ventral branch forms a process which is articulated with the pleural wing

24 SYNTHORAX, VENTRAL VIEW

25 INTERNAL VIEW OF VENTRAL PORTION

26 POSTERIOR VIEW OF X-SEC. BEHIND FP₃

27 ANTERIOR VIEW OF X-SEC. BEHIND FP₃

28 PROTHORACIC LEG, ♂

29 PROTHORACIC TIBIA, DORSAL VIEW

30 PRETARSUS, VENTRAL VIEW

FIGS. 24-30.—Synthorax and legs.

process and is connected with the subalare by tough membrane. Thus the base of $R+M$ has the same function as the second axillary of other orders of insects. It is probable that the second axillary sclerite is formed by detachment of a portion of the base of $R+M$ or R.

AXILLARY SCLERITE. Regarding the axillary sclerite (s), special attention is given to (1) the number and (2) the origin, since there appears to be a considerable amount of confusion in the literature regarding these considerations. In the species studied here there is only one, i.e., the *first axillary sclerite* (1AX), described previously. This sclerite has the same shape and is situated at the same position as that illustrated by Snodgrass (1909) for *Pachydiplax longipennis*. Another small sclerite between the adnotal sclerite and the anteromesal margin of the axillary plate is probably detached from the adnotal sclerite. Its homology is not certain.

Crampton (1924) mentioned that in Palaeopterygota "there are frequently no alar ossicles, or at the most but one." Forbes (1943) maintained that in the dragonflies there are no basal sclerites dorsally, or "no trace of dorsal axillary sclerites as separate elements." Snodgrass (1909) pointed out that "only one distinct axillary is present" in the dragonflies. This axillary sclerite is clearly illustrated by him in this paper (1909, fig. 17, 1Ax), but not mentioned or illustrated in his later paper (1930) or his well-known "Principles of Insect Morphology" (1935). The present studies are in agreement with Snodgrass but not with Forbes.

As to the origin of the axillary sclerites, Crampton and Forbes differ in opinion. Forbes (1943) mentioned that "the extreme bases of the veins are modified into a series of thickened knobs, the axillary sclerites." Crampton (1942) maintained that "the axillary sclerites, alar ossicles or pteralia . . . are apparently formed, in part, as detached portions of the lateral region of the notum, and partly as detached basal portions of the wing veins, or as sclerotized areas at the bases of the veins." He considered, on the basis of numerous comparative studies, that the first axillary or the notopterale (notale) "probably represents a detached portion of the lateral edge of the notum." Crampton's opinion is adopted in this paper since in *Anax junius* the condition of fusion of the first axillary with the anterior notal wing process is perhaps indicative of such an origin.

PLEURAL WING PROCESS and EPIPLEURITES. At the dorsal end of each pleural suture the pleuron is produced into an inverted foot-shaped *pleural wing process* (PLP). The tip of the foot (the posterior longer arm of the wing process) acts as the principal pivot for the articulation of the wing. The heel of the foot (the anterior shorter

arm of the process) is connected to the humeral plate by membrane and does not seem to form an articulation with the latter. The anterior *basalare* (BA) and the posterior *subalare* (SA), collectively called the epipleural sclerites or paraptera, are present. They are very small externally and so deeply imbedded in the membrane as to be easily overlooked. Internally each has a very large apodeme which has a stalk greatly expanded apically into a large surface for the attachment of the depressor muscle. The basalare is connected by tough fibrous membrane to the lateral portion of the anterior lobe and, to a lesser extent, to the posterior lobe of the humeral plate. The subalare is connected by similar membrane to the ventral branch of the base of R+M. It is also interesting to point out that the presence of the basalare and the subalare in dragonflies was probably correctly determined for the first time by Forbes (1943). They were considered as "cap-tendons" by earlier workers (Calvert, 1893; Tillyard, 1917). Snodgrass (1935) mentioned that "there are no epipleural sclerites in the dragonflies." Probably he also considered the epipleural sclerites as tendons, since in the same works he mentioned that "in Odonata there are two anterior wing muscles . . . inserted by long *tendons* directly on the large humeral plate of the wing base," and that "two posterior pleural wing muscles take their origins on the ventral edge of the epimeron in each alate segment and are inserted directly on the axillary plate of the wing base." However, they seem to be more appropriately considered as basalare and subalare instead of tendons, since (1) they are distinct, though small, sclerites imbedded in the membrane in the same positions in which the epipleurites are found in other orders of insects; (2) they serve for the attachment of direct muscles as they also do in other winged insects; and (3) they are connected to the wing base by tough membrane as in other winged insects. Particular attention is called to the connection between the subalare and the ventral branch of the fused bases of R+M—a condition similar to the connection between the subalare and the second axillary sclerite.

WING MUSCLES. Nine wing muscles in dragonflies have been recognized by Berlése (1909), Calvert (1893), and Tillyard (1917), but the apodemes of some sclerites to which the muscles are attached were called cap-tendons, and the sclerites considered to be of no morphological importance. Of the nine muscles, three are very large: (1) The principal elevator, (2) the anterior depressor, and (3) the posterior depressor. The principal elevator (see Tillyard, 1917, p. 204, fig. 89, A, pe_1 and pe_2) is attached to the geat apodeme (AP_2, AP_3) produced internally from the detached plate of the scutum. The an-

terior and posterior depressors are attached to the basalare and subalare respectively.

Snodgrass (1935) classifies flight muscles into two types, *direct* and *indirect*. The direct muscles are the axillary and epipleural muscles and the indirect are the dorsal and tergosternal muscles. The tergosternal muscles, according to Snodgrass, "are attached dorsally on the anterior lateral areas of the tergum, and ventrally on the basisternum before coxae." The present study shows, however, that dragonflies have both types of flight muscles. This interpretation differs from what Forbes (1943) states that in Odonata the indirect muscles are "nonfunctional" or that "only direct wing muscles" are present. The direct (epipleural) muscles have been discussed before. There are several pairs of indirect muscles, the most important of which are the principal elevator muscles, which are attached to the detached portions of the scutum dorsally and to the "squame of furca" (produced internally from the pleurosternal sutures) ventrally. They have been homologized with the "first tergosternal" of other insects by Berlése (1909) whose opinion is adopted by Tillyard (1917). The dragonfly wing mechanics appear therefore to be not fundamentally different from those of higher groups of insects.

ARTICULATORY POINTS. Each wing is articulated with the thorax in three places: (1) The ventral branch of $R+M$ articulates with the posterior arm of the pleural wing process. This is the principal pivot of the wing. (2) The humeral plate articulates with the prealare. (3) The axillary plate articulates with the posterior notal wing process. The prealare-humeral articulation is particularly interesting in two respects: First, the prealare normally "extends laterad or ventrad to the episternum and thus supports the notum anteriorly on the pleural wall of the segment" (Snodgrass, 1935). In the present species, the prealare is separated from the episternum by a large membranous region. It does not offer any support to the notum anteriorly; the latter thus moves up and down freely and synchronously with the movement of the wings. Secondly, the prealare-humeral articulation is probably unique to dragonflies, since in other winged insects the wings are articulated with the anterior wing processes instead of the prealares.

MECHANICS OF FLIGHT. Since the author has not studied the muscles involved in controlling the wing movements, a discussion on the possible mechanics is based on inferences concerned with the sclerotized structures described on a previous page.

The wing mechanics in the dragonflies are similar to those of higher winged insects in two fundamental respects: (1) The wings

are primarily controlled by the antagonistic indirect elevator muscles and the direct depressor muscles attached to the detached lateral plates of scutum and epipleurites respectively; (2) the subalare is connected to the wing base very close to the fulcrum while the basalare is far in front. This latter condition indicates that a pull upon the posterior depressor muscles would strongly depress the wing while a pull upon the anterior depressor not only would depress the wing but also deflect the anterior part of the wing to produce the sculling type of flight.

On the other hand, the wing mechanics in dragonflies differ from those of higher winged insects in two important respects: (1) The prealare-humeral articulation is probably unique in dragonflies. This articulation forms the anterior part of the hinge line and differs from that in other winged insects in which the anterior notal process forms an important articulatory point. (2) Another feature probably also unique in dragonflies is that the terga are connected to the pleura by membrane only and the phragmata produced internally along the antecostal sutures are very small. The latter fact indicates that the longitudinal dorsal muscles attached to the phragmata would be small, such as illustrated by Berlése (see Tillyard, 1917, p. 204, fig. 89, A, *pt*). The small size of the dorsal muscles probably indicates that they do not produce an effective antagonistic action to the tergosternal elevator muscles. Judging from the above facts, it seems that the terga must probably move up and down during flight without distortion. This condition differs from that of other winged insects in which "the restoration of the dorsal curvature of the back by the contraction of the longitudinal dorsal muscles" will effect, in part, the down-strokes of the wings (Snodgrass, 1935, p. 234).

As to the control of the direction of flight, the fore wings are probably more important in this action than the hind ones. This contention is based on the fact that the articulatory plates of the scutum are distinctly separated from the main body of scutum (detached plates) in the mesothorax but firmly fused with it in the metathorax. Thus the hinge line and consequently the pitch of the fore wing can be changed, but that of the hind wing appears to be fixed.

WING VENATION

(Figures 31, 32)

The wings are transparent and supported by numerous veins forming a complicated network. The *fore wings* (fig. 31) are widest at the *nodus* (N) which is located at the middle of the anterior margin

of the wing. The *hind wings* (fig. 32) are slightly shorter and about one-fifth again as wide as the fore wings (the widest portion of the former is a little basal to the nodus which is situated at the basal two-fifths of the wing). In the male the inner margin of the hind wing is excavated and fringed with a narrow white edge, the *membranule* (mb), and the anal angle, or *tornus* (Aa), angulated. In the female the inner margin of the hind wing is not excavated and the anal angle is rounded.

Both pairs of wings have a very conspicuous *pterostigma* (Pt) of the same size, shape, and color. The pterostigma is also called stigma or anastomosis, the latter being very rarely used. The term "stigma," though frequently used, is rather confusing because it may refer also to the spiracles. It is a thickened area between Sc (Fraser, 1948) and R_1 near the apex of the wing, dark brown or black in color, elongate, about four times as long as wide, with its shorter sides oblique and parallel to each other; with its longer sides concave, surmounting about six cells; and with a strong vein, the *brace vein* (br. v.), extending down from its basal side.

Several systems of notation of the venation have been proposed. Originally, de Selys gave a name to each vein without notation in use. Later on, Needham gave an interpretation based on the larval wing tracheation, with a notation based on the Comstock-Needham system. This system has been widely used in the last thirty years or so. Tillyard (1926) gave a different interpretation, based on the study of fossil forms. His system, with a few modifications, has been generally accepted by later entomologists. Borror (1945) summarized in two tables the different systems of terminologies used by different authorities, such as de Selys, Kirby, Needham, Tillyard, Tillyard and Fraser, and others. Forbes (1943) gave very different notations. Fraser (1948) modified the costal vein and the anal veins. The present paper uses Tillyard's system (1926) with a few modifications by subsequent workers. To summarize the points, a table (p. 31) is prepared to show a comparison of terminology of the principal longitudinal veins of the dragonfly wing.

PRINCIPAL LONGITUDINAL VEINS. The principal longitudinal veins are costa, subcosta, radius (4 branches with 2 intercalaries), media (a single vein), posterior cubitus, and anal.

The *costa* (C), or costal vein, is a simple and strong vein which, according to Fraser (1948), extends from the base of the wing to the nodus.

The *subcosta* (Sc) is a long vein posterior to the costa. According to Fraser (1948), its course is from the base of the wing to the nodus

TABLE 1.—*Comparison of terminologies of odonate wing venation*

The principal longitudinal veins

| Terminology used in this paper | | Selysian system | Needham (1903) | Tillyard | | Tillyard and Fraser (1938) | Forbes (1943) |
Name	Abbreviation			(1917)	(1926)		
Costa+subcosta..........	C+Sc	Costa	CC	C	C	C	C
Subcosta...............	Sc	Subcosta	Sc	Sc	Sc	Sc	Sc
Radius+media.......... (Wing base to arculus)....	R+M	Median	R+M	R+M	R+M	R+M	R_1 $Rs+M+Cu$
First radius............	R_1		R_1	R_1	R_1	R_1	R_1
Radial sector...........	R_3	Upper sector of arculus	M_{1+3}	M_{1+3}		Rs	
Second radius...........	R_2	Principal sector	M_1	M_1	R_2	R_2	R_2
Second radius intercalary....	IR_2	Postnodal sector	M_{1a}		IR_2	IR_2	
Third radius............	R_3	Nodal sector	M_2	M_2	R_3	R_3	R_3
Third radius intercalary......	IR_3	Subnodal sector	Rs	Rs	IR_3	IR_3	R_4
Fourth+fifth radius.........	R_{4+5}	Median sector	M_3	M_3	R_{4+5}	R_{4+5}	M
Anterior media............	MA	Lower sector of arculus	M_4	M_4	MA	MA	Cu_1
Posterior cubitus...........	CuP	Superior sector of triangle	Cu_1	Cu_1	Cu_2	Cu_2	P_1
Anal.................	A	Postcosta	A	A_1		A^1	
First anal..............	A_1	Inferior sector of triangle	Cu_2	Cu_2		1A	1Ax
Second anal............	A_2	Proximal sub-basal sector	A_2	A_2			3Ax

where it makes a distinct curve anteriorward toward the costal margin, at which level it straightens out again along the margin of the apical half of the wing.

The *radius* and *media* have a common stem $(R+M)$ which forms the anterior border of a large cell, the *basal space* (bs), at the base of the wing. From the anterior external angle of the basal space the $R+M$ gives off two branches, namely R_1 and the anterior portion of the *arculus* (arc). R_1 extends to the apex of the wing. It is parallel to Sc and forms the posterior border of the *pterostigma* (Pt). The arculus is an oblique vein between $R+M$ and CuP. It forms the external border of the basal space. It consists of two portions, namely, the anterior portion and the posterior portion. The anterior portion is the fusion of the *radial sector* and *media* $(Rs+M)$. They separate from the middle of the arculus. Rs is then called the *superior* or *anterior sector of arculus* and media the *inferior* or *posterior sector of arculus*. The radial sector has three branches, with two intercalary veins between them. The three branches are R_2, R_3 and R_{4+5}. The two intercalary veins are IR_2 and IR_3, the former being posterior to R_2 and the latter to R_3. Near the base of R_3 there is an *oblique vein* (O) $(=LO$, lestine oblique vein of Fraser, 1944) between R_3 and IR_3. The basal portion of IR_3 from its base to the oblique vein is called *bridge* or *bridge vein* (br) by Needham. This bridge was regarded by Needham as a secondary extension of Rs backward toward the base of the wing. Tillyard (1922, p. 7) believed that "it was never formed backwards as a bridge vein but was always the basal portion of a strongly formed main longitudinal vein arising from R_{4+5} or sometimes from R_{2+3} as in most recent forms." On the other hand, Fraser (1944) stated that "IR_3 never originated from a basal source but extended inwards from a peripherial one."

The *media* (MA) is a simple vein extending from the arculus to the apical third or fourth of the posterior margin of the wing. It is called by Lameere (1922) and Tillyard (1926) *anterior median* (MA). Its basal portion forms the anterior border of the *hyper-triangle* (h).

The *posterior cubitus* (CuP) is a crooked vein. It extends from the base of the wing to a point beyond the arculus and then bends abruptly posteriorly almost at a right angle, forming the common side of the *triangle* (t) and the *subtriangle* (s). From the posterior apex of the triangle CuP extends to a point slightly beyond or basal to the middle of the posterior margin of the fore and hind wings respectively. Lameere called this vein the *posterior branch of cubitus* (CuP), and in this has been generally followed by subsequent authors on
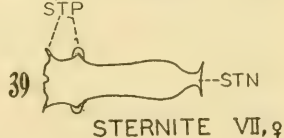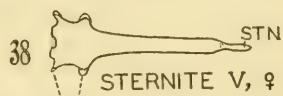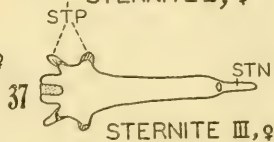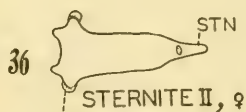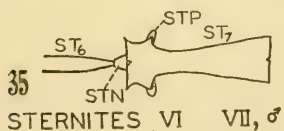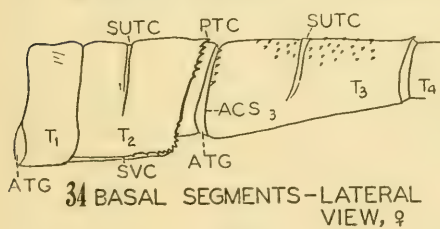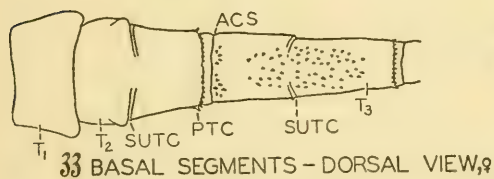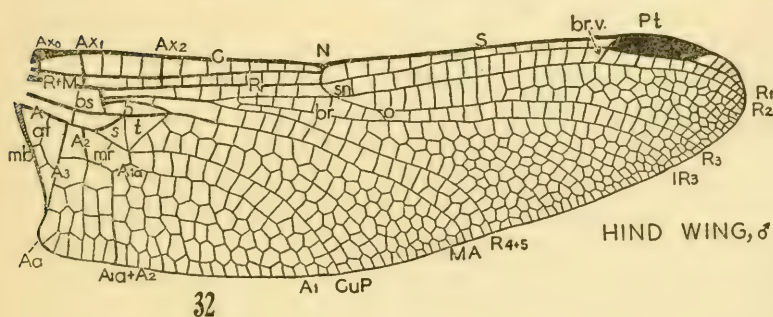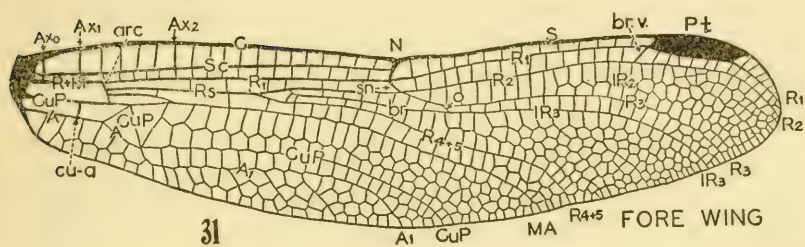
FIGS. 31-39.—Wings and abdomen.

dragonflies (e.g., Fraser, 1940; Borror, 1945). Forbes (1943) called this vein the *plait vein* (Pl) which, according to him, corresponds to the anal furrow of insects of other orders. The basal portion of this vein is regarded as the common stem of the *cubitus* (Cu) by Needham (1903) and as the common stem of $Cu_2 + 1A$ by Tillyard and Fraser (1938).

The *anal vein* (A) is slightly undulated at its basal portion. It meets with CuP at the apex of the triangle. The apical portion of the anal vein (A_1) from the apex of the triangle to the posterior margin of the wing is parallel to CuP in the hind wing. On the other hand, in the fore wing it is parallel to CuP for a long distance and then diverges from the latter. The notation A used in this paper refers to the vein from the base of the wing to the posterior apex of the triangle. A_1 denotes its extension. Tillyard (1926) regarded the basal portion (A) as a backward extension of IA toward the base of the wing. He designated the portion from the posterior apex of the triangle to the *cubito-anal cross vein* (cu-a) as Ab (anal bridge) and the portion between cu-a and the base of the wing as A'. Fraser (1938) demonstrates that the anal vein in the Odonata has an independent origin from the base of the wing. (The present notation A equals Ab + A' of Tillyard.) In the hind wing the anal area is greatly expanded. There are three distinct anal veins, namely, A_{1a}, A_2, and A_3. A_{1a} and A_2 become fused not far from their origins thus forming a 2-celled *anal loop* (AL). The vein that separates the anal loop into two cells is called the *anal supplementary* (mspl) or *midrib* (mr). Forbes (1943) used a new term, "axillary" (AX), for the veins often called "anal" but which, according to him, are distinct from the original anal vein which is usually the Pl of his system.

CROSS VEINS. The more important cross veins are as follows: Nodal, subnodal, antenodal and postnodal, primary antenodal, brace vein, arculus, oblique vein, and cubitoanal vein. The *brace vein, arculus,* and *oblique vein* have been mentioned before and will not be repeated again.

The *nodus,* or *nodal vein* (N), is a thick vein situated between the costal margin and R_1. Both notations N and n have been used but the former is adopted in this paper. Their positions in the fore and hind wings have already been mentioned before. The anterior portion of the nodal vein coincides with the bending part of Sc. The extension of the nodal vein between R_1 and R_2 is called *subnodus* (sn). Between the costal margin and R_1 there are many cross veins, those between the base of the wing and the nodus being *antenodal cross veins* (Ax) and those between the nodus and the basal end of the

pterostigma being *postnodal cross veins* (Px). The first and the fifth or sixth antenodal cross veins are thickened and are called *primary antenodal cross veins* (Ax_1 and Ax_2). It should be noted that Forbes (1943) used the same notation Ax for the veins which he called *axillary veins*. This has been mentioned before. The number of the nodal veins varies. In systematic work the *nodal index* such as $\frac{13-16 \mid 16-12}{13-11 \mid 11-13}$ has been often used and indicates the number of the antenodal and postnodal cross veins in the left and right fore and hind wings respectively. The nodal indices of ten specimens are shown as follows:

$$\frac{13-16 \mid 16-12}{13-11 \mid 11-13}, \text{♂}; \frac{11-14 \mid 15-11}{10-11 \mid 11-11}, \text{♂}; \frac{13-18 \mid 18-11}{14-13 \mid 13-14}, \text{♀}; \frac{12-15 \mid 14-12}{12-10 \mid 10-12}, \text{♂};$$

$$\frac{12-17 \mid 16-11}{-12 \mid 13-11}, \text{♂}; \frac{12-16 \mid 19-12}{12-11 \mid 13-11}, \text{♂}; \frac{12-19 \mid 18-10}{12-10 \mid 10-12}, \text{♀}; \frac{13-16 \mid 15-12}{13-11 \mid 13-13}, \text{♀};$$

$$\frac{12-17 \mid 16-12}{12-12 \mid 12-13}, \text{♂}; \frac{13-16 \mid 18-11}{13-11 \mid 11-12}, \text{♂}.$$

The *cubito-anal cross vein* (cu-a) is a vein between CuP and A, basal to arculus for a considerable distance. Different notations have been given to this vein, such as ac (anal crossing, Needham), Cu_x (Tillyard, 1917), Ac (Tillyard, 1926), AC (Fraser, 1940), and cu-a (Borror, 1945); the last notation is used in this paper. The different terminologies are accounted for largely by the different interpretations of the anal vein.

CELLS and SPECIAL AREAS. The important cells and special areas are as follows: Pterostigma, basal space, triangle, hypertriangle, subtriangle, discoidal field, basal anal area, anal loop, anal field, and anal triangle. The *pterostigma* (Pt) has been mentioned before and will not be considered again.

The *basal space* (bs) is an area at the base of the wing, bounded anteriorly, posteriorly, and apically or externally by $R+M$, CuP and *arc* respectively, the first two being subparallel and the last slightly slanting. It is also called by different names, such as median space, midbasal space, sub-basal space, and basilar space. It is about $3\frac{1}{2}$ to 4 times as long as wide.

The *triangle* (t) is a distinct and almost isosceles-triangular space formed by CuP basally and two cross veins anteriorly and apically (or externally) respectively. A space anterior to the triangle from *arc* to the apex of the triangle is called *hypertriangle* (h), which is also called by different names such as supratriangle, hypertrigone, or supratrigone. It is a narrow space bounded basally by the posterior

portion of the arculus or m-cu, anteriorly by a portion of MA, and posteriorly by a vein which is composite. The basal portion of this composite vein is a part of CuP and the distal portion a cross vein between CuP and MA. This cross vein is also the anterior side of the triangle. Its direction is such that it looks like part of a longitudinal vein. The *subtriangle* (s), or internal triangle, is also an isosceles triangle. It is situated basal to the triangles with the vertical part of CuP as their common side. It is bounded externally by the vertical part of CuP, posteriorly by a part of A, and basally by a slanting cross vein between CuP and A. Phylogenetically the triangle and the subtriangle are collectively called the *cubital area,* which is homologous with the *discoidal cell* or quadrangle of Zygoptera. The area apical to the triangle between MA and CuP is called the *discoidal field.* The discoidal field in the fore wing is of almost the same width throughout except that the portion beyond the level of nodus is slightly widened, while that of the hind wing is considerably widened at the posterior margin of the wing. The difference in shapes of the discoidal fields in both wings is accounted for by the different positions of the apical portion of the CuP.

The *basal anal area* is a narrow space posterior to the basal space. It is situated between CuP and A and is limited by the cross vein cu-a.

The *anal loop* (AL) is a 2-celled area in the hind wing bounded by A, A_{1a}, and A_2 on its anterior, apical, and basal sides respectively. It is bisected by a short vein, the *anal supplementary,* or *midrib* (mr).

The *anal field* refers to the area bounded by A, A_3, $A_{1a} + A_2$, and the posterior margin of the wing. It includes the anal loop in the hind wing. In the fore wing its apical limit is about at the level of the posterior apex of the triangle. The anal field has two rows of cells between A and the posterior margin of the fore wing, whereas there are five rows in the hind wing.

The *anal triangle* (at) is a 4-celled space at the extreme base of the hind wing in the male, bounded anteriorly, externally, and basally by A, A_3, and the basal margin of the wing respectively. The basal margin of the hind wing is flanged by a narrow whitish membrane, the *membranule* (mb). In the female the anal triangle is 8- or 9-celled.

LEGS

(Figures 28-30)

The legs are small in comparison with the size of the body. They are strongly armed with spines. The prothoracic legs are the smallest, being slightly smaller than the mesothoracic legs, which in turn are

considerably smaller than the metathoracic legs. The difference in size of the legs is accounted for especially by differences in length of the femur, tibia, and tarsus, since the coxa and trochanter are not conspicuously different in lengths in the three pairs of legs.

The COXA (CX) is of moderate size, more or less conical in shape, with its outer surface much longer than its inner surface which is conspicuously bulged. The basal portion of the outer surface is modified to form the *pleural articular socket* which is articulated with the pleural process of the thorax. The basal end of the coxa is girdled by a submarginal *basicoxal suture* (BCXS), along which a ridge, the *basicosta,* is produced internally. The basicosta is enlarged on the outer surface posterior to the pleural articular socket. The basicostal suture sets off a marginal flange, the *basicoxite* (BCX), which is enlarged on the outer surface posterior to the pleural articular socket. Distally the coxa bears an anterior and a posterior *articular socket* to which the *trochanteral articular condyles* are attached.

The TROCHANTER (TR) is a slender segment, about as long as the coxa, having a short outer surface so that its distal end is obliquely truncated. A transverse constriction gives this segment a superficially 2-segmented appearance. The basal portion is attached to the coxa by an articular membrane. It is also articulated with the coxa by an anterior and a posterior *trochanteral articular condyle*. The coxotrochanteral condylic hinge is a right angle with the pleurocoxal articulation so that it there forms a "universal joint" which allows a wide range of motion of the leg. A condylic hinge is also present at the distal end of the trochanter. This operates at a right angle to the coxotrochanteral condylic hinge, but permits of much less freedom of motion than the latter since nearly the entire basal rim of the femur is closely attached to the distal end of the trochanter.

The anterior surface of the articular membrane between the coxa and trochanter is invaginated to form a deep pouch, the posterior wall of which is thickened and tendonlike in structure. This undoubtedly serves for the attachment of a muscle internally.

On the inner wall of the trochanter there is a group of short and robust spines. There are only four or five spines on the basal, and the same number on the distal, portion of the trochanter of the prothoracic leg, whereas there are many on the distal portion of the trochanter of the mesothoracic and metathoracic legs. These spines are arranged at random: they are not arranged in a definite row to form a *trochanteral brush* such as reported by Cowley (1937) to occur in some other dragonflies.

The FEMUR (FE) is the longest segment of the leg, nearly cylindri-

cal, armed with short stout spines on its inner surface which faces ventrally in its natural position. The front femur is slightly curved and therefore fits nicely along the side of the thorax. The hind femur is straight, slightly compressed, and is held beneath the thorax. Its spines are more irregularly arranged on the basal portion than on the distal portion where they are distributed in two distinct rows. Proceeding distalward the spines are progressively larger and more widely separated. The area between the two rows of spines is smooth, flat, or slightly grooved, fitting it for the reception of the tibia when the latter is flexed close against the femur. The distal margin of the femur is crowned with a few short spines.

The TIBIA (TI) is a slender segment, convex on its dorsal or outer surface, flattened on its ventral or inner surface, armed laterally with a row of flattened spurs and dorsally with two parallel rows of short spines. It is constricted and slightly bent near its basal end which is articulated with the former by an anterior and posterior condyle. The articular membrane between the femur and the tibia has the same condition of invagination as that found in the membrane between trochanter and femur.

The flattened lateral spurs are of two types: (a) The short and swordlike type; and (b) the elongate type. The short swordlike spurs number about 8 or 9 in a row, situated on the apical half of the anterior margin of the prothoracic tibia in either sex. They are collectively called *tibial comb* (TIC) which was first pointed out by St. Quentin (1936) to be present on the prothoracic tibia of all dragonflies. Each spur is set on a socket which is oblong in shape. The spur is not evenly sclerotized, but has one edge unpigmented and thinner than the other edge. The elongate type of spur is long, undulated, and pointed at the apex. Along the anterior margin of the tibia there are four such spurs basal to, and one apical to, the tibial comb on the prothoracic leg, whereas there are eight on the mesothoracic or metathoracic leg where the tibial comb is absent. Along the posterior margin of the tibia there are eight to ten such spurs. Proceeding distalward these spurs are progressively shorter but broader.

The function of the tibial comb is unknown. Garman (1917) said that it might be used for the cleaning of the mouth parts and antennae. Needham and Haywood (1929) said that it might serve to hold the dragonflies' food. St. Quentin (1936) mentioned that it might be used for the cleaning of compound eyes.

On the ventral surface of the tibia there is a group of bristles along the base of the tibial comb and a nonsclerotized structure near the distal end of the tibia. This nonsclerotized structure is elevated and

elongated. It is present on the prothoracic tibia of the male sex only. As far as my knowledge goes, this special structure occurs in many species of gomphine dragonflies which I have examined. It has apparently not been reported heretofore. Its function is not obvious to me.

The distal end of the tibia is notched and somewhat socketlike and therefore fitted for the reception of the bulbous basal region of the basitarsus.

The TARSUS (TA) is 3-segmented; the basal segment or *basitarsus* (BTA) is the shortest; the distal segment or *distitarsus* (DTA) is the longest. The latter is about as long as the basitarsus and the middle segment taken together. Each segment is armed with a few spurs on its lateral margin. The *distitarsus* (DTA) bears a ventrodistal projection, the *plantella* (PTL), which is well developed.

The PRETARSUS (fig. 30) or terminal region of the leg consists of a pair of claws, empodium, and unguitractor. The *claws* (CL) are the largest parts of the pretarsus, and they articulate with a small dorsal process of the distitarsus. Each claw bears a ventral tooth and a narrow, wavy, ridgelike structure on each side of it. Ventrally the bases of the claws are connected with membrane which is also closely attached to the mesally located *unguitractor*. The *unguitractor* is a ventral sclerite which is partially hidden by the distal projection of the distitarsus, the plantella. An *empodium* (EMP) is attached to the distal end of the unguitractor. The distal portion of the empodium is enlarged.

ABDOMEN

(Figures 33-50)

The abdomen is composed of 10 distinct segments and, according to Tillyard (1917), also of the reduced remnants of the 11th and 12th segments. It is long and slender; the basal two segments tumid and slightly compressed, becoming thin, slender, and cylindrical from segments 3 to 7 (more pronouncedly so in the male); dilated and depressed from the posterior half of segments 7 to 9 (more pronouncedly so in the male), widest across the apical end of segment 8; segment 10 ringlike (in male) or depressed (in female). The proportional lengths of the segments from base to apex are approximately as follows: 1.8:4.5:6.0:7.0:7.0:6.5:5.5:4.6:2.5:1.5.

The male differs from the female in (1) having *auricles* (AU) on segment 2, (2) in having accessory sexual organs (figs. 40-44) on the ventral surfaces of segments 2 and 3, (3) the relatively great dilation of segments 7-9, and (4) the relatively great length of the anal appendages (figs. 45-50) at the extreme apex of the abdomen.

MALE TERGITES

The tergites are convexly arched. They occupy not only the dorsal region but also the whole of the lateral regions of the segments. The lateral edges of the posterior half of tergite 3 and also of tergites 4-6 almost meet midventrally, partially hiding the sternites from view. With the exception of segments 1 and 10, the tergites are distinctly separated from the sternites by pleural membrane. Tergites 1 and 2 are weakly sclerotized middorsally; 3-7 weakened along the midline; and 8-10 not so weakened. Tergites 3-7 are adorned with minute spines middorsally and also along the posterior transverse and submarginal ventral carinae. The dorsal spines are absent on the tergites of the other segments. Tergites 3-6 are similar to one another, while those of the other segments differ from the former in various ways. Tergite 4, to be described first, illustrates the generalized condition.

TERGITE 4 is strengthened by the formation of both internal ridges and external carinae. Basally it is girdled by a submarginal *antecostal suture* (ACS), which is very narrow and usually obscured by the apical portion of the preceding tergite. Dorsally the tergite is weakened along its midline but, conversely, is strengthened by a *supplementary transverse carina* (SUTC) which is situated at a point one-fourth the distance from base to apex of the segment. Posteriorly it is strengthened by the submarginal *posterior transverse carina* (PTC) which is continuous with the submarginal *ventral carinae* (SVC), one on each side along the ventral margins of the tergite. The posterior transverse carina is conspicuous and adorned with small spines. The submarginal ventral carinae are poorly formed and weakly sclerotized.

TERGITE 1 is separated from the sternite by narrow pleural membranes except anteriorly where it is fused with the latter. Dorsally it is adorned with a pair of tufts of long, fine hairs each on a slightly elevated subapical area. Lateroventrally the *acrotergite* (ATG) is enlarged and produced into a pouchlike evagination on each side. All carinae are absent except the submarginal *ventral carinae* (SVC) which are very poorly developed, with or without a few minute spines.

TERGITE 2 is peculiar in having a pair of lateral outgrowths, the *auricles* (AU). These are situated in an oblique position on the anterior portion of the tergite, and are weakly sclerotized except along their crests, which are denticulate ventrally. The *supplementary transverse carina* (SUTC) is situated slightly anterior to the middle of the tergite and extends downward on each side posterior to the auricle. A similar but much shorter structure is present posterior to the supplementary transverse carina. The submarginal *posterior transverse*
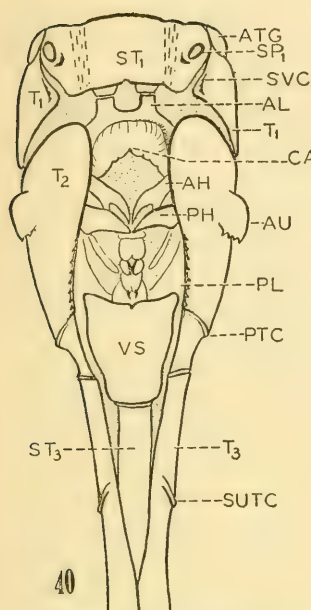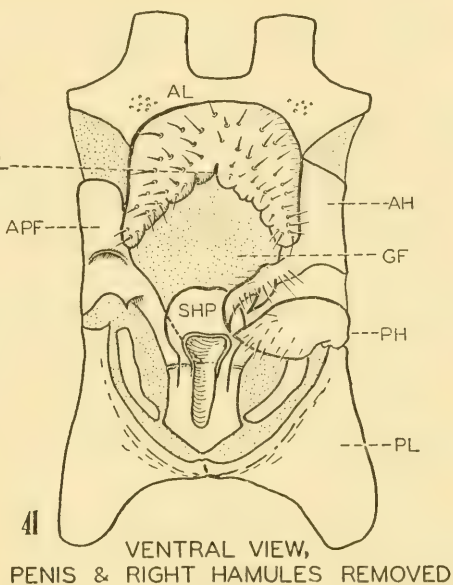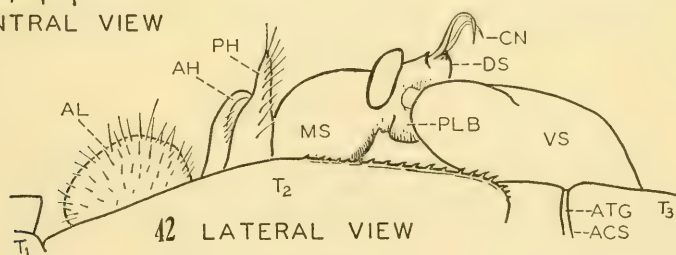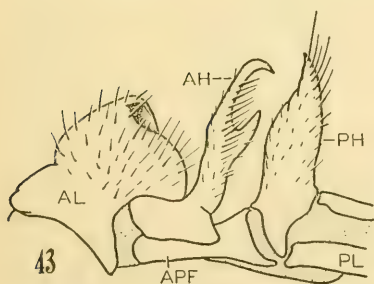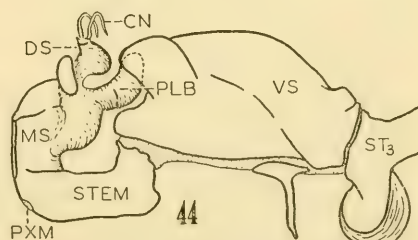
FIGS. 40-44.—Basal abdominal segments and male accessory sexual organs.

carina (PTC) is more prominent dorsally than laterally. The submarginal *ventral carinae* (SVC) are adorned with long hairs anteriorly and with spines posteriorly.

TERGITE 7 (fig. 45) is peculiar in having the median area of the submarginal posterior transverse carina raised considerably and the submarginal ventral carinae dilated into leaflike structures, the *pseudolateral dilations* (PLD) (Fraser, 1934).

TERGITE 8 (fig. 45) is peculiar in having a pair of submedian, low, rounded, transversely wrinkled tubercles. The supplementary transverse carina is absent. The submarginal posterior carina is raised medially where it is deeply notched. The submarginal ventral carinae are greatly expanded to form pseudolateral dilations.

TERGITE 9 is similar to the preceding one except that (1) it is without submedian tubercles, (2) it is submedially slightly constricted on both sides, and (3) its submarginal posterior carina is slight notched medially.

TERGITE 10 is completely fused with the sternite to form a ring. Dorsally it is deeply concave on its apical margin, with a pair of subbasal, very low, ovoid, transversely wrinkled tubercles followed by dorsal wrinkles paralleling the edge of the apical concavity. All carinae are absent: the position of the submarginal posterior carina is indicated by a few small spines laterally.

MALE STERNITES

STERNITE 1 (fig. 40) is short, transversely rectangular, anterolaterally fused with the tergite. Posteriorly it is produced into two short processes which are inflected and obscured from view by the main portion of the sternite. These processes are connected with the anterior processes of the *anterior lamina* of sternite 2. Laterally the sternite has a pair of ovoid spiracles and a pair of small pits mesoposterior to the former. From these pits short hornlike apophyses are produced internally.

Sternite 2 and the anterior portion of sternite 3 are greatly modified into complicated accessory sexual organs which are collectively known as the *copulatory apparatus*. The main structure of the apparatus consists of a *penis* which is lodged in a membranous depression, the *genital fossa,* and is protected by various organs derived from sternite 2. Different parts of the apparatus will be described in detail as follows.

STERNITE 2 (figs. 40-43) is modified to form the following parts: genital fossa, anterior lamina, posterior lamina, supporting framework, sheath of the penis, anterior hamules, and posterior hamules.

The *genital fossa* (GF) is a membranous depression strengthened by anterior lamina, posterior lamina, and lateral supporting frameworks. The *sheath of the penis* (SHP) is located on the posterior part of this membrane.

The *anterior lamina* (AL) is a large sclerite, situated at the anterior third of the second abdominal segment. It is differentiated into distinct anterior and posterior portions. The anterior portion is flat, comparatively weakly sclerotized, anteriorly produced into two processes which are connected with similar processes of the preceding sternite. The posterior portion of the anterior lamina is strongly sclerotized, convex, and adorned with many minute tubercles and hairs. The posterior margin of the anterior lamina is V-shaped, irregularly indented, and with a short median cleft, the *cleft of the anterior lamina* (CAL).

The *posterior lamina* (PL) is a large sclerite situated at the posterior end of the second abdominal segment. It is weakly sclerotized, constricted medially, and greatly expanded laterally.

The *supporting frameworks,* or the *anterior portions of the frameworks* (APF) (Thompson, 1908) are a pair of sclerites on the lateral sides of the genital fossa between the anterior and the posterior laminae. Each is an elongate sclerite, slightly convex ventrally, with a subapical mesodorsal process which supports the base of the *sheath of the penis* (SHP). Ventrally the sclerite has a low transverse ridge to which the posterior margin of the base of the *anterior hamule* (AH) is attached. Posteriorly the sclerite is emarginated to form, together with the anterior extension of the *posterior lamina* (PL), a socket to which the *posterior hamule* (PH) is attached.

The *sheath of the penis* (SHP) is a placoid structure composed of a scooplike structure arising ventrally from the base which is imbedded in the membranous genital fossa. The scoop is supposed to be for the protection of the penis. The base of the sheath is five-sided, medially with a broad shallow groove. The anterior margin of the base is articulated with and supported by the two arms of the paired supporting frameworks. Each of the posterolateral angles of the base is connected with a small slender sclerite, the outer end of which is articulated with the posterior margin of the base of the posterior hamule.

The *anterior hamules* (AH) each consists of a long bifurcated process produced ventrally from the posterior portion of an elongate sclerite which is attached to the low ridge of the supporting framework. Mesally it is attached to the lateral margin of the anterior lamina. The two processes are of unequal length, pointed apically. The anterior process is hooked apically, about twice as long as the posterior process, and is subequal in length to the stem.

Each of the *posterior hamules* (PH) is a robust structure attached to the socket formed by the supporting framework and the posterior lamina. It is about as long as the anterior hamule, pointed, with more bristles on its mesal surface and apex than elsewhere.

TABLE 2.—*Designations for the segments of the penis of anisopterous dragonflies*

AUTHOR	Williamson (1920)	Kennedy (1922)	Borror (1942)	Fraser (1940)	Present author
DRAGONFLIES STUDIED	*Desmogomphus*	*Libellula*	*Erythrodiplax*	Gomphidae	*Onychogomphus ardens*
SEGMENTS	Vesicle	Segment 1	First or basal segment	Vesicle	Vesicle
	Segment 1	Segment 2	Second segment	Stem or first joint	Stem
	Segment 2	Segment 3	Third segment		
			Fourth or terminal segment	Median or second joint	Median segment
	Segment 3	(Elongation of distal meatus of segment 3)		Glans or distal joint	Distal segment

STERNITE 3 is modified anteriorly into a penis and posteriorly into a long, narrow sclerite; the former is abutted to the truncated end of the latter. Anteriorly the narrow sclerite bears a large, round, internal, apodeme on each side.

The *penis* (fig. 44) is a complicated organ consisting of several segments. Different designations for each of the segments of the penis of anisopterous dragonflies have been proposed by various taxonomists. A table is here given to show the different terminologies. Those terms used by Fraser (1940) in his paper on the penes of a large number of gomphine dragonflies are adopted in the present paper with a few modifications.

The VESICLE (VS) is a robust structure, heavily sclerotized except for its dorsal surface which is membranous, having a small sclerite imbedded in its posterior portion. This sclerite is connected to the

posterior extensions of the posterior lamina by a pair of small sclerites. These slender sclerites apparently have not been recorded in the literature. When viewed ventrally (fig. 40) the vesicle is slightly constricted near the base, widened apically, slightly protruded on its apical angles, and with a short median cleft. The cavity of the vesicle is filled with fluid, and is continuous with those of the succeeding segments of the penis, but not with the haemocoele of the abdomen. The latter fact is contrary to the opinion maintained by Kennedy (1922) and probably also by Borror (1942).

The vesicle is an important organ in relation to the erection of the penis, but the exact role that it plays remains obscure. Kennedy (1922) mentioned that the cavity of the vesicle is continuous with the haemocoele of the abdomen, and that the erection of the penis is accomplished by forcing blood from the latter through the vesicle to the cavity in the apical segments of the penis. This opinion is adopted by Borror (1942) with modification. Fraser (1940) says that "when pressure is raised in the vesicle . . . the penis" is "at once erected." But he does not mention how the pressure is raised in the vesicle. From the present studies it appears that the raising of pressure in the vesicle is accomplished by exerting a force on the small sclerite imbedded in the dorsal membrane of the vesicle. This contention is based on the observation that the cavity of the vesicle is not continuous with the haemocoele and that the wall of the vesicle is rigid except for the dorsal surface which is membranous. Thus a force exerted on the small sclerite imbedded in the membrane will depress the latter and force the fluid in the vesicle to flow into the apical segments so that the penis is erected.

The STEM (STEM) is L-shaped, attached to the dorsal membrane at the anterior end of the vesicle. Apically it bears a large round membrane which has a long narrow opening, the *proximal meatus* (PXM). The presence of this proximal meatus probably indicates that the stem is a composite segment, i.e., consisting of the second and the third segments of Borror (1942) fused together. This contention is based on the fact that (1) in *Erythrodiplax* and *Libellula* the proximal meatus is always present in a small and distinct segment, i.e., the third segment of Borror, and that (2) the apical limit of the preceding segment is indicated by the presence of a short dorsal spur (Kennedy, 1922), or knoblike protuberance (Borror, 1942). In gomphine dragonflies this spur is absent in many species, such as shown by Fraser (1940), but present in some other species, e.g., *Gomphus agricola, G. suzukii, Onychogomphus flexuosus, O. circularis, Megalogomphus hannyngtoni, Progomphus pygmaeus, Cyclophylla signata,* and *Stylo-*

gomphus inglisi. The latter fact indicates the distal limit of a segment proximal to the segment bearing the proximal meatus. The suture between these two segments is generally obliterated in gomphine dragonflies.

The MEDIAN SEGMENT (MS) is short, perpendicular to the basal segment, and distally inflated. The inflated portion is weakly sclerotized and bears a large lobe, the *posterior lobe* (PLB) (Kennedy, 1922; Borror, 1942), also called *preputial fold* or *prepuse* (Fraser, 1940). Anteriorly the median segment is medially grooved. Dorsally it bears a pair of very heavily sclerotized structures to which the bilobed *distal segment* (DS) is attached.

The DISTAL SEGMENT (DS), or *glans* (Fraser, 1940), is bilobed. Each lobe bears a curled *flagellum* (Fraser, 1940) or *cornua* (CN) (Kennedy, 1922). The *distal meatus* is situated deeply between the two lobes.

STERNITES 4 and 5 (see fig. 38, sternite V, ♀) are elongate sclerites. Each is differentiated into an anterior subquadrate area followed by a long, narrow piece which is slightly constricted near the apex and ending in a small piece, the *sternellum* (STN) (Tillyard, 1917). Anteriorly the subquadrate area is produced into a pair of short processes. At the four angles of the subquadrate area, the sternite is produced internally and laterally into two pairs of *sternal processes* (STP) for the attachment of the segmental muscles. The anterior pair is small and linear and the posterior pair is fairly large and scalelike.

STERNITE 6 (fig. 35) is similar to the preceding sternite except that its sternellum is enlarged apically.

STERNITE 7 (fig. 35) is peculiar in that the anterior pair of sternal processes is very small, and the long piece following the subquadrate area is widened apically; without sternellum.

STERNITE 8 (fig. 46) is a large sclerite, subtrapezoidal in shape, basally with a low median keel, and laterally slightly sinuate.

STERNITE 9 (fig. 46) is sclerotized on its basal half and very weakly so on its apical half. The sclerotized portion is 4-lobed, two on each side of a pair of median ovoid sclerites, the *valvules* (VV), which, according to Tillyard (1917), are homologous with the lateral processes of the ovipositor of the female. The valvules cover the *male genital pore;* the latter is guarded by a sclerotized ring.

STERNITE 10 (fig. 46) is fused with the corresponding tergite. Its posterior margin is deeply emarginated.
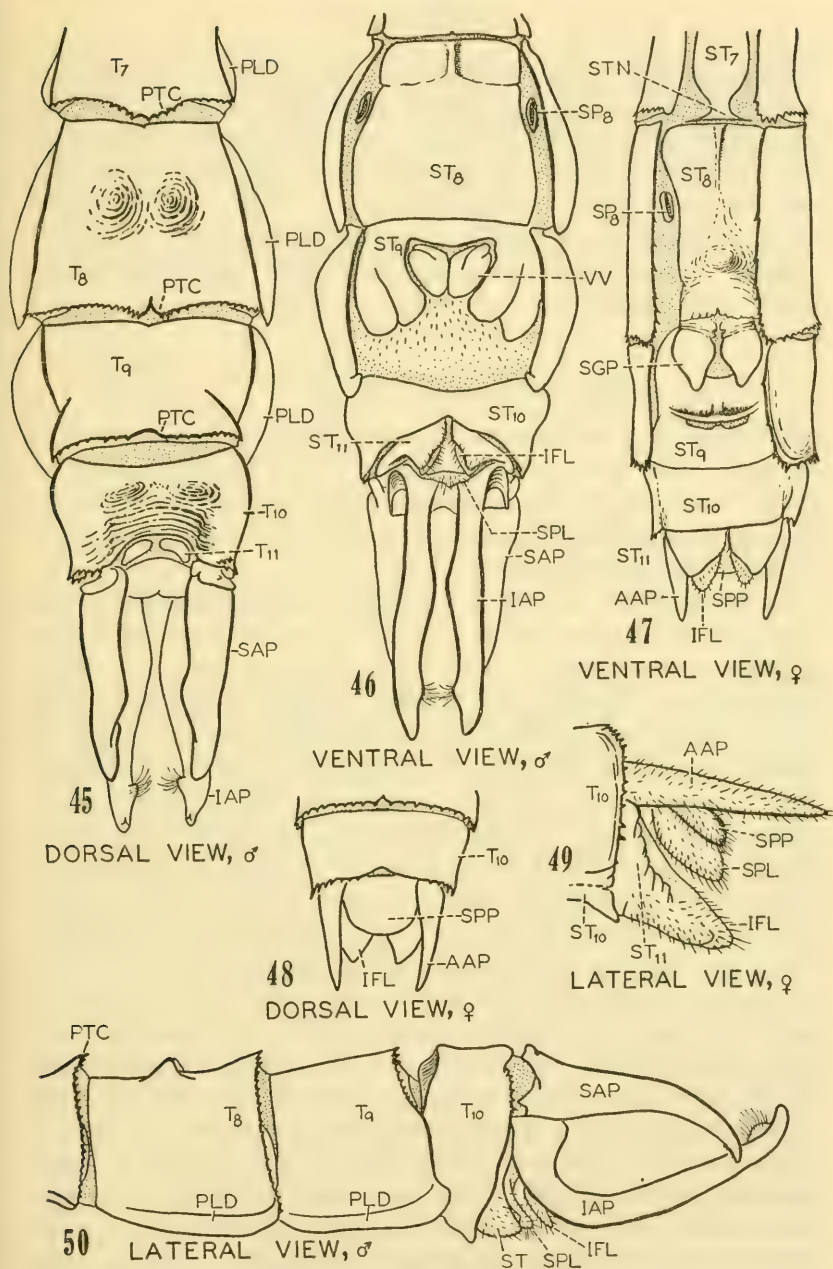
FIGS. 45-50.—Terminal abdominal segments.

SPIRACLES

There are eight pairs of abdominal *spiracles* (SP). The first pair is situated in the first sternite, described previously. The next six pairs are situated in the pleural membranes near the posterior sternal processes in each of the abdominal segments 2 to 7. They are ovoid in shape and oblique in position. The eighth pair is situated on the pleural membrane close to the middle of the lateral margins of the eighth sternite. It is almost twice as large as the other spiracles, elongate ovoid, and parallel to the long axis of the body.

FEMALE TERGITES AND STERNITES

The tergites of the female are fundamentally the same as those of the male, except for some sexual dimorphic characters mentioned before. TERGITE 10 (fig. 48) differs from that of the male in that dorsally it is not wrinkled nor tuberculate, and apically it forms a straight line instead of being deeply concave.

Of the *sternites,* the first, fourth, fifth, and sixth are the same as in the males. STERNITE 2 (fig. 36) differs from the more generalized condition of the above in that it is rather wide, with the anterior transverse area bearing a pair of lateral sternal processes only. STERNITE 3 (fig. 37) is similar to the generalized sternite except that the anterior and lateral processes are comparatively longer. STERNITE 7 (figs. 39, 47) is comparatively broad, with very small sternellum. STERNITE 8 (fig. 47) is large, elongate rectangular, laterally sinuate, basally with a low median keel, subapically with a low protuberance, and apically with a pair of *subgenital plates* (SGP) which are about two-fifths as long as sternite 9. The two sclerites of the subgenital plates are called *valves* (or vulvar scales, anterior processes) of the ovipositor, probably synonymous with some other terms such as ventral valves and first valvulae. STERNITE 9 (fig. 47) is broad, basally emarginate and separated from the preceding sternite by a large semi-circular membrane. The *female genital pore* is situated in this membrane and is covered by the subgenital plates. At a point one-third the distance from apex to base of the segment a low arc-shaped ridge is produced, which is apically bordered by a narrow membrane; the latter is constricted in the middle. This ridge might possibly be the remnant of the median process of the ovipositor (Tillyard, 1917) (also called inner valves or second valvulae). STERNITE 10 is transversely rectangular, apically not emarginated as in the male.

END SEGMENTS

The end segments, as used by Tillyard (1917), consist of various structures apical to the segment 10. These structures differ morphologically and phylogenetically in different suborders and in the two sexes. The following table shows their homologies (modified from Tillyard, 1917, p. 225).

TABLE 3.—*Occurrence and homologies of terminal abdominal structures*

Seg-ment	Name of parts	Male	Female
10	Tergite Sternite Cercoids	Present Present Superior anal appendages	Present Present Anal appendages
11	Tergite Sternite (bipartite) Appendix dorsalis Cerci	Rudimentary Fairly large Inferior anal appendages Absent	Median dorsal appendage Fairly large Absent Absent
12	Tergite Sternite (two laminae anales)	Rudimentary Rudimentary	Rudimentary Rudimentary

In the male the superior and inferior anal appendages are very well developed. The SUPERIOR ANAL APPENDAGES (SAP) are elongate, more than double the length of the segment 10, declined in their apical halves, slightly sinuate in dorsal view, and ventrally serrate at the apices. The INFERIOR ANAL APPENDAGES (IAP) is a bifid structure with its two branches slightly longer than the superior anal appendages. Its base bends down vertically for a short distance and bears two apposing arms which curve upward gently toward their rather acute apices. Each branch of the inferior appendage has a minute dorsal subapical tooth and a fairly large, low, internal ridgelike tubercle just opposite the apex of the superior appendage; the tubercle being adorned with fine hairs. The remnants of the 11TH STERNITE (figs. 46, 50) are divided into two fairly large sclerites, collectively called the bipartite 11th sternite, situated along the ventral and lateral margins of the segment 10. The 12TH TERGITE and STERNITE are represented by *superior* and *inferior anal laminae*. Both are weakly sclerotized and adorned with minute hairs. The *superior anal lamina* (SPL) is attached to the anterior surface of the base of the inferior anal appendage. The *inferior anal laminae* (IFL) consist of two pieces, one attached to each of the bipartite sternites. The *anal opening* is situated at the bases of the anal laminae.

In the female the end segments are comparatively short, consisting of anal appendages, median dorsal appendage, and the remnants of the 11th and 12th segments. The ANAL APPENDAGES (AAP) are a pair of slender conical structures, situated laterally above the dorsal appendage, slightly longer than the 10th tergite. The *median dorsal appendage,* or *supra-anal plate* (SPP), is a subsemicircular sclerite, convex above, about half as long as the anal appendages. The BI-PARTITE 11TH STERNITE (fig. 47) consists of a pair of fairly large sclerites which, when viewed ventrally, are triangular in shape. The remnants of the 12th tergite and sternite are represented by *superior* and *inferior anal laminae.* The former is weakly sclerotized, attached to the ventral surface of the median dorsal appendage. The *inferior anal laminae* (IFL) are bipartite, attached to the 11th sternite, and exceed the length of the latter.

ABBREVIATIONS

Aa, tornus
AAP, anal appendage
AAR, anterior mandibular articulation
AAS, antealar sinus
AB, anterior lobe of prothorax
ACL, anteclypeus
ACS, antecostal suture
AES$_2$, AES$_3$, mesothoracic or metathoracic anepisternum
AH, anterior hamule
AL, anterior lamina
AN, adnotal sclerite
AP$_2$, AP$_3$, apodeme of detached plate of mesothoracic or metathoracic scutum
APF, anterior portion of framework
ARB, anterior rib of anterior tentorial arm
arc, arculus
ARG, antealar ridge
at, anal triangle
ATA, anterior tentorial arm
ATG, acrotergite
AU, auricle
AWP, anterior wing process
Ax$_1$, Ax$_2$, primary antecostal cross veins
1AX, first axillary sclerite
AXC, axillary cord
AXP, axillary plate

BA, basalare
BCD, basicardo
BCX, basicoxite
BCXS, basicostal suture
BH, brush
BPL, basal plate
br, bridge vein
br.v., brace vein
bs, basal space
BS, basisternum
BTA, basitarsus

C, costal vein
CAC, cleft of anterior lamina
CAR, posterior mandibular articulation
CEP, cephaliger
CL, claw
CN, cornua
COL, collar
CT, corporotentorium
cu-a, cubito-anal cross vein
CuP, posterior cubitus
CX, coxa
CXC, coxal cavity

DC, dorsal cervical sclerite
DCD, disticardo
DCR, dorsal carina
DS, distal segment of penis

DTA, dorsal tentorial arm
DTP, dorsal tentorial pit
DTTA, distitarsus

EC, eucervicale
EH, end hook
EMP, empodium
EPM, epimeron
EPX, epipharynx
ES, episternum
ESR, epistomal ridge
ESS, epistomal suture
EYE, compound eye

F, furca
FE, femur
FL, flagellum of antenna
FM, foramen magnum
FP, furcal pit
FR, frons
FS, furcasternum
FT, flexor tendon of mandible

G, gena
GF, genital fossa

h, hypertriangle
HM, hypostoma
HMS, hypostomal suture
HP, humeral plate

IAP, inferior anal appendage
ICS, incisors
IFL, inferior anal lamina
IL, inner lobe
IP, intermediary piece
IPLA, interpleural apodeme (=intersegmental apodeme)
IR$_2$, IR$_3$, intercalary radial veins

KEP, katepisternum

LL, lateral lobe
LR, labrum

M, media
MA, anterior median
mb, membranule
MB, median lobe of pronotum
MD, mandible
MDP, mandibular process
MH, movable hook
ML, middle lobe of labium

MLS, midlateral suture (=intersegmental suture)
MN, mentum
MO, mola
mr, midrib of anal loop in hind wing
MRB, midrib of anterior tentorial arm
MS, median segment of penis
MSC, mesostigmatic lamina
MX, maxilla
MXP, maxillary process

N, nodus
NC, neural canal

o, oblique vein
OC, ocellus
OCC, occiput
OCCD, occipital condyle
OCCH, occipital horn
OCCM, occipital margin
OCS, ocular sclerite
OL, outer lobe
OS, ocular suture

P, pedicel
PA, papilla
PB, posterior lobe of prothorax
PC, postcervicale
PCL, postclypeus
PCX, postcoxale
PF$_2$, prefurca
PFS, parafrontal suture
PFST, postfurcasternum
PG, postgena
PH, posterior hamule
PL, posterior lamina
PLA, pleural apodeme
PLB, posterior lobe of penis
PLD, pseudolateral dilation
PLF, sternal fold
PLS, pleural suture
PM, pleurostoma
PMS, pleurostomal suture
POCC, postocciput
POCS, postoccipital suture
POS, postocellar suture
PRA, prealare
PRB, posterior rib of anterior tentorial arm
PS, parastipes
PSA, peristigmatic apodeme

PSC, prescutum
PSCL, postscutellum
PSTN, pseudosternum
Pt, pterostigma
PTA, posterior tentorial arm
PTAR, pretarsus
PTC, posterior transverse carina
PTL, plantella
PTP, posterior tentorial pit
PWP, posterior wing process
PXM, proximal meatus

R, radius
ROOC, rear of occiput
Rs, radial sector
RT, retractor tendon of mandible

s, subtriangle
S, scape
SA, subalare
SAG, subalar ridge
SAL, salivarium
SAP, superior anal appendage
Sc, subcosta
SCL, scutellum
SCS, sternocostal suture
SCT, scutum
SG, sutural groove
SGP, subgenital plate
SHP, sheath of penis
SM, submentum
sn, subnodus

SP, spiracle (ISP, IISP, mesothoracic and metathoracic spiracles; SP_1, SP_2, etc., abdominal spiracles)
SPD, spiracular dorsum
SPL, superior anal lamina
SPP, supra-anal plate
SQ, squame of labium
ST_1, ST_2, etc., abdominal sternites
IST, IIST, mesosternum, metasternum
STEM, stem of penis
STI, stipes
STN, sternellum
STP, abdominal sternal process
SUTC, supplementary transverse carina
SVC, submarginal ventral carina

t, triangle
T, tergite
TA, tarsus
TFR, top of frons
TI, tibia
TIC, tibial comb
TN_1, squame of precostal apodeme
TR, trochanter

UT, unguitractor

V, vertex
VC, ventral cervical sclerite
VS, vesicle
VV, valvula

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Charles D. and Mary Vaux Walcott
Research Fund

THE GEOLOGY OF CHACO CANYON
NEW MEXICO

IN RELATION TO THE LIFE AND REMAINS
OF THE PREHISTORIC PEOPLES OF
PUEBLO BONITO

(With 11 Plates)

BY
KIRK BRYAN

PLATE 1

Pueblo Bonito, from the north cliff. The east and west refuse mounds lie close beyond the ruin. At the left, the embankment of Wetherill's reservoir; at the right, midway between ruin and camp, a ring of dirt marks pit No. 3. (Photograph by O. C. Havens, 1924.)

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(With 11 Plates)

BY
KIRK BRYAN

(Publication 4140)

FOREWORD

The geology of Chaco Canyon in relation to its prehistoric inhabitants was a subject that greatly interested Kirk Bryan. Born and schooled in New Mexico, he had seen hundreds of ruined Pueblo villages, mostly abandoned before advent of the Spaniards in 1540, and had given much thought to the reasons behind their desertion. Warfare may have been one cause but it obviously was not the only one.

A geologist with the United States Geological Survey and engaged primarily in a study of groundwater resources of the Southwest, Dr. Bryan seemed to us especially qualified to seek out the factors that had invited, and then repelled, colonization of Chaco Canyon in the days of Pueblo Bonito. He accepted with enthusiasm our invitation to undertake this study but was able to devote only two brief vacation periods to field work, in the midsummers of 1924 and 1925. His observations in Chaco Canyon, admittedly incomplete, prompted like inquiries in other valleys during the decade that followed.

In 1926 Dr. Bryan left the Geological Survey to accept a call from Harvard University, and thereafter academic commitments and summers in the field allowed him but little leisure. In consequence, he never found an opportunity to finish this report on his Chaco Canyon researches. A first draft, dated March 1925, and written before his second visit to the canyon, was repeatedly revised and expanded as his continuing investigations annually provided new data. He appears to have made no change in the text after 1940. For these several reasons some sections of the report lack references to the more recent literature.

Following Dr. Bryan's untimely death in the summer of 1950, his unfinished manuscript was forwarded to me by Mrs. Bryan. I have undertaken to arrange its several parts in conformity with his original table of contents and to eliminate repetitions of subject matter and phraseology. The various stratigraphic columns Bryan examined and the course he plotted for an arroyo more or less contemporary with the decline of Pueblo Bonito are shown on the accompanying map of Chaco Canyon. Stratigraphic sections 10 to 23 were studied in 1925, but we have descriptions for numbers 15 and 17 only, and a third, without number but adequately located in relation to the expedition's camp.

Test pit No. 3, about midway between camp and the west refuse mound, was among those I had caused to be dug in 1922 in connection with an analysis of Chaco Canyon soils. When it was deepened three years later at Bryan's request and was found to penetrate the buried channel he was then trying to isolate, a common impulse was to extend the exploratory trench we had previously dug through the west refuse mound and thus reveal the original surface between buried channel and the old village dump. Pit No. 4, dug expressly for Dr. Bryan, was so named because of its proximity to his section 4, where the buried channel stood exposed near the southeast corner of Pueblo del Arroyo. Thus test pits 3 and 4 and the extended west-mound trench enabled Bryan to plot the course of that prehistoric arroyo as it passed Pueblo Bonito, and led to his search for traces of it as far east as Pueblo Wejegi. The extent of this ancient channel, together with evidence of alternating periods of erosion and sedimentation, formed the basis for Bryan's growing conviction that a slight change in climate was the most likely cause for disruption and dispersal of the Chaco Canyon population in the early twelfth century. His conclusion is certain to exert a profound influence upon future interpretation of past history in the Southwest.

I gladly acknowledge our obligation to Mrs. Kirk Bryan and to two of Dr. Bryan's former students, Dr. John T. Hack and Dr. Luna B. Leopold, both of the United States Geological Survey, for their cooperation in the preparation of this report. Two members of my Pueblo Bonito staff, O. C. Havens and Lynn C. Hammond, and several of our Zuñi workmen assisted Dr. Bryan in Chaco Canyon. The illustrations are mostly from photographs by Mr. Havens.

It was originally intended that this paper appear as fourth in the series reporting the results of the National Geographic Society's Pueblo Bonito Expeditions. But the series was discontinued after the first number, "Dating Pueblo Bonito and Other Ruins of the Southwest," by Dr. A. E. Douglass (1935). Early in 1953 the Society made the present manuscript available to the Smithsonian Institution, which proposed to publish it under the Charles D. and Mary Vaux Walcott Research Fund.

The life and achievements of Dr. Kirk Bryan are briefly reviewed by Frederick Johnson in American Antiquity, vol. 13, No. 3, p. 253, January 1951.

Neil M. Judd.
*Leader of the National Geographic
Society's Pueblo Bonito Expeditions.*

Washington, D. C.
June 1953.

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THE GEOLOGY OF CHACO CANYON NEW MEXICO

IN RELATION TO THE LIFE AND REMAINS OF THE PREHISTORIC PEOPLES OF PUEBLO BONITO

By KIRK BRYAN [1]

(With 11 Plates)

INTRODUCTION

On the initiative of Neil M. Judd, leader of the National Geographic Society's Pueblo Bonito Expeditions, and on the recommendation of Dr. John C. Merriam, then president of the Carnegie Institution of Washington, the present writer was selected to undertake an inquiry into the geologic history of Chaco Canyon. Two brief periods were devoted to field work: July 28 to August 9, 1924, and July 10 to August 1, 1925. In the well-ordered camp of the expedition he was received with gracious hospitality, and to all members of the staff he owes much in kindness. Mr. Judd placed every facility at his disposal including a number of excavations especially designed to bring to light geologic facts and thus expedite the investigation.

Application of the stratigraphic methods of geology to archeological problems is no longer new, and knowledge of these methods forms a part of the equipment of every modern archeologist. Our inquiry into Chaco Canyon geology has proved (1) that the alluvial deposits of the canyon carry various relics of prehistoric peoples and (2) that the deposits can be separated into divisions of differing age. In recent years knowledge of these generalizations has become widespread and additional data have been gathered. It appears that we are now on the brink of establishing in the Southwest an alluvial chronology based on a sequence of episodes of erosion and alluviation. This sequence of geologic events gives a key to the fluctuations of climate of late geologic time and yields a proximate cause for the sudden decay of the great Pueblo communities of the San Juan country. (Bryan, 1941.)

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[1] Dr. Bryan died on August 23, 1950.

Previous work on the general geology of this region is referred to hereinafter. During the summers of 1899 and 1901, Prof. Richard E. Dodge made a geological survey of Chaco Canyon as part of the extensive plans for the Hyde Exploring Expedition. His work was done after archeological excavation had ceased, and, unfortunately, his results were published only in skeleton outline in the report of the expedition (Pepper, 1920, pp. 23-25) and in three abstracts (Dodge, 1902a, 1902b, 1910). Even so, these brief sketches record a number of observations of interest that are referred to in the following pages. They indicate that Professor Dodge was on the verge of discovery and, with more archeological help, the geological theory herein set forth would doubtless have been advanced by him 20 years earlier. The 1877 observations of W. H. Jackson (1878) were keen and penetrating, and from exposures no longer visible he made the original discovery of the buried channel whose description and interpretation form such a large part of this report.

The long delay between initiation of this study and its publication has not been without advantage. During the interval we have learned that the geologic history of Chaco Canyon is not unique. Other valleys have similar histories, as will appear from the data on these other valleys summarized hereinafter. Generalizations on the cause of the alternations from erosion to alluviation and on the effect of these events on human affairs now rest upon a foundation of fact much larger than would have been possible in 1924 and 1925.

PLAN OF THE REPORT

This Chaco Canyon study was begun as an isolated project. It was an attempt to relate recent geology to the life of prehistoric peoples in the area. The results proved so successful, however, that other studies were subsequently undertaken. The alternate periods of alluviation and erosion discovered in Chaco Canyon and related to the tree-ring dates of Douglass (1935) have been found in other localities. The periods of alluviation are, so far as evidence now exists, nearly synchronous over the whole Southwest. Thus there has been developed an alluvial chronology still imperfect but valuable as a measure of time in the dating of archeological events. It is presumably still more valuable as a measure of alternating periods favorable or unfavorable to floodwater farming, an important method of agriculture in the area. Still more important are the inferences on fluctuations in climate parallel with alternations in the regime of streams.

The report begins with a general consideration of the area and its

CENTRAL PORTION
OF THE
CHACO CANYON NATIONAL MONUMENT
SHOWING THE LOCATION OF
PUEBLO BONITO

FROM SURVEYS BY THE
PUEBLO BONITO EXPEDITIONS
OF THE
NATIONAL GEOGRAPHIC SOCIETY
Topography by Robert P. Anderson
1925

Contour Interval 20 feet
• Navaho Hogans
□ Ancient Ruins
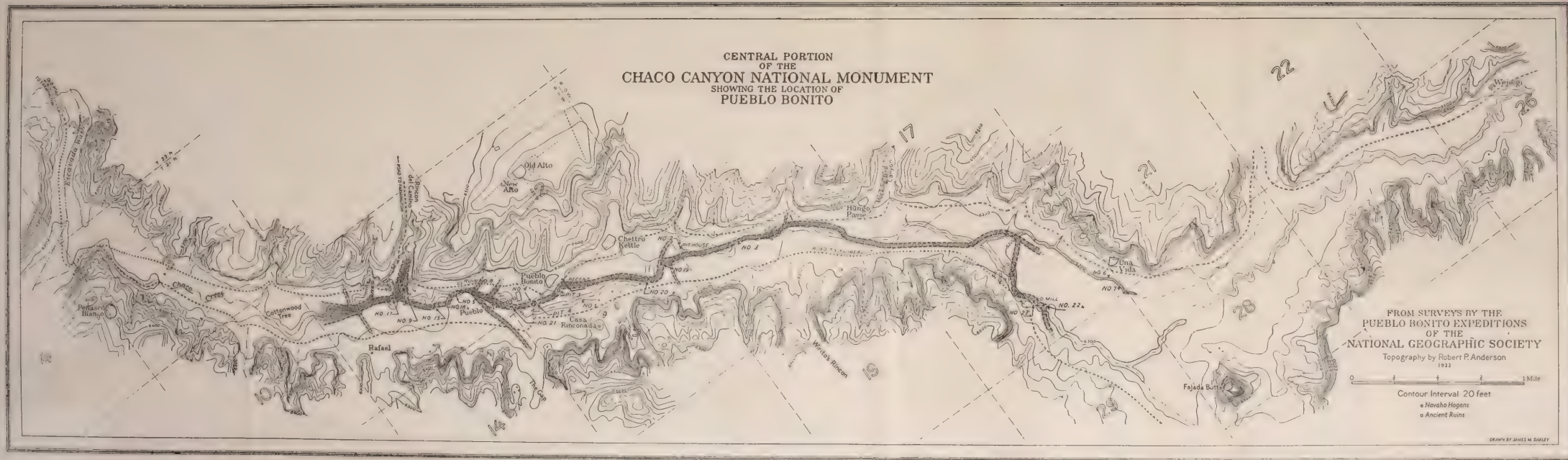
FIG. 1.—The buried, or post-Bonito, channel in relation to the present arroyo in Chaco Canyon.
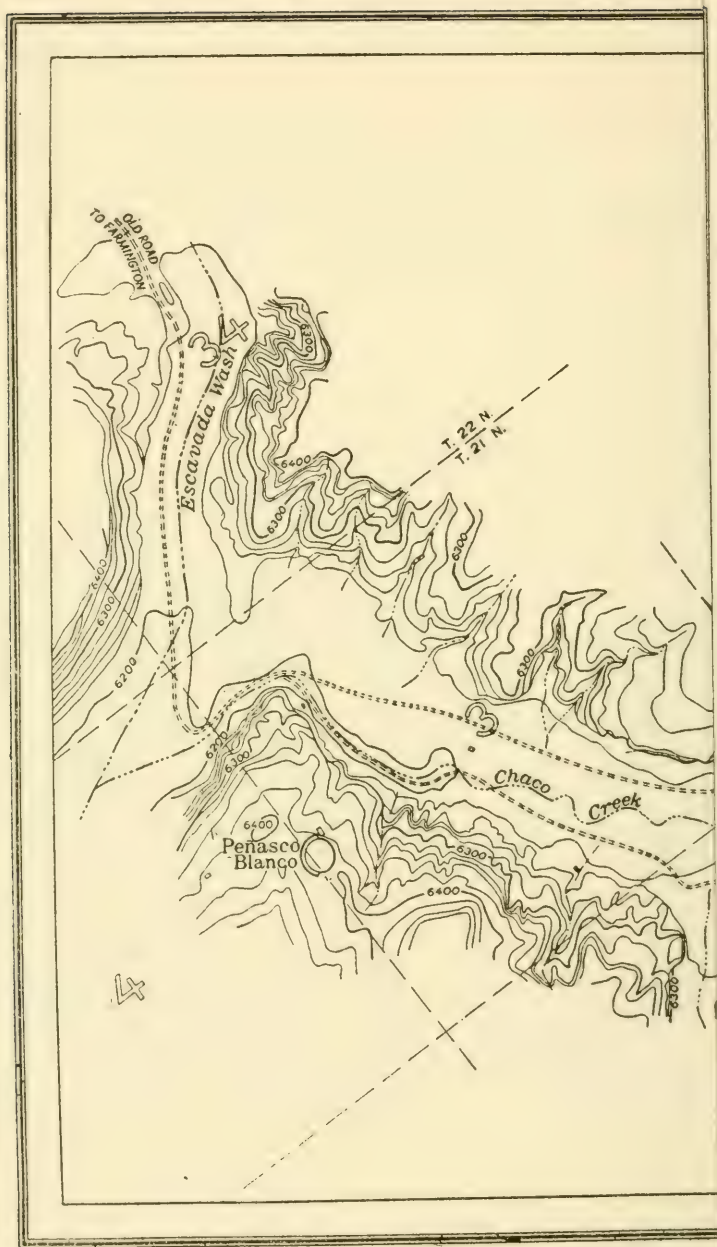
climate, with such information as is available on the age of the present arroyo in Chaco Canyon, with rather detailed studies of geologic processes now current there, and a description of the alluvium of the valley floor. It then presents evidence that this alluvium is divisible into three parts: the terrace, the main valley fill, and the post-Bonito channel. The antiquity of these divisions and their correlation with similar alluvial formations elsewhere are also considered. The importance of floodwater farming in the Southwest and the effect of the recent epicycle of erosion on this type of agriculture are next set forth.

The cause of the alternation from alluviation to erosion in southwestern valleys is next discussed and the argument advanced that simultaneous alternations in the regimes of widely separated streams must be due to synchronous climatic changes. The concurrent effects of climatic change and change in stream regime throughout the known human history of the Southwest affords a clue to fluctuations in human culture otherwise unattainable.

PHYSIOGRAPHY OF CHACO CANYON

GENERAL RELATIONS

Chaco Canyon lies in northwestern New Mexico on the upper reaches of Chaco River, a tributary of San Juan River (fig. 1). Chaco River, about 100 miles long, is an ephemeral stream such as is characteristic of arid regions. Its sandy bed throughout the greater part of the year is dry and the stream is dignified by the name of river only because of its considerable length and the violence of its floods. The stream begins in the high plains country north of Chacra Mesa at an altitude of 6,900 feet and flows a little north of west for 68 miles. Here the course changes sharply to the north and the river flows nearly parallel to, and on the east side of, the ridge known as the Grand Hogback for 26 miles and thence, breaking through the Hogback in a narrow canyon, it reaches San Juan River in 7 miles. The total length of the stream is thus about 100 miles, of which, however, only 15 or 20 miles of the upper course lies in a canyon worthy of the name. About 12 miles of this canyon, the portion with which we are concerned, is shown on the accompanying map (fig. 1).

Chaco Canyon lies in the southwestern part of the great Plateau province which occupies northwestern New Mexico, northern Arizona, western Colorado, and eastern Utah. The province is noted for its extensive flat surfaces, long lines of cliffs, and deep canyons. The flat surfaces are in part developed on the more resistant beds of nearly horizontal sedimentary rocks, although in part they consist of large

outflows of lava, and in part they are the remnants of extensive plains of erosion. In northwestern New Mexico the largest unit of the Plateau province is the San Juan Basin, a vast area in which the rocks dip gently from the periphery toward the center. Chaco Canyon lies near the southern part of this area with a dip of about 2° to the north and east.

Sandstone and shale are the characteristic rocks. The shale is eroded into broad, flat surfaces or gently sloping valleys; the sandstone stands out as ridges or plateaus, bounded, especially on the south, by cliffs. The order and succession of these rocks have been studied by a number of geologists [2] interested primarily in the occurrence of coal or of vertebrate fossils.

Chaco Canyon is cut in the Cliff House sandstone, the upper member of the Mesaverde group. This sandstone member is 369 feet thick as measured by Reeside on Meyers Creek, a few miles northwest of Pueblo Bonito. It is underlain by dark shale containing thin sandstone and coal (Menefee formation) which crops out in the cliffs on the south side of Chaco Canyon and in a few places on the north side. The Mesaverde group is overlain by the Lewis shale which forms the plain north of Pueblo Alto and has a thickness of about 70 feet. Above the Lewis shale lie the Pictured Cliff sandstone and higher formations.

The Cliff House sandstone consists of two massive sandstones separated by relatively thin bedded sandstone. Consequently, weathering tends to produce two cliffs separated by a bench of gentler slope. The lower of these two massive sandstones is buff-colored and about 140 feet thick. The cliffs which make the northern wall of Chaco Canyon are carved from this rock by processes considered more in detail on pages 18-20.

CLIMATIC CONDITIONS AFFECTING GEOLOGIC PROCESSES

The climate of the Chaco country is arid, but such a simple statement does not adequately summarize the effect of climate on the geologic processes. Aridity has many gradations from the almost total lack of rainfall characteristic of parts of the Libyan desert of Africa, and of certain areas on the west coast of Peru, to the tempered aridity of California where trees and grass thrive in areas having relatively low rainfall. Aridity is thus an inclusive term embracing climates having varying amounts of precipitation up to a quantity fixed arbi-

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[2] Holmes, 1877; Endlich, 1877; Schrader, 1906; Shaler, 1907; Gardner, 1909; Sinclair and Granger, 1914; Matthew, 1897; Brown, 1910; Bauer, 1917; Bauer and Reeside, 1921; Reeside, 1924.

trarily around 20 inches of rainfall a year. The many shadings and
gradations of aridity are dependent on such factors as the propor-
tion of the precipitation that may occur as rain or as snow, on the dis-
tribution of precipitation throughout the year, and on the incidence
of rainfall whether in hard showers or gentle drizzles. Similarly the
daily or seasonal range of temperature and the extremes of heat and
cold with their incidence and duration are all factors in aridity.

Climatic elements directly affect various subprocesses involved in
the weathering of rocks and indirectly influence the nature of streams
which act as the agents of removal and of transportation of weathered
rock. Slight differences in degree of aridity often have marked in-
fluence in the growth of a vegetative cover, one of the greatest single
factors influencing and delimiting erosive and sedimentary processes.
In the account of these processes given hereinafter it will be seen that
the scant vegetation of an arid region is a necessary prerequisite to the
relative intensity of action, or even the existence, of many of the sub-
processes. It follows, therefore, that any past or anticipated climatic
change, provided it is sufficient to alter the existing vegetation, may
have relatively large effect on geologic processes.

The available rainfall records of the Navaho Country up to the end
of 1913 were collected by Gregory (1916, pp. 51-59) and the factors
of climate in Chaco Canyon are now being recorded by the National
Park Service. Herein only such general elements of climate are de-
scribed as seem necessary for the purpose of defining climate in respect
to geologic processes.

The climate of the Plateau province may be considered moderately
arid. On the higher portion, between the valleys of San Juan River
and the Little Colorado, there is greater precipitation than in the low-
lands. In the mountains doubtless as much as 20 inches may fall each
year, but current rainfall stations are all on lower ground. St. Mi-
chaels, Ariz., altitude about 6,950 feet, has a mean of 13.72 inches
based on records for 29 years out of a period of 68 years; Crown-
point, altitude 6,800 feet, has 10.93 inches, based on an incomplete
record extending over 11 years. At lower elevations, especially to the
north and south of Chaco Canyon, the precipitation is less. Holbrook,
Ariz., altitude 5,069 feet, has 9.38 inches with 25 years of record out
of a total of 33 years. Places in the San Juan Valley have a lower
rainfall: Fruitland, N. Mex., altitude 4,800 feet, 6.38 inches with 7
years of record; Farmington, N. Mex., altitude 5,220 feet, 9.23 inches
with 7 years of record; Aneth, Utah, altitude about 4,700 feet, 4.96
inches. It seems likely the Chaco Canyon district has a precipitation
similar to that at Crownpoint with a little less rainfall on the floor of

the canyon which is 300 to 400 feet lower than the adjacent cliffs. For the purpose of this study it will be assumed that Chaco Canyon has a mean of about 10 inches.

A large part of this precipitation falls during the so-called summer rainy season in July and August. This period is characterized by sharp local or general rains from cumulus clouds or thunderheads. The rate of rainfall is high but the storms seldom last long. The incidence of the rains is also variable in time and space. Small areas are deluged and adjacent areas are left dry. The rains may come as early as June or as late as September, or may be inconsiderable in amount for a whole summer.

Gregory (1916, p. 63) summarizes many observations as follows:

The area covered by a shower is frequently only a few square miles, and on two occasions showers of 20 to 30 minutes' duration resulted in wetting less than 300 acres. Many of the showers result in a heavy downpour, and the total precipitation for a month is not infrequently the result of a single shower. . . . Generally the intense heat preceding a shower is reestablished within an hour or two after rain has ceased, especially at elevations below 6,000 feet. . . . Lightning is the almost invariable accompaniment of summer showers and constitutes a real danger to travel. . . . My records of thunderstorms for the Navaho Reservation during the field seasons 1909, 1910, 1911, and 1913 are 38, 26, 33, and 23, respectively, and it is believed that the annual number exceeds 40.

The winter precipitation falls gently and is likely to be widely spaced in time, but on the average totals nearly as much as the summer rainfall. At elevations above 6,000 feet there are 17 to 25 inches of snow, and at lower elevations some snow is possible each winter.

The distribution of precipitation throughout the year and its effect on agriculture is best expressed in the following table compiled by Gregory and amplified in a quotation also from him (ibid., pp. 61-62):

Season	Months	Precipitation in percent of mean rainfall
Summer	July, August, September	37
Early winter	October, November, December	25
Later winter	January, February, March	26
Spring	April, May, June	12

It will be noted that the season of least rainfall, April to June, is the growing season for most crops, and that therefore the seasonal distribution of rain is unfavorable for agriculture or for the vigorous reproduction of many grasses. Half an inch of rain per month for the period April, May, and June is an unusually large precipitation for most parts of the reservation, and during many years the combined precipitation of these three months is less than one-half inch. Moreover, plants obtained only a portion of this meager supply, for evaporation

is most effective during the clear, dry, hot days of early summer. The moisture in the ground, supplied by the rains of winter supplemented by the scattered showers of spring, is sufficient to allow seeds to germinate and to send their stalks above ground, but is insufficient to bring a crop to maturity. The rainfall of July becomes therefore the critical factor in the life of the Navaho. If his prayers to the rain gods are answered his corn crop is assured, and grass springs up from the desert floors; if his prayer is denied the crop is a failure. . . . For a large part of the reservation corn, without irrigation, fails to mature every second or fourth year.

The variation in rainfall from year to year is of the greatest importance. The amount ranges between half the normal and twice the normal. For the 29 years of record at Fort Defiance and St. Michaels the year of greatest rainfall was 1854 with 22.44 inches; the year of lowest rainfall was 1900 with 6.52 inches. It is obvious that in years of severe drought like 1900 almost nothing grows. Such years are periods of starvation for a population dependent on agriculture or on the pasturage of animals.

Similarly the native vegetation must be able to resist these extremes of drought and precipitation. In general, sagebrush and scattering grass grow in the dryer areas, and perennial grasses where precipitation is more generous. With a slight additional increase of rainfall, cedar (juniper) forms sparse groves and a total precipitation of 15 to 20 inches is adequate for the open pine forests of mountain areas. These vegetative zones are, however, not strictly bounded by lines of equal rainfall because slope, exposure, and soil are all factors in the growth of plants. Near Chaco Canyon the flat parts of the plateau are generally underlain by clayey soils derived from shale or by loams formed by the admixture of sand from the sandstone beds with clay from the shale areas. These soils, under the influence of the local climate, support a fairly continuous cover of perennial grasses. The outcrops of sandstone have a rough and broken topography without soil or with only a thin sandy soil. Here grow scattered cedars, occasional woody bushes, and patches of "sand grass" but large portions of such areas are bare rock. The floor of Chaco Canyon supports a growth of greasewood (chico) with, in areas overflowed by storm water, a fair growth of perennial grass. A few cottonwood trees have survived from the period when the stream bed was shallow and are evidence that, with a slightly higher water table or less interference by man, domestic animals, and floods, many of these trees would again grow in the valley.

The temperatures of the region are, when expressed in yearly or monthly means, those of a temperate region. Yearly means range from 47.6° F. to 60.6° according to the altitude of the station. The

annual and daily ranges in temperature are, however, very great. The maximum range recorded for various stations in the region is as follows: Fort Defiance–St. Michaels, 122° (98° to –24°); Fruitland, 124° (110° to − 14°); Holbrook, 127° (106° to −21°); Crownpoint, 103° (98° to −5°). Temperatures exceeding 100° normally occur for 10 to 20 days each summer and 5 to 6 days of below-zero weather are likely each winter. The daily ranges in temperatures may amount to as much as 40° to 50° and, although doubtless effective in producing the disruption of rocks, are somewhat mitigated in their effect on man and beast by the low humidity of the air.

The growing season, or number of days between the last killing frost of spring and the first killing frost of autumn, ranges at various stations from 89 days to 161 days. In general, localities of lowest altitude have the longest growing season but there is at all stations a variability from year to year in the length of the growing season that may be shorter than the mean by as much as a month. Fort Defiance, at an altitude of 7,000 feet, has experienced killing frost in every month of the year except August. Obviously these variations in the length of the growing season add an additional hazard to agriculture in a region where rainfall is scant and also highly variable in incidence and amount. The data also give an index of the probability of changes in temperature that cross the frost line and these changes are the ones effective in the disruption of rock by frost action.

EXCAVATION OF CHACO CANYON

One who climbs the north wall of Chaco Canyon to Pueblo Alto is rewarded by magnificent views of a region that appears to be flat on all sides. To the south, beyond the canyon, he sees a vast plain from which rise a few low hills and, far to the southwest, high mesas that close in the horizon south of Crownpoint. To the north, the valley of Escavada Wash is a prominent feature bordered by ragged bluffs, but beyond lies a plain similar to the one on which he stands. This high level plain occurs generally on the more elevated parts of the San Juan Basin and is more or less independent of the hardness of the underlying rock. Canyons divide this plain into several parts that are obviously remnants of a once continuous erosion surface that formerly extended over the entire region. The plain has been too little studied to warrant strict definition or to hazard correlation with the Mojave peneplain which Robinson (1907) believes to have existed over the whole of northwestern New Mexico and northeastern Arizona.

Bryan and McCann (1936) imply that this surface is older than the

Ortiz surface and other surfaces which, in the drainage of the Rio Puerco (of the East), are graded to the Rio Grande.

From the evidence near Chaco Canyon it seems possible to postulate two or more erosion cycles during each of which the region was reduced to very low relief. Whether a single peneplain or a more com-

FIG. 2.—Northwestern New Mexico showing the location of Chaco Canyon and Pueblo Bonito.

plex series of erosion cycles will be demonstrated by further work in the area, Chaco River and the adjacent streams gained their courses in a region of such moderate relief that the direction of flow was more or less independent of the distribution of hard and soft rocks. After a general uplift of the Plateau country, the "Canyon Cycle of Erosion" was initiated and the great canyons of the Colorado River system were cut.

Chaco River, a distant and rather feeble tributary of the Colorado, also lowered its bed. In some places it excavated canyons and in others fairly broad valleys. That its canyon cutting was not continuous is evidenced by a well-marked erosional terrace near the mouth of Escavada Wash, a terrace capped by gravel largely derived from the local rocks and lying at an elevation about 150 feet above Chaco River. How important or general this pause may have been awaits field work over a larger area.

The general course of the river appears to have been controlled by undiscovered factors on the ancient plain already mentioned, but details of the carving of the rocks within Chaco Canyon, as we see it, result from the interaction of forces of erosion normal to the climate and the structure of the rocks.

The most notable feature of the canyon is its asymmetry. The north, or rather northeast, wall is steep and but little indented; the south or southwest wall is gentler and broken by branching canyons. Asymmetry is not an uncommon feature of valleys and canyons in New Mexico that have an east-west trend. For example, the relatively smooth, boulder-strewn slope of the south wall of Canyon del Rito de los Frijoles, near Santa Fe, contrasts strongly with the sheer cliffs of its north wall, in which Indians carved caves for occupancy in pre-Spanish times. Yet this canyon, cut in lava and tuffs having a slight dip downstream, is essentially alike in the two walls. The south side, however, is shaded for much of the day, a condition that leads to lower evaporation both of rain and snow, and consequently plants thrive. Small bodies of soil are held in place by grass and bushes; chemical erosion is promoted; talus heaps become overgrown with trees and mantle the rock slopes. In contrast, the north wall with its slope exposed to the sun is relatively dry. The mechanical forces of erosion are in full swing here and debris once loosened from the wall falls clear from rock surfaces which are thereby again exposed to the weather.

Chaco Canyon also has an almost east-west course and is subject to the same influences. A more important factor in creating a difference in the slopes of the canyon walls is, however, a northeasterly dip of the rocks. This inclination varies from 1 to 2 degrees with the result that the base of the Cliff House sandstone lies at or below the floor of the canyon on the north side, whereas it is from 50 to 100 feet above on the opposite side. In consequence the south cliff is undermined with relative ease by sapping of the underlying soft sandstone and shale. The fall of blocks is also assisted by a slight inclination of the bedding planes. Consequently, numerous and relatively large branch canyons
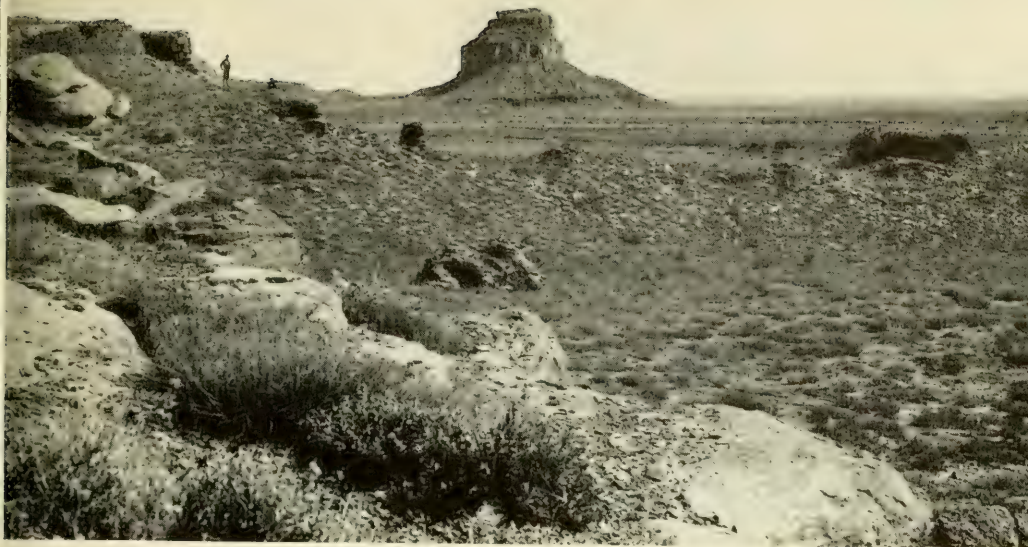
PLATE 2

Upper: Fajada Butte from Pueblo Una Vida, with the present arroyo dimly seen beyond the ruin, and, at the right, the treeless plateau extending southward toward Crownpoint. (Photograph by Neil M. Judd, 1920.)

Lower: A small ruin in a northern branch of Chaco Canyon between Una Vida and Wejegi. Seepage has deposited an incrustation of gypsum along the rear wall of the cave. (Photograph by Neil M. Judd, 1926.)
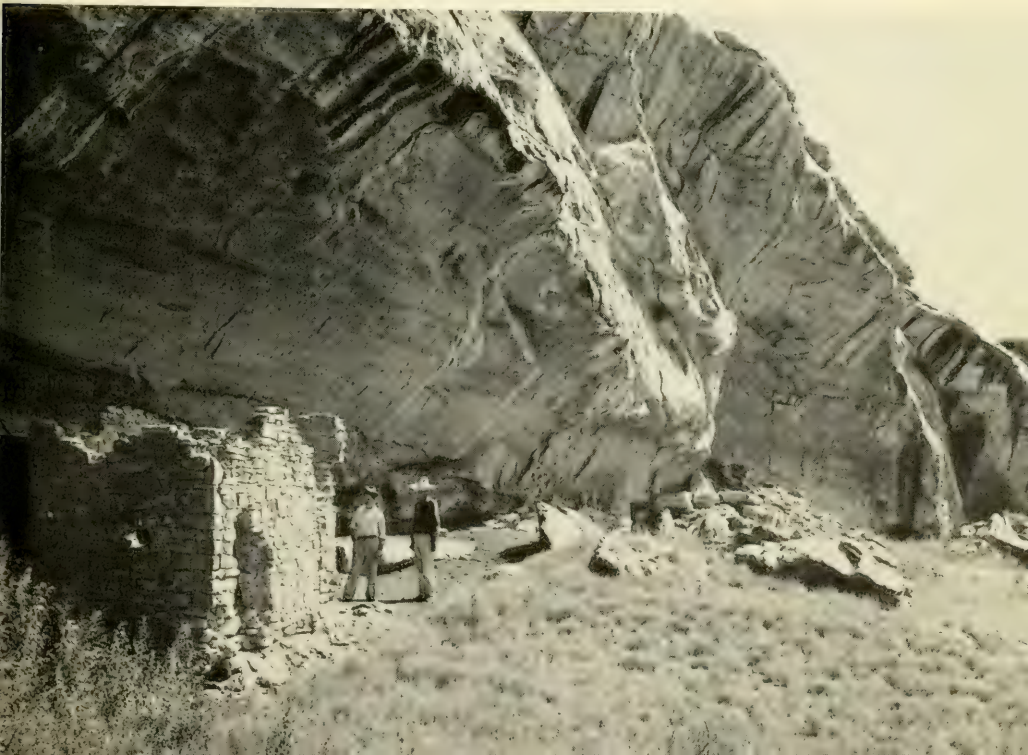
Plate 3

Left: Carved by wind and water, this niche reveals the characteristic cleavage planes of the lower Cliff House sandstone in the north wall of Chaco Canyon.

Right: A feature at section 5 was this slab-sided Pueblo III fireplace 5 feet below the present surface.
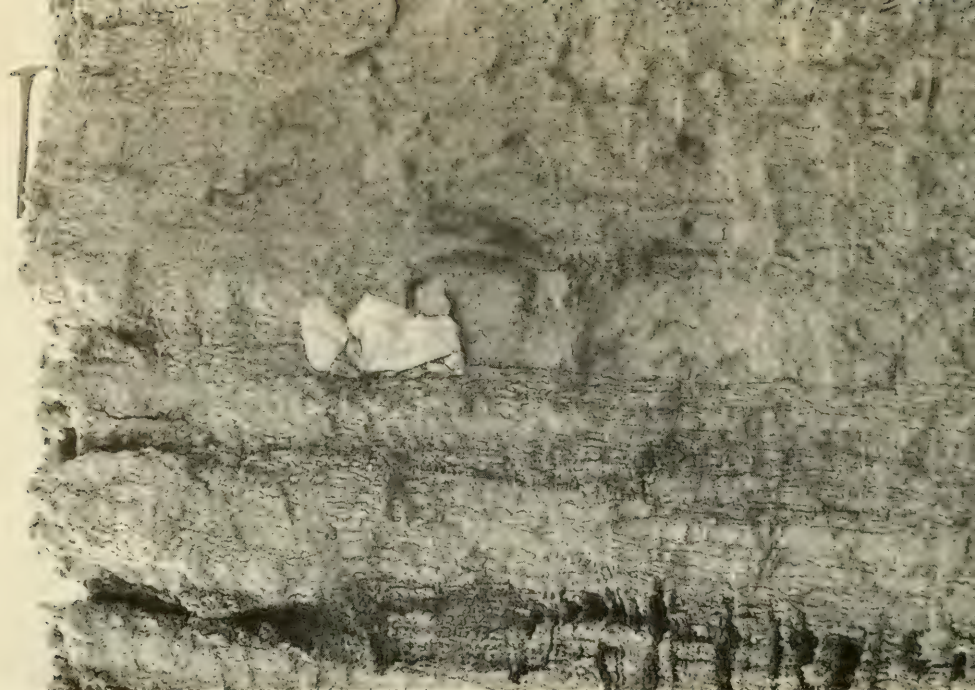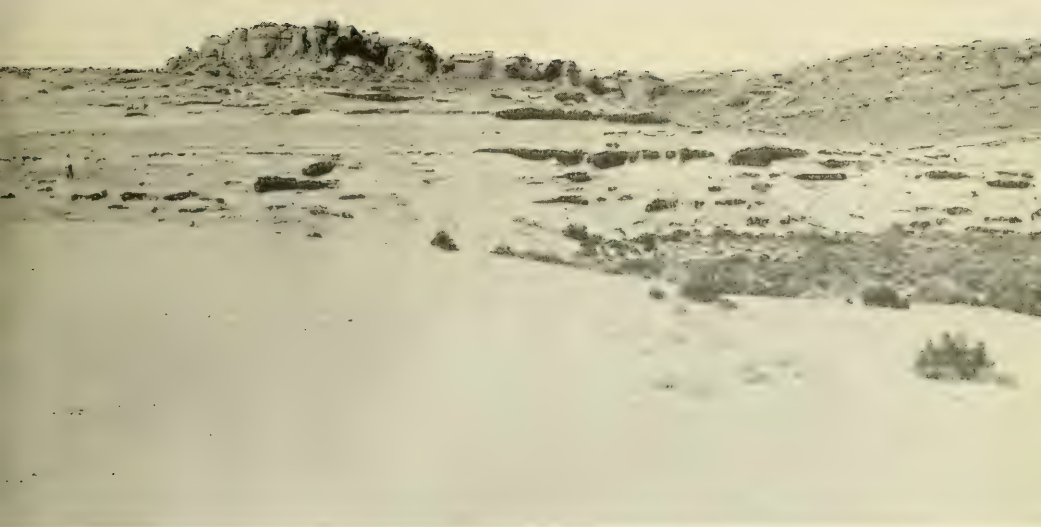
(Photographs by O. C. Havens, 1924.)

Upper: Near the mouth of the Escavada Wash the lower Cliff House sandstone in the north wall of Chaco Canyon has been scoured and blasted by wind-driven sand. Dunes have blocked the old road to Farmington.

Lower: Rainwater percolating through sandstone often results in a type of weathering called "stonelace." On the rock in the background water issuing from holes has left vertical streaks.

(Photographs by O. C. Havens, 1924.)
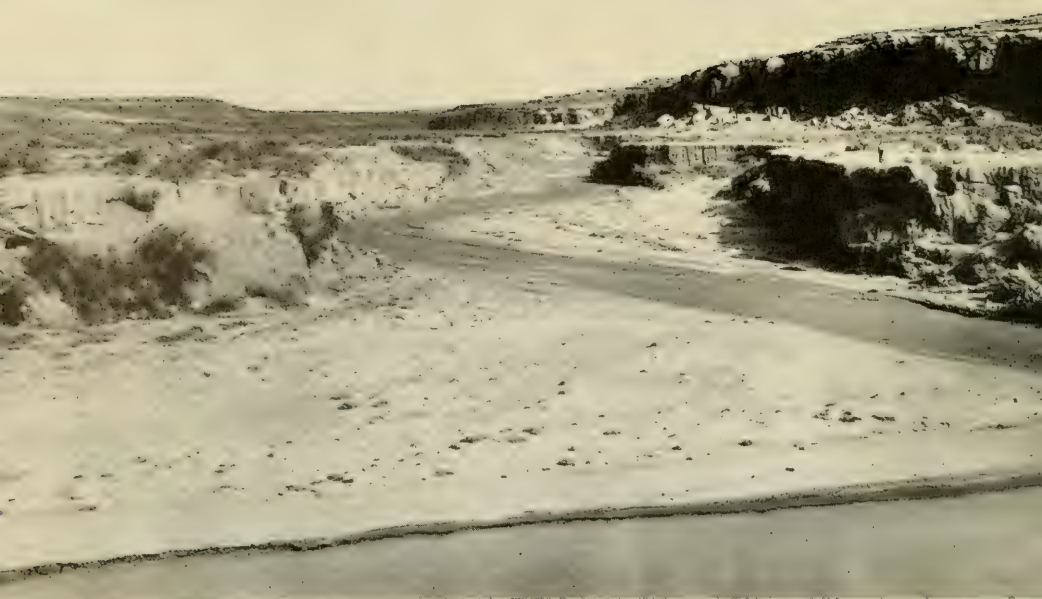
PLATE 5

Upper: Looking down Chaco Canyon from Pueblo del Arroyo. The irregular mass of Peñasco Blanco is seen on the horizon at left center. At the right a sunlit cliff in the middle distance marks the mouth of Rincon del Camino; between it and the standing figure are the broken walls of Ruin No. 8.

Lower: A newly fallen section of bank immediately west of Pueblo del Arroyo.

(Photographs by O. C. Havens, 1925.)

have developed. In the vicinity of Fajada Butte a large tributary drainage has completely destroyed the south canyon wall and enters through a valley broader than that of Chaco River (pl. 2, upper).

On the north side of the Chaco the base of the Cliff House sandstone lies below the canyon floor from Escavada Wash to Mockingbird Canyon. This part of the escarpment is characterized by having a sheer cliff surmounted by a bench and a more gentle cliff above. Its tributary canyons are generally less than half a mile in length and many are mere indentations in the cliff, of the type commonly called "rincons." From Mockingbird Canyon upstream the base of the sandstone lies above the valley floor and the lower cliff is benched rather than sheer, the tributaries are longer and the aspect of the canyon wall is more like that of the southwest wall.

Excavation of the canyon is a process long since interrupted, for the main stream nowhere runs on rock today, nor is it cutting laterally against the walls of the canyon. The process of canyon cutting was succeeded by a period of alluviation resulting in deposition of a valley fill to the level of the present valley floor (see below). Filling of the canyon has also been interrupted by formation of the present arroyo (p. 35).

ALLUVIATION OF THE CANYON FLOOR

After cutting Chaco Canyon to a depth somewhat greater than at present, the stream changed its habit and began to deposit more material than it removed. The gradual character of this filling and details of the process are here recounted at some length. This change from erosion to sedimentation was not confined to Chaco Canyon. Other canyons of the Plateau province and other streams throughout the Southwest were also filled and alluviation was the characteristic process up to a time within the memory of man. The isolation of Chaco Canyon has prevented the accumulation of definite historical data on characteristics of the canyon during this recent period of alluviation. However, canyons of adjacent parts of the Plateau province furnish reliable and analogous data since they lie at similar elevation, and are cut in like rocks under similar conditions of climate and settlement.

During the surveys of Powell and Dutton in 1878-1880, the canyons were undergoing alluviation as attested by the following statement (Dutton, 1882, pp. 228-229):

Most of these lateral canyons . . . are slowly filling up with alluvium at the present time, but very plainly they were much deeper at no remote epoch in the past. The lower talus in some of them is completely buried and the alluvium

mounts up on the breasts of the perpendicular scarps. In some cases a smooth floor of alluvium extends from side to side of what was originally a canyon valley.

Such conditions no longer exist and had, even in Dutton's time, ceased in certain parts of the San Juan drainage. At present every main canyon in the area is occupied by an arroyo with vertical banks from 10 to 100 feet high. The streams now run at a level lower than the flat floors Dutton described by an amount equal to the height of their banks. These arroyos began at or near the lower end of canyons and progressed headward by a receding fall. The upper (or falls) portion of an arroyo is ordinarily marked by a vertical bank or a chaos of jagged, vertical banks and great blocks of detached alluvium. In many canyons the head of the arroyo has not yet completed its advance and, generally, only in the lower and larger tributaries have branch arroyos been formed.

In the undissected parts of canyons and in minor tributaries there can still be seen at work the processes by which their flood plains were built up during the period of alluviation that has so recently been brought to a close. The flat floor of such a canyon slopes downstream at a grade dependent on the ratio of the volume of water in floods to the supply of sediment carried. In general there is no well-marked central channel, but numerous small discontinuous and branching channels mark the central part of the canyon floor. Low alluvial fans consisting of sediment carried in from minor tributaries diversify the plain. Some of these fans are so large they have partly dammed flood waters of the main canyon and thus created temporary lakes or leveled broad stretches of the canyon floor. In such places perennial grasses may grow in quantities great enough to be cut for hay. However, the features of these canyon floors constantly change, since floods vary in volume, in quantity of material carried, and in the time of their occurrence in the annual cycle. Obviously a flood that occurs after a long dry season during which vegetation has been reduced to a minimum by the dryness of the soil will readily change the minor features of the plain over which it flows. However, generally speaking, the parched soil will absorb so much that only when it is present in large volume will floodwater be able to run the full length of a canyon. On the other hand, a heavy rain and small flood in early summer may produce such a rapid growth of vegetation that the plain will, for the rest of the summer, be protected against erosion by much greater floods.

Obviously, also, floods down the axis of a canyon tend to produce a slope more or less uniform at any locality but of decreasing declivity—the so-called graded slope of a stream. Floods in the tributaries, how-

ever, tend to dump material on the floor of the main canyon and interrupt this "graded slope." Opposite the fan of a tributary, therefore, the main stream may have a marked channel that is constantly renewed and shifted in position. Such discontinuous channels must be sharply differentiated from the arroyos characteristic of dissection.

Discrimination of these minor channels from continuous channels that indicate a new cycle of erosion is not always easy. Both are commonly described in the Southwest as arroyos. The character of discontinuous channels can best be explained by an example. The Cañada del Magre, located about 90 miles southeast of Pueblo Bonito, is a narrow, flat-floored canyon tributary to the Rio Puerco (of the East). Its walls are of buff Cretaceous sandstone similar in color, massiveness, and porosity to the Cliff House sandstone. A tributary, the Cañada de Bernardo, is similar. In 1909 a steep-walled gully about 25 feet deep extended from the arroyo of the Rio Puerco across the abandoned flood plain of that stream and a quarter of a mile within the Cañada del Magre where it ended in a chaos of blocks of alluvium and an intricate dry falls. This was the head of the new arroyo representing the readjustment of grade of the Rio Puerco—a readjustment gradually affecting all its tributaries. Upstream from this arroyo head the floor of Cañada del Magre was a grassy flat for a distance of about half a mile. There the center of the flat became sandy and this sandy stretch was enclosed in low banks which gradually increased upstream until they were about 6 feet high and which closed in from the sides until they were only 10 feet or so apart. Here there was another dry falls, more or less grassed over. Some grass also grew on the floor of the arroyo. Above this latter falls was another grassy flat, succeeded at irregular distances by similar gullies and similar grassy flats. It is evident that these discontinuous channels are merely a phase in the process of transportation and deposition on the floor of such a valley. If the grade is locally out of adjustment but the grass cover prevents the easy removal of a thin sheet of alluvium over the whole floor, more sand and clay become lodged in the grass. Alluvium thus continues to be deposited even though the floor is above grade. Finally the strong currents of an exceptional flood break through the grass cover and initiate a gully which then increases headward rather easily. The overpour at the head of the gully so increases the ability of floods to erode that the gully is carried deeper than necessary and its lower end begins to fill with coarser sediment derived from the upper end. The manner in which these gullies disappear can only be inferred from the characteristics of certain ones which are very broad and low-banked at the downstream end and shallow and almost obliterated by

the growth of grass at the upper end. Evidently lateral erosion in the lower and middle parts of a gully removes material lying above normal grade, and since the head of the gully stands below this grade it is, with the help of vegetation, gradually filled in.

That such discontinuous gullies existed during the alluviation of Chaco Canyon there seems no reason to doubt. The kind of sediment in the floor and the nature of rocks in the drainage area are so similar to those of the Cañada del Magre and other canyons of the Rio Puerco drainage as to preclude the possibility that dissimilar conditions existed. Cross sections of the valley fill exposed in the banks of the modern arroyo show numerous irregularly placed channel deposits from 10 to 40 feet wide and 2 to 10 feet deep that may well have been deposited in discontinuous gullies.

The existence of channels of this type adds much uncertainty to the usefulness of the accounts of travelers in dating the initiation of modern arroyo systems. Thus Simpson (1850) states that in 1849 the banks of the Rio Puerco were 10 feet high and had to be cut down to allow the passage of artillery at a point 7 miles above Cabezon. Banks of similar height at the crossing of Arroyo Torrejon (Torreones) and the Arroyo Cedro are also recorded. Yet even in 1926 the upper portions of the Cañada (en) Medio, a tributary of the Torrejon, and the Cañada de Piedra Lumbre were undissected and their flat floors were farmed by Navaho Indians. A recent investigation (Bryan, 1928a) has, however, shown that the early discontinuous channels of the Rio Puerco were relatively shallow and narrow compared to the existing arroyo which was initiated between 1885 and 1890.

These minor features of the canyon floor, though constantly changing, doubtless had a marked similarity from year to year for there is a balance between the forces involved that could only have changed gradually with the progressive fill of sediment. The experienced observer can easily predict what areas of such a canyon floor will be gently flooded and what areas will be scored and eroded by tumultuous waters. Only gently flooded areas will be suitable for floodwater farming.

The process of filling Chaco and other canyons was doubtless a slow one and for each foot of material permanently added many feet were deposited temporarily and later shifted downstream. The irregularities in bedding produced by this process preclude an estimation of the time involved in deposition by any method now known.

At various places wind is effective in shifting material and thereby adding complexity to minor features of a canyon floor. Much of the material dropped by floods adjacent to channels of greatest flow is

incoherent and sandy. It is easily picked up by the wind and piled in low mounds or dunes. Such material is often in motion within an hour after recession of a flood. Nevertheless, these piles of sand are often effective in changing the courses of channels and in spreading floods. Areas so affected are small and usually are confined to three locations, here listed in the order of their relative importance: 1, Adjacent to channels; 2, on alluvial fans of tributaries carrying sandy debris; 3, outcrops of sandstone.

The work of winds in the vicinity of human habitations is notable and is described on pages 21-22.

DATE OF RECENT STREAM TRENCHING

Historical records at Chaco Canyon are meager, and it is impossible to fix precisely the beginning of its present arroyo. That this is recent and that the process is still continuing is self-evident. Many of the tributary canyons, such as Mockingbird, were yet undissected in 1925, although a falls that receded each year marked the head of their respective arroyos. Since 1925, extension of these gullies probably has destroyed the alluvial plains in the tributaries. That the main Chaco arroyo has increased since early expeditions to the canyon was recognized by Dodge (1910) and the evidence is here reviewed. Not only are its physical features recent but they resemble in every detail those of other arroyos in the Southwest whose date has been fixed with some assurance (Bryan, 1925a, 1928a). It seems reasonable to assume, therefore, that the trenching of Chaco Canyon took place at about the same time as the trenching of other valleys.

During a military expedition against the Navahos in 1849 under command of Col., afterward Gen., John M. Washington, Chaco Canyon was visited and a description of its ruins recorded by Lt. J. H. Simpson. According to this account (Simpson, 1850, p. 78), the "Rio Chaco" had, on August 27, 1849, a width of 8 feet and a depth of $1\frac{1}{2}$ feet at the expedition's camp near Una Vida. It is evident that this description applies to the muddy water then flowing. No mention is made of a gully although Simpson described the steep-walled arroyos of three other streams that were crossed on the way to Chaco Canyon.

Lt. C. C. Morrison (1879, p. 367) visited the Canyon in 1875 but does not mention an arroyo. Oscar Loew (1879) was there about the same time, but his description of the topography of the canyon is too vague to be of value.

William H. Jackson, whose pioneer archeological work in the Southwest is of great accuracy as to detail, spent five days in Chaco Canyon

in 1877. Five or six miles above Pueblo Pintado the arroyo was so shallow that Navahos had formed "water pockets" (reservoirs) by obstructing the channel; nearer Pintado the arroyo was 10 or 12 feet deep (Jackson, 1878, p. 433). Between Pueblo Pintado and Wejegi the depth of the arroyo almost entirely cut off communication from one side of the canyon to the other. Numerous small cottonwoods grew along the bank. Near Una Vida Jackson noted that the arroyo was dry where Lt. Simpson had found running water in 1849 and explains that his own visit was made in the spring, when floods are rare, whereas Simpson was there in August when floods are more common (ibid., pp. 436-437). At Pueblo del Arroyo the arroyo was 16 feet deep and 40 to 60 feet wide, as stated and also shown by his sketch map (ibid., p. 443 and pl. 59); 250 yards below this ruin there were shallow pools of stagnant water and here Jackson camped. New grass among young willows and cottonwoods in the bed of the arroyo extended for half a mile up and down stream (ibid., p. 446). The rapidity with which this channel has developed may be judged from the fact that, at Pueblo del Arroyo where Jackson recorded a depth of 16 feet and a width of 60 feet, the arroyo is now (1925) 30 feet deep and 150 to 300 feet wide.

Mr. Judd has diligently collected local traditions on past conditions in Chaco Canyon. Jack Martin, a long-time freighter in the region, said that between 1890 and 1900 the arroyo was so shallow most freight wagons could be hauled across without doubling the teams. The favored crossing was just south of Pueblo del Arroyo and part of the dugway down the north bank is still recognizable. In 1925 Padilla, an old Navaho who lives 7 or 8 miles west of Pueblo Bonito, stated to Mr. Judd and also to me that in his boyhood the arroyo was an "arroyito" not more than breast deep (about 5 feet) and that along it grew cottonwoods and willows. Since his boyhood it has continually widened and deepened.

Later the same year Wello, a Navaho thought to be about 75 years old, told Mr. Judd that Chaco River had no channel when he was a boy; that there were cottonwood and willow trees on the flat opposite Pueblo Bonito and grass was knee high. Water was close to the surface of the ground. Padilla was present at this interview and agreed that these things were so. He may be 5 to 10 years younger than Wello and doubtless based his agreement on knowledge gained from older men, but he still insisted on the truth of his previous statement that, in his boyhood, the "arroyito" was only breast high. If we can accept 1860 as the period to which these elders referred then we have an approximate date for the beginning of the Chaco arroyo. It was 5 feet

deep when Padilla was a boy; about 10 years earlier there was no channel at all, according to Wello. Simpson did not mention an arroyo because such a feature did not exist in 1849.

The original notes and maps of the townships surveyed under contract for the U. S. Land Office Survey in the early 1880's have been inspected. These records contain gross errors, and some of the township surveys appear to be entirely fictitious. Hence no useful information was obtained from them.

In attempting to determine a proper date for the beginning of arroyo cutting in Chaco Canyon, the problem is to decide whether the arroyo described by Jackson in 1877 is a portion of a through-going and complete arroyo system. It may have been merely a discontinuous arroyo with a head in the broad areas of the valley near Fajada Butte and a fan near the entrance of Escavada Wash downstream. Our information refers only to this part of the river and we have no data on conditions farther down the Chaco. It seems necessary, therefore, to assume that the arroyo of 1877 was the headward portion of a new system and that the present arroyo is its successor.

The year 1877 cannot be the beginning of this arroyo and allowance must be made for growth of the one described by Jackson. Some weight must also be given to statements of the two Navahos, Padilla and Wello. If Padilla is 70 years old he cannot remember farther back than 1860 to 1865. Wello, an older man, remembers, or remembers statements by others, that there was once no arroyo. Balancing these considerations, it seems that 1860 is as early a date as is possible since it affords 17 years for cutting the arroyo Jackson saw and is consistent with the stories of the two old Indians. The date must be considered as an arbitrary choice, however, and not very precise.

Elsewhere in the Southwest existing evidence indicates that the phenomenon of arroyo cutting began at slightly different times, stream to stream. A considerable period elapsed between initiation of a given channel and its completion throughout the length of its valley floor. The date of beginning is apparently earlier in southern Colorado, northern New Mexico, and northern Arizona than elsewhere, and may easily fall in the decade 1860 to 1870. On Rio Puerco, however, a nearby and similar stream, the date has been satisfactorily placed within the years 1885 to 1890, and in the Hopi country, arroyos were not cut until after 1900.

The effect of arroyo cutting on native vegetation and on habitability of the area affected is very considerable. In southern Arizona, meadows of coarse-top sacaton with groves of cottonwood and walnut have been drained by arroyos, and dense forests of mesquite have since

sprung up. On the Rio Puerco, natural hay fields of fine-top sacaton and other grasses once naturally irrigated have dried up and the deep-rooted chamiso, "wafer sage," has replaced the grasses. Areas near San Ignacio and San Francisco that were once irrigated by use of crude ditches or by natural flooding are now 30 feet above the stream bed. Since these areas can no longer be farmed, the towns have been abandoned.

Instances of similar change in native vegetation and of the abandonment of fields could be multiplied (see references given in Bryan, 1925a, 1928b). The present lack is a quantitative estimate of the decrease in vegetation and consequent lessened opportunity for man under the changed conditions. Primitive man, without domestic animals, would not suffer from decrease in forage or from loss of hay fields but, to the extent that he was dependent on floodwater farming, might have his very existence jeopardized by these changes. On the other hand entrenchment of Moenkopi Wash, near Tuba City, Ariz., has, according to Gregory (1915), increased the low water flow of the stream and thereby provided more water for irrigation during the critical period of plant growth. An old Hopi farming village here, after long abandonment, was reoccupied in 1880 and is now a thriving community of about 300 people.

PRESENT GEOLOGIC PROCESSES

WEATHERING AND EROSION OF THE CLIFFS

The asymmetric form of Chaco Canyon is due to its east-west course and to the prevailing dip of the rocks, as explained on pages 10-11. The processes now at work on the cliffs differ from those of the past only because of two factors: (1) The relatively recent valley fill which covers the lower part of certain cliffs; (2) the possible differences between present and past climates. The first factor can have little effect on the nature of the processes; the second affects only the rate of erosion, as the probable changes in climate do not involve a change to a strictly humid climate. When past climates were wetter than the present but still relatively arid, cliff recession was doubtless accelerated; when the climate was drier, the process was slowed down.

Chaco cliffs can be divided into two sorts in two locations: The lower division of the Cliff House sandstone generally forms vertical cliffs but these differ in detail according to whether the base of the sandstone lies below or above the level of the alluvial plain. The upper division has domelike forms and generally produces low cliffs either stepped or rounded where the base is above the alluvium. In lateral

canyons the base of this upper member falls below the level of the alluvium and here crenulated and rounded cliffs occur.

Erosion of the lower part of the Cliff House sandstone is largely due to differential sapping at its base. Rainwater entering the sandstone above emerges below. If the base is above the level of the flood plain, the water emerges at the top of the friable sandstones, coal, or shale of the somewhat variable underlying Menefee formation. This material is decomposed and carried away partly by this seepage water and partly by direct rainwash. As a result the cliff is undermined and blocks break off along characteristic joint planes. Perhaps because the edge of the cliff settles and these joints are open some distance back from the face, the cliffs of these localities are less sheer than those of the same rock where the base of the sandstone is below the level of the alluvial plain, as in the north wall of the canyon near Pueblo Bonito. Here water absorbed by the overlying sandstone emerges at or near the level of the alluvial plain. It dissolves the cement of the rock and appears as an efflorescence of a white salt. The sandstone becomes friable and grains are loosened from the surface. These grains fall by gravity, especially during windstorms, or are loosened and carried off by the sheet of water that covers the face of the rock in rains. Thus cavities or niches (Bryan, 1928c) are formed like the one shown in plate 3, left. With the formation of these cavities the rock splits on its characteristic vertical joints; as loosened blocks fall, the vertical face of the cliff is renewed. Narrow slabs several hundred feet long, partly loosened, are fairly common features, and one directly back of Pueblo Bonito has excited much interest because massive masonry below it shows that the prehistoric peoples attempted to brace the slab against falling. [It actually did fall, on January 22, 1941.— N. M. J.]

The upper member of the Cliff House sandstone tends to weather in domal forms. Widely spaced vertical joints more or less at right angles to each other afford points of attack for the weather and the resulting, nearly cubical blocks are then rounded on the corners. The process of sapping takes place in this sandstone also. There is, however, a relatively irregular zone of slabby and shaly sandstone below, at which the water may emerge. On the double cliffs back of Pueblo Bonito the sapping takes place over such a thick and irregular zone that the upper cliff is discontinuous and in many places is replaced by a series of benches. In canyons and rincons that enter Chaco Canyon from the north, this contact passes below the level of the alluvium and the zone of seepage emergence is more or less confined. The rounded

bosses are undercut. Where temporary waterfalls cascade over the cliffs during rains, niches are formed.[3]

Such a niche, in Rincon del Camino, is notable because water emerges under the overhang throughout the year and in sufficient quantity to constitute a spring. Other niches may have only enough seepage to support a few green bushes or there may be merely a damp place on the rock. It requires, however, no stretch of the imagination to perceive that with a slightly greater rainfall springs would exist in these and similar situations.

The rate at which cliffs recede according to the processes just reviewed is necessarily slow. That parts of some cliffs are newer than others is attested by their bright, unstained surfaces and the lack of talus. Other parts have relatively ancient, iron-stained surfaces and have shed no fragments since completion of the alluvial plain which laps their bases. Some cliff faces are marked by carvings or pictographs; others have had holes cut in them to support the roof timbers of abutting dwellings. Often blocks at the foot of a cliff are so like the cliff face in color they must be of equal age. In general it can be said that, except for fall of a few blocks here or a mass of debris there, the Chaco cliffs are essentially the same as they were when the canyon was inhabited by prehistoric peoples.

The blocks of sandstone that fall at the foot of a cliff also slowly weather and disappear. There are relatively few such occurrences in Chaco Canyon; rarely are the blocks numerous enough to form a heap or talus. The lack of talus may usually be explained as owing to burial of all blocks formed previous to alluviation of the valley floor. Exposed blocks are mostly recent falls and some of them are so little weathered that they can easily be correlated with scars they left on the cliffs. Others are much weathered and disintegrated. The principal process of weathering appears to be the solution of cement by rainwater that percolates through the blocks and emerges on the side or near the base. Numerous fantastically shaped holes are thus produced, as illustrated in plate 4, lower. The movement of water through such rocks was particularly observed on August 3 and 4, 1924. A sharp shower occurred about 2 p.m. August 3 in which 0.14 inch of rain fell. After the shower several rocks of this type were examined. The exposed portions were wet, and part of the dust under the larger overhang was eroded by the splash of falling rain, but the cavities were dry. Next morning parts wet the day before were dry but the cavities

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[3] Bryan's negatives were not found, but those he intended to use here are reproduced in Zeitschrift für Geomorphologie, 1928, pl. 3, A, B.

were damp, and some were almost wet. Evidently within 12 hours water absorbed at the top had percolated through the rock. In rainstorms of greater duration water must pour out of such cavities in considerable volume and carry with it sand grains resulting from previous solution of the cement.

WIND WORK

In various places on the cliffs, especially on the bench between the upper and lower sandstones, there are patches of windblown sand. This sand, evidently derived from disintegration of the nearby sandstone, accumulates in places more or less sheltered from the wind. Some heaps are fixed in position by the growth of grass. That such heaps accumulate is proof that a much greater quantity of sand is moved by the wind and either blown off the cliff altogether or into position where it is carried away by rainwater. How much the movement of this sand scours the rock is difficult to evaluate. It seems likely that the scouring effect is small, for the rock at the surface is soft and crumbly. At the mouth of Escavada Wash, where the Farmington road left the Chaco prior to 1920, the wind has heaped up sand out of the wash to form a group of dunes that encroaches on cliffs similar to those upcanyon (Bryan, 1928c). Here the sandstone has the same domes, niches, pinnacles, and other characteristic details, yet the surface is hard and firm (pl. 4, upper). Tiny iron concretions stand above the surface like collar buttons. The surface is continuously scoured by sand and is in marked contrast, by reason of its firm texture, to the soft and crumbly surfaces seen elsewhere. Nevertheless, the total erosion is obviously less than it seems, for otherwise the domes, niches, etc., would disappear and be replaced by new details equally dependent for their shapes on the process of wind scour.

Near Pueblo Bonito, dust is easily raised on any windy day and windblown sand accumulates, as it has in the past, in every sheltered nook and cranny. Between the ruin and the cliff sand had collected to a depth of 4 to 6 feet between 1900, when the Hyde Exploring Expedition concluded its excavations, and 1921, when the National Geographic Society inaugurated its researches. Similarly, windblown sand near other ruins of the region evidences more wind work than appears at places of otherwise similar location.

These conditions are easily understood when the activity of man and his domestic animals is considered. Near his habitations man and his animals continually disturb the surface soil and thus make the work of wind easy. In addition the soil is made pulverant by abnormal

quantities of organic matter consisting of the excrement of men and animals, the debris of crops gathered and brought in, the refuse of building materials and fuel, and litter of all sorts swept up and carried out of houses. These organic substances added to the surface soil serve to make it friable in the same way that manure improves the tilth of a field. The soil, when wet, is no longer a gummy mass that becomes pavement-hard on drying. It is less muddy when wet, and when dry is loose and friable and thus easily picked up and transported by the wind.

With only dogs and turkeys to help in the processes just described, prehistoric peoples probably did not create as much dusty ground as the same number would today. Yet their refuse mounds testify to an enormous quantity of rubbish discarded systematically and enable one to picture the proportion of such litter that must have been scattered about the inhabited areas. The quantity of windblown sand and wind-reworked material found buried in the refuse heaps of Pueblo Bonito evidences a considerable amount of wind work in prehistoric time that, on the grounds set forth above, may be considered as influenced by the habits of prehistoric man.

ALLUVIAL FANS

At the foot of the cliffs, and particularly at every indentation in them, alluvial fans are now forming. These are composed largely of buff and yellow sand derived from disintegration of the sandstone of the cliffs and talus blocks. During every rain, sheets and streams of water pour over the cliffs; the largest flows naturally occur at the indentations. Alluvial fans deposited by these streams are more or less proportional in size to the indentation and, by inference, to the area of surface drained. In a few places the sand of alluvial fans is picked up by the winds and formed into low heaps, but, as was pointed out above, currently there is more wind-moved material in and around the various ruins than at other places in Chaco Canyon.

The soil of these alluvial fans is loose and sandy and doubtless formed the best agricultural land in prehistoric time. During and after rains, waters that pour from recesses in the cliff could easily be directed over the fans. The problem of directing and spreading such runoff so it will wet without gullying the land is a difficult one which must have taxed the ingenuity of the prehistoric farmer. It is possible, but by no means certain, that part of these floodwaters were directed over the more clayey areas in the middle of the valley not only for the purpose of irrigation but also to mix water-borne sand with the less tractable clay.

ADOBE FLATS

Adobe flats still constitute a large part of the floor of Chaco Canyon and are added to each season by storm waters draining from adjacent areas. They are, however, no longer built up by the marginal waters of main stream floods or by deposition in temporary lakes. Progressive cutting of the arroyo has left these flats mere relics of past conditions, but the method by which they were formed can be interpreted from observations in such undissected tributaries as Mockingbird Canyon.

EROSION IN THE ARROYO

The initiation of dissection and the formation of arroyos has already been discussed (pp. 12-13). The present (1925) arroyo varies in width from 150 to 500 feet, and in depth from 10 feet near Escavada Wash to 30 feet at Pueblo Bonito. Upstream, however, the height of the bank again decreases to about 20 feet near Wejegi.

The vertical walls are formed by undermining the alluvium which then breaks off in blocks parallel to an obscure jointing. Undermining is largely due to the lateral cutting of floods in swirls and eddies on the outside of bends. It seems probable, however, that water absorbed in the alluvial plain seeps into the arroyo at the base of these banks, softening and helping to undermine them. The rate of such lateral cutting is rapid, and significant changes may occur in a single year (pl. 5, upper and lower).

THE VALLEY ALLUVIUM

MATERIALS OF THE FILL

The alluvial fill of Chaco Canyon consists largely of sand, yet so much of its surface is covered by a layer of dark sandy clay (locally called "adobe"), that the true character of the fill is not evident except where exposed in the arroyo. Even there the degree of sandiness can be detected only by close inspection, for rains wash mud down over the vertical walls and this, like a film of plaster, conceals the sand and gives the impression that the whole bank is made of clay. The relative quantities of sand and clay will appear from the measured sections on pages 51 to 59; in the following paragraphs, each class of material is described separately.

Small discontinuous bodies and lenses of gravel occur sparingly. The gravels contain much fine sand and mud and are thus similar to the small bodies of gravel found in the present arroyo bed. Like the latter they are obviously the deposits of tumultuous and muddy floods.

The pebbles are mostly partly rounded fragments of sandstone and of limy concretions derived from the Mesaverde and Pictured Cliffs sandstone, but there are also a few water-worn pebbles secondarily derived from the Tertiary rocks. These pebbles may vary in diameter from half an inch to 2 inches, but angular stones up to 6 or 8 inches in diameter are also found.

The sands are of several types not wholly distinct in character that grade into one another even in the same bed. Some sands have almost no bedding or lamination and consist of yellowish, rusty grains such as result from disintegration of the sandstone of the canyon walls. These accumulations seem to have been deposited by outwash and are parts of ancient fans similar to those now being formed at the foot of the cliffs. Lenses of clean white sand, laminated and crossbedded, were laid down by the stream of the main canyon, just as like lenses are being deposited today. Somewhat similar but generally finer-grained sands may have very minute and irregular crossbedding that is a remnant of wind-made ripples. Such beds clearly have been subject to wind action but it seems likely that the sand was first deposited by water and subsequently reworked by the wind. The very same process may be seen today when sand recently deposited in the channel by a flood is reworked by wind shortly afterward.

Gray or brown silt in beds that are minutely though irregularly laminated make up a considerable part of the alluvium. Ripple marks, current marks, and mud cracks are common on the surface of the laminae; a few rusty streaks, some parallel and some at large angles to the laminae, are doubtless the impressions of stems and roots. In many places the silt beds are 2 to 4 feet thick, but in others silt occurs as thin layers in sand or clay. Obviously it was deposited in outer portions of the channel by the main stream or in nearby parts of the flooded area.

The clay of the valley fill locally known as adobe is mostly gray or brown and contains appreciable amounts of sand and silt. A more realistic name would be "sandy or silty clay" or "clayey fine sand." The usual clay bed is from 6 inches to 3 feet thick and is nearly uniform in color and texture. Lamination is not always apparent to the unaided eye but it probably is a constant feature since it has been detected under the microscope and doubtless would be readily visible were it not for vertical jointing and a tendency to "check."

Well-laminated, less sandy clays occur in discontinuous lenses a few feet long and varying from 2 to 12 inches in thickness. These lenses appear to have been deposited by floodwater that was ponded in abandoned and shallow channels. In contrast, the more abundant sandy

clay is the result of sheetlike overflows of the main stream and of its tributaries. These overflows formed flats or meadows of alkali sacaton grass. The imperfect lamination and reticulated structure are probably to be accounted for by successive drying of the mud on exposure after each overflow and by the influence of grass roots. The dark color is due to finely divided organic matter incorporated in the clay. In such flats the rate of soil formation is rapid and the reticulated (chernozem) soil structure is quickly attained.

ARRANGEMENT OF THE MATERIALS

The walls of Chaco arroyo and its various branches afford ample exposure in which the several sorts of material just described are displayed. The dominant characteristic is lack of continuity. No bed, however uniform over a short distance, extends very far, nor does a like sequence of beds occur in the wall of the arroyo at any two places.

In general clay beds are the most continuous and some of them have a length of nearly a quarter mile. Such beds rest on, and in turn are covered by, essentially parallel beds of different composition from place to place. These changes in lithology imply that there are many minor unconformities between beds. In some places sharp and definite erosion surfaces cut clay beds which are overlain by sand deposited in the channel responsible for the erosion. Less definite evidences of erosion contemporary with deposition occur, but no one of these episodes of erosion within the formation has any time value, for such irregularities are to be expected in the deposits of ephemeral streams. Each large flood forms new channels of flow and destroys in part the work of its predecessor. In such localities the measure of erosion or sedimentation is the algebraic sum of the erosion and deposition of successive floods.

In several places a cross section of a much older channel is exposed in the wall of the arroyo. These exposures generally show a round-bottomed channel, filled with crossbedded sand to a depth of 2 to 10 feet, and the lenticular character of adjacent clay beds. Such channels are evidently interformational for they are shallow, occur at all levels, and are covered by beds that are conformable with others, adjacent and contemporaneous. Evidently these channels are of the discontinuous type described on pages 13-14 and are to be distinguished from the relatively recent, buried channel discussed on pages 32-37.

DEPTH OF THE ALLUVIUM

Tangible evidence on the total depth of the valley fill is wanting in Chaco Canyon. The well at the Society's Pueblo Bonito camp was dug
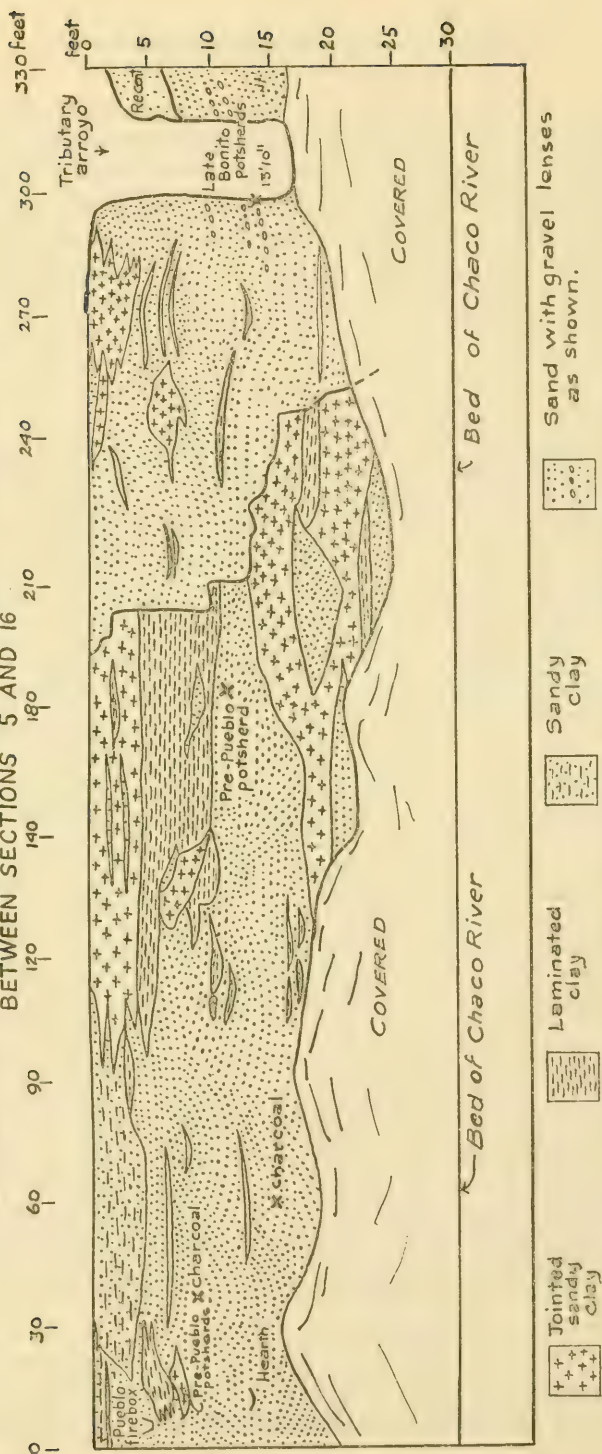
Fig. 3.—Diagrammatic sketch of the valley fill between sections 5 and 16.

PLATE 6

Upper: Annually since 1877 Chaco floods gnawed at this small Pueblo III ruin until the last vestige of it disappeared in 1948. Pueblo del Arroyo stands at the right, beyond the sheds. (Photograph by Charles Martin, 1920.)

Lower: A Pueblo I pit house with roof 6 feet below the valley surface was revealed by caving of the arroyo bank during the 1921 flood season. (Photograph by Neil M. Judd, 1922.)

Plate 7

Upper: The buried channel as exposed at section 16. Here Late Bonitian potsherds were found at a depth of 13 feet 10 inches. (Photograph by O. C. Havens, 1925.)

Lower: The author stands below a cross section of the post-Bonito channel at section 4, near the southeast corner of Pueblo del Arroyo. (Photograph by O. C. Havens, 1924.)

PLATE 8

Upper: As it did in the days of Pueblo Bonito, the Rincon del Camino comes in from the north to join the main Chaco arroyo. (Photograph by O. C. Havens, 1924.)

Lower: Lateral erosion caused by drainage from The Gap. View looking north across the Chaco toward Pueblo del Arroyo in left middle distance. (Photograph by Neil M. Judd, 1929.)

PLATE 9

Upper: About half a mile west of Ruin No. 9 a disarticulated skeleton was found in the arroyo bank 6 feet below the surface.

Lower: Hearth at depth of 12 feet 8 inches, section 9, at mouth of Rincon del Camino.

(Photographs by O. C. Havens, 1925.)

about 10 feet below the level of the stream bed in the arroyo, here 30 feet deep, and thus shows at least 40 feet of alluvium. About 1900 a well said to have been 350 feet deep was drilled between Richard Wetherill's old home and the southwest corner of Pueblo Bonito and was promptly abandoned because the water was brackish. No record of the material passed through is available.

In other, somewhat similar canyons and valleys, the alluvium is known to be relatively shallow. As recorded by Gregory (1916, p. 160), wells at Leupp, in the Little Colorado Valley, northeastern Arizona, and along Oraibi Wash, farther north, show a depth to bedrock ranging from 60 to 80 feet. In the Puerco Valley, 50 to 70 feet of alluvium is found. At Gallup, near the Arizona line in New Mexico, there is 175 feet of alluvium above bedrock.

From these data one may assume that the alluvium in Chaco Canyon probably does not exceed 100 feet in depth. Thus there is exposed only about one-third, or 30 feet, of the total. The generalizations of this paper are based on an examination of this exposed third but we may be sure an equally thorough examination of the lower and unexposed portion would reveal equally interesting and significant information.

HUMAN RELICS IN THE VALLEY FILL

During investigation of the sediments exposed in the walls of Chaco arroyo, relics of man's activity were observed repeatedly. These relics consisted mostly of hearths, charcoal, stones, bone fragments, and potsherds. Remnants of masonry structures were also found, although infrequently. Most of the hearths are not constructed fireplaces but, rather, surfaces more or less blackened or reddened by heat and overlain with charcoal. They are merely places where fires had been built and obviously represent no more than temporary camps. Some may have been used for only a day; others, to judge from the depth of the burnt ground and the amount of charcoal, could have been used for a period of weeks. Some hearths have been buried by sand or clay laid down so gently by running water that the charcoal was not eroded. They are thus good evidences (1) that the contemporary surface at that place was occupied by people during the period of alluviation and (2) that alluviation was accomplished in part by gently moving sheets of water which did not destroy previously existing surfaces.

Scattered charcoal, on the other hand, is not conclusive evidence of the presence of man since it may have been incorporated in the sediments by erosion of areas where the vegetation was burned by fires of natural origin. However, as previously pointed out, the character of

the sediments indicates that the region has always been an arid one. In such a region fires of natural origin are, because of the scarcity of burnable vegetation, likely to be small in extent and thus produce small amounts of charcoal. Certainly charcoal is not common in the stream beds of the present time, either in this area or in the Southwest generally. It seems more likely, therefore, that occurrences of scattered charcoal in the Chaco fill are due to the erosion of hearths or refuse dumps. Since charcoal is soft and friable, it cannot be carried far and indicates human occupation at no great distance upstream.

Isolated stones in the fine-grained sediments occur in many places, but, however others may have reached their present positions, those found near hearths were probably brought in by man. Their presence thus tends to confirm such evidence of onetime human occupation as worked flints, stone and bone artifacts, and fragments of pottery.

Bone fragments are not positive proof of man's presence unless showing signs of human workmanship but, like scattered stones, may be confirmatory when in association with man-made objects.

Potsherds are resistant to erosion and provide durable and unquestioned evidence of man's presence in the past. They have such large surfaces in proportion to their weight that they may be carried in currents unable to transport small stones and thus often occur in fine-grained deposits. Generally, however, they are associated with gravels. Some potsherds, found singly in fine-grained beds, may have been dropped on the surface and simply buried by the mud of the next flood. Deposition by floods on uneroded surfaces was doubtless common, as shown by the lack of erosion of charcoal in hearths. Potsherds also have a genuine stratigraphic value because pottery made by prehistoric peoples at different periods differs in texture and decoration and can be identified with some certainty. Thus, if collected systematically, potsherds can be used as fossils are used to identify the age of sediments.

COMPLEX CHARACTER OF THE VALLEY FILL

The nature of the sedimentary deposits comprising the main fill of Chaco Canyon is clearly revealed in the walls of the present arroyo. Here 30 feet and more of successive strata have been laid bare and one has only to read the story they tell.

Before discussing the significance of these exposures and the methods used, some of the difficulties we encountered will be mentioned for the benefit of future workers. Study of arroyo banks involves the tiresome traversing of the stream bed, which is soft and sandy when

dry and may be dangerously boggy just after a flood. The banks are a monotonous brown and in many places are covered with a film of mud washed down from above.

Like a coat of calcimine over a fresco, this film obscures the characteristics of the materials of the bank. The freshest exposures are usually on the outside of bends for here the stream cuts laterally with greatest activity. On the inside of bends, temporary bars or heaps of windblown sand accumulate and may cover the bank to half its height. Frequently there has been left adhering to the bank a remnant of such a bar formed at some past time in the process of cutting the arroyo. Occasionally these remnants form little terraces 3 to 20 feet wide and 4 to 6 feet lower than the top of the bank. They consist of Chaco River deposits similar to the rest of the valley fill and are so deceptive in appearance we came to call them "false banks." Sometimes the "false bank" contains sheep dung and recency of deposition is thus definitely established. Elsewhere one must rely upon the form of the bank or some local difference in bedding, in color, or in grain of the clays and sands to distinguish the false from the true bank.

In full sunlight the relatively small variations in color and texture of beds are almost invisible. Therefore each locality was scrutinized at least twice, once in the morning and once in the afternoon so that, as nearly as possible, every part of the exposure could be seen in the shade.

Detailed descriptions of the valley fill at each of the 23 sections examined would merely weary the reader. A number of such descriptions are offered hereinafter (pp. 51-58) for those interested primarily in the geological aspect of this study, but our present purpose will be served by a single example. Typical conditions are shown at a locality on the south bank of Chaco River, opposite Ruin No. 8 and approximately half a mile west of Pueblo Bonito (fig. 1). Our diagram (fig. 3) was constructed by measuring the beds on verticals spaced 10 feet apart and by sketching the form of the several bodies of material in the intervals.

On the left are shown the irregularly continuous beds of the main valley fill at section No. 5. A conspicuous feature here is a fireplace of nearly vertical stone slabs built when the surface was 5 feet lower than it is now (pl. 3, right). Archeologists consider this type of fireplace characteristic of the period of settlement known as Pueblo III. Nearby, both in the bank and on the surface, are potsherds of that age. A few feet to the west, however, and at a depth of 6 feet 3 inches, sherds of indeterminate age were found. A second hearth at a depth of 12 feet 8 inches, and charcoal at 16 feet 3 inches, are doubtless rec-

ords of the presence of people earlier than Pueblo III. Near vertical 180 a potsherd of distinctive type attributable to pre-Pueblo (P. I) times was found in a loose block of earth. This block retained the shape of the bank so perfectly there is no doubt the sherd came from a depth of 11 feet 3 inches.

At the right of vertical 180 is represented the coarse, sandy filling of an ancient arroyo at section 16 (pl. 7, upper). In the gravel lenses of this old channel and at a maximum depth of 13 feet 10 inches, potsherds of the type characteristic of the latest phases of Pueblo Bonito were found. The sherd collection here was comparatively large because the gravel lenses could be followed for 50 feet at right angles to the section in the lateral tributary of the modern arroyo.

Generally speaking, material within this ancient arroyo is sandier and more crossbedded than that of the main valley fill. In other sections examined the laminations dip from both sides of the channel toward the middle and at or near the bottom there are one or more lenses of gravel. These lenses are, on the average, 3 to 12 inches thick and 2 to 4 feet long. The gravel is clayey and dirty and similar to gravel beds of the valley fill or those in the present stream bed. However, potsherds are relatively plentiful and most frequently of Pueblo III type. The unusual number of these late potsherds is in itself significant and, so far as my experience goes, an infallible indicator of the presence of the buried channel. Connecting channels of contemporary age are commonly filled with coarser material similar to that in the present tributary arroyos.

Typical conditions are thus recorded in the main valley fill between sections 5 and 16. The current arroyo has exposed its predecessor and bared evidences of human occupation in times past. To depths of 4 feet and more, rarely 6 feet, potsherds of Pueblo III type are fairly common. Below this horizon the sherds are of definitely earlier types or of indeterminate age. Here, as elsewhere, we detect no physical division between the lower and upper sedimentary beds, merely a separation of the early and late pottery fragments found in them.

RELATION OF HUMAN RELICS TO MAIN VALLEY FILL

The various relics of man's activity found exposed in the walls of the modern arroyo indicate that man inhabited Chaco Canyon during the latter part of the period of alluviation. The greatest depth at which potsherds were seen during the course of our investigation was in a bed ranging from 17 feet to 20 feet 6 inches below the surface of the valley floor (section No. 3, fig. 1). At another site, section 8, charcoal

was found at a depth of 21 feet. Man may have been present during the earlier phases of sedimentation but his presence during deposition of the last 21 feet of fill is definitely established. It seems a fair inference that in the prehistoric period most streams in this region were building up their flood plains and primitive man witnessed the process.

Chaco Canyon was by no means unique in this respect. Ashes, pottery, artifacts, and like evidences of man have been recovered at various depths in the alluvium of other Southwestern valleys. Published records are not so numerous as might be expected but those available, together with some of the present writer's observations, are tabulated herewith: [4]

Relics of man in the recent alluvium

State	Name of stream valley	Feet below surface	Author	Reference
Arizona	Rio de Flag	9	A. E. Douglass	1924, pp. 238-239
	Santa Cruz	10	E. Huntington	1914, p. 24
	Navaho Country	..	H. E. Gregory	1915
	Navaho Country	..	A. B. Reagan	1924a, pp. 283-285
	Pueblo Colorado Wash	10	A. B. Reagan	1924b, pp. 335-344
Sonora	Sonoita River	12	C. Lumholtz	1912
Colorado	Montezuma Canyon	2	G. O. Williams	1925, pp. 201-202
New Mexico	Chaco Canyon	17	R. E. Dodge	1920, pp. 23-25
	Chaco Canyon	14	W. H. Jackson	1878, pp. 431-450
	Coyote Canyon, Sandia Mts.	6	Kirk Bryan	1925a
	Rio Puerco	6	Kirk Bryan	1926b
	Nutriosa Creek Zuñi drainage	6	Kirk Bryan	1926b

In Chaco Canyon, potsherds and other artifacts were collected from noteworthy depths at many different places. Generally, sherds from the upper 4 to 6 feet of the valley fill are of relatively late types of pottery (Pueblo III). Earlier types are found at greater depths. From our data it seems clear that the upper 4 to 6 feet of the main valley fill is not only younger than the lower horizons but that the division between the prehistoric periods known as Pueblo II and III lies at the base of this layer.

Two Pueblo I pit houses in Chaco Canyon were excavated and described by Judd (1924). One of them, so far as critical evidence was preserved, may have been built after alluviation had filled the valley

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[4] It is to be emphasized that this paper was begun in 1925 and was added to from time to time until 1940, when it was left incomplete. Hence the absence of later references.—N. M. J.

to its present level. It was situated at the base of the talus on the south side of the canyon, opposite Pueblo Bonito. The other and more perfect example, at the locality marked "Pit House" on figure 1, was evidently occupied when the surface of the alluvial plain was 5 feet 11 inches or, in round numbers, 6 feet below the present surface (pl. 6, lower). Because potsherds of precisely the same type as those recovered from these two P. I pit houses have been found repeatedly in the valley fill, one can scarcely avoid the conclusion that during the time when strata at depths of 4 to 21 feet were being deposited, Chaco Canyon was occupied predominantly by people of this cultural stage.

The exact relationship between the Pit House people and later inhabitants of the valley is not wholly clear at this writing. Pottery similar to that from Judd's two pit houses has been found in and below rubbish associated with the older parts of Pueblo Bonito and portions of a slab-lined pit house were encountered 12 feet beneath the west court of the great ruin. I leave solution of this puzzle to the archeologists but, at the moment, it would seem as though the inhabitants of Chaco Canyon had passed rather abruptly from a P. I to a P. III society. So direct a transition in human culture appears physically possible for the valley fill records no break in sedimentation; hence the environment must have been relatively uniform during the change.

As previously stated, numerous relics of the Pueblo III people have been found in the upper 4 feet of the main body of the valley alluvium. Most distinctive of these remains are house walls which, in a number of instances, rest on undisturbed material 3 feet or more below the general surface. There is no better example than the small house on the south bank of the arroyo, opposite Pueblo del Arroyo. Its relationship to the underlying strata is clearly shown in plate 6, upper. One corner had recently been undermined when Jackson first noted its precarious situation in 1877. Since then the little house has paid annual tribute to Chaco floods and its complete destruction is only a matter of time.

Near section No. 2 (p. 53) the foundations of another small building reach a depth below the surface of 8 feet, but this is exceptional. Apparently at this site the alluvial fan of the adjacent tributary has been built up several feet above the normal level.

THE BURIED CHANNEL AND ITS SIGNIFICANCE

One of the notable discoveries of W. H. Jackson during this keen observer's visit in 1877 was a buried channel just south of Pueblo del Arroyo, 14 feet deep and containing numerous potsherds, flint

chips, and other human relics (Jackson, 1878, pp. 443-444). Unquestionably this exposure was among those later seen by Prof. Richard E. Dodge and reported in published excerpts from his field notes of 1899 and 1901 (*in* Pepper, 1920, pp. 23-25). It is perhaps only natural, therefore, that the present writer, although these earlier discoveries were unknown to him at the time, should have happened upon the same ancient channel mentioned by Jackson and Dodge.

As shown in plate 7, lower, this buried channel is round-bottomed and crescentic in cross section. Its boundaries are sharp and clearly cut across the horizontal bedding of the older valley fill. The materials within the channel are such as might be expected: gravel and cross-bedded sand 3 to 4 feet thick form the base of the deposit and are succeeded by clay which, in turn, is overlain by successive beds of sand and sandy clay. The first clay bed seems to indicate a ponding of floodwater in this channel while the main floods were diverted into another. A series of sandstone blocks in the clay bed resembles stepping stones placed to provide a passage over the mud but such an explanation of the blocks, though plausible, can scarcely be considered as established.

Buried potsherds, broken bones, and beads were revealed also in a reentrant of the modern arroyo which existed in 1924 and 1925 a few yards from the south wall of Pueblo del Arroyo and a hundred feet, more or less, west of the exposure described above. The potsherds included some of the latest varieties of pottery made in Pueblo Bonito and were, according to Mr. Judd, produced somewhere around A.D. 1100. Although this deposit was visible for about 75 feet its lateral contacts were, at the time of my examination, unfortunately obscured by a small gulley on the east and by unusually severe weathering on the west.

With two exposures in line, extension of this buried channel eastward under the plain before Pueblo Bonito was obvious. To provide a third contact, a test pit (pit No. 4) was dug 60 feet back from the edge of the bank where the channel was first observed. At a depth of 18 feet sherds of the latest Pueblo Bonito pottery were found, proving this pit to be located in the buried channel.

Nearer Pueblo Bonito, Judd's test pit No. 3 was deepened and more late pottery was discovered. Next, a trench previously dug through the west refuse mound as a means of studying its composition was extended out into the flat. In this extension the north bank of the buried channel was clearly profiled. The channel filling, marked by coarser material, rests unconformably on the edge of the old refuse mound and on strata of the main valley fill.

Farther east, an outcropping in the north wall of the present arroyo gave still another point and thus enabled us to indicate the course of the buried channel as it passed Pueblo Bonito. In 1936 Senter (1937) dug pits near Pueblo Chettro Kettle and likewise exposed a buried channel containing potsherds of late date. From the position given, however, I would judge his buried channel to be a branch of the arroyo produced by the stream which drained the reentrant in the cliffs back of Chettro Kettle.

A careful reading of Jackson's account shows that there was in 1877 an abandoned side channel 8 feet deep, or half that of the main arroyo, between the latter and the ruins of Pueblo del Arroyo. This side channel ("old arroyo" of his map) still existed, in part at least, in 1925. It must be distinguished from Jackson's buried channel which he describes as 14 feet deep and marked by "an undulating stratum of broken pottery, flint chippings, and small bones firmly embedded in a coarse gravelly deposit." This stratum he first observed below masonry walls exposed by the side channel above referred to—walls that did not show on the surface. He traced the stratum upstream "several rods" in the vertical north bank of the main arroyo, noted its presence also on the opposite side, and followed it thence farther upstream to the small ruin shown in plate 6, upper. The stratum reached its lowest level 14 feet below the surface, or 2 feet above the bed of the main arroyo, a fact that led to Jackson's conclusion: "Since the desertion of this region the old bed has become filled to the depth of at least 14 feet, and through this the arroyo has made its present channel." (Jackson, 1878, p. 444.)

In 1924 and 1925 the walls of the "side channel" were much weathered and waste from the Society's excavation of Pueblo del Arroyo had been dumped into the main arroyo southeast of the ruin in an effort to check further erosion. The exposures described by Jackson had been destroyed in the widening and deepening of this arroyo but in an excavation made for a storage cellar back of the old Wetherill "hotel," the northern border of a channel containing late Bonito pottery could still be seen.

When considering the significance of the buried channel described above, I have often thought of it as the "post-Bonito channel" because late Bonito potsherds on the bottom of it identify the channel with the final years of Pueblo Bonito or even later. In 1925, by means of test pits in the plain that lies in front of Pueblo Bonito, we traced this old channel eastward from the exposure near Pueblo del Arroyo for more than 1,000 feet. The lenses of clayey gravel and other materials found in those pits were thoroughly characteristic of channel deposits. Late

Bonito pottery fragments were found from 10 to 18 feet below the surface in test pit No. 3 and from 7 to 15 feet below in pit No. 4. Additional exposures enabled us to plot the channel's course with a high degree of accuracy for several miles.

That this buried channel is part of a continuous arroyo once extending the full length of Chaco Canyon seems definitely established. The existence of such a through channel is proof that there intervened during alluviation of the valley a period of arroyo formation and dissection similar to the present. To put it another way, an early period of alluviation, represented by the main valley fill, was followed by a period of dissection that included our post-Bonito channel. After an unknown interval alluviation was again resumed, the arroyo system was filled up and some slight addition made to the valley deposits, and alluviation, or at least a balance between alluviation and erosion, was continued down to the year 1860 to be interrupted in the ensuing decade by formation of the present arroyo.

Such a history appeals to the imagination by reason of its symmetry and because of the nice correlation with human history that can be made, as outlined in a later part of this paper. However, the importance of the issues involved requires that available evidence be examined with care.

The buried channel, as exposed in various places, is round-bottomed although vertical side walls have been detected in a few instances. Vertical walls are to be expected in any through-flowing arroyo. However, as previously pointed out, local conditions often prevented a critical study of side contacts of the old channel. The present arroyo, which coincides very closely with this post-Bonito channel throughout much of the area under examination, has, by reason of its greater width, removed all traces of the buried channel over considerable distances. Sections of the old channel have been discovered largely through search for lenses of gravel containing late-Bonito potsherds, and in many localities the side contacts of the old channel are poorly exposed. The best evidence found that however round-bottomed the channel may have been, its walls were generally vertical, is its known length and presumed extension both ways.

Supporting evidence that the post-Bonito channel is part of a continuous arroyo is given by the existence of lateral channels representing its important tributaries. A mile downstream from Pueblo Bonito there is an indentation of the north canyon wall which we called "the Rincon del Camino." The present road to Farmington and Aztec goes this way. Drainage from a considerable area falls over the cliffs at the head of this rincon and reaches the main arroyo through a half-mile-

long tributary (pl. 8, upper). The material exposed in this tributary
consists of irregularly bedded yellow sand, numerous lenses of dirty
gravel, and a few lenses, 2 to 6 inches thick, of laminated dark clay.
All this material, except the clay, is similar to that now carried by the
tributary stream and was undoubtedly derived exclusively from the
drainage of Rincon del Camino. Similar sand and gravel are exposed
in the north wall of the main arroyo for about 300 yards east of the
tributary.

There is thus a triangle of material derived from the alluvial fan of
the side stream extending from the main arroyo to the head of the rin-
con, as outlined in figure 1. This triangular mass contains no material
from upstream except the clay beds, and evidently the area could not
have been occupied by the main stream of the canyon during deposi-
tion of the fan. All other evidence, however, leads to the conclusion
that during the period of alluviation the main stream wandered at will
over the canyon floor. If, however, an arroyo similar to the present
one had been formed, contemporary drainage from Rincon del Camino
might easily have excavated a tributary large enough to carry away
and destroy the main valley fill over the entire triangular area shown
on the map. If conditions of alluviation were restored thereafter and
the main arroyo began to fill up, the excavated area would also be
filled. The waters of the main arroyo could, however, enter the area
only as a gentle overflow or backwater from which clay similar to that
of the clay lenses would have been deposited. Most of the filling would
consist of sand and gravel brought in by the tributary stream. It seems
obvious, therefore, that the fan of Rincon del Camino is later than the
main valley fill and was deposited after a period of erosion.

That the area was occupied by human beings during this episode is
evident from discovery, at the place marked section 9 on figure 1, of
several hearths from 10 feet to 12 feet 8 inches below the surface
(pl. 9, lower). A short distance away two potsherds were found in
gravel lenses, but they are undecorated ware of indeterminate age. A
small sherd collection, gathered among lumps fallen from the bank of
the main arroyo but derived from the fan of Rincon del Camino, con-
sists also of fragments indeterminate as to age.

The human remains before us, therefore, do not afford reliable evi-
dence of the synchronous erosion and refilling of the post-Bonito chan-
nel and the triangular area at Rincon del Camino. However, it seems
impossible to account for the type of sand and gravel found here ex-
cept on the theory that it was deposited in an area excavated during
an earlier period of erosion. The alluvial fan of Rincon del Camino
presents general evidence, if not conclusive proof, of a period of ero-

sion and sedimentation contemporaneous with the cycle postulated from a consideration of the post-Bonito channel.

The sequence of geologic events in Chaco Canyon, if the post-Bonito episodes of erosion and sedimentation be accepted, may be summarized as follows:

Recent geologic events in Chaco Canyon

Process	Event	Date
Erosion	Formation of existing arroyo system	1860 to present
Sedimentation	Filling of channels	After completion and perhaps after abandonment of Pueblo Bonito
Erosion	Formation of a main arroyo for full length of canyon and formation of tributary arroyos	Probably post-Bonito
Sedimentation	1. Deposition of upper 4-ft. zone transitional with lower zone	Pueblo III period
	2. Deposition of zone from 21 to 4 ft. below surface	Pre-pueblo (Pit House and earlier?) period
	3. Deposition of unknown amount	Unknown, probably post-Pleistocene

Possible alternations of erosion and sedimentation not as yet differentiated.

Erosion	Formation of canyon	Unknown, probably Pleistocene

The twofold character of the valley fill is thus well established. The buried channel has been traced from near Una Vida to a point about 1½ miles below Pueblo Bonito where it becomes so large that remnants of the main valley fill cannot be identified.

BURIED CHANNELS SIMILAR TO THE POST-BONITO CHANNEL ON OTHER STREAMS

Discovery of the post-Bonito channel led to a search for a similar division of the flood plains of other streams in northwestern New Mexico. The data obtained are here summarized although it is recognized that the importance of the subject requires additional field study and more complete description.

In 1925 buried channels were detected in the walls of Arroyo en Medio and Arroyo Cedro, both tributaries of the Rio Puerco by way of Arroyo Chico. In 1927 a well-defined buried channel was

found and mapped for half a mile in the arroyo of Rio Puerco, between the towns of Cuba and La Ventana. In neither of these localities were potsherds or other human relics found in the deposits of the channel. On Rio Puerco I picked up two sherds of black-on-white pottery that clearly had fallen with a portion of the arroyo bank, but the exact position in which they were deposited is not known. They merely indicate that part of the valley fill was laid down during a time when prehistoric Puebloan peoples inhabited the valley.

In 1929 buried channels were also discovered in the floors of Tijeras and Coyote Canyons on the west slope of Sandia Mountains. In Coyote Canyon many evidences of human occupancy during deposition of the valley fill were found. Hearths, bones, charcoal, and potsherds occur but the localities are so disposed that none provided the critical data that would date the channel.

In 1928 a buried channel was discovered on Galisteo Creek at the town of Galisteo, in Santa Fe County. A similar one occurs west of the road crossing and rock falls on San Cristobal Creek, just below the pueblo of San Cristobal. The channel on Galisteo Creek was carefully traced and mapped. It obviously underlies and therefore must be older than Pueblo Galisteo (Bryan, 1941, p. 231). This particular ruin (Nelson, 1914) contains potsherds which are all of glazed types and no part of it appears to be older than the Pueblo IV period, comparable to Pecos Glaze II (personal communication from A. V. Kidder).

GEOLOGIC EVIDENCE ON THE MEANS OF LIVELIHOOD OF CHACO CANYON PEOPLES

All peoples known to have occupied Chaco Canyon in prehistoric times were dependent for sustenance largely upon agriculture. The Navaho now living there are principally stock raisers, but nearly all of them plant fields of a sort. Two small patches of corn were to be seen near Pueblo Bonito in 1924; farther upstream, beyond Pueblo Pintado, fields were larger and more numerous. The Bonitians, however, lacked domestic animals and although the hunting in their day may have been better than it is now the major part of their food supply doubtless came from cultivated plots.

As pointed out heretofore, the present climate of the Chaco area is unfavorable to agriculture by reason of the unreliability of rainfall, particularly in June and July, and because of the comparatively short growing season. Elsewhere irrigation makes possible the growth of most crops common to the temperate region; corn, beans, and squash, still staples of Indian tribes throughout the Southwest, are known from

frequent finds in excavations to have been the main crops in prehistoric times. During the course of this investigation we were constantly on watch for evidence of local irrigation with living water—and found none.

The floor of Chaco Canyon has no irregularities that are not entirely natural in origin except wagon roads, mounds covering ruins, and an ill-advised ditch built some years ago by a white man. The banks of the modern arroyo were carefully inspected for traces of ancient irrigation ditches but none was found in the main valley fill. Such negative evidence would be of little value were it not a fact that in every country in which living water is used for irrigation the ditch banks are routes of travel and are thereby compacted. It is inconceivable that, if ditches had been used by the ancient inhabitants of Chaco Canyon, all their compact ditch banks would have been destroyed, especially when the processes of alluviation were so gentle that charcoal in hearths was buried with little disturbance. Under such conditions the hard-packed surfaces of ditch banks should also have been preserved.

Materials of the valley fill, as already described, do not indicate that there ever was a stream of living or perennial water in Chaco Canyon during the two periods of alluviation determined by these investigations. Such materials all appear to have been laid down during muddy floods similar to those now characteristic of Chaco River. Irrigation by means of a system of ditches continuously maintained is hardly practical on such a stream. Thus geologic interpretation confirms the negative evidence of the ditches and indicates that the prehistoric peoples of Chaco Canyon did not practice irrigation as we commonly understand it. However, in selected places they could have farmed successfully by irrigating with flood water or, as it is usually called, "floodwater farming." For this method the floor of Chaco Canyon, save for the presence of its modern arroyo, is entirely suitable.

FLOODWATER FARMING

The ordinary rainfall throughout most of the southwestern United States and northern Mexico is insufficient to grow crops. Such lands, however, as are overflowed by the muddy water of ephemeral streams or by rainwash from hillsides will support a hazardous agriculture. Floodwater farming was first adequately described by Gregory (1916, pp. 103-105) and a rather complete account with maps of fields has recently been published by the present writer (Bryan, 1929). The additional data given herewith apply particularly to conditions that once obtained in Chaco Canyon.

Gregory (1916, pp. 104-105) outlines, as follows, the methods and results of floodwater farming in the Navaho Country, an area that includes Chaco Canyon:

From experience and tradition the Indians have learned to know the areas liable to be flooded during occasional showers as well as those annually inundated by the successive rains of July and August. Along the flood plains of the larger washes the practice is to plant corn at intermediate levels in widely spaced holes 12 to 16 inches deep. The grain germinates in the sand and rises a foot or more above the surface before the July rains begin. With the coming of the flood the field is wholly or partially submerged. After the water has receded parts of the field are found to have been stripped bare of vegetation and other parts to have been deeply buried by silt; the portion of seeded ground remaining constitutes the irrigated field from which a crop is harvested. The Hopis, and to a less extent the Navajos, sometimes endeavor to direct the floods and to prevent excessive erosion within the fields by constructing earthen diversion dams a few inches to a foot or more in height—dams which require renewal each season. . . . Much work is done by the Indians while the flood is in progress, and an everyday sight during showers is the irrigator at work with hoe or stick, or even with his hands, constructing ridges of earth or laying down sagebrush in such a manner as to insure a thorough soaking of his planted field. By these methods of flood irrigation the Navajo and Hopi together cultivate about 20,000 acres of land widely distributed over the reservation in fields about 3 acres in average size, rarely exceeding 200 acres.

Similar methods of cultivation are in wide use throughout the plateau of Mexico and in New Mexico and Arizona (Hoover, 1930, pp. 437-438; Hack, 1942, p. 26). The Mexican calls such a field *sombrado* (planting) or *temporal* (temporary field). The Nahuatl word *milpa* is also used. In favored localities and usually at high elevations these terms are applied to fields dependent on rainfall alone but generally flood irrigation from the rainwash of higher slopes or from ephemeral streams is essential to a crop.

Since they were first visited by whites in 1698 and doubtless long before, the Papago Indians of southern Arizona have supported themselves largely by floodwater farming pursued on the broad plains of their undissected desert valleys. Corn, squash, and *tepari* beans are their main crops (Lumholtz, 1912; Bryan, 1925b; Hoover, 1929).

Floodwater farming for the production of stock feed is widely practiced in northern Nevada. Quinn River valley (Bryan, 1923b) may be taken as typical. The valley—

is bordered on the east by the Santa Rosa and Buckskin mountains and on the west by the Quinn River Mountains. It heads in Oregon about 10 miles north of the Nevada line and extends southward about 45 miles to the Slumbering Hills, which separate it from the broad valley of Humboldt River. The valley is 10 to 12 miles wide and is drained by Quinn River, which runs southward through it for about 40 miles, turns west, and, passing south of the Quinn River

Mountains, is lost in the Black Rock Desert. The river is formed about 4 miles south of the Oregon line by the union of East Fork of Quinn River and McDermitt, Washburn, and other creeks. Its drainage basin includes about 1,164 square miles.

The valley floor consists of plains formed of beds of sand, gravel, and clay deposited by the existing streams. A small part of the valley bounded by a line of bluffs that extends from the Oregon line east of McDermitt southeastward to the National mine differs from the larger part in that the streams flow in flat-bottomed valleys that lie 50 to 100 feet below the level of sloping plains formed by the same streams at an earlier time, when they flowed at a higher level. In general, however, each stream, on leaving the mountains, wanders through circuitous and branching channels over the alluvial slopes to the axial flat, where it joins in grassy meadows the small meandering channel of Quinn River.

The region is arid, none of the streams containing water throughout the year. The principal streams carry considerable water or are in flood in the spring, when the snow on the mountains is melting. The spring floods are not violent, and the water, which may be almost clear, is easily diverted into semi-permanent ditches to irrigate the cultivated fields. In the axial flat there are large fields that are irrigated from Quinn River or from its tributaries. Near the mouths of the canyons of the principal mountain streams there are smaller fields, many of which are irrigated by the water of streams that seldom reach the lower, larger fields. About 14,000 acres is irrigated. Native grasses, which are used both for pasture and for hay, form the principal irrigated crops, but there are also fields of alfalfa and small grain.

Paradise Valley lies east of the Santa Rosa Mountains and is enclosed on the north and northeast by unnamed volcanic plateaus and mountains and on the east by the mountain range that culminates in Hot Springs Peak. It is drained by Little Humboldt River, which is formed by the union of Indian, Martin, and other creeks with the east fork of Little Humboldt River. The topography of this valley is like that of Quinn River Valley, though the central flats are wider and the area irrigated is larger.

In both valleys communication with centers of population elsewhere is difficult. The distance from some of the ranches to Winnemucca, the nearest railroad station, is more than 60 miles. Only cattle on the hoof can be readily marketed, and the irrigated land is devoted to the raising of stock-feed. In April and May the cattle are turned loose in the plains and lower foothills, where they browse on the sage, weeds and grass, and as the snow melts they gradually climb higher into the hills, reaching the summits in midsummer. As the cattle leave the valleys the ranchers begin to irrigate their land, starting with the first floods and continuing to use the water as long as it lasts. In August great quantities of hay are made from the native grass and from alfalfa.

The cattle begin to come down from the hills late in August and early in September—according to the local saying, "as soon as they hear the mowing machines." Late in September and during October the ranchers bring the last of the cattle out of the hills to the owners' fields, where they are pastured on the still green native grass and on greasewood until it is necessary to feed them hay. In ordinary years the cattle are brought through the winter in excellent condition.

About 13 miles east of Pueblo Bonito and beyond Pueblo Pintado, small Navaho fields are cultivated in the floors of valleys more or less obstructed by sand dunes. The effect of sand dunes in spreading the floods of ephemeral streams and in providing localities suitable for floodwater farming is also of large importance in the Hopi country (Hack, 1942). In canyons tributary to Arroyo Salado, in the Rio Grande drainage and some 70 miles east of Pueblo Bonito, there is limited floodwater farming. The Cañada (de) las Milpas doubtless had, before the existing deep arroyo was formed, enough fields to justify its name. Here, as late as 1922 on hill slopes at Juan Chaves's ranch, there were two small fields irrigated by the runoff from high bluffs. In 1921 the writer saw in Rincon de Lopez 40 to 50 acres of corn and beans that had been irrigated by floodwater.

About 10 miles from Cañada las Milpas is Bernalillito, a locality so called because people from Bernalillo on the Rio Grande 35 miles distant formerly moved there each summer to plant and tend their fields. Bernalillito Wash heads on the eastern escarpment of the Mesa Prieta and flows in a broad flat valley eroded in shales and sandstones about 10 miles east to a narrow gap in a massive sandstone cliff. Below this cliff there is a canyon in places broad and in others narrow. About half a mile below the cliff is the single ranch house of Bernalillito. Nearby is one field of 15 acres suitable for planting corn and beans and to one side a smaller area where hay may be cut. The sandy alluvial fan of a tributary gulch causes the main flood to spread and the gentle overflow makes possible the cultivation of the field and the growth of grass on the meadow. The flood is also caused to spread more widely by a low dam of brush and stone (*atarque*) at the lower end of the field. Just below field and meadow is the headwater falls of an arroyo which has already dissected similar flats in the canyon below and now threatens to destroy the remaining fields. In 1920 this ranch came under the control of H. M. Bryan, who has planted with the results shown in the table on the following page.

The years 1920 to 1923 were generally unfavorable in this part of New Mexico and similar planting in years of greater rainfall might have produced better results. However, the flood of September 1921, which broke down and washed out part of the corn, is an incident that might happen any year. When this flood arrived, a bean crop estimated at 1,000 pounds was ready for harvesting but only 200 pounds —the equivalent of the seed planted—were saved. Similarly, the loss from intruding cattle that broke through the outside fence to obtain water in 1920 and 1922 might have been avoided. Such hazards are, however, a part of this type of farming although the prehistoric flood-

Upper: The Chaco in flood. Tents of a General Land Office surveying party at left; men on opposite bank and rider at right stand on approaches to the wagon crossing. Pump on Wetherill's well, destroyed a few weeks later, is seen above the fourth horse from the right. (Photograph by Neil M. Judd, 1921.)

Lower: Middle south wall of Pueblo del Arroyo with a partially refilled section of Jackson's "old arroyo" in the foreground. (Photograph by Neil M. Judd, 1920.)
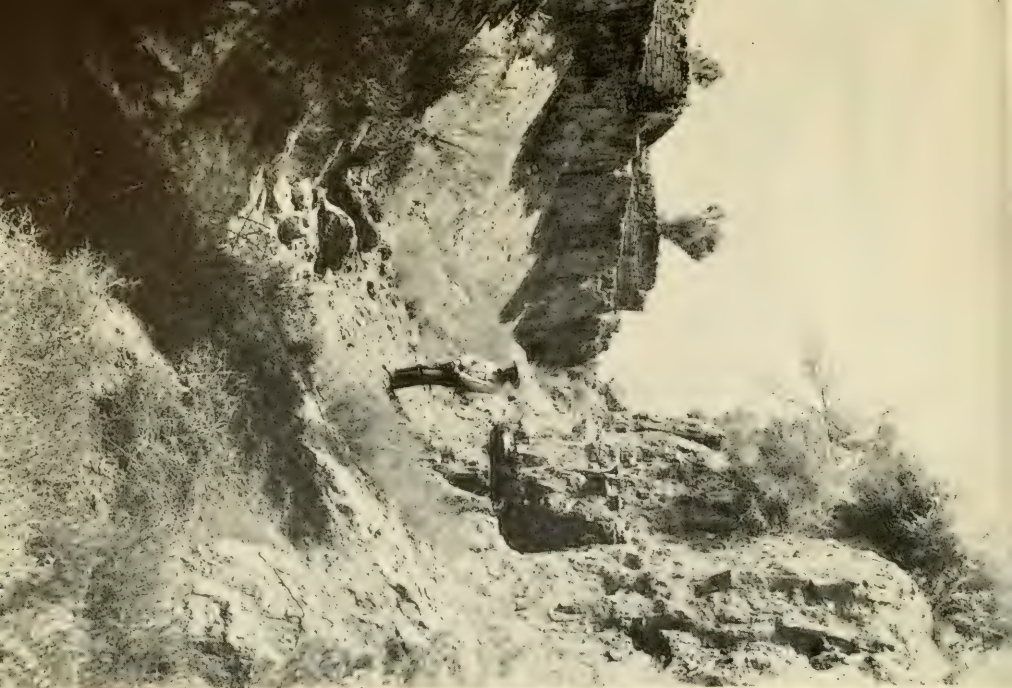
PLATE 11

Left: A pit house with floor 13 feet 6 inches below the present surface, 9 miles east of Pueblo Bonito, had been long forgotten before the Pueblo III village was constructed on an upper level a few feet distant. (Photograph by Neil M. Judd, 1926.)

Right: An Early Pueblo cooking pot covered with a sandstone slab lay 6 feet below the surface of a sand dune in Wirito's Rincon, about 1½ miles southeast of Pueblo Bonito. (Photograph by Neil M. Judd, 1927.)
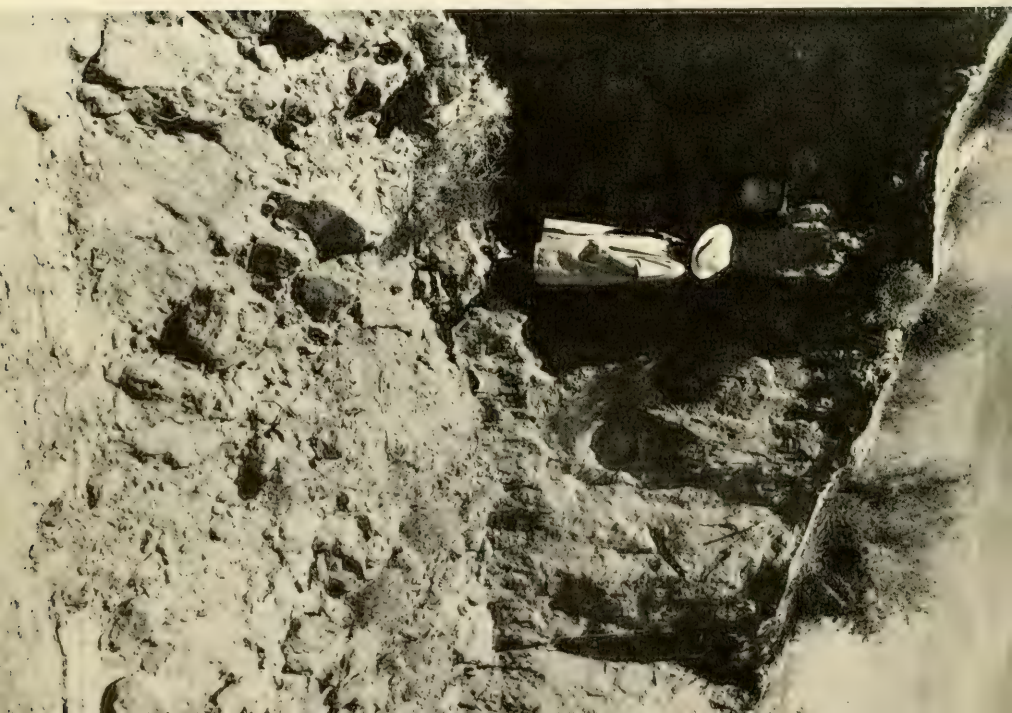
Crops at Bernalillito, N. Mex., 1919 to 1925
(Data furnished by H. M. Bryan)

Year	Corn	Cropped forage	Beans	Natural hay	Remarks
1919	Not planted	Not planted	Not planted	10 tons	Good year; no planting
1920	None	None	None	None	Good year; no planting
1921	Fair	5 tons corn fodder	200 pounds	Fair, pastured	Flood in September destroyed 800 pounds of beans and destroyed corn fodder
1922	Few good ears	None	None	None	June flood gave corn good start but it was eaten by cattle. $100 crop damage collected
1923	50 bushels gathered	Corn fodder	None	2 tons	Corn not properly cultivated, but favorable year
1924	Small crop	2 tons barley hay	About half of expected crop	8 tons hay and Russian thistle	Three floods in August and September made harvesting difficult
1925	Not planted	Not planted	Not planted	Pastured	Floods, Aug. 8, 15, and 16, Oct. 9 and 12

NOTE.—In 1925 no planting was done and the land was encouraged to revert to grass. In the fall of that year a stand of grass about 30 percent of full stand had been attained.

water farmers were saved at least the risk due to domestic animals. It is true also that this piece of ground was poorly farmed during these years. The owner at the time was a sheep man whose herds during the summer season were in the mountains more than 60 miles away. Consequently the farming was done during intervals of other, more important work, and by hired labor. Cockleburs and Russian thistle grow so rapidly that strict attention to cultivation is necessary. Because this attention could not be given, the owner converted the plowed land into meadow with the intention of cutting hay for winter use.

The record of these six years indicates that, with an adequate reserve for lean years, this field would support a family requiring no more than was necessary for prehistoric Pueblo peoples. But this family would need to give the crop the constant attention which modern Hopi lavish on their own fields.

It is obvious that the condition of aggradation that once prevailed in the valleys and canyons of the Southwest was favorable to floodwater farming. At that time the floods spread widely and were confined to channels at only a few places. Small localized showers that fell on the walls of canyons, if sufficient to produce runoff, flooded the adjacent flat floor, whereas now the runoff flows into an arroyo below the general level of the plain.

Water that soaked into the ground could not so easily drain away and consequently underlay the valley floors at moderate depths. It was thus available to supply the roots of trees and bushes which doubtless once flourished in valleys where they are now absent. At favorable places, lakes and swamps existed in which grew the rushes (tule) frequently found in prehistoric ruins. Because of this higher water table a thinner layer of earth was dried out between floods; smaller floods were sufficient to wet the dry ground. These smaller floods also covered larger areas since less of their flow was absorbed by the dry ground. The result of such a regimen was a denser vegetation on the canyon floors.

Of this denser vegetation an important part was perennial grasses. Even today where floods spread widely over the floors of undissected tributaries to Chaco Canyon there is a fairly dense cover of perennial grass, usually alkali sacaton. Meadows of this type were so numerous in the Rio Puerco region, 80 miles to the southeast, that a principal occupation of the Mexican inhabitants in the late 1890's was the cutting of hay to be hauled 30 miles or more to market in Albuquerque.

The presence of these meadows was advantageous to white men, and their destruction by the formation of arroyos has been a distinct loss. The forage they were capable of producing naturally was of no

value to prehistoric farmers without domestic animals to feed, and their agricultural potentialities remained untested because those same prehistoric farmers lacked tools adequate to the task of uprooting sod. At the present time grass is apt to grow thickest on the more clayey soils and, to the extent that they are effectual in spreading flood-waters, grassy areas tend to postpone arroyo cutting. The inhabitants of Pueblo Bonito undoubtedly planted on the sandier soil bordering such grassed areas, on alluvial fans below the cliffs, and along the vague and meandering course of the main stream. Such soils were more or less disturbed by successive floods but, despite annual loss of part of the planted crop, they were doubtless recognized as the best agricultural land because of their superior tilth and relative freedom from deep-rooted perennial grasses.

In 1921 Mr. Judd dug a trench 20 feet in depth to study the stratigraphy of the west refuse mound at Pueblo Bonito. Four years later when he extended it out into the flat fronting the mound, the trench cut across several obviously artificial canals or ditches. They ran parallel to the front of the refuse mound and, therefore, essentially east and west. They were from 4 to 10 feet wide and were enclosed on the downhill (south) bank by walls of slushed mud (adobe) laid with care and in places supported by the dumping of house refuse. Filled with both fine and coarse materials, including Late Bonito potsherds, these ditches presumably had carried floodwaters from upcanyon, perhaps from the rincon of Chettro Kettle, to fields west of Pueblo Bonito. As each filled up or was washed out, a new one was constructed along the same route. Such more or less temporary ditches for the spreading of water are fairly common features of floodwater fields in New Mexico. If these before Pueblo Bonito were more elaborately constructed than is usual, it is doubtless because they lay close to the village where labor was readily available. The data Mr. Judd has gathered relative to comparable structures for control of floodwaters in Chaco Canyon will be presented by him in connection with the subsistence problem of the Bonitians.

ARROYO FORMATION AND FLOODWATER FARMING

From the foregoing it should be evident that in Chaco Canyon conditions were favorable for floodwater farming from the beginning of alluviation. The area available also gradually increased as the plain widened with the filling of the canyon. The canyon, therefore, afforded a locality for the initiation and development of a civilization based on agriculture. That this agriculture was precarious and that crops might fail owing either to lack of rain and consequently of floods, or to the

occurrence of unusually cold seasons, does not constitute a factor that would prevent the development of a local community of relatively high culture. These hazards merely limit the number of people and fix their standards of living. In pre-Spanish times the Hopis are said to have insured themselves against crop failure from these causes by the storage of a year's supply, or more. A like necessity may have been one of the compelling causes which led to development of more houses and a house cluster more elaborate than the simple pit dwelling.

The same comments may be applied to the problem of water. Lack of a local water supply does not prevent the use of suitable floodwater fields, for at the present time the Hopi farmer may cultivate tracts 10 or even 20 miles from his home. Moenkopi, 40 miles northwest of Oraibi, was a farming community when seen by Oñate in 1604 and remained so until the Navaho forced its temporary abandonment about a century ago. An alluvial plain in the process of sedimentation always has local depressions which fill with water after rains or floods. These pools or *charcos* (Bryan, 1920) afford a limited water supply during the growing season. The Papagos of southern Arizona were entirely dependent on charcos during the planting and harvesting of their crops until, within the past few years, the United States Indian Service drilled wells at the fields. Before coming of the Spanish, these Indians not only cultivated the same fields while dependent on charco water but carried the crop on their backs to winter residences located at permanent, or at least longer lasting, water many miles distant. Thus lack of permanent water is not necessarily a hindrance to floodwater farming, although it may be an obstacle to permanent residence.

In Rincon del Camino one of the Navaho workmen employed by the Pueblo Bonito Expedition developed a small spring in a rock shelter or niche under a cliff. At other similar localities on the north side of Chaco Canyon the rock is damp and covered by an efflorescence of salts. Here it might be possible to develop water by systematic digging, and springs of this type may have been the principal source of domestic water to the ancient people. It is certain that a very slight increase in rainfall over the present annual average would produce springs in such localities.

Conditions of alluviation lead also to a relatively high water table. At present, water may be obtained by digging about 10 feet below the bed of the arroyo, or some 40 feet below the plain. Before the modern arroyo was cut the stream ran in a shallow channel and ground water must have saturated the valley fill to within 10 feet of the surface, a distance comparable to the present depth of water below the bed of the arroyo. As the dry season advanced, the prehistoric peoples may have scraped holes in low places and thus formed a primitive type of well.

No evidence of such wells has been found but the digging of them would have been entirely feasible for the inhabitants of Pueblo Bonito even though they lacked metal tools.

The formation of an arroyo similar to the present one, or the one we have called the post-Bonito channel, confines floodwaters to a narrow belt below the level of the plain. The ground-water level is also lowered and floods from tributaries are less effective in wetting the ground. Farming by means of floodwater is consequently impossible over the whole plain and is limited to insignificant areas.

If, therefore, the geologic chronology tentatively outlined on page 37 be accepted, Chaco Canyon enjoyed a relatively long period of alluviation with conditions favorable to floodwater farming. As indicated by finds of potsherds and other relics, people of Early Pueblo culture occupied the valley at least during the time required to build the fill from a level 21 feet below the present surface to 4 feet below. The favorable conditions then existent led to development of the relatively complex civilization of the Great Pueblo period, a culture that flourished during deposition of the upper 4 feet of valley fill.

Formation of the arroyo system represented by the post-Bonito channel may be given as the approximate cause for abandonment of the valley by these Pueblo III people, although other factors such as war, invasion, disease, or gradual decrease in means of subsistence may also have had their effect. However great the changes these other factors might have produced, it seems unlikely that any one or two of them would have kept out of use for long a place so eminently suitable for floodwater farming as Chaco Canyon.

CAUSE OF ALTERNATE EROSION AND SEDIMENTATION

If, as outlined in the preceding pages, the alternate erosion and sedimentation in Chaco Canyon resulting in the production of a plain of alluviation suitable for farming at successive times and the dissection and partial destruction of this plain in the intervening intervals is an adequate cause for the rise and destruction of human cultures, the ultimate reason for changes in the habit of streams becomes of large importance. A river or stream deposits sediment when it has a load greater than it can carry on a given grade. It erodes when it can carry more material than is furnished to it. The quantity of water, variations in this quantity, grade, supply of sediment, size of grain of the sediment, and shape of the channel are factors which determine the habits of a stream. The complex interrelationships of these factors are difficult to determine quantitatively, and are summed up in the

word "regimen." The regimen of streams in the Chaco Canyon region is such that they now erode whereas formerly they deposited material on the canyon floors.

As this change in regimen is general, general causes must be sought. A number of writers [5] attribute the present epicycle of erosion to introduction of livestock. Formation of trails and destruction of vegetation by overgrazing are supposed to have concentrated floodwaters and to have allowed these floods to erode the present channels. The argument of these writers is best expressed by Duce (1918, p. 452) : "We may, therefore, summarize the effect of cattle by saying that they increase the rapidity of the run-off and the rate of erosion by destroying vegetation, by compacting the soil, and by forming channels for the passage of water."

The apparent coincidence in time of the initiation of overgrazing and the beginning of dissection is significant and more data on this phase of the problem are needed. Coincidence of settlement and the deepening of the channel of Rio Puerco seems well established (Bryan, 1928a). The theory that erosion is caused by a slight uplift and increase in the gradient of streams has been generally rejected because erosion of about equal magnitude affects streams of different drainage systems that flow in all possible directions. Uplift so nicely adjusted to the drainage pattern is inconceivable.

Huntington (1914, pp. 33-34) was doubtless the first to advocate a climatic change as the cause of erosion, and Bryan (1923a, pp. 77-80) has brought together available evidence that a slightly wetter climate was characteristic of southern Arizona at the time of the first Spanish explorations.

Gregory (1917, pp. 131-132) advocates climatic change and rejects the argument for overgrazing in the following words:

It is important to note in this connection that the balance between aggradation [alluviation] and degradation [erosion] is nicely adjusted in an arid region where the stream gradients are steep, and that accordingly small changes in the amount of rain, its distribution, or the character of storms and changes in the amount and nature of the flora result in insignificant modification of stream habit. Even the effect of sheep grazing is recorded in the run-off, and this influence combined with deforestation has been considered by many investigators as the sole cause of recent terracing in the Plateau province. For the Navajo Country these human factors exert a strong influence but are not entirely responsible for the disastrous erosion of recent years. The region has not been deforested; the present cover of vegetation affects the run-off but slightly, and parts of the region not utilized for grazing present the same detailed topographic features as the areas annually overrun by Indian herds.

[5] Dodge, 1910; Thornber, 1910; Smith, 1910; Rich, 1911; Duce, 1918; Olmsted, 1919.

Reagan (1922, 1924a, 1924b) presents the interesting hypothesis that prehistoric peoples, by means of small reservoirs, check dams, and embankments designed to spread floods, used or distributed most of the water so that floods of the main arroyos were decreased in volume and violence. Hence, sediment was deposited and the arroyos filled up. When these ancients disappeared and their structures fell into decay, erosion was resumed. Reagan also supposes that the prehistoric peoples killed off the game, and thereafter the vegetative cover increased until it gave a maximum of protection to the soil. This cover was destroyed with introduction of domestic animals after the Spanish conquest. Thus Reagan assumes that the structures built by prehistoric men were sufficient to reduce floods without complete consideration of the difficulties involved. He ignores the fact that alternation between erosion and alluviation began before entrance of the Puebloan peoples into the area. The earlier epicycles could not have been influenced by such causes as Reagan advances.

Olmsted (1919, p. 88) estimated the cost of check dams and bank structures for control of Gila River above the San Carlos dam site at a total of $6,401,029. Elaborate as these plans seem, engineers by no means agree that they are adequate to control floods on Gila River, much less to restore channel conditions to those obtaining before 1880. In recent years the Soil Conservation Service has built structures for control of erosion which exceed in magnitude anything possible to the ancients. Success has been rare and modest. That primitive man could erect barriers sufficient in number and size to accomplish this result seems improbable. If such attempts had been made, remnants should remain to be easily identified.

All the investigators mentioned above considered that they were dealing with only one period of sedimentation and one period of erosion, although Huntington thought these minor changes of the geological Recent were the latter part of a series of such changes running back into Pleistocene time. If the post-Bonito channel represents a valid cycle of erosion and sedimentation then three complete local cycles of erosion and sedimentation and part of a fourth must be explained. These events may be put in tabular form, as follows:

Cycles of erosion and sedimentation in Chaco Canyon

1st cycle	Erosion of canyon or later part of this erosion	Sedimentation and formation of terrace
2d cycle	Erosion of terrace	Sedimentation and formation of main valley fill
3d cycle	Erosion of post-Bonito channel	Sedimentation and fill of post-Bonito channel
4th cycle	Erosion of present arroyo	Future?

Presented in this form it seems evident that a postulate of climatic change has greater inherent possibilities as a true explanation of the facts. Domestic animals certainly cannot be charged with inception of the post-Bonito erosion. However great the influence of overgrazing, therefore, it must be regarded as a mere trigger pull which initiated an epicycle of erosion that was brought about by other causes.

Reagan (1924a, p. 285) has carried the factor of overgrazing into prehistoric times and suggests that incoming and increasing hordes of herbivorous animals may have overgrazed the country and thus caused formation of arroyos. Thereafter, the animals having starved to death or left the region, vegetation would again spring up and sufficiently protect the land surface so that streams would again begin to aggrade. Thus he postulates recurrent overgrazing with consequent cycles of erosion and aggradation. That animals in a state of nature would overgraze an area is an assumption without proof. It seems best to pass this interesting postulate since there exists ample evidence that at least one period of sedimentation in the not-distant past was wetter than the present.

Douglass [6] has described briefly the valley deposits of the Rio de Flag, a small creek near Flagstaff, Ariz. Here an arroyo dating from 1890 to 1892 has dissected a valley fill; standing stumps of pine trees are found from 4 to 16 feet below the surface and prostrate logs in the upper 4 feet. Both stumps and logs belong to the living species, *Pinus ponderosa*, now growing on the adjacent hillside. The stumps, however, have wide growth rings similar to those found in trees of humid lands. The prostrate logs have narrow rings like living trees of the region. It seems evident, therefore, that the zone from 4 to 16 feet below the surface was deposited under a climate much wetter than now. In addition, human relics have been found in the fill at depths from 4 to 9 feet but their relation to the stumps is uncertain. Evidence in the valley fill of the presence of man seems to indicate that the humid period demonstrated by the stumps is not very ancient. It may represent one of the cycles of sedimentation disclosed in Chaco Canyon or an older cycle not yet identified there.

Study of the Chaco Canyon deposits has not produced incontestable evidence that wetter climates prevailed there in the past. From the main valley fill—2d cycle of the table, page 49—we collected a few fresh-water shells but similar shells were also found in the post-Bonito channel. In some of the sandy and silty beds of the main valley fill impressions that resemble rushes were noted. The adobes are dark

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[6] 1924, pp. 238-239. This reference supplemented by an oral communication, and by inspection of the locality by me in September 1921.

brown from included organic matter, but this might have derived from a heavy growth of grass or other vegetation.

There is, however, nothing in the character of these sediments that precludes their deposition under a slightly wetter climate. It is possible there may have been a sufficiently greater rainfall so that pine trees grew in favored places on the hills, cottonwood and willows may have bordered the river, the valley floor may have had large areas of perennial grass and in a few places there may even have been marshy ground with cattails. Currently existing damp places under the north cliffs may have been small springs in times past. Such an environment seems compatible with the type of alluvium deposited and yet sufficiently favorable to have provided an adequate food supply for the peoples of the thirteen villages of Chaco Canyon. Such a climate cannot be inferred from the nature of the sediments themselves but, on the other hand, those sediments present no evidence that a relatively slight modification of climate did not exist when they were being deposited.

[NOTE.—Bryan's speculations in the foregoing paragraphs have been substantiated in large measure by data from our excavations and from further exploration. Our old Navaho neighbors reported pine stumps at various places about the valley; dead and prostrate pines were photographed on the south cliff and a couple of dozen trees and stumps were seen at the head of the canyon, 16 miles to the east (Douglass, 1935, p. 46). These last few remnants of former forests suggest that the annual rainfall in their time was considerably greater than our postulated 10-inch average for the present. Even more suggestive is the fact that thousands of logs, large and small, went into construction of Pueblo Bonito and its neighboring villages between A.D. 900 and 1100. The forests that furnished those logs must have been close at hand since none of the timbers we uncovered was scarred in transportation and such forests, at 6,500 feet, could have flourished as they did only in a climate somewhat wetter than that of today. Indeed, many of the old ceiling timbers from Pueblo Bonito exhibited growth rings so uniform in width they obviously had grown where moisture was fairly constant year after year. In addition, we know that rushes were then abundant and readily accessible, for quantities were utilized in the building of Pueblo Bonito.—N. M. J.]

DETAILED SECTIONS IN THE RECENT ALLUVIUM

SECTIONS IN THE MAIN VALLEY FILL

The following sections, measured at various places along the main arroyo, record the character and thickness of the several strata from

the top of the bank to its base, and give a record of human relics found therein. Each station is indicated on the accompanying map, figure 1, by its corresponding number.

Section 1

South bank of main arroyo, 200 yards east of expedition camp. No potsherds were recovered in this section but opposite, in the north bank, plain ware of coarse texture was found at a depth of about 12 feet.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Laminated dark clay and sand, more clayey above	4	0	4	0
Silt with streaks of clay........................	3	0	7	0
Sand	2	0	9	0
Laminated dark silt...........................	0	6	9	6
Silt and sand with thin streak of clay 18 in. above base	3	4	12	10
Dark clay, with shells........................	0	8	13	6
Sand	3	0	16	6
Covered below.				

PIT HOUSE

At the place on the map marked "Pit House" there was discovered in 1922 a structure partly destroyed by erosion of the arroyo bank. What remained was excavated and studied by Neil M. Judd, who has described it at length (Judd, 1924). It consisted of a single circular room with the middle of its slightly concave floor 12 feet 2 inches below the present surface. The original excavation was 6 feet deep (pl. 6, lower). The builders of this subterranean house lived when the flood plain was 6 feet lower than it now is, and doubtless they or their contemporaries are responsible for the human relics at deeper levels shown in the sections to follow.

Section 2

In a small tributary entering the main arroyo from northwest of Pit House.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Soil and clay, more sandy above...............	1	10	1	10
Sand	0	2	2	0
Clay	0	2	2	2
Sand	0	7	2	9
Clay	1	7	4	4
Hard compact sandy clay with fragments of charcoal and 2 potsherds........................	1	4	5	8

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Clay with scattered bits of charcoal and with fireplace at base marked by crescentic streak of charcoal and burned ground below...........	0	5	6	1
Sandy adobe	3	0	9	1

Near section 2 and in the same small arroyo, there is a ruined house now almost destroyed by erosion. Its foundations reach to a depth of 8 feet below the surface, yet the walls appear to be quite similar to masonry of the neighboring great pueblos and the potsherds are of both early and late types.

Two alternatives must be considered, either the pit house and this small pueblolike dwelling are contemporaneous, which is unlikely, or, granting that the pit house is older, the pueblo-type dwelling and section 2 are located in a later deposit.

Section 3

Section 3, on the south bank about 300 yards east of the pit house, represents a normal succession of beds. A potsherd at 4 feet below the surface is of undetermined type. Sherds found between depths of 17 feet and 20 feet 6 inches, are of Pit House or older age. This is the greatest depth at which potsherds were found.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Soil and clay, upper 8 in. the most clayey.......	2	6	2	6
Silt	1	0	3	6
Alternate layers of clay and silt; potsherds 6 in. from top of this layer and 4 ft. from surface..	1	6	5	0
Clay	1	0	6	0
Sand	2	6	8	6
Alternate layers of clay and silt..............	1	6	10	0
Silt and sand laminated and crossbedded and grading into lower layer....................	7	0	17	0
Clayey sand; much scattered charcoal, sandstone fragments, some of which are reddened by fire, potsherds and worked cores of quartzite and agate	2	0	19	0
Sand, with a few sandstone fragments and potsherds at bottom. Marks base of culture layer.	1	6	20	6
Sandy adobe darker than that above with plant impressions	3	5	23	11
Covered to bed of arroyo......................	7	1	31	0

Section 4

In the north bank of the main arroyo and near the "store" at southeast corner of Pueblo del Arroyo (pl. 7, lower). The section was measured in the middle of a channel deposit which lies beneath a horizontal clay layer. The deposit itself is 13 feet 5 inches thick at the deepest point exposed, and its base is 15 feet below the level of the adjacent plain. Nearby, in 1877, Jackson found potsherds, bones, and a human skull at a depth of 14 feet, as discussed on page 32.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Clay	1	8	1	8
Sand, with lenses of fine gravel and clay which dip toward center of old channel. Crescentic lense of laminated clay; depth of lowest part 12 ft., thickness 6 in. Sandstone blocks imbedded in this clay like steppingstones. Gravel layer at base. Many fragments of bones, broken rocks, a few shells and many potsherds especially near base............................	13	5	15	1
Clay and laminated silt, scattered charcoal to depth of 21 ft. 6 in........................	7	0	22	1

Section 5

South bank of main arroyo opposite Ruin No. 8 and a short distance east of section 16 (see pp. 29-30). Of special note is a Pueblo III fireplace (pl. 3, right) built when the surface was 5 feet lower than it is now, a second hearth at 12 feet 8 inches, and charcoal at 16 feet 3 inches.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Dark clay, a fairly continuous layer that thickens and thins	0	8	0	8
Fine-grained sand, finely laminated and cross-bedded, with impressions of roots............	0	8	1	4
Clay	0	2	1	6
Sand, laminated and containing streaks of charcoal and chunks of clay......................	1	6	3	0
Dark clay and laminated sand. Clay is in irregular thin layers which slope from south to north and fade out in irregular broken chunks of clay imbedded in sand. A firebox formed of nearly vertical sandstone slabs at depth of 5 ft. is of P. III type................................	2	9	5	9

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Compact rusty sandy clay with fragments of stone, potsherds, and charcoal. Potsherds are 6 ft. 3 in. from surface and of indeterminate type	0	6	6	3
Crossbedded sand to crescentic hearth 12 ft. 8 in. below top of section; scattered charcoal at 14 ft. 8 in. and, 50 ft. south of section, at 16 ft. 3 in.	13	0	19	3

Covered below.

Sections 6 and 7

Sections 6 and 7 are near each other and in the north branch of the main arroyo opposite Una Vida (fig. 1). The bedding is very irregular in this vicinity, and none of the layers listed is persistent. Section 6 has potsherds considered to be of Pueblo III type between 4 feet 6 inches, and 5 feet below the surface. Section 7 shows a very large hearth 8 feet from the surface.

Section 6

In north bank of north channel, near Una Vida.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Dark clay. Potsherds at 4 ft. 6 in. and 5 ft......	5	0	5	0
Crossbedded sand, with lenses of clay a few feet off the line of the section....................	3	6	8	6
Clay	1	6	10	0
Crossbedded sand and silt......................	2	6	12	6
Clay	2	0	14	6
Clayey silt to bottom of arroyo................	4	0	18	6

Section 7

In south bank of north channel, 100 yards upstream from section 6.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Clay	3	0	3	0
Sand	3	0	6	0
Clay, with open hearth at base. Hearth is 8 ft. long and burnt (red) ground is nearly 1 ft. thick with much charcoal above..............	2	0	8	0
Sand and silt.................................	1	2	9	2
Adobe	1	5	10	7
Sand and silt to bottom of arroyo..............	3	7	14	2

Section 8

South bank of main arroyo 2 miles east of Wejegi and outside the area of our map.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Dark clay	2	0	2	0
Laminated and crossbedded sand with a few lenses of gravel. At depth of 10 ft. 4 in. there is a streak of charcoal resting on burnt (red) earth; at 13 ft. 2 in., a second streak of charcoal, directly below the first but no red earth; scattered charcoal occurs to depth of 21 ft.....	25	4	27	4
Covered below.				

Section 9

In arroyo of Rincon del Camino, about 300 feet south of the road and in the fan of the rincon.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Compact rusty sandy clay with fragments of stone and charcoal; potsherds at 6 ft. 3 in.....	6	3	6	3
Crossbedded sand with impressions of plant stems and scattered charcoal to depth of 14 ft. 8 in. At depth of 12 ft. 8 in. there is a hearth crescentic in section and consisting of baked and reddened floor 2 ft. 1 in. across and rising 3 in. at the ends with layer of charcoal from $\frac{1}{2}$ to $1\frac{1}{2}$ in. thick. South 50 ft. from this section, scattered charcoal occurs to a depth of 16 ft. 3 in. from top of bank......................	13	0	19	3

Section not numbered

North bank of main arroyo west of 1924 dump. [South of the Wetherill corrals and 100 yards, more or less, west of the expedition camp.—N. M. J.]

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Apparently uniform indurated sand mixed with adobe and a little silt........................	6	0	6	0
Laminated clay interbedded with slightly indurated sand. Fine interbeddings well defined and nearly parallel. Lower 0.7 ft. has broader laminae	2	7	8	7
Indurated sand laminated without adobe........	1	6	10	1
Fine white sand slightly indurated and finely laminated	1	0	11	1

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Nonlaminated clayey sand, indurated...........	0	5	11	6
White sand slightly and inconspicuously laminated	0	9	12	3
Well-indurated inconspicuously laminated sand with large content of fine silt or clay.........	2	8	14	11
Gray sand slightly laminated and indurated.....	2	8	17	7
Clay containing sand and showing tendency to granulate and fissure on shrinkage (adobe)....	2	8	20	3
Fine nonlaminated sand slightly indurated.......	1	2	21	5
Clay containing some sand and showing tendency to granulate and fissure on shrinkage.........	2	7	24	0
Pulverant loamy sand containing minute black fragments (moist)	3	0	27	0

Section 15

In middle of buried channel, on south bank of main arroyo and 200 yards upstream from mouth of Rincon del Camino.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Alternate bands of sandy clay with internal cracks and compact sand....................	4	0	4	0
Compact sand	1	7	5	7
Sandy clay with internal cracks and streaks of compact sand	1	2	6	9
Minutely crossbedded compact sand with a few lenses of clay 3 to 4 ft. long near base........	3	4	10	1
Crossbedded compact sand with lense of gravel 1 ft. thick and 4 ft. long at base, containing burnt sandstone blocks up to 6 in. across, clay pellets, blocks of clay, and potsherds of late type, base of buried channel..................	3	0	13	1
Crossbedded sand, crossbedding on larger scale, streaks of pieces of black shale and coal......	2	3	15	4
Compact crossbedded sand.....................	2	7	17	11
Covered	5	0	22	11

Section 17

At the mouth of Rincon del Camino a narrow point projects into the main arroyo from the north. On the east face of this point a well-defined buried channel is exposed. Section 17 was measured in the middle of this exposure.

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Yellow pulverant sand derived from Rincon del Camino	0	6	0	6

	Thickness		Depth	
	Feet	Inches	Feet	Inches
Sandy clay with internal cracks................	1	0	1	6
Yellow pulverant sand derived from Rincon del Camino	1	4	2	10
Sandy clay with internal cracks contains sand lense to south of section....................	2	8	5	6
Gray, minutely laminated sand; laminae slope to south, are interbedded there with clay layers..	4	10	10	4
Yellow crossbedded compact sand with gravel lenses. To the south a clay lense. Upper gravel at 13 ft. 7 in., lower at base, contains clay balls, pellets, and potsherds of late type in both lenses	5	8	16	0
Sandy clay, upper part has internal cracks; base of buried channel...........................	2	4	18	4
Compact laminated sand with lenses of clay having internal cracks to bed of arroyo.......	6	2	24	6

SECTIONS IN THE BURIED, OR POST-BONITO, CHANNEL

In 1922 Mr. Judd had dug a number of pits in the vicinity of Pueblo Bonito in order to obtain soil samples for analysis. None of these pits exceeded 10 feet in depth because that appeared to be well below the level of fields once cultivated by the villagers and subsequently overlain by post-Bonito alluvial deposits. Pit number 3, located in the plain between the expedition camp and the ruin, had been fenced and left open for possible further tests. When this pit was deepened at my suggestion in 1925 we were all surprised to find late Bonito potsherds at depths of 10 to 18 feet. This meant we were right in the middle of the buried channel. Some fragments showed the influence of contact with the Mesa Verde culture, thus further identifying the channel fill as contemporaneous with the last years of Pueblo Bonito or even later and, of course, much later in age than the main valley fill.

Log of test pit number 3

Between Pueblo Bonito and expedition camp

Materials found	Thickness		Depth		Potsherds	Found at	
	Feet	Inches	Feet	Inches		Feet	Inches
Dark sandy clay (adobe)..........	2	0	2	0			
Laminated fine sand and silt........	2	2	4	2			
Dark sandy clay (adobe)..........	0	9	4	11			
Sand with thin layers of laminated silt and clay.....................	1	11	6	10			
Laminated layers of silt and dark clay	4	1	10	11		10	
Dark sticky clay...................	0	11	11	10	A few	to	
Laminated fine sand...............	2	5	14	3		12	2

Materials found	Thickness		Depth		Potsherds	Found at	
	Feet	Inches	Feet	Inches		Feet	Inches
Laminated clay	0	7	14	10			
Laminated and minutely crossbedded coarse sand. This bed grades to south into gravelly clay that extends to depth of 16 ft. 10 in.......	1	5	16	3	Many	⎰16 to 16	1 8
Dark clay	0	5	16	8			
Fine sand	0	2	16	10			
Gravelly clay containing large and small stones, grades into sand to south	1	5	18	3	Numerous	⎰17 to 18	3 3
Fine sand	0	3	18	6			

Log of test pit number 4

Sixty feet east from arroyo bank at section 4

Materials found	Thickness		Depth		Potsherds	Found at	
	Feet	Inches	Feet	Inches		Feet	Inches
Gray-brown sandy clay (adobe)....	1	10	1	10			
Laminated sandy adobe, a lense....	0	2	2	0			
Hard brown sand with pieces of charcoal	2	2	4	2			
Brown sand in part finely laminated with lenticular streaks of dark laminated clay ½ to 1 in. thick and spaced 2 to 10 in. apart...........	3	3	7	5	One only " "	7 7	0 2
Hard brown sand, containing at north end of pit an irregular lense of sandy and gravelly adobe containing charcoal and bones.......	2	5	9	10	Many	9	6
Dark sandy clay (adobe) with small lense of gravel..................	4	7	14	5	Many in gravel	⎰10 to 10	6 8
					Many	⎰11 to 11	6 8
Sand (a lense) that extends to 15 ft. at north end of pit..............	0	3	14	8	.		
Adobe to bottom of pit............	0	9	15	5	Many	15	0

SUMMARY

Chaco River, a river only during occasional floods, entrenched itself at some past time, doubtless Pleistocene, in a broad plain that then existed in the San Juan Basin of northwestern New Mexico. In the nearly horizontal sandstones and shales that underlie San Juan Basin,

the Chaco River flows, when it flows at all, alternately in broad valleys and narrow canyons. To one of these latter the name Chaco Canyon is applied almost exclusively, and here, in a stretch of about 12 miles, there are numerous ruins of prehistoric villages, the largest of which is Pueblo Bonito.

Chaco Canyon, after its excavation, was partly refilled with sand and silt during a period of alluviation common to most streams of the southwestern United States. On the flat floor of the canyon, resulting from this alluviation, the prehistoric peoples lived and left evidence of their long-time occupation in hearths, scattered charcoal, potsherds, and other relics. These remains extend to a depth of 21 feet below the present surface of the alluvium. An ancient type of dwelling known as a pit house has been found at a depth of 6 feet below the surface, but the typical Pueblo III type of construction has not been surely identified below 4 feet.

Alluviation in Chaco Canyon and generally throughout the Southwest has more recently been interrupted by the formation of an arroyo or steep-sided gully in which the floods of the stream are now wholly confined. The Chaco Canyon arroyo is presently 20 to 30 feet deep and from 150 to 400 feet wide, yet a military expedition of 1849 did not mention the gully, if it then existed. In 1877 an arroyo 16 feet deep and 60 to 100 feet wide was reported. Available evidence indicates that the arroyos of other streams were mostly formed in the decade 1880 to 1890 and that the process is still going on. The beginning of the Chaco arroyo appears to have been somewhat earlier and the date may, with some assurance, be placed in the decade 1860 to 1870.

A study of the deposits that make up the valley fill indicates that Chaco River never had a permanent low-water flow. No signs of irrigation ditches or other diversions of flowing water have been found in the alluvial deposits. It seems probable, therefore, that the prehistoric inhabitants of the canyon practiced floodwater farming, a form of agriculture still in use in the region. For this type of farming wide-spreading floods are a prerequisite, and the beginning of erosion, with formation of an arroyo that confines the floods and lowers the water table, puts an end to agriculture of this type.

The main body of the valley fill is of unknown depth. Only the upper 30 feet is exposed and of this the uppermost 21 feet contains relics of man. Pottery made by the ancient people varies in texture and design according to locality and age. Differences between the kinds of pottery typical of different stages in human culture are not wholly known, nor has a definite chronology of the stages been deter-

mined, but broad distinctions can be made between the older and younger civilizations.

Collections of potsherds can therefore be used as fossils in studying the stratigraphy of the valley alluvium. Generally, only a few potsherds are found at any one place and many of these are indeterminate, hence of no diagnostic value. Somewhat meager collections of sherds from depths of 6 to 21 feet have been examined by the expedition's archeologists who identify them as mostly a coarse ware characteristic of the Pit House culture. On the basis of these fragments, therefore, we may draw the inference that people of the Pit House period were the principal inhabitants of Chaco Canyon during the time required for deposition of those 15 feet of alluvium.

Potsherds collected from the zone of valley fill less than 6 feet below the surface are generally of Pueblo III type. This fact, together with ruins whose foundations are partly buried in alluvium, indicate that Pueblo III people occupied the valley during the period represented by the last 6 feet of alluviation.

In the bank of the arroyo near Pueblo del Arroyo there is exposed a buried channel which extends to a depth of 15 feet below the present surface. At this point the channel is a well-defined ancient arroyo that had been refilled and then buried under an additional 2 feet of sediment in the interval between abandonment of Pueblo Bonito and American Army penetration of Chaco Canyon in 1849. Potsherds removed from the gravel lenses of that buried channel included fragments of the latest Pueblo Bonito types. The channel, therefore, must have been refilled late in the occupancy of Pueblo Bonito or after its abandonment.

By means of test pits in which similar pottery was found, we traced this buried channel for about 1,000 feet across the plain fronting Pueblo Bonito and later discovered remnants of it both up and down the canyon. This buried channel clearly represents a period of dissection and arroyo formation for the full length of the valley and, assuming that the dissection occurred late in the occupancy of Pueblo Bonito, an adequate cause exists for abandonment of the canyon by aboriginal farmers whose floodwater fields were destroyed by confinement of the floods within this channel, and by concurrent events.

Our examination of the main valley fill suggests alternate dissection and alluviation of Chaco Canyon: three periods of dissection and two of alluviation. If this alternation represents a true cycle, we may expect the present arroyo to run its course and then be refilled and perhaps covered over. However plausible it may be to attribute formation of the present arroyo to destruction of the vegetative cover by

overgrazing, the previous dissection and subsequent alluviation were in no way affected by domestic animals. It seems probable, therefore, that the ultimate cause of this periodic change in the regime of streams is climatic. A slightly increased rainfall would increase the vegetative cover and thereby both reduce the violence of floods and protect the soil from erosion. Any decrease in rainfall would produce a reversed effect. Although the deposits of Chaco Canyon contain no definite evidence of a more humid climate during the two periods of their deposition, it seems likely that an increased humidity did exist and was a factor in development of the distinctive Chaco culture. The subsequent change to more arid conditions was doubtless of less effect until it culminated in formation of the twelfth-century arroyo that unexpectedly became a dominant feature of this study.

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FURTHER ADDITIONS TO THE BIRDS OF PANAMÁ AND COLOMBIA

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During work of recent months on our extensive collections of birds from Panamá and northern Colombia, several hitherto unrecognized forms have been found that merit description to give better understanding of the geographic variation in the species concerned. With these I have included records of three others that have not been reported previously from Colombia.

Family CRACIDAE

ORTALIS RUFICRISSA LAMPROPHONIA, new subspecies

Characters.—Similar to *Ortalis ruficrissa ruficrissa* (Sclater and Salvin)[1] but smaller; feet smaller; tail shorter; lower breast and abdomen whiter; back and wings more grayish brown.

Description.—Male adult, U.S.N.M. No. 368535, from the Serranía de Macuire, above Nazaret, Guajira, Colombia, collected May 5, 1941, by A. Wetmore and M. A. Carriker, Jr. (orig. No. 11792). Crown chaetura drab, feathers of forehead edged with a wash of light olive-gray; ear coverts drab; remainder of side of head mouse gray, the feathers with fuscous shafts; hindneck deep mouse gray, shading into the color of the upper back; upper back and wings between olive-brown and deep olive; rump and upper tail coverts slightly darker than buffy brown; primaries light olive-brown, with a slight grayish wash on outer webs; central rectrices deep olive, tipped indefinitely with buffy brown; outer rectrices dark greenish olive (slightly iridescent), tipped widely with white; foreneck and sides of neck light grayish olive with a slight brownish wash; multiple line of feather shafts, extending longitudinally down center of bare throat, black, becoming fuscous where they merge with upper portion of feathered foreneck; webs of

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[1] *Ortalida ruficrissa* Sclater and Salvin, Proc. Zool. Soc. London, November 1870, p. 538 (Valledupar, Magdalena, Colombia).

feathers bordering bare throat pale smoke gray; lower breast and upper abdomen white, washed with pinkish buff on upper portion of breast, this buffy wash extending down onto the sides; flanks and under tail coverts tawny; tibiae pinkish buff to cinnamon-buff; under wing coverts with outer half light grayish olive, inner half clay color. Tip of bill horn color; rest of distal half castor gray; basal half neutral gray; tarsus and toes fuscous; claws drab (from dried skin).

Range.—The Serranía de Macuire, at the eastern end of the Guajira Peninsula, Colombia.

Measurements.—Males (2 specimens): Wing 195-202 (198), tail 227-235 (230), culmen from base 25.7-27.2 (26.4), tarsus 64.0-65.4 (64.7) mm.

Females (2 specimens): Wing 195-200 (197), tail 217 (in both), culmen from base 25.8-26.0 (25.9), tarsus 59.5-62.3 (60.9) mm.

Type, male: Wing 202, tail 235, culmen from base 27.2, tarsus 65.4 mm.

Remarks.—*Ortalis ruficrissa ruficrissa,* named many years ago by Sclater and Salvin from Valledupar, was known prior to our work in northeastern Colombia from two specimens, the type in the British Museum and one from Dibulla on the north coast, about 35 miles west of Riohacha, in the Carnegie Museum. We found it first at Maicao, Guajira, and later Carriker secured a series that extend the range of the typical race from the western Guajira at Maicao, into northeastern Magdalena, from La Cueva in the eastern foothills of the Sierra Nevada de Santa Marta southward, along the western base of the Sierra de Perijá, to Casacará. This excellent series is sufficient to demonstrate the distinctness of the isolated colony on the Serranía de Macuire, which is cut off by many miles of barren desert, where there is no suitable habitat for these birds, from the more-forested section of the western Guajira inhabited by *Ortalis ruficrissa ruficrissa.* Measurements of the typical race are as follows:

Males (7 specimens): Wing 206-238 (217), tail 240-272 (253), culmen from base 26.0-29.8 (27.8, average of 6), tarsus 64.0-73.1 (69.2) mm.

Females (5 specimens): Wing 196-217 (205), tail 230-253 (239), culmen from base 26.0-28.2 (26.7), tarsus 62.0-67.0 (64.1, average of 4) mm.

In the series of *ruficrissa* there is one bird in somewhat worn plumage, from Camperucho, Magdalena, that is as white on the breast as the four *lamprophonia,* but it has the upper breast and foreneck and the dorsal surface darker, the feet larger, and the tail definitely longer.

The name for the new race is given because of the raucous voice that carries for long distances.

Family BUCCONIDAE

NONNULA FRONTALIS STULTA, new subspecies

Characters.—Similar to *Nonnula frontalis frontalis* (Sclater),[2] but somewhat grayer, less rufescent above; crown duller brown; averaging very slightly duller brown on breast and foreneck.

Description.—Type, U.S.N.M. No. 445077, male, El Uracillo, Province of Coclé, Panamá, February 23, 1952, A. Wetmore and W. M. Perrygo (orig. No. 16946). Forehead, sides of head extending to area above eye, and including the lores and erectile feathers above the anterior end of the eye, gray (dark gull gray); anterior portion of crown between verona brown and warm sepia, shading to bister on nape; rest of upper surface, including wings and tail, sepia, with wing coverts, primaries, and secondaries edged lightly with Saccardo's umber, and the ends of the rectrices shading to clove brown; outermost rectrix drab, the second pair edged externally and tipped rather widely with drab, the others with the drab less extensive; extreme base of the feathers on chin at the base of the bill white; throat, foreneck, and breast between cinnamon and sayal brown; flanks clay color; abdomen whitish; under tail coverts white; edge of wing cinnamon; under wing coverts tawny-olive; inner webs of secondaries and inner primaries cinnamon-buff. Bill, tarsus, and toes blackish slate (from dried skin).

Measurements.—Males (12 specimens): Wing 55.2-58.8 (57.1), tail 52.3-58.7 (55.1), culmen from base 22.3-24.8 (23.5), tarsus 13.0-14.7 (13.6) mm.

Females (17 specimens): Wing 55.1-62.0 (58.1), tail 53.6-59.6 (57.1), culmen from base 22.4-25.6 (24.0), tarsus 12.2-14.2 (12.6) mm.

Type, male: Wing 55.7, tail 54.8, culmen from base 23.7, tarsus 13.5 mm.

Range.—Panamá from northeastern Coclé (El Uracillo) and the Canal Zone (Lion Hill) through eastern Province of Panamá (Tocumen, Pacora, Chepo), through Darién (Jesucito, Río Esnape, El Real, El Tigre, Boca de Cupe, Capetí, Cana) to extreme northern Chocó (Acandí), Colombia. Found mainly on the Pacific slope.

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[2] *Malacoptila frontalis* P. L. Sclater, Ann. Mag. Nat. Hist., ser. 2, vol. 13, 1854, p. 479 (interior of Colombia).

Remarks.—This attractive little bird, while somewhat more active than the larger members of its family, shares with them the habit of resting quietly for long periods. I have found it in brushy areas or low down in tracts of gallery forest. In the main, in Panamá it ranges on the Pacific slope, thus far having been found in the Caribbean drainage near the head of canoe navigation on the Río Indio in northern Coclé, at Lion Hill (before the Panama Canal was constructed), and at Acandí, Colombia, on the western shore of the Gulf of Urabá. Specimens from Unguía, Chocó, on the western side of the lower Río Atrato, are *N. f. pallescens*.

This species has two color phases, one rufescent, in which the dorsal surface is decidedly brown and where brown extends over the entire ventral side except the center of the abdomen and the lower tail coverts, and the other grayish, where the lower surface especially is paler, with the white of the abdomen more extensive.

Nonnula f. stulta differs from *pallescens* of extreme northern Colombia in being darker colored and also duller brown, less rufescent, above.

Family TROCHILIDAE

COELIGENA ORINA, new species

Characters.—Similar to *Coeligena bonapartei* (Boissoneau)[3] but crown uniform, without frontal spot; body color uniform dark green, without bronzy sheen on lower breast, under tail coverts and rump; under tail coverts uniform green, without cinnamon edgings; tail dark green without bronzy reflections; wings dull black (not fuscous); spot on foreneck decidedly brighter blue; under wing coverts darker green; bill more slender.

Description.—Type, U.S.N.M. No. 436219, male adult, Páramo de Frontino, at 10,500 feet, Antioquia, Colombia, August 27, 1951, collected by M. A. Carriker, Jr. (orig. No. 21016). Feathers of crown, sides of head, and hindneck iridescent elm green, margined with black, the green being evident clearly only when viewed at an appropriate angle; back, and lesser and middle wing coverts iridescent spinach green; rump and upper tail coverts strongly iridescent, varying from lettuce green to Cosse green; remiges and greater wing coverts aniline black, with a faint violet-purple sheen, the inner greater coverts edged with shining lettuce green; outer primary margined lightly on external web with avellaneous; rectrices iridescent yellowish oil green, with lightly indicated edgings of dull black; chin chaetura black;

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[3] *Ornismia bonarpartei* [sic] Boissoneau, Rev. Zool., 1840, p. 6 (Bogotá).

foreneck and upper breast iridescent spinach green, the feathers margined lightly with black; a spot of glittering salvia blue on foreneck; lower breast, sides, flanks, and under tail coverts shining lettuce green; center of abdomen, in a small area, dull white; tibiae cinnamon-buff; under wing coverts iridescent elm green. Bill black, toes fuscous, claws black (from dried skin).

Measurements.—Male, type: Wing 75.2, tail 44.0, culmen from base 33.6 mm.

Range.—Known only from the Páramo de Frontino at 10,500 feet, above Urrao, Antioquia, Colombia.

Remarks.—The single male seen appears closer to *Coeligena bonapartei* than to others of the genus, and apparently is a representative of that group in the western Andes. It is so different, however, that I have no doubt as to its being a distinct species. The specimen appears fully adult, so that absence of the frontal spot may not be ascribed to immaturity. Compared to *C. bonapartei* the bill, in addition to being more slender, is longer.

This is one of the handsomest of the novelties obtained during the present ornithological exploration of Colombia. Carriker noted on the label that the bird was taken in forest below the open páramo.

Family TYRANNIDAE

MYIARCHUS FEROX AUDENS, new subspecies

Characters.—Similar to *Myiarchus ferox panamensis* Lawrence [4] but grayer above, with the crown more nearly uniform with the back; slightly paler yellow below.

Description.—Type, U.S.N.M. No. 443502, female, Nuquí, Chocó, Colombia, collected on March 5, 1951, by M. A. Carriker, Jr. (orig. No. 19780). Crown and auricular area between hair brown and deep grayish olive, with an indefinite wash of chaetura drab on central portion along shafts; neck, back, lesser wing coverts, and upper tail coverts slightly darker than deep grayish olive; rump grayish olive; middle and greater wing coverts chaetura drab, tipped rather widely with grayish olive to produce two indistinct wing bars; primary coverts, primaries, secondaries, and rectrices chaetura drab; secondaries margined prominently and inner primaries lightly with dull white; outer rectrix with outer web dull buffy brown, the others edged with grayish olive, more prominently at the base, all tipped lightly with a wash of olive-buff; lores, and an indistinct line above

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[4] *Myiarchus panamensis* Lawrence, Ann. Lyc. Nat. Hist. New York, vol. 7, May 1860, p. 284 (Atlantic slope of Canal Zone on the Panama Railroad).

eye pale olive-gray; a mixture of dull white immediately in front of eye, with whitish feathers extending back over the lower eyelid; chin indistinctly whitish; throat, foreneck, and upper breast light olive-gray, lined indistinctly with dull white on throat and upper foreneck; lower breast and abdomen chartreuse yellow; sides and under tail coverts sea-foam yellow; edge of wing and under wing coverts between Marguerite yellow and primrose yellow; inner webs of primaries and secondaries pale olive-buff toward base. Bill, tarsus, and feet dull black (from dried skin).

Measurements.—Female (3 specimens): Wing 86.0-91.1 (89.4), tail 78.2-86.4 (83.3), culmen from base 20.2-21.6 (20.8), tarsus 21.8-22.7 (22.2) mm.

Type, female: Wing 91.1, tail 86.4, culmen from base 21.6, tarsus 22.7 mm.

Range.—Known only from near Nuquí, Department of Chocó, northwestern Colombia.

Remarks.—The three skins on which this new race is based have been compared with a large series of *M. f. panamensis* covering the area from western Panamá across northern Colombia. They stand out clearly from all in the definitely gray coloration. The nearest specimens of *panamensis* seen are from Jaqué, Darién, across the border in Panamá, and from Nicoclí and Villa Artiaga, Antioquia, in Colombia. It is probable that the new race ranges immediately back of the beaches along the coast, as the species as a whole does not penetrate into heavy forests such as are found inland in the Chocó. Its distribution, therefore, may be through a relatively narrow belt, east and west.

It is pertinent to add here that *Myiarchus ferox australis Hellmayr* is also to be included in the list of birds found in Colombia, as shown by a male in the U. S. National Museum taken at Villavicencio, Meta, by Hermano Nicéforo María in December 1939. Zimmer [5] records four specimens from this locality as intermediate between *M. f. ferox* and *australis,* but nearer *australis.* In a later paper by Zimmer and Phelps,[6] describing *M. f. brunnescens,* these four skins from Villavicencio were, through some error in printing, included under *brunnescens* instead of *australis* in their list of specimens examined. It was this, apparently, that caused De Schauensee [7] to include Villavicencio under the range he assigns to *brunnescens,* and to omit *australis* from his list.

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[5] Amer. Mus. Nov. No. 994, June 2, 1938, pp. 12, 15.

[6] Amer. Mus. Nov. No. 1312, March 12, 1946, p. 11.

[7] Caldasia, vol. 5, No. 24, July 10, 1950, p. 826.

PHAEOMYIAS MURINA EREMONOMA, new subspecies

Characters.—Similar to *Phaeomyias murina incomta* (Cabanis and Heine)[8] but dorsal surface lighter, grayer; slightly smaller in size.

Description.—Type, U.S.N.M. No. 400534, male, taken on the Río Santa María, 4 miles north of París, Herrera, February 24, 1948, by A. Wetmore and W. M. Perrygo (orig. No. 13500). Crown, sides of head, hindneck, back, and lesser and middle wing coverts between drab and grayish olive; the feathers of the back becoming drab at the tips; rump and upper tail coverts drab; superciliary stripe, extending from the front of the eye back along the sides of the crown, and the feathers encircling the edge of the eyelids, dull white; lores light grayish olive; primaries, secondaries, and greater coverts dull hair brown; lesser wing coverts edged indefinitely with dull tilleul buff, forming an indistinct wing bar; middle and greater coverts tipped widely with somewhat dull pale pinkish buff, forming two prominent wing bars, in addition to the third indistinct one on the lesser coverts; inner secondaries margined and tipped broadly with dull white; outer webs of outer secondaries and primaries edged very narrowly with pale olive-buff; rectrices dull hair brown, tipped and margined narrowly on the external webs with pale olive-buff; throat and foreneck dull white; upper breast and sides washed with pale smoke gray; lower breast and abdomen light primrose yellow; under tail coverts Marguerite yellow; under wing coverts light primrose yellow, lined with hair brown on bend of wing. Maxilla and tip of mandible fuscous-black; base of mandible light grayish olive; tarsus, toes, and claws black (from dried skin).

Measurements.—Male (16 specimens): Wing 54.8-60.5 (56.8), tail 48.7-56.2 (51.5), culmen from base 10.0-11.6 (10.8), tarsus 17.0-18.3 (17.7) mm.

Females (13 specimens): Wing 49.8-55.9 (52.8), tail 44.5-48.3 (46.7, average of 12), culmen from base 9.9-11.5 (10.4, average of 12), tarsus 15.8-18.3 (16.9) mm.

Type, male: Wing 55.8, tail 48.7, culmen from base 10.7, tarsus 17.5 mm.

Range.—Lowland areas of the Pacific slope of Panamá, from the valley of Río San Pablo in southern Veraguas (Soná, Río de Jesús), and the eastern side of the Azuero Peninsula (Los Santos, Parita, París, Potuga, El Barrero) through Coclé (Aguadulce) to the western section of the Province of Panamá (Nueva Gorgona, La Campana).

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[8] *Elainea incomta* Cabanis and Heine, Mus. Hein., vol. 2, 1859, p. 59 (Cartagena, Colombia).

Remarks.—Since 1948, when I first found this small flycatcher in the Provinces of Los Santos and Herrera on the eastern side of the Azuero Peninsula, I have been assembling material for comparison from elsewhere in Panamá, and from Colombia, since it seemed doubtful that the Panamanian birds, separated from the Colombian group by the whole of Darién and the lower Atrato basin, were the race *incomta,* named from Cartagena, to which they have been referred. It was found immediately that so many were in worn plumage, due to the intense light and lack of deep shade in their brushy haunts, that there was considerable fading in color. Finally, enough have been obtained to demonstrate the differences outlined above, through comparison of birds in reasonably fresh dress. Panamanian birds, in addition to being lighter, grayer above, average more yellow below. The latter difference however is variable from specimen to specimen, and is useful only in examining series, so that it is not included in the formal diagnosis.

The size difference between the newly described race and *incomta* is not great but is illustrated by examination of the following measurements of the latter form, from Colombian specimens.

Males (23 specimens): Wing 60.1-64.4 (62.2), tail 51.0-58.9 (54.9), culmen from base 10.3-11.7 (10.9), tarsus 16.4-19.4 (18.4) mm.

Females (16 specimens): Wing 55.5-60.1 (58.3), tail 46.5-53.5 (58.4), culmen from base 9.8-11.0 (10.4), tarsus 16.3-19.3 (17.1) mm.

Zimmer [9] has recorded one from Panamá from El Villano, a locality that I have not found on available maps.

In the field this species is liable to confusion with the beardless flycatcher (*Camptostoma obsoletum*), often encountered in the same localities, in spite of the larger size of *Phaeomyias murina,* because of similar habits.

PHYLLOMYIAS GRISEICEPS QUANTULUS, new subspecies

Characters.—Similar to *Phyllomyias griseiceps cristatus* Berlepsch,[10] but grayer, less greenish, on the back; pileum darker, more brownish; under surface slightly paler, the yellow of breast and abdomen being lighter, and the sides and upper breast paler, with less olive wash.

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[9] Amer. Mus. Nov. No. 1109, May 15, 1941, p. 10.

[10] *Phyllomyias cristatus* Berlepsch, Journ. Orn., vol. 32, April 1884, p. 250 (Bucaramanga, Santander, Colombia). This description was repeated on page 300 in the succeeding issue for July-October.

Description.—Type, U.S.N.M. No. 420014, male adult, Cana, 1,800 feet elevation, Darién, Panamá, June 1, 1912, E. A. Goldman (orig. No. 15783). Crown and hindneck fuscous-black; a narrow superciliary, extending from well behind eye to nostrils, dull white; lores chaetura drab; hindneck, back, and scapulars deep olive; rump and upper tail coverts citrine-drab; wing coverts hair brown, with very slight paler borders; primaries and secondaries chaetura drab, the innermost secondaries margined narrowly with pale olive-buff; rectrices hair brown, the outermost with slight tipping of pale olive-buff; sides of head chaetura drab, with the lower eyelid dull white, and numerous thin lines of dull white across auricular area; chin and throat dull white; rest of under surface in general reed yellow, becoming primrose yellow on the abdomen and under tail coverts; sides of breast lightly washed with citrine-drab; axillars barium yellow; under wing coverts primrose yellow; inner webs of primaries and secondaries edged prominently with Marguerite yellow. Bill fuscous, tarsus and toes fuscous-black (from dried skin).

Measurements.—Male, type: Wing 49.3, tail 43.1, culmen from base 9.7, tarsus 13.9 mm.

Range.—Known only from near Cana, Darién.

Remarks.—The single specimen on which this form was based was taken by E. A. Goldman toward the close of his work near Cana. While Nelson identified it correctly to species, later the skin was not entered in the museum catalog with the rest of Goldman's collection, coming to attention only recently in examining the rest of this series. It seems appropriate to describe it, since I find no duplication of its characters in more than 30 skins of *griseiceps* examined, including examples of the subspecies *griseiceps, cristatus, caucae,* and *pallidiceps.* It is the only record for the species in Panamá.

It is probable that a bird recorded by de Schauensee [11] from the Río Juradó, across the border in Chocó, Colombia, also belongs to this new race.

The name *quantulus,* "how small," is given because of the tiny size of these little flycatchers.

Family FRINGILLIDAE

SICALIS LUTEOLA EISENMANNI, new subspecies

Characters.—Male similar to that of *Sicalis luteola chrysops* Sclater [12] but clearer, brighter yellow on under surface; dark streaking

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[11] Caldasia, vol. 5, No. 24, 1950, p. 864.

[12] *Sycalis chrysops* Sclater, Proc. Zool. Soc. London, 1861 (Feb. 1, 1862),

on back heavier; sides of head more greenish. Female like that of *S. l. chrysops,* but lighter, brighter yellow below and on rump; sides of head more grayish brown.

Description.—Type, U.S.N.M. No. 449369, male adult, taken 2 miles east of Antón, Province of Coclé, Panamá, June 20, 1953, by A. Wetmore (orig. No. 18159). Forehead wax yellow, extending back over eye as an indefinitely delimited superciliary line, and shading posteriorly into the sulphine yellow of the crown; hindneck olive lake with a slight grayish overwash; crown, behind the level of the eyes, and hindneck streaked narrowly with chaetura drab; auricular region and side of neck yellowish citrine; lores wax yellow, feathers of the lower half and those behind rictus being white basally, forming an indefinite whitish spot; feathers of upper back chaetura black, edged with olive-yellow, producing heavy dark streaks outlined by narrower lighter ones; lower back yellowish citrine; rump and upper tail coverts slightly brighter than sulphine yellow; wing coverts in general chaetura drab; lesser coverts edged with light yellowish olive, which is more extensive on the inner feathers; middle coverts margined with deep olive-buff; greater coverts edged with pale olive-buff; primaries and secondaries chaetura drab; central portion of outer webs of primaries edged narrowly with olive-citrine, distal portion and secondaries margined with dull white; rectrices chaetura drab, edged basally with yellowish citrine; under surface lemon chrome, deepening on sides of throat and foreneck to apricot yellow; under tail coverts wax yellow; sides of upper breast washed with strontian yellow; under wing coverts lemon yellow; inner webs of primaries edged indistinctly with pale olive-buff. Maxilla and tip of mandible chaetura black; sides of mandible fuscous, base olive-buff; tarsus and toes clove brown (from dried skin).

Measurements.—Males (9 specimens): Wing 60.4-64.8 (62.8), tail 38.5-45.0 (41.3), culmen from base 8.9-10.0 (9.5, average of eight), tarsus 14.2-15.8 (15.0) mm.

Female (1 specimen): Wing 60.1, tail 37.3, culmen from base 9.3, tarsus 15.4 mm.

Type, male: Wing 62.3, tail 45.0, culmen from base 9.7, tarsus 14.9 mm.

Range.—The savannas of southern Coclé Province, Panamá; recorded to date from west of Río Hato to near Aguadulce, and north to Penonomé.

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p. 376. (Mexico merid. = Orizaba, Veracruz, designated by Brodkorb, Journ. Washington Acad. Sci., vol. 33, No. 2, Feb. 15, 1943, p. 34).

Remarks.—This interesting subspecies is described from 10 specimens taken near Antón and Penonomé. From the race of the species found in southern México, named *Sicalis luteola mexicana* by Brodkorb (in the reference cited above), which is known from Morelos and Puebla, the form described here is distinguished by brighter color, and by slightly smaller size. The Panamanian form furnishes an interesting link between the races of South America and those of the southern half of México.

This bird was first recorded through a sight observation near Penonomé late in January 1951, by Dr. R. T. Scholes, who recognized that it was unknown. Eugene Eisenmann and John Bull, in July 1952, found it fairly common, several small colonies being located. In crossing through this area in May 1953, I collected one near Antón, and later, on June 20, I secured the rest of the series from which this description was written. On the June excursion I had the pleasure of the company of Dr. Eisenmann, in whose honor the race is named in recognition of his studies of living Panamanian birds.

The birds are found in the nesting season in little colonies that may be overlooked because of the brilliant light of the savanna areas which often obscures the yellow breast color, so that the *Sicalis* may be confused with the seed-eaters that abound in the same habitat.

OTHER ADDITIONS TO THE LIST OF BIRDS RECORDED FROM COLOMBIA

Crax daubentoni Gray:

Crax Daubentoni G. R. Gray, List Birds Brit. Mus., pt. 5, Gallinae, 1867, p. 15 (Venezuela).

M. A. Carriker, Jr., found these birds fairly common in the forested foothills of the Sierra Negra, where he collected specimens near Monte Elías, Magdalena, August 13, and at El Bosque, Guajira, above Carraipía, in the Montés de Oca, June 10 and 14, 1941. The occurrence is to be expected since the species has been taken in the drainage of the Río Negro on the Venezuelan side of the Sierra de Perijá.

Chaetura chapmani viridipennis Cherrie:

Chaetura chapmani viridipennis Cherrie, Bull. Amer. Mus. Nat. Hist., vol. 35, May 20, 1916, p. 183 (Doze Octobre = Doze de Outubro, Mato Grosso, Brasil).

A female taken at El Real, on the Río Nechí, March 10, and a pair from Tarazá, shot April 28, 1948, constitute the second report

of this race since its description from specimens taken in Mato Grosso. Both of the Colombian localities are in Antioquia.

Myiarchus ferox venezuelensis Lawrence:

Myiarchus venezuelensis Lawrence, Proc. Acad. Nat. Sci. Philadelphia, 1865, p. 38 (Venezuela).

A female taken near Nazaret, Guajira, in the foothills of the Serranía de Macuire, on May 13, 1941, is a well-marked example of this race.

INSECT METAMORPHOSIS

BY

R. E. SNODGRASS

Collaborator of the Smithsonian Institution and of the U. S. Department of Agriculture

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U. S. Department of Agriculture*

INTRODUCTION

Ancient mythologies are replete with stories of the transformation of one creature into another, called metamorphosis. So the early students of natural history who first observed a caterpillar turn into a butterfly had a term ready made for the phenomenon they witnessed, and today in entomology we commonly think of metamorphosis as the transformation of a larval insect into the imago. In so doing, however, we overlook the fact, quite as extraordinary, that a caterpillar hatches from the egg of a butterfly. We might truly say, then, that the real metamorphosis in the life history of the species is that which has changed a young butterfly into a caterpillar, the subsequent change of the caterpillar into the butterfly being merely the return of the metamorphosed young to the form of its parents. The transformation of the caterpillar into the butterfly is a visible event re-enacted with each generation; the change of the young butterfly into a caterpillar has been accomplished gradually through the past evolutionary history of the Lepidoptera. Today, there is not even any recapitulation of the butterfly stage in the ontogeny of the caterpillar; the butterfly's egg develops directly into the caterpillar form of its species. The idea that the caterpillar, because of its abdominal "legs," represents a primitive stage in the ancestry of insects is quite out of harmony with the modern structure of the caterpillar's head and with the fact that the caterpillar has wings developing beneath its cuticle. Both the caterpillar and the butterfly are modern end results of evolution, but along different lines of development.

In attaining their present distinctive forms, the butterfly has followed out the evolutionary path adopted by its adult ancestors, and therefore represents the adult line of descent; the caterpillar, on the other hand, in its evolution has departed from the ancestral path and has become a new and distinct juvenile form of its species. Since the caterpillar leads an independent life in a very efficient manner as an

individual, it would seem that it might be capable of developing its reproductive organs to maturity and thus dispensing with the butter-fly stage entirely. The caterpillar, however, has limited powers of locomotion; the winged butterfly, therefore, retains the reproductive function because it can widely distribute the eggs for the next genera-tion of caterpillars and thus prevent overpopulation in any one place. The same principle applies to all winged insects, and it is easy to see the advantages insects have attained in acquiring wings, together with specialized types of feeding organs and organs for mating and egg laying. It is to be presumed then that the specialized forms and habits of many young insects also are of some advantage to the species as a whole. In short, we can readily perceive a reason for metamorphosis, but how the differences between young and adult have come about, and how two distinct creatures can develop from one egg are questions difficult to answer.

Since there can be no doubt that the early insects lived on land and developed without metamorphic changes, the metamorphoses that we know among modern insects are of relatively late origin, and have no relation to the more primitive metamorphoses of the annelids and crustaceans. Even among the insects themselves metamorphosis has been independently developed in several groups, though the reason for it may be deduced from pretty much the same premises in all cases.

Wherever a pronounced metamorphosis occurs in the life of an insect it is generally, but not always, true that the young and the adult lead different lives or inhabit different media, and are structurally modified in adaptation to their individual habitats or ways of feeding. Very probably the presence of functional wings only in the adult stage, or conversely, the flightless state of the young, was an impor-tant condition that led to structural differentiation between the juve-nile and imaginal stages. The winged adult insect has opportunities of extending its activities far beyond the range of the wingless young insect, and, as is amply shown in modern insects, various new ways of life are open to the winged insect if it is free to develop special structures, particularly feeding organs, that enable it to take advan-tage of them. Likewise, to the wingless young insect there are pre-sented in nature various possible habitats and sources of food, some of which might better its condition if it were free to make the ana-tomical adjustments that would accommodate it to a new way of liv-ing in some special environment. However, as long as the usual mechanism of inheritance makes it necessary that newly acquired adult characters be transmitted through the young, and that charac-

ters acquired in the juvenile stage must be passed on to the adult, neither the adult nor the young could be free to develop structures that would be detrimental to the other. Consider, for example, the plight of the caterpillar if it had to inherit the mouth parts of the butterfly, or that of a young mosquito equipped with blood-feeding organs but lacking wings. The adult flea, it is true, has mouth parts highly specialized for a blood diet, and still is wingless, but it has substituted the power of jumping for that of flight. The Hemiptera are another exception to the rule that specialized adult mouth parts depend on wings, but here the mouth parts are just as practicable to the flightless young as to the adults.

A prerequisite of metamorphic differentiation between the young and the adult, therefore, is the inhibition of some of the ordinary processes of heredity. The young insect can then vary to any extent by the development of adaptive structures for its own use so long as its new characters are suppressed at the change to the adult; and the adult, on its part, can acquire special feeding organs that would be entirely impracticable to the wingless young. The individual, furthermore, thus derives whatever advantages there may be in living a double life, or that may accrue from inhabiting successively two different media. Moreover, the different specializations of the young and the adult may be mutually advantageous and therefore beneficial to the individual as a whole. The larva, for example, usually becomes the chief, and sometimes the only, feeding stage, thus giving the adult a large measure of freedom for the functions of mating and procreation.

When the divergence becomes too great between the young insect and the adult, especially with regard to habitat, a liaison between the two must be established by compensating instincts in order to maintain continuity of the individual life history. The adult female, for example, must know where to lay her eggs so that the emerging larva shall find its proper food, or be in its appropriate environment. The egg-laying instinct must be more and more precise as the habits of the larva become more restricted. The parent of an aquatic larva has only to deposit her eggs in some suitable place in the water, but the parent of a parasitic larva specific to some particular host must be able to insert her eggs into a member of this same host species. It has been shown by Thorpe (1938, 1939) that the egg-laying response of the adult may be a result of conditioning during the feeding of the larva. Likewise the larva, on its part, must be endowed with an instinct that brings it to undergo its transformation at some place

appropriate for the ecdysis of the winged adult. Most aquatic larvae come out of the water to pupate, some crawl up on rocks or plant stems, others travel inland; the parasitic larva emerges from its host; overwintering species find protection from the cold in concealed places or within the ground, and do not transform until the return of warm weather.

Changes of structure adaptive to environmental conditions, however, are not limited to the postembryonic stages of insects. The embryo itself may acquire adaptive characters as well as the larva. The embryo is commonly said to recapitulate ancestral stages in the evolution of its species, but, shut up in an egg shell, it can hardly be expected to follow in all ways the course of evolution that was practical to its free-living progenitors, and it needs special features for its own purposes. The insect embryo, for example, may have amniotic folds for protection, perhaps a trophamnion for its nourishment, a tooth on its head for breaking out of the egg shell. Then there are those embryonic organs on the first abdominal segment of some insects known as pleuropodia, but which take on special embryonic functions quite foreign to the usual purpose of a leg. All such adaptations of the embryo to life in an egg shell are just as truly aberrations from phylogenetic evolution as are the adaptive characters of free-living larvae that fit them to their particular environments, such as gills of aquatic species or the abdominal "legs" of crawling and climbing species.

A most interesting case of adaptive embryonic metamorphosis is seen in scorpions of the family Scorpionidae (Mathew, 1948; Vachon, 1950, 1953), in which the eggs are provided with very little yolk. The embryos undergo their development in follicles of the ovarial tubes, and are nourished on material from the blood of the mother absorbed into slender apical diverticula of the follicles. Each diverticulum is traversed by an inner feeding tube reaching to the mouth of the embryo. As a special adaptation on the part of the embryo, the movable digits of the chelicerae take the form of flat pads or long vesicular arms that clasp the feeding tube and bring it against the mouth, into which the food material is sucked by the muscular pharyngeal pump. At birth the young scorpion retains the embryonic chelicerae until the first moult, when these organs revert to the adult form.

The embryonic modification of phylogenetic evolution forced upon the embryo because of its development in the egg is well illustrated by the manner in which the insect embryo commonly forms its stomach. The food of the embryo, the yolk, is stored in the egg and thus

comes to be inside the body of the embryo; consequently it cannot be ingested in the ancestral manner by way of the mouth. In embryonic development, therefore, the stomach grows around the yolk, a method of "gastrulation" certainly that does not in any sense recapitulate stomach formation in the evolution of a free-living ancestor whose food had to be taken in from the outside. The embryo simply follows a modified process of gastrulation in adaptation to life in an egg shell, but in the end it produces an alimentary canal the same as that which its free-living ancestors produced by quite different evolutionary methods.

The insect embryo may develop into a juvenile form resembling its parents except in matters of immaturity, such as the rudimentary nature of the wings and the organs of reproduction. In such cases the young insect successively approaches the adult structure at each moult and finally assumes the imaginal form. At the other extreme, the embryo throws off all adult ancestral influences and develops into a creature having no likeness to its parents. There is here no phylogenetic recapitulation, the young insect in its growth takes no steps toward the adult structure; development of the adult, except for the growth of invaginated appendage rudiments, is inhibited until the young insect has accomplished its particular function in the life history of its species. Then the juvenile tissues disintegrate and the imago is rapidly built up in the form of its parents.

Inasmuch as the terminology of metamorphosis is not standardized, the same names being used in different ways by different zoologists, it will be necessary before proceeding with a further discussion of insect metamorphosis to explain a few common terms as they will be applied in the following pages.

Metamorphosis.—The word "metamorphosis" means merely a "change of form." In general zoology any pronounced change of form during growth, such as the changes of a crustacean larva in its development from the nauplius to the adult, or the changes of a tadpole in becoming a frog, is called metamorphosis. Entomologists, on the contrary, are inclined to restrict the idea of metamorphosis to the final change from a differentiated juvenile form to the imago, whether the change is direct or accomplished in an intervening pupal stage. Such a definition of metamorphosis is clearly too restrictive, since it would eliminate the use of the term as commonly used in other branches of zoology, and even in the insects there may be pronounced metamorphic changes between larval instars. Students of the action of hormones in the postembryonic development of insects commonly refer to the change to the adult as the "metamorphosis" of the insect

regardless of the degree or nature of the change. Bodenstein (1953b, p. 879), for example, says: "We speak of metamorphosis when the animal shows adult characters after a molt." Wigglesworth (1953a) finds that in *Rhodnius,* in addition to the full development of the wings and reproductive organs at the final moult, the epidermal cells now lay down an imaginal cuticle that is totally different in structure and color pattern from that of the nymph, and hence he calls the changes at the last moult the metamorphosis of the insect. Such final changes as those that occur in most of the Heteroptera, however, would appear to involve merely the completion or final acquisition of adult characters, and are therefore not comparable to the metamorphic changes in other insects resulting from the suppression of juvenile aberrations in form or structure.

It will probably be useless to attempt to write a definition of metamorphosis, since none would be generally acceptable. With nearly all insects there is necessarily a change of some kind or degree from one instar to the next, since the insect grows by stages, and the change at the last moult is usually greatest because the insect now takes on the fully developed adult characters. However, regardless of definitions, we must distinguish between changes that are consequent on growth from youth to maturity, and those that result from structural aberrations on the part of the young insect from the direct line of development. True metamorphic characters, as here understood, are adaptive structures, temporarily assumed usually by the young insect for its own purposes, that have no phylogenetic counterpart in the adult evolution, and which are discarded at the transformation to the imago. Metamorphic changes may take place between the immature stages of the insect, but metamorphosis is most pronounced at the change to the adult because it now involves the assumption of imaginal characters as well as the discarding of juvenile characters. However, if the assumption of imaginal characters alone is called "metamorphosis," then all insects undergo metamorphosis in some degree at the last moult, and the term has no specific meaning.

If the metamorphic change between the young and the adult is of small degree it is termed *paurometabolism.* If the young insect differs conspicuously from the adult or has distinctive adaptive characters of its own, but still makes the change to the adult at one moult, the insect is said to be *hemimetabolous.* When two moults are involved in the change and a pupal stage thus intervenes between the young and the adult, the insect is said to be *holometabolous.* These terms, of course, have no literal significance. An insect may be classed as *ametabolous* if it goes through no changes during its development

that are not related to growth from youth to maturity, but such changes may be considerable and are often difficult to distinguish from paurometabolism.

Nymph.—In its biological application this term is almost exclusively entomological, but entomologists are not consistent in its usage. According to American and most English usage a "nymph" is generally the young of an insect without a pupal stage, while with European entomologists a "nymph" is more commonly the pupa. In the following discussion the term *nymph* will be limited to the young of ametabolous or paurometabolous insects that in all essential respects, except those of immaturity, resemble their parents and have no important characters that obscure their likeness to the adult.

Larva.—In general zoology the term "larva" is commonly used to designate the immature stages of any invertebrate animal, or even the tadpole stage of frogs and salamanders. Some entomologists limit its application to the young form of insects that have a pupal stage in their life cycle; others call any juvenile insect a "larva." Definitions may be arbitrary, but it is better if a scientific term has some relation to the original meaning of the word involved. If we take the word "larva" in one of its Latin meanings, that of a *mask,* it becomes an appropriate term for any young form, particularly of an arthropod, that differs so much from its parents that its identity is not apparent in its structure, being "masked" under a specialized juvenile disguise. A *larva,* in this sense, may be defined specifically as an immature post-embryonic stage that has acquired for its own use adaptive characters that its adult ancestors did not possess, and which are not carried over into its own winged instar. Unfortunately, the insects will not always conform with definitions. There are some young insects that are essentially nymphs, and yet have a few special characters of their own. Such borderline cases, however, only show how easily a nymph might become a larva.

True larval forms among modern arthropods occur principally in the crustaceans and the insects, but in these two groups the larvae are not equivalent ontogenetic stages. The crustacean larva in most cases is hatched at an early stage of embryonic development long before body segmentation is completed. The earliest larval form in the **Crustacea** is the *nauplius,* a minute creature without body segmentation, but provided with three pairs of appendages, which are the first and second antennae and the mandibles, a simple nervous system, a single median eye, and an alimentary canal with oral and anal apertures. The swimming nauplius serves for the distribution of its species, and,

though it is derived from an early stage of ontogeny, it is specifically modified in adaptation to an aquatic life, and therefore in its form and structure does not recapitulate any primitive ancestral form in the evolution of the Crustacea. In its growth the crustacean larva goes through subsequent stages in which body segmentation appears, and both the segments and the appendages increase in number until the final organization is attained. The young of a terrestrial animal could not survive if hatched at such an early stage of development as that of the nauplius. The insect larva, with a few exceptions among parasitic species, is hatched with the definitive body segmentation, and thus in its youngest stage represents a relatively late period of development. The typical crustacean larva is *anamorphic,* the insect larva is *epimorphic.* Here are two more terms that will need some attention farther on.

In both the crustaceans and the insects the larva may be *heteromorphic* in that it develops through a series of different forms. In the Crustacea the heteromorphic larva progresses toward the adult structure; with the insects successive larval forms are adaptations to different functions or living conditions of the larva itself and have no relation to the adult. Larval metamorphosis among the crustaceans, however, especially in parasitic species, is often retrogressive and ends in the production of a greatly modified or highly degenerate metamorphosed adult form. With the insects, simplified, or "degenerate," forms occur mostly in the early larval stages of heteromorphic parasitic species, which have normal adults.

Pupa.—There is no ambiguity in the use of this term; the pupa is the stage of a holometabolous insect in which the final development of the imago takes place. There is, however, a difference of opinion as to the nature of the pupa. A common idea is that the pupa represents the last nymphal instar of an ametabolous insect; another is that it is a condensation of all the former nymphal instars of its species; a third sees in the pupa a preliminary sketch of the adult furnishing a mold for the proper reconstruction and attachment of the adult musculature. The respective merits of these several pupal concepts will be discussed later.

The degree to which reconstructive processes take place in the pupa varies with different insects. In some cases most of the larval tissues are merely made over into corresponding parts of the adult, in others the larval tissues go into a state of dissolution and the adult organs are built up from special groups of undifferentiated embryonic cells, called *imaginal discs* or *histoblasts,* which are carried by the larva but form no essential part of the larval structure. That the larva

is a "double" organism, as it is often said to be, is thus seen to be true only in the more specialized members of some of the holometabolous orders. The embryo, however, is charged with the double potentiality of forming first a larva and then an imago; the larval structure is completed in the egg, the latent adult structure is built up in the pupa. Of all the reconstructive processes that take place in the pupa the most important is that of the muscular system, which is perhaps the primary reason for the pupa. The dissolution of the larval muscles before the imaginal muscles are formed at least accounts for the immobile condition of the pupa, though, since all the larval muscles are not destroyed at the same time and some may go over intact from the larva to the adult, various pupae retain some degree of activity.

The imago.—Rarely does the adult insect undergo any metamorphic changes after it emerges from the pupal skin. There is the curious case of the streblid fly *Ascodipteron,* however, which is parasitic on bats. As described by Jobling (1939) the female fly pierces the skin of the host with her enormous proboscis and pulls her body into the wound. The legs and wings are then cast off, while a circular fold of the integument grows forward over the abdomen and thorax until the body acquires a flask-shaped form. On a posterior setose knob of the body, which alone projects from the skin of the host, are situated six spiracles and the slitlike aperture of a chamber containing the openings of the vagina and rectum.

Anamorphosis.—The term *anamorphosis,* as usually defined, refers to the completion of body segmentation after hatching. Though anamorphosis thus involves a "change of form," it should not be confused with metamorphosis; it is merely a way of growing. The manner by which body segments are formed in anamorphic development is always essentially the same. Just anterior to the terminal lobe of the body, or telson, is a mass of undifferentiated tissue, the *zone of growth,* which is capable of active cell proliferation, and it is here that the new segments are generated. As each new segment is formed it lies between the segment before it and the zone of growth, so that the animal extends its length posteriorly, but the anterior segments are the oldest. This method of growth from behind forward, which may begin in the embryo or be completed in the embryo, is in general known as *telogenesis.* Anamorphosis, by definition, therefore, is telogenesis continued after hatching. The number of segments added by anamorphosis depends on how many segments the young animal has on hatching and on the number of segments it will have when mature.

Anamorphosis is characteristic of the polychaete annelids; it was the mode of development in the trilobites; it still prevails in most of

the crustaceans, in two groups of chilopods, in all the diplopods, pauropods, and symphylans; and a remnant of it persists among the hexapods in the Protura. It would seem, therefore, that anamorphosis was the primitive method of growth in the arthropods, and that it is an inheritance from their remote common ancestry with primitive annelids.

The addition of new segments in the arthropods takes place at the moults, and is usually accompanied or followed by the formation of new segmental appendages. If the growing animal takes on a different form or distinctive characters at successive anamorphic stages, as is common among the Crustacea, such features are metamorphic aberrations or adaptations superposed on anamorphosis. Anamorphosis, therefore, may be accompanied by larval heteromorphosis.

Epimorphosis.—The development of an animal is said to be *epimorphic* when the maximum number of definitive segments is present at hatching, though some segments may be suppressed later. The segments in some cases are formed teloblastically as in anamorphosis by generation from a subterminal zone of growth, but in most epimorphic arthropods, as in insects, the prospective body is first laid out as an unsegmented *germ band,* which later becomes segmented. Segmentation in the germ band commonly begins anteriorly and proceeds posteriorly, and the segmental appendages appear in the same order. In this case, therefore, metamerism might appear to have no relation to a supposedly primitive anamorphic method of growth, and the anteroposterior progress of development has been regarded as indicative of a "metabolic gradient" in the embryo, meaning that the developmental processes are most intense first at the anterior pole and proceed posteriorly. However, since in anamorphic growth the anterior segments are the oldest, the apparent formation of segments and appendages from before backward in an epimorphic animal may be merely the visible results of delayed segment differentiation in the germ band. Epimorphosis is clearly a specialized and more expeditious way of growing than is anamorphosis; it delivers the young animal into the world in a more nearly mature condition, and therefore in a more practical stage of development for meeting the contingencies of a free existence.

I. METAMORPHOSIS AND CLASSIFICATION

Insects cannot be classified taxonomically according to the type of metamorphosis they undergo. Hemimetabolism occurs among several unrelated orders, and holometabolism is not limited to the group

of orders formerly known as the Holometabola. Even among the orders that are typically ametabolous there may be juvenile changes during growth sufficient to warrant the term paurometabolism.

The ametabolous and paurometabolous insects include the Apterygota, and, among the pterygote orders, the Dermaptera, Orthoptera, Embioptera, Isoptera, Zoraptera, Corrodentia, Mallophaga, Anoplura, Heteroptera, and most of the Homoptera. Growth changes among the ametabolous insects are often fairly conspicuous, since they may include the acquisition of abdominal styli, developmental changes in the mouth parts, antennae, legs, wings, and the external reproductive organs, and furthermore they may involve changes in the shape and proportions of the head, thorax, and abdomen, accompanied by changes in the shape of the sclerites, and possibly in the number and arrangement of setae. Changes of this kind, however, are for the most part merely alterations that a young animal must go through in attaining the adult form, and are not of the adaptive kind here treated as true metamorphosis. Marked changes in the nymphal instars of an insect, furthermore, may be due to some specialized development of the imago, as is well illustrated by the Tingitidae, in which the apparent metamorphoses of the nymph are merely juvenile steps leading up to the unusual form of the adult insect, and have no adaptive significance for the immature stages themselves.

The postembryonic development typical of ametabolous insects is well exemplified in the nymphal growth of a cockroach or a grasshopper. The newly hatched insect may differ considerably in shape from its parents, but its form is the result of its having been developed in an egg, and is not an adaptation to its juvenile life. As the young insect grows it takes on more and more of the adult form at successive moults; the wings grow out as padlike extensions of the back plates of the mesothorax and metathorax, the head becomes relatively smaller, the abdomen larger, and the external genitalia develop. There may perhaps be changes of color, or minor features found only in the immature stages, but such characters are insignificant. The young insect generally mingles with its parents in the same habitat, feeding on the same kind of food with the same kind of mouth parts. The adults on their part have taken no advantage from their wings to lead a different kind of life. In short, it may be said of the orthopteroid insects in general that they lead the normal life of most other animals instead of adopting a dual existence as do those with metamorphosis. They should, therefore, be the direct descendants of more primitive winged insects, the young of which never wandered from the parental habitat, or took on a form or characters that had to be

discarded at the moult to the imago. In a study of metamorphosis the orthopteroid insects are thus of particular interest in that they show us the simple course of postembryonic development in winged insects, one that has not been complicated by the addition of juvenile characters for the specific use of the young.

The insects here classed as hemimetabolous are the Plecoptera, the Ephemeroptera, the Odonata, and some of the Homoptera. The metamorphoses of these insects undoubtedly have been developed independently in each group; they have nothing in common and need no further discussion here since each order will be treated in a separate section following.

The holometabolous insects include the males of Coccidae, the Thysanoptera, the Neuropteroidea, Coleoptera, Strepsiptera, Trichoptera, Lepidoptera, Mecoptera, Siphonaptera, Diptera, and Hymenoptera. The presence of a pupal stage in the life history is diagnostic of holometabolism, but it is probable that the pupa is not in all cases a homologous stage. It is the intensity or degree of the transformation processes, particularly the reconstruction of the muscular system, that characterizes holometabolism and makes a resting stage necessary between the larva and the imago.

The larvae of holometabolous insects are endopterous and some of them are endopodous, that is, they have no external wing rudiments, and may have no functional legs. The "wingless" condition of the larva, as well as the "legless" condition, however, is apparent rather than real, since wing and leg rudiments are usually present but concealed within pouches of the epidermis beneath the outer cuticle. A truly apodous larva, therefore, is rare or perhaps does not exist, and probably the only wingless larvae are those of insects that have no wings in the adult stage. Wing rudiments, however, are sometimes present on the pupae of wingless adults, and in such cases are preformed in the larva.

The endopterous condition of the larva is not entirely characteristic of any particular taxonomic group of insects. In the Coccidae the wings of the male do not appear externally until the third or fourth moult, and in Aleyrodidae they do not become external until the last moult. The winged males of Embioptera also, as shown by Melander (1903), develop their wings internally up to the last nymphal stage. In the case of the male coccids and the aleyrodids a variable degree of metamorphosis, aside from the wing and leg development, may accompany the larval growth, but the embiids show no juvenile changes that do not lead up to the adult structure. It is evident that

the endopterous condition of the larva has been acquired independently by different insects, and it is questionable whether it is to be regarded necessarily as a metamorphic feature, or merely as a device for protecting the wings during the early stages of their growth. Clearly it is an advantage to the young insect to have temporarily useless appendages removed from the surface.

Inasmuch as the type of metamorphosis that an insect goes through, or whether the young insect is exopterous or endopterous, does not in all cases conform with the insect's taxonomic relationships, it will be more appropriate to discuss the metabolous insects according to their usual classification rather than according to their kind of metamorphosis. Among the ametabolous insects special attention must be given to the Apterygota, because certain features of hemimetabolous and holometabolous larvae have been thought to be derived from adult ancestral forms resembling the modern thysanurans.

II. HORMONES AND METAMORPHOSIS

The transformations of insects have long furnished a popular theme for writers on the "marvels of insect life," but in recent years serious investigators have given more and more attention to the vital mechanisms that control the phenomena of metamorphosis. Though their studies have not eliminated the mystery, they have revealed something of its nature, and insect metamorphosis has now become a subject for experimentation rather than one that merely excites our visual curiosity. The young insect contains two opposing forces in the nature of hormonal secretions that regulate its growth and development; one maintains the juvenile status, the other stimulates moulting and normal development that culminates in the production of the imago.

Though insect endocrinology is still a youthful science, it has many devotees. The insects are excellent experimental subjects; they submit to amputations, graftings, and transplantations without complaint and apparently without discomfort. It would go too far beyond the scope of the present discussion to list the great number of papers now available on the endocrine organs of insects, or to review all the experimental evidence of the action of hormones in controlling the metamorphic processes. The student may find ample bibliographies in the more recent papers to be cited in connection with the following summary of what may now be regarded as known concerning the organs of internal secretion and the hormones that regulate metamorphosis.

The endocrine organs of insects that control nymphal and larval

growth, moulting, development, pupation, transformation of the nymph or larva to the imago, and the ripening of the eggs in the ovaries include the following: (1) Secretory cells in the intercerebral part of the brain, (2) the corpora cardiaca, (3) the corpora allata, (4) pericardial glands, (5) perhaps glands in the posterior ventral part of the head, (6) thoracic glands, and (7) the ring gland of cyclorrhaphous Diptera.

Secretory cells of the brain.—In insects of most of the principal orders secretory nerve cells that play an important part in moulting and imaginal development are present in the pars intercerebralis of the protocerebrum. According to Scharrer and Scharrer (1944) such cells have been shown to be present in Orthoptera, Hemiptera, Neuroptera, Coleoptera, Trichoptera, Lepidoptera, Hymenoptera, and Diptera. In the blattid *Leucophaea,* these authors observe, some of the cells of the pars intercerebralis contain varying numbers of distinctly staining colloid inclusions, which are continued for some distance into the cell axons. The fibers from the secreting cells go downward in the brain, where most of them cross from one side to the other, and then turn backward through the nerves of the corpora cardiaca to innervate these bodies. It has been shown by Wigglesworth (1940) and others that the brain secretion has to do with the induction of moulting, but from further research it is now known that moulting and imaginal development depend on a hormonal complex derived from the brain and the prothoracic glands. According to Williams (1948) there are two groups of secretory cells in the larval brain of the *Cecropia* moth producing two different hormones, both of which are necessary to induce moulting.

The corpora cardiaca, or paracardiaca.—The corpora cardiaca (fig. 1 A,*Cc*) are usually paired oval or elongate bodies lying behind the brain, with which they have nerve connections, and are closely attached to the sides of the aorta. They arise, however, as cellular outgrowths from the dorsal wall of the stomodaeum at the sides of a similar median outgrowth that becomes the hypocerebral ganglion of the stomodaeal nervous system (*hcGng*). According to Pflugfelder (1937) the corpora cardiaca in an early embryonic stage of the phasmatid *Dixippus* lie against the lower surfaces of the cardioblasts, but when the cardioblasts unite to form the aorta, they push into the aortic wall; the lower cells remain as compact masses which are soon differentiated into ganglion cells, while the others appear to be secretory.

An extensive comparative account of the corpora cardiaca in most of the principal groups of insects is given by Cazal (1948), who more

appropriately calls these bodies *paracardiaca,* since their connection with the heart is entirely secondary. Typically each corpus cardiacum is connected with the back of the brain by two nerves (fig. 1 A,*ccNvs*), one lateral, the other median. The lateral nerves have their roots in the lateral parts of the protocerebrum, the median nerves arise in the
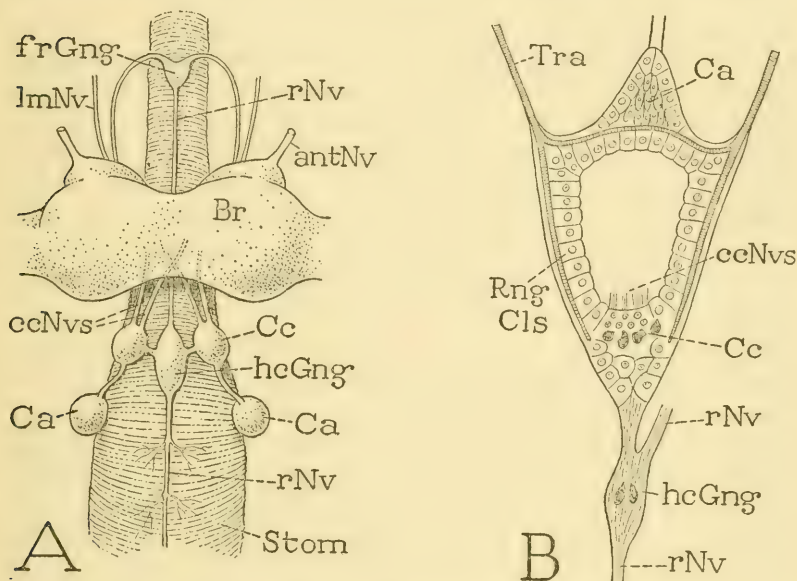

Fig. 1.—The retrocerebral endocrine organs.

A, diagram of a simple, perhaps generalized, arrangement of the corpora cardiaca and corpora allata on dorsal surface of stomodaeum behind the brain in association with the hypocerebral ganglion. B, diagram of ring gland of larva of *Calliphora* (from M. Thomsen, 1951).

AntNv, antennal nerve; *Br,* brain; *Ca,* corpus allatum; *Cc,* corpus cardiacum; *ccNvs,* corpus-cardiacum nerves; *frGng,* frontal ganglion; *hcGng,* hypocerebral ganglion; *lmNv,* labral nerve; *RngCls,* ring cells; *rNv,* recurrent nerve; *Stom,* stomodaeum; *Tra,* trachea.

pars intercerebralis and cross each other from one side to the other. Nerve fibers traversing the corpus cardiacum form a nerve connection between the latter and the corpus allatum of the same side.

Because of the intimate nerve relation of the corpora cardiaca to the secretory cells of the brain, and the observation that colloid granules similar to those in the brain can be traced along the nerve fibers into the corpora cardiaca, Scharrer and Scharrer (1944) point out that "the pars intercerebralis and the corpus cardiacum of insects may be viewed as one neuro-endocrine complex rather than as two separate sources of hormones." The presence of a brain hormone

concerned with moulting and development is now well known, but the specific function of the corpora cardiaca has been but little investigated. It is noted by Pfeiffer (1942) that removal of the corpora cardiaca from nymphs of *Melanoplus* is followed by a delay in moulting, but does not prevent moulting. This observation suggests that a corpus-cardiacum hormone is a part of the hormone system that activates moulting and imaginal development. The most definite information we have on the action of the corpus-cardiacum hormone, however, has to do with its effect on crustaceans. It had been known that extracts of the head of insects injected into blinded shrimps would cause a contraction of the chromatophores, just as does the hormone of the crustacean sinus gland in the eyestalk. M. Thomsen (1943) then showed that the activating element of the insect head comes from the corpora cardiaca, since transplantation of these bodies into a shrimp with amputated eyestalks had the same effect as head extract.

The corpora allata.—The corpora allata (fig. 1 A,*Ca*) are typically a pair of small oval bodies lying usually behind or laterad of the corpora cardiaca, with which they are connected by nerves, but in some insects the two bodies on each side are united, and the corpora allata themselves may be fused into a single mass. Variations in the relative position and connections of the corpora allata and cardiaca, and their association with the hypocerebral ganglion are illustrated in various insects by De Lerma (1937), Nesbitt (1941), and Bickley (1942) ; an exhaustive review of the structure of the retrocerebral organs in most of the insect orders is given by Cazal (1948). The first general description of the histology of the organs is due to Nabert (1913).

The corpora allata arise during embryonic development from the head ectoderm between the mandibular and maxillary segments, and are later transposed, as the name "allata" implies, to their definitive position behind the brain. In most insects they come to lie above the stomodaeum ; according to Cazal (1948) they lie below the stomodaeum in Ephemeroptera and Odonata. Formerly it was thought that corpora allata are absent in the Thysanura, but Chaudonneret (1949) has given reasons for believing that small glandular bodies in these insects lying against the outer surfaces of the adductor muscles of the maxillae are the corpora allata in a relatively primitive position.

The action of the corpus-allatum hormone is better known than that of the other incretory organs. The experiments of Wigglesworth

on the hemipteron *Rhodnius,* of Scharrer (1946a) on the blattid *Leucophaea,* of Pflugfelder (1937, 1938) on the phasmatid *Dixippus,* of Bounhiol (1938) on lepidopterous larvae all go to show that the corpus-allatum secretion in the young insect is the factor that maintains the juvenile status. This hormone, therefore, is known as the *juvenile hormone.* Wigglesworth (1951a) summarizes the results of his experiments on *Rhodnius* demonstrating the inhibitory effect of the corpus-allatum hormone on adult development as follows: "If the corpus allatum is removed from one of the young stages and implanted into the abdomen of a fifth-stage larva, when this moults it turns into a giant or sixth-stage larva instead of undergoing metamorphosis to an adult. Even a seventh-stage larva has been produced this way, and some of the sixth-stage larvae have transformed successfully into giant adults." Scharrer (1946a) obtained the same results from experiments on *Leucophaea.* Removal of the corpora allata from the last (8th) instar of the cockroach had no visible effects on development, but removal at earlier stages resulted in an abbreviation of development and the production of small adultlike forms, the adult characters being more accentuated with the age of the operated insects. Pflugfelder (1938) working with *Dixippus,* found that removal of the corpora allata from first and second instars was followed by a degeneration of certain tissues, including the fat bodies, the mesodermal sheath of the nervous system, muscles, and the Malpighian tubules. These changes are those that normally take place at the end of larval life in holometabolous insects, showing that it is the corpusallatum hormone that maintains the integrity of the juvenile tissues, and that the dissolution of specialized larval tissues is due to the weakening or cessation of secretory activity by the corpora allata in the last juvenile stage. Similar results have been obtained in Lepidoptera by Bounhiol (1938) and other investigators (see Hinton, 1951). Removal of the corpora allata from a young caterpillar brings on precocious pupation, but removal of the organs from a last-stage larva has no effect on pupation. It is noted by Wigglesworth (1936), furthermore, that "the corpus allatum also determines the characters of each nymphal instar by limiting the degree of differentiation toward the adult form which occurs during the moults."

In the adult insect the corpora allata again become active, but now their secretion is operative on egg production in the female and on secretion by the accessory genital glands in the male. The effect of eliminating the corpora allata from the adult insect has been studied by various investigators, including Wigglesworth (1936, 1948), Pfeiffer (1939, 1942, 1945), and Scharrer (1946b). From experiments

on the grasshopper *Melanoplus,* Pfeiffer (1939) found that complete removal of the corpora allata from adult females prevents the production of ripe eggs in the ovaries and of secretion in the oviducts. The eggs will develop without corpora allata until they reach the stage at which yolk deposition normally begins, but after that time they stop development, degenerate, and are resorbed. In later work on the same insect Pfeiffer (1945) showed that in normal females, during the early period of adult life before yolk formation in the ovaries, the fatty acid content of the body increases, the fat body hypertrophies by rapid storage of fat, nonfatty dry matter increases in correlation with fatty acid increase, and the blood volume moderately increases. These changes, however, do not take place if the corpora allata are removed at the beginning of the adult stage. In the normal female the metabolic processes are reversed after yolk formation begins. From these findings Pfeiffer concludes that "the corpora allata control egg production principally, if not entirely, through the agency of a metabolic hormone, and that a primary function of this hormone is to facilitate the mobilization or production of materials necessary for egg growth." According to Scharrer (1946b) the corpora allata are necessary in the blattid *Leucophaea* for approximately the first third of the total period required for egg development, which time corresponds to the period of growth and yolk deposition. Reimplantation of corpora allata into females from which these organs had been removed caused the eggs to develop and produce normal nymphs.

It is a curious fact that the corpus-allatum hormone of the adult seems to be the same as that which inhibits adult development in the young insect. By implanting from two to six corpora allata from young adult females of *Melanoplus* into a nymph, Pfeiffer (1942) found that the nymphs never transformed into adults, though some of them made one or two further moults. The same hormone apparently is present in both the female and the male, since Wigglesworth (1936) reports that in *Rhodnius* the corpora allata of the male will induce egg development in the adult female, and those of the female will activate the accessory glands of the male. He concludes (1948), therefore, that "it is probable that the yolk-forming hormone and the juvenile hormone are identical." On the other hand, Wigglesworth finds that the moulting hormone of the nymph will not induce egg formation, nor will the egg-forming hormone of the adult induce moulting in the nymph. A dual function of an apparently single hormone, Wigglesworth notes, recalls the multiple action of thyroxin in Amphibia. In the case of the insect, however, it now appears that the principle of "tissue competence" emphasized by Bodenstein (1943)

and by Bounhiol (1938, 1953) plays an important part in the action of a hormone. With respect to the corpus allatum, Bounhiol (1953) says, it is very probable that it has only a general effect on metabolism, and that it is the variable state of sensitivity in the different organs, or in any one organ according to its age, that determines the varying responses. Evidently, what is a stimulus in one case may be an inhibition in another.

Though the corpus-allatum hormone acts as an inhibitor of development in the larval tissues between moults, the rudiments of imaginal organs developing in the larva, such as the antennal, leg, and wing buds, continue to grow during the larval instars. Eassa (1953) gives measurements of the antennal growth in the larva of *Pieris brassicae* between moults, and notes that mitosis may be observed in the antennal cells. It would appear, then, either that the larval corpus-allatum hormone is selective for larval tissues, or that imaginal tissues are not affected by it.

Pericardial glands.—These glands were first described by Pflugfelder (1938) in the phasmatids *Dixippus* and *Phyllium,* but later (1947) he reported them present also in Ephemeroptera and Plecoptera. The glands of *Dixippus* and *Phyllium* lie in the posterior part of the head close above the dorsal blood vessel, mesad of the pericardial cells, from which they are distinctly different. The pericardial glands, according to Pflugfelder, arise from the lateral walls of the head coelom, and are therefore mesodermal organs. They attain their greatest development in the last nymphal stage, and in the adult they soon degenerate and disappear, from which facts it is deduced that the pericardial glands are endocrine organs, though there is no direct evidence of their function. It is probable, as will be explained later, that the pericardial glands compose the major part of the ring gland of cyclorrhaphous fly larvae, and that functionally they are equivalent to the thoracic glands of other insects.

Ventral glands of the head.—These organs are small glandular bodies lying ventrally in the posterior part of the head, described by Pflugfelder (1938) first in Phasmatidae, but later (1947) reported as present also in Ephemeroptera, Odonata, Plecoptera, Dermaptera, Acrididae, Blattidae, and Isoptera. They are of ectodermal origin and degenerate after the last moult except in the workers and soldiers of termites. Williams (1948) suggests that the glands may be homologous with the prothoracic glands, but it is said by Hinton (1951) that prothoracic glands also are now known to be present in Odonata and Orthoptera.

The prothoracic glands.—Glands of the prothorax were described in a caterpillar by Lyonet as "granulated vessels," and little further attention was given to them until recent times. It is now well demonstrated that these glands are important endocrine organs, probably present in most insects; according to Hinton (1951) they are known to occur in Odonata, Orthoptera, Hemiptera, Lepidoptera, Hymenoptera, and Diptera. They are said by Toyama (1902) to arise in the early embryonic development of the silkworm as epithelial invaginations of the lateral part of the second maxillary segment and to extend into the thorax. In lepidopterous larvae the glands are loose, branching masses of cells associated with the tracheae in the sides of the prothorax. Their structure has been described by Williams (1948) in the larva of *Platysamia cecropia,* and a well-illustrated comparative account of them in various lepidopterous species is given by Lee (1948). Prothoracic glands in the hemipteron *Rhodnius* are described by Wigglesworth (1951b, 1952a).

The probable function of the prothoracic glands is best known from experiments by Williams (1947) in connection with the pupal diapause of *Playtsamia cecropia.* It appears that there is an intimate functional relation in the caterpillar between the prothoracic glands and the brain. The pupa of the Cecropia silkworm as soon as it is formed goes into a prolonged state of diapause, which normally is broken only when the pupa is exposed to low temperatures. It is shown by Williams, however, that if the brain is removed from a diapausing pupa, chilling has no effect and further development permanently ceases. On the other hand, if the brain from a chilled pupa is implanted into a brainless pupa, normal development takes place. It is evident, therefore, that the chilling of the brain renders it competent to release its developmental hormone. However, further experiments by Williams showed that a pupal abdomen severed from the thorax will not develop even if a chilled brain is implanted into it, but when reattached to the thorax such an abdomen proceeds with development. The head and the thorax, on the contrary, develop when a chilled brain is inserted. Normal development, in short, requires besides a chilled brain the presence of the thoracic glands, which do not need exposure to cold for activation. Thus the brain, Williams points out, evidently exerts a controlling action on the prothoracic glands. In other words, the resumption of normal development in the diapausing Cecropia pupa is brought about by the interaction of a hormone from the brain and another from the prothoracic glands, but the gland hormone, Williams says, "most probably, has the ultimate action on the tissues in terminating diapause." The same rela-

tion between the brain hormone and a prothoracic hormone has been demonstrated in the hempiteron *Rhodnius* by Wigglesworth (1952b). The brain hormone activates the thoracic gland, which latter "then produces the factor initiating growth and moulting."

Considering, then, the intimate relation of the secretory cells of the brain both to the corpora cardiaca and to the prothoracic glands, it is evident that the brain is of primary importance in the activation of imaginal development. It is to be noted, however, that in this case the brain does not function in the usual manner by nervous control, but through having taken on a secondary function of hormone secretion. The secretory action of the brain, however, is induced by nerve activity.

The ring gland of cyclorrhaphous Diptera.—In the larvae of cyclorrhaphous Diptera a glandular structure surrounding the aorta behind the brain is known as the *ring gland*. Though formerly regarded as the corpus allatum, it is now known to be a complex endocrine organ that includes the corpora allata and corpora cardiaca of other insects embedded in a ring of cells of different origin. In the lower Diptera there is no ring gland. As shown by Cazal (1948) corpora allata and corpora cardiaca are present in the usual manner in Nematocera, either separate or united. In *Tabanus* and other Brachycera the corpora allata are united above the aorta and are connected by nerves going around the aorta to the ventrally placed corpora cardiaca, which are separate. In *Melophagus ovinus,* according to Day (1943), the corpora allata are paired bodies in the larva and the corpus cardiacum is a single median organ.

Investigators are mostly in accord as to the structure of the ring gland in the Cyclorrhapha, and we may follow the account of the organ given by M. Thomsen (1951). The larval ring gland of *Calliphora erythrocephala* as illustrated by Thomsen (fig. 1 B) is triangular rather than circular; its wide anterior part is prolonged forward as a median tongue above the aorta, its narrow posterior part lies below the aorta. A trachea (*Tra*) enters on each side and the two lateral trunks are connected by a commissure through the anterior part of the gland. The major part of the organ is formed of large cells termed the *ring cells* (*RngCls*). Within the anterior tongue in front of the tracheal commissure is a group of small cells (*Ca*) representing the corpora allata of other insects. In the posterior angle of the ventral part of the ring is a second group of small cells (*Cc*) apparently representing the corpora cardiaca. The ring cells themselves were formerly regarded as the corpora cardiaca, but it was sug-

gested by Ellen Thomsen (1942) that they correspond with the pericardial glands described by Pflugfelder in the phasmatids, and M. Thomsen concurs in this view, which is now generally accepted. Furthermore, there is reason to believe that both the pericardial glands and the lateral cells of the ring gland represent the thoracic glands of other insects. Though Poulson (1950) says the lateral ring gland cells of *Drosophila* arise from the roof of the stomodaeum, and would therefore appear to be the corpora cardiaca, M. Thomsen shows that the usual four corpora-cardiaca nerves (*ccNvs*) from the brain go to the group of small cells in the posterior angle of the ring gland, which fact would suggest that these cells alone are of corpuscardiacum origin. Lying behind the ring gland of *Calliphora,* and connected with its posterior end by a short nerve is the hypocerebral ganglion (*hcGng*) of the recurrent nerve (*rNv*). In *Drosophila* Bodenstein (1950) shows that the corpus cardiacum and the hypocerebral ganglion are apparently united in the posterior end of the ring gland.

From experimental work it is known that the ring gland of cyclorrhaphous larvae is necessary for the inducement of moulting and pupation. Burtt (1938) observed that removal of the gland from larvae of *Calliphora* prevents pupation and that growth of the imaginal buds is arrested. Day (1943) reports that experiments on *Lucilia* and *Sarcophaga* suggest that the ring gland produces a hormone concerned with normal development; in the larva it induces puparium formation. Bodenstein (1944) showed that larval moulting is dependent on the presence of a ring-gland hormone. Possompès (1950), however, demonstrated that the action of the ring gland as an effector of metamorphosis depends on its stimulation by a hormone from the brain. He suggests that the ring-gland elements thus activated from the brain are the lateral cells ("peritracheal glands"), which thus correspond at least in function with the thoracic glands of other larvae. There appears to be no experimental demonstration of the specific function of the corpus-allatum element of the ring gland on the larva, but presumably it is the same as in other insects.

The ring gland of the larva moves backward in the pupa and comes to lie in front of the proventriculus. In the newly emerged adult of *Calliphora,* according to Ellen Thomsen (1942), the ring gland is present, but in the mature fly all of it except the corpus-allatum component disappears. In the adult of *Drosophila,* Bodenstein (1950) says the lateral ring cells degenerate, but the anterior group of cells remains as the corpus allatum, and the cells of the posterior part form

an elongate body representing the corpus cardiacum and the hypo-cerebral ganglion. The metabolic changes that the ring gland produces in the adult fly are those that are ordinarily attributed to the corpora allata. The action of the ring gland in the adult fly according to Day (1943) is seen "first in changes which occur during the breakdown of the larval fat body cells and subsequently in the changes undergone by the adult fat body cells, the oenocytes, and the development of the ovaries." Bodenstein (1950) attributes to the corpus-allatum remnant of the ring gland in the adult female of *Drosophila* the formation of a hormone that regulates egg maturation. The necessity for the presence of the ring gland in the adult fly for the ripening of the eggs is well attested by the works of Ellen Thomsen (1940, 1942) and others.

The nature of hormonal action.—The hormones concerned with growth and metamorphosis are not in themselves the determiners of development; the course of development is determined by hereditary factors inherent in the tissues of the animal. The hormones are mere regulators, and in most cases they are found to be nonspecific as to species, a hormone from one insect having the same effect when introduced into another, regardless of different species structure. Furthermore, the effect of a hormone depends not entirely on the nature of the hormone, but also on the receptive state of the affected tissue.

Most of the experimental work that has been done on the hormones of insects has had as its object the ascertaining of the effect of specific hormones. It is now coming to be recognized, however, that the various endocrine glands and their secretions interact upon one another, and that the hormonal effect at any one time may depend on the relative amount of a particular hormone or hormone complex present in the blood. As stated by Bodenstein (1953a) the insect is able to keep a hormonal balance by "a mechanism of compensating hypertrophy or atrophy of its glands." The glands are in constant interaction with one another so that the amount of any hormone in relation to the others can be changed. "It is the hormone balance at a given time that determines the specific activity of the humoral system." In further work on the endocrine glands of insects Bounhiol (1953) says "it will be necessary to study more and more the action of the glands on one another," or, in the words of Bodenstein (1953a), "to disentangle the complicated relationships existing between the various hormones and to understand their action in physiological terms, not forgetting the vital role played in all these responses by the reacting systems."

III. APTERYGOTA

The insects of this group, which are wingless at all stages, as presumably were their ancestors, go through no truly metamorphic changes in their postembryonic growth. They might, therefore, be omitted from a discussion of metamorphosis were it not for the fact that they have certain structures that have been thought to recur in the larval stages of some winged insects, and which thus give them a theoretical value in the interpretation of juvenile characters among the metabolous insects. Of the several groups of apterygote insects, the Thysanura are the most closely related to the Pterygota. Though thysanurans are known in paleontology only as far back as the Tertiary, while winged insects were fully developed in the Carboniferous, a thysanuran (fig. 2 A) undoubtedly gives us a concrete example of what the wingless ancestors of the winged insects were like.

The organs of the Thysanura that are of particular interest in connection with a study of the larvae of the higher insects are the abdominal *styli* and the associated *eversible vesicles*. As typically developed in the Machilidae, there may be a pair of styli on the venter of each abdominal segment from the second to the ninth inclusive (fig. 2 A), and a pair of vesicles (E,*Vs*) on each of the first seven segments, or two pairs on some of the intermediate segments. In each segment the styli and vesicles are borne on lateral plates of the venter (C,D,E,*Cx*) commonly regarded as the bases of otherwise suppressed abdominal limbs. In the embryonic development of *Lepisma*, Heymons (1897) has shown that rudiments of appendages are formed on the first ten abdominal segments, but with the dorsal growth of the body wall they are stretched transversely and become flattened until finally they form merely the lateral parts of the definitive abdominal sterna. Eversible vesicles are absent in the lepismatids, and styli are present only on the eighth and ninth segments, or also on the seventh segment. In the machilids the so-called coxal plates (C,D,E,*Cx*) bearing the styli and vesicles remain separated from a median sternal plate (*S*). That the styli are coxal appendages and not limb vestiges is shown by their occurrence on the coxae of the middle and hind legs (B,*Sty*). The abdominal styli, therefore, are appurtenances of former limbs, but do not themselves represent abdominal legs. The same evidently is true of the eversible vesicles. Both styli and vesicles occur also among the other groups of apterygote insects, and among the pterygotes styli are present on the ninth abdominal segment of the adult male in the cockroaches, mantids, and termites. We may reasonably conclude, therefore, that the

immediate ancestors of both the wingless and winged insects had abdominal styli.

In Thysanura and Diplura the abdominal styli and vesicles are provided individually with muscles that arise on the supporting plates (fig. 2 D,E). The styli are flexibly movable on their bases; the vesicles are retracted by their muscles, and protracted probably by blood pressure. The styli are developed during postembryonic growth; ac-
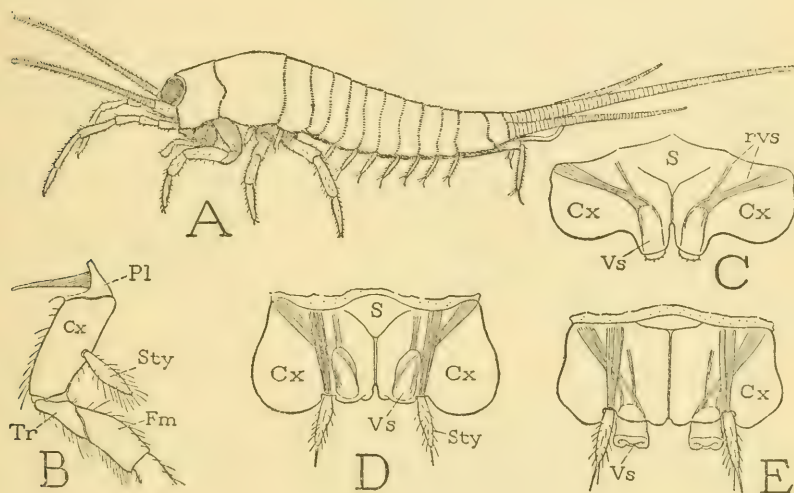

FIG. 2.—Structural details of Machilidae.

A, *Machilis* sp., whole insect, showing thoracic and abdominal styli. B, *Neso-machilis maoricus* Tillyard, middle leg, showing stylus on coxa. C, same, ventral surface of first abdominal segment, vesicles retracted. D, same, ventral surface of second abdominal segment, with vesicles and styli. E, same, ventral surface of sixth abdominal segment, vesicles everted.

Cx, coxa; *Fm,* femur; *Pl,* pleuron; *rvs,* retractor muscles of vesicle; *S,* sternum; *Sty,* stylus; *Tr,* trochanter; *Vs,* eversible vesicle.

cording to Heymons (1897, 1906), Adams (1933), Sweetman and Whittemore (1937), and Lindsay (1939) they first appear on the fourth or fifth instar of lepismatids, or even on much later instars.

Thysanurans moult many times throughout life, the number of moults depending on how long the insect lives. Sweetman and Whittemore (1937) record as many as 42 observed moults for one individual of *Thermobia domestica,* and they state that both moulting and growth continue long after the first eggs are laid. The lifelong periodic moulting of the Thysanura suggests that in this respect the primitive insects resembled the other wingless arthropods. With the acquisition of wings, moulting became too arduous, and among modern winged

insects a moult in the active imaginal stage occurs only in the Ephemeroptera.

The few structural changes that the thysanurans go through during their postembryonic life are merely those of development from youth to maturity. Body scales do not appear until after the first moult, the rings of the antennae and of the caudal filaments increase in number, the abdominal styli are formed at various moults, the leg styli of *Machilis* are said by Heymons (1906) to be absent on the first instar, there are some changes in the shape and proportions of the parts of the body, and the external genitalia develop during late stages. Such changes, however, do not constitute a true metamorphosis; they are progressive toward the adult structure, and do not give rise to adaptive juvenile characters.

The fossil records of early insects give no evidence as to how insects acquired their wings. There is no doubt that insects were hexapods before wings were developed, and it seems highly probable that wings were evolved from paranotal lobes on the thoracic segments that first served as gliders.

IV. PLECOPTERA

Among all the "orthopteroid" insects the stoneflies are the only ones of which the young have adopted a medium different from that of the adults, and, though the young stoneflies live in the water, their structural adaptation to aquatic life is relatively little. Aside from features of immaturity, such as the unfinished development of the wings, there is little to distinguish a young stonefly from an adult other than the presence of gills for aquatic respiration, and differences in the shape and proportions of the parts of the body. The stonefly larvae have no outstanding features common to all species by which they differ from the adults, and they could hardly be mistaken for anything other than immature Plecoptera.

A typical stonefly larva has well-developed compound eyes and frontal ocelli; the antennae are long, slender, and multiarticulate; at the end of the body are two caudal filaments representing the orthopteroid cerci, but no median filament; there are three subsegments in the tarsi, and two pretarsal claws; the fully exposed wing pads undergo a gradual development. In all these characters except those of immaturity the stonefly larva is essentially like the adult, and is entirely comparable to an orthopteran nymph; in short, it is simply a nymph that has taken to the water, where most species have acquired gills of a simple kind. If there is a difference in the mouth parts or

in the length of the caudal filaments between the larva and the imago, the difference is usually due to a reduction of these structures in the latter. The life cycle of the larva varies, according to the species, from one to three or four years, and there are correspondingly many instars, as many as 33 being recorded by Schoenemund (1912) for *Perla cephalotes.*

The gills of the stonefly larva are mostly tufts of delicate filaments penetrated by tracheae; they are generally present on the sides or sternal region of the thorax, but sometimes on the abdomen, particularly at the posterior end around the anus. Gills of a different type, however, may occur on the bases of the legs. As described by Lauterborn (1903), these leg gills in *Taeniopteryx nebulosa* L. are soft, "3-segmented," tapering processes arising singly from the mesal ends of the coxae, and are retractile by muscles. When retracted the three "segments" are telescoped into each other until only a soft papilla remains visible externally. Lauterborn compares these gills with the coxal sacs of Diplopoda; they might be likened to the eversible vesicles of Thysanura, but their position on the mesal ends of the coxae precludes a comparison with styli. Similar tapering gill processes are present on the sides of the first six segments of the abdomen in the genus *Eusthenia,* as illustrated by Tillyard (1926) in *E. spectabilis* Wwd. Though these abdominal gills are suggestive of styli, it seems probable that all the gills of stonefly larvae are special developments and have no relation to any other structures, including the gills of mayfly larvae. Besides the gills there may be a subepidermal system of tracheoles serving for respiration direct through the body wall. Wu (1923) has described in the larva of *Nemoura* the presence of numerous tufts of tracheoles on the epidermis of the submentum, the coxae, the ventral sides of the femora, and on the first eight sterna of the abdomen. A group of long tubular processes arising in the anterior end of the rectum he regards as "blood gills" because they do not contain tracheae.

The stonefly larva generally retains the feeding habits of the adults; most species feed on vegetable matter (see Claassen, 1931), only members of the family Perlidae being carnivorous. The mouth parts are modified according to the nature of the food, and there may be differences also in the general form of the body between vegetarian and carnivorous species. When the larva is ready to transform into the adult it crawls out of the water onto a stone or log, and may go some distance from the shore, showing that it has not entirely lost the ability to comport itself on land. The adult stonefly does not depend on the larva for stored nourishment to the extent that do insects

with more specialized larvae. Though the adult mouth parts are more or less reduced in some species (Lucy W. Smith, 1913), in others they are well developed, and such species feed extensively in the adult stage on vegetation. The female stonefly goes back to the water to discharge her eggs.

In the Plecoptera we have an example of metamorphosis in its simplest form, and one that shows very clearly that insect metamorphosis can have its inception in the adaptation of the juvenile stage to a medium different from that inhabited by the adults. The higher degrees of metamorphosis, therefore, arose from more extensive structural modifications of the young in adaptation to a secondarily adopted medium or way of living. Probably the nymph of the primitive stonefly simply found that it could obtain a better living in the water than on land, and natural selection then eventually furnished it with gills for a permanent aquatic existence.

V. EPHEMEROPTERA

The young mayfly (fig. 3 A) is distinctly more specialized in its adaptation to life in the water than is the young stonefly. Still, the young mayfly is simply a juvenile insect of generalized structure; it has compound eyes and frontal ocelli, well-developed legs, mouth parts of the biting type, and during its growth it develops wing pads that increase in size up to the last moult. In these characters the young mayfly has the developmental status of an orthopteroid nymph, and that it was primarily a land-inhabiting nymph may be deduced from the presence of an elaborate tracheal system in both the adult and the larva. Since the young of the earliest known fossil mayflies, found in the Permian, already had gills, the mayfly larva has come down to us with surprisingly few changes.

The larval gills of the mayflies are organs of particular interest because of their apparent likeness to the abdominal styli of Thysanura. In modern species the gills are present on the sides of, at most, the first seven segments of the abdomen; larvae from the lower Permian, however, had nine pairs of gills, and some Jurassic species had eight. The gills are highly variable in form in different species, but they are borne singly on lateral lobes of the abdominal segments (fig. 3 B,C) interpolated between the tergal and sternal regions. The gill-bearing lobes fall directly in line with the bases of the thoracic legs (Cx), and thus may be likened to the stylus-bearing plates of *Machilis*. Moreover each gill is movable by muscles arising in the supporting lobe (C,D). The movements of the mayfly gills has been made the
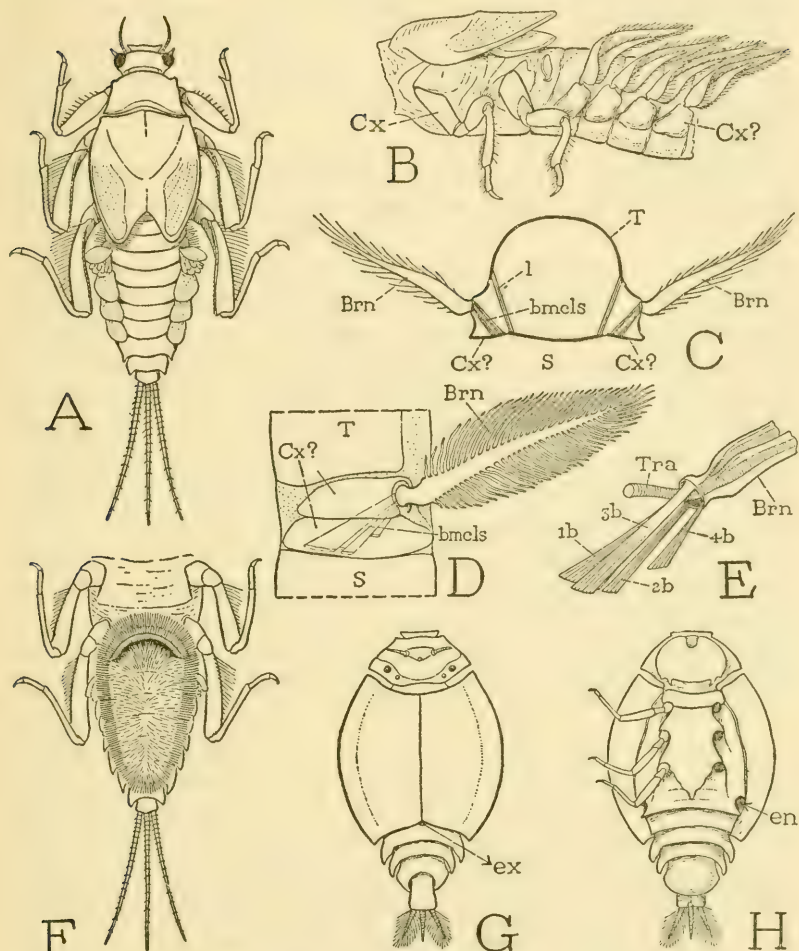
FIG. 3.—Characters of larvae of Ephemeroptera.

A, *Ephemerella* sp. B, *Ephoron* sp., part of thorax and abdomen, showing gill-bearing lobes in line with coxae of legs. C, diagrammatic cross section of abdomen. D, a single gill, showing muscles arising in supporting body lobe. E, base of gill, with tracheal trunk and muscles. F, *Ephemerella* sp., showing adhesive disc on venter of abdomen. G, *Prosopistoma foliaceus* Fourcroy, dorsal (from Vayssière, 1890). H, same, ventral (from Vayssière, 1890).

1b-4b, bmcls, branchial muscles; *Brn,* branchia, gill; *Cx,* coxa of leg; *Cx?,* gill-bearing lobe of abdomen; *en,* respiratory entrance; *ex,* respiratory exit; *l,* lateral body muscle; *S,* sternum; *T,* tergum; *Tra,* trachea.

subject of a special study by Eastham (1938, 1939). Just as the thysanuran styli do not appear until after the first moult, so the gills of the mayfly larva are absent in the first instar. It is said by Ide (1935) that all the gills appear with the first moult in some species, but that in other species most of them may be delayed until several moults later.

Gills of the simplest form are slender processes penetrated by tracheae, others are fringed with long filaments, some are lamelliform, and most of them are branched. According to Ide (1935) all the gills are at first uniramous, and some that eventually become lamelliform grow out first in the form of filaments. It would appear to be true, therefore, as Spieth (1933) says, that the primitive gills of the ancestral mayflies were simple slender tubular structures, into which the tracheae enter, and that the compound gills of the present-day forms have arisen as modifications of the primitive type. If the modern gills do represent styli, we may suppose that the young mayfly in its primary terrestrial life may have had abdominal styli similar to those of the Thysanura and Diplura, which, when it took to the water, were readily converted into gills. That the mayfly gills have been derived from styli, however, is merely a theoretical concept, but considering that the Ephemeroptera are relatively primitive insects the concept is sufficiently reasonable to be accepted as not too improbable. Unlike styli, however, the mayfly gills are discarded at the moult to the subimago.

Some remarkable larval modifications occur in connection with the gills. In the genus *Baetisca,* described by Vayssière (1934), the mesonotum is extended posteriorly to the middle of the sixth abdominal segment to form a carapace covering the gills and the metathoracic wing pads, the pads of the first wings being fused with its under surface. In *Prosopistoma* (Vayssière, 1882, 1890) a carapace is even more extensively developed (fig. 3 G) and covers a respiratory chamber enclosing the gills, which is shut in ventrally (H) by the pleural regions of the thorax and lateral extensions of the first five abdominal sterna. The *Prosopistoma* larva thus resembles a small crustacean in appearance. Water has entrance to the respiratory chamber by way of lateral openings (H,*en*) between the carapace and the sternum, and is discharged through a median dorsal aperture (G,*ex*) in the notch of the posterior end of the carapace. A preliminary stage in the development of a carapace is suggested in the larva of *Ephemerella* (A) in which the mesonotum including the fore wing pads is extended posteriorly over the base of the abdomen and completely covers the hind wing pads.

In various lesser ways the mayfly larva may be characterized by special juvenile structures. In some forms the incisor processes of the mandibles are produced into a pair of long tusks. The larvae of *Ephemerella* that live in swift currents have an adhesive disc on the under side of the abdomen (F) formed of a dense fringe of soft marginal hairs. In the anterior part of the disc is a deep transverse cavity behind a strong semicircular lip, which possibly has something to do with creating a suction when the disc is applied against the surface of a rock.

It is noted by Ide (1935) that at each moult of the mayfly larva there is some structural change adapting the larva to environmental changes resulting from the growth of the larva. Such changes involve the mouth parts, the wing pads, external genitalia, the claws of the legs, and the caudal filaments. The larva moults many times before changing to the winged imago; observations by Ide show that *Ephemera simulans* goes through about 30 larval moults, and *Stenonema canadense* as many as 40 to 45 moults. The large number of moults Ide attributes to the necessity for making adjustive physical changes to the environment, rather than to growth, since the larva increases but slowly in size. Some of these adaptive changes of the larva might be regarded as a feeble hypermetamorphosis, but the lack of gills and a tracheal system in the first instar and the expansion of newly formed gills into lamellar gills, cited by Joly (1872) as examples of hypermetamorphosis, are simply developmental changes.

The structural adaptation of an animal to a special environment is much easier to see as a fact, than it is to explain how it came about. The young mayfly larva can breathe through its skin, but as it gets larger it needs gills; the first one that entered the water, therefore, must have suffocated if it persisted in keeping submerged. However, if it possessed tracheated styli, it was but a simple evolutionary process to convert these organs into gills. Adaptation can seldom be one-sided; in the case of an aquatic larva of a terrestrial or aerial adult, the adult must be adapted to the way the larva lives. The female mayfly, therefore, has an instinct for returning to the water to discharge her eggs.

The changes that the mayfly larva undergoes in its metamorphosis to the adult are not due entirely to the special characters of the larva. The adult mayfly lives so short a time that it needs no food, and as a matter of economy its mouth parts are reduced to a functionless condition. Murphy (1922) says the "atrophy of the mouth parts is progressive during the aerial life of an individual," but "varies in extent among members of species." The ingestion apparatus and the

alimentary tract, however, are fully preserved, but for the purpose of swallowing and retaining air. The stomach is shown by Pickles (1931) and by Grandi (1950) to be transformed in the adult into a thin-walled air sack. The air probably serves to make the body more buoyant and by compression to expel the eggs.

Most mayflies undergo a moult after they have attained the state of a winged imago, the adult stage being thus subdivided into two winged stages, distinguished as the *subimago* and the *imago*. Concerning the subimago of *Cloeon dipterum*, La Baume (1909) says that it usually issues from the larval skin toward evening either on the surface of the water or on the shore. The quickness of the change is most noticeable, particularly the almost instantaneous spreading of the wings. The insect now flies to vegetation along the shore, where it remains quiet until the next moult, which, according to the species, may occur in a few minutes, a few hours, or several days. There is probably no specific reason why the adult mayfly should moult again; it is the only winged insect known to moult in the active adult stage, and even some mayfly species omit a second moult. Evidently the imaginal moult is simply a holdover by a primitive insect from wingless ancestors that shed the cuticle periodically throughout life as do the Thysanura and most other wingless arthropods. Extraction of the wings from the old cuticle is a difficult matter and other insects have simply discarded a useless and dangerous habit.

It is clear that the mayfly undergoes a greater degree of metamorphosis than does the stonefly because the young mayfly is more extensively modified in adaptation to life in the water. Inasmuch as the larva in the two cases is differently modified for the same purpose, metamorphosis has arisen independently in the two groups.

VI. ODONATA

The Odonata present an example of metamorphosis much more accentuated than that of either the Plecoptera or the Ephemeroptera, and there is no relation between the special characters of the odonate larva and those of the other two groups, again showing that larval structures in adaptation to aquatic life have been independently developed in these three orders. In common with other aquatic larvae, the odonate larva has been adapted in its body form and its means of respiration to life in the water, but in addition it has evolved a very special modification of the labium by which this organ is greatly enlarged and converted into an efficient device for the capture of active prey.

The Odonata are predaceous both as larvae and as adults; their mouth parts are of the biting type of structure. The adults entrap their insect prey on the wing by means of their hairy legs, and their mouth parts are not unusually modified. The short body of the adult
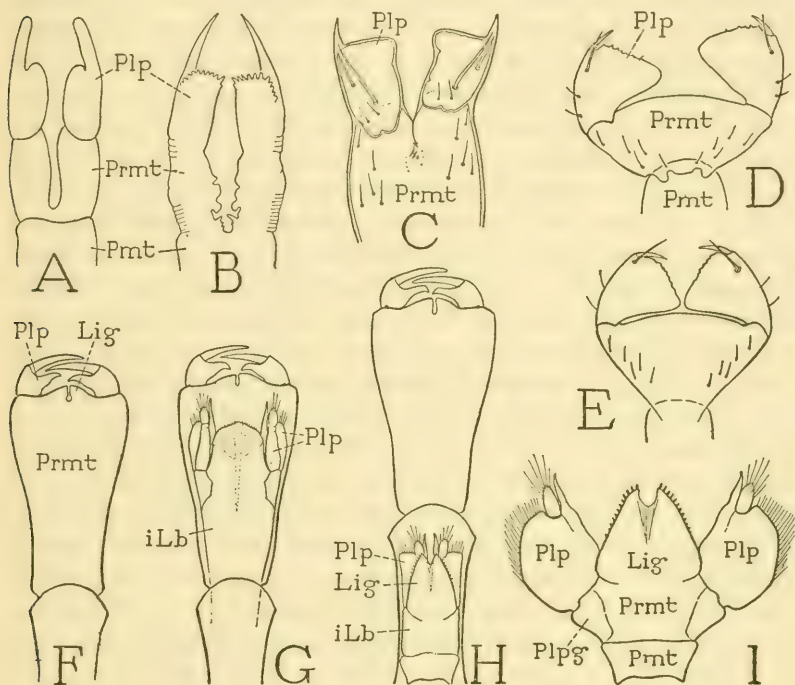

FIG. 4.—Odonata; development and metamorphosis of the labium.

A, *Anax junius* Drury, labium of 17-day embryo (from Butler, 1904). B, same, 20-day embryo (from Butler, 1904). C, *Sympetrum striolatum* (Charp.), labium of pronymph containing labium of second instar (from Corbet, 1951). D, same, free labium of second instar, expanding (from Corbet, 1951). E, same, fully expanded labium of second instar (from Corbet, 1951). F, *Anax* sp., labium of mature larva, posterior. G, same, larval labium and early stage of formation of imaginal labium in the prementum. H, same, later stage, the imaginal labium retracted into postmentum of larva and taking on the adult structure, posterior. I, same, imaginal labium from H unrolled and spread out.

iLb, imaginal labium; *Lig,* ligula; *Plp,* labial palpus; *Plpg,* palpiger; *Pmt,* postmentum; *Prmt,* prementum.

labium (fig. 4 I) consists of a distinct postmentum and a prementum; the prementum bears a large median ligular lobe, and two small lateral lobes (*Plpg*) that support the short, thick palpi (*Plp*). The larval labium is more simple in form than that of the adult, but both the postmentum and the prementum are greatly elongated, and are articulated on each other by a freely movable elbow. The larval postmen-

tum is unusual in that, instead of being as in most insects a plate on the under side of the head, it is produced into a long, free stalk supporting the prementum on its distal end. The prementum is highly variable in form in different genera; in the common *Anax junius* (F) it is a long flat lobe somewhat expanded distally where it bears the relatively small palpi, each of which is armed with a long sharp claw. In the passive position of the labium the postmentum is turned posteriorly against the mesosternum of the thorax (fig. 5 A); the prementum in some species is pressed against the under surface of the head (A), in others it is applied like a mask over the lower part of the face (C). In action the postmentum swings downward and forward on the head, the prementum is lowered (B), and the entire labium is then projected far beyond the mandibles to seize a prospective victim. Associated with the larval labium is a long T-shaped apodeme developed from the base of the hypopharynx that extends posteriorly through the head, and the crossbar is embedded in the posterior edge of the base of the postmentum. The labial musculature is surprisingly simple, but it is probable that blood pressure from the abdomen plays an important part in the projection of the labium. While undoubtedly the larval labium is specialized by comparison with the adult labium, the labium of the embryo develops directly into that of the larva, and at metamorphosis the adult labium develops within the larval organ. The hypopharyngeal apodeme is either greatly shortened in the adult or reduced to a ligamentous band.

The embryonic labium of *Anax junius* (fig. 4 A,B), as illustrated by Butler (1904), has a primitive feature in the almost complete separation of the stipital lobes of the prementum (*Prmt*); the unsegmented palpi (*Plp*) bear fingerlike processes (A) that will become the apical hooks (B). In the pronymph of *Sympetrum* (C), according to Corbet (1951), the prementum is undivided and the palpi arise close together from its distal end, but during ecdysis of the second instar (D) the prementum stretches transversely, and later (E) becomes more elongate. The embryonic labium thus goes from a primitive labial structure directly into the specialized structure of the larval labium. The labium of the adult as described by Munscheid (1933) is first formed in the distal part of the larval labium about five days after the larva ceases to feed. At first it takes on approximately the form of the larval labium, but later it becomes shorter until four days after its formation it occupies only the basal two-thirds of the larval postmentum. A further three days now elapses before ecdysis of the imago.

At an early stage of the labial transformation in *Anax junius* the imaginal labium may be seen retracted into the anterior part of the larval prementum (fig. 4 G, *iLb*). The principal changes that have taken place affect the palpi and the ligula, which have become elongated. On the palpus, the movable claw of the larval organ is replaced by a short setigerous lobe, as in the adult (I), and the fixed finger has become a slender tapering median process. At the base of each palpus a palpigerous plate is differentiated. In a later stage (H) the imaginal labium has withdrawn into the postmentum of the larval labium, where it is much compressed and its lateral parts are rolled anteriorly. When the imaginal labium at this stage is removed from the larval labium, unrolled and spread out (I), it is seen to have approximately the form of the adult labium except for the triangular shape of the ligula and its deeper apical notch. The palpi have taken on the form and size of the adult palpi, the prementum and postmentum are distinct in the body of the labium, and the palpigers are well defined. The triangular ligula finally becomes transversely oval.

It is of interest to note that the odonate labium begins its development in the embryo as a labium of primitive structure (fig. 4 A,B). In its later growth it develops directly into the specialized labium of the larva; then finally the more generalized labium of the adult is derived from the larval labium. It is not clear what phylogenetic deductions may be made from these facts, but it seems reasonable to suppose that the larval labium in the first place must have been evolved from a generalized labium approximately of the adult type of structure; if so, it carries the potentiality of reversal.

The transformation period from larva to imago is said by Munscheid (1933) in *Aeschna cyanea* to occupy about 12 days. During this time the structural changes of the labium are accompanied by a total histolysis of the larval labial muscles, followed by regeneration of the imaginal muscles and the formation of new tonofibrillar muscle attachments on the imaginal cuticle. Two pairs of larval muscles are destroyed and not replaced. The processes of muscle histolysis and histogenesis are described in detail by Munscheid, who points out that the transformation of the odonate labium and the regeneration of its muscles is comparable to the pupal metamorphosis in holometabolous insects, except that in the Odonata the process is limited to a single organ instead of affecting the entire insect, which otherwise is hemimetabolous. The long quiescent transformation period apparently allows the regenerated muscles to become attached directly on the new imaginal cuticle without the interpolation of a second moult.

Aside from the specialization of the labium, the principal adaptive characters of the odonate larva are the organs that serve for respiration. In the Anisoptera a spacious rectal sac contains six longitudinal tracheated folds of the walls which are the larval gills. The muscular apparatus of the rectum for the inhalation and exhalation of water becomes also a means of locomotion by the forcible ejection of spurts
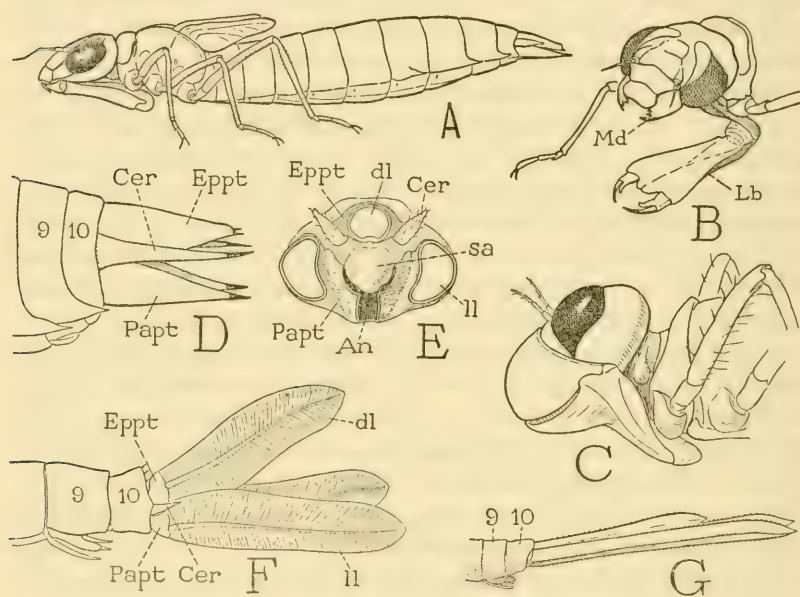

Fig. 5.—Odonata; general features of larvae.

A, Larva of *Anax* sp., labium in passive position. B, same, labium lowered and partly protracted. C, *Crocothemis servilis* Drury, labium applied against the face. D, anisopterous larva, posterior segments and lobes enclosing the anus. E, *Agrion virgo* L., posterior end of body with gill lobes removed. F, *Archilestes grandis* (Rambur), end segments of body and gill lobes. G, *Agrion virgo* L., end segments and apical lobes.

An, anus; *Cer,* cercus (cercoid); *dl,* dorsal gill lobe; *Eppt,* epiproct; *Lb,* labium; *ll,* lateral gill lobe; *Md,* mandible; *Papt,* paraproct; *sa,* supra-anal lobe.

of water. Zygopterous larvae are provided with three external gill lobes of various forms at the end of the body, one median and dorsal, the other two lateral, borne on basal plates surrounding the anus. Typically these caudal gills are thin lamellae (fig. 5 F), but they may be sacciform, and in some species they are slender horny blades (G) that do not appear to be suitable for respiratory purposes. The gills are weakly attached to the supporting plates so that they are easily broken off, but they regenerate at the next moult.

The current interpretation of the zygopterous larval gills, taken

from Heymons (1904), is that the dorsal gill represents a median dorsal filament and that the lateral gills are the cerci. Arising on each side between the bases of the gill-supporting plates is a small cercus-like process (fig. 5 F,*Cer*), the "cercoid" of Heymons, who says it is developed during larval life. The gill-bearing plates (*Eppt,Papt*) surround the anus (E, *An*) in a manner so exactly comparable to the epiproct and paraprocts of an orthopteroid insect that their identity as such is hardly to be questioned, and the "cercoids" (*Cer*) have the usual relation of cerci to these plates. The lateral gill lobes (E, *ll*, removed at their bases) therefore appear to be mere outgrowths from the paraproctial plates, and as such they could hardly be cerci. In the anisopterous larva (D) the gill-bearing plates of the zygopterous larva are produced into long valvelike lobes enclosing the anus, and there is no apparent reason for not identifying these lobes (*Eppt,Papt*) with the usual epiproct and paraprocts in the same position. The gills are cast off at the transformation to the adult, except as said by Tillyard (1917) that the lateral gills ("cerci") of the male leave a pair of small processes developed within their bases. If the lateral gills are cerci, it is an unusual thing for an insect to lose these organs.

In some zygopterous larvae, in addition to the caudal gills, there are paired lateral gills in the form of tracheated filaments along the sides of the abdomen (see Calvert, 1911; Needham, 1911; Tillyard, 1917). The tracheal system of the Odonata is present in the newly hatched larva, but according to Calvert (1898) the tracheae do not fill with air until the first moult. Spiracles are present in the larva but ordinarily are not functional except for the withdrawal of the tracheal linings at ecdysis. The early development of the tracheal system and the presence of spiracles in the larva, Calvert points out, attest that the immediate ancestors of the Odonata were air-breathing insects.

The structural changes that take place during larval life of the Odonata have been summarized by Tillyard (1917) under nine headings. Such changes, however, as the growth of the compound eyes, development of the ocelli, increase in the number of antennal joints and of subsegments in the tarsi, changes in the shape of the thorax correlated with development of the wings, progressive changes in the nervous system, and increase in the number of Malpighian tubules are merely stages in the postembryonic development of the adult organs. These are not true metamorphic changes such as those producing the general form of the larval body, the modification of the labium, and the development and differentiation of the rectal and

caudal gills. In addition to these changes, however, there takes place during the transformation period a radical change in the sclerotization pattern of the abdominal segments, accompanied by an almost total destruction of the larval abdominal musculature and the formation of a much more simple musculature for the adult. The Odonata might almost be said to be holometabolous insects without a pupal stage.

As in the case of other insects having aquatic larvae, the adult female of the Odonata has one instinct of responsibility to her offspring, namely, that which impels her to go back to the water to deposit her eggs. Some are so conscientious in this respect that they even enter the water and insert their eggs in the stems of submerged water plants.

VII. HEMIPTERA

The Hemiptera differ from most other insects having specialized mouth parts in the mature stage in that the adult type of mouth parts is just as practical for the young as for the imago. The adult hemipteron has not evolved feeding organs useful only to an insect with functional wings. The piercing and sucking mouth parts in Hemiptera, therefore, are developed in the embryo and are functional as such in the newly hatched insect. The same is true of the Thysanoptera and Anoplura. If there are metamorphic changes between the young and the adults of these insects, they do not affect the essential nature of the feeding organs, and all instars of a species can live and feed together in the same habitat.

Among the Heteroptera postembryonic development is principally a succession of growth stages from the young to the adult; the Heteroptera, as the Orthoptera, are essentially ametabolous. Though the change between instars may be accentuated at the last moult, there is in general little, if any, structural deviation on the part of the young insect that must be suppressed in the imago. However, a definite case of juvenile aberration in the Heteroptera is to be seen in a species of mirid described by China (1931) in which the nymph (fig. 6 F) is armed on the head, thorax, and abdomen with large dorsal prongs. Though the adult of the species has not been certainly identified, no adult mirid is known to possess any such armature.

Among the Homoptera there is a distinct though sporadic tendency for the young insect to develop special characters of its own that are not carried over into the adult stage, or to take on a form quite different from that of its parents. The aberration of the young insect may even become so pronounced that the final transformation to the imago approaches or actually attains a condition of holometabolism.

A good example of simple metamorphosis in the Homoptera is seen in the structural adaptation of the young cicada to a subterranean life by the modification of its front legs for digging (fig. 6 D). The nymphal structure of the leg is not present in the embryo (A); it appears first on the nymph with the shedding of the embryonic cuticle just after hatching (B) and becomes more fully developed in succes-
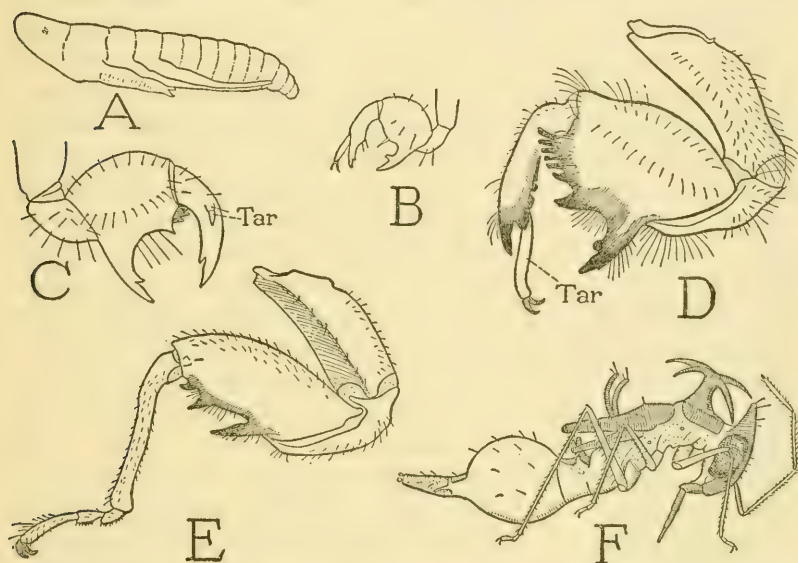

FIG. 6.—Examples of simple juvenile metamorphic characters in Hemiptera.

A, *Magicada septemdecim* (L.), newly hatched nymph still in embryonic cuticle. B, same, left front leg of first instar (from Marlatt, 1923). C, same, front leg of third instar, mesal view showing reduced tarsus (*Tar*). D, same, front leg of mature nymph, lateral. E, same, front leg of adult. F, *Paracarnus myersi* China, nymph, Heteroptera-Miridae (from China, 1931).

sive instars (C,D). The tarsus of the first instar (B) is reduced in later stages to a small spur on the inner surface of the tibia (C,*Tar*), but it is fully restored in the mature nymph (D). At the transformation to the adult, the special features of the nymphal leg are much reduced or obliterated (E). The newly hatched cicada has a pair of small eye spots, but in subsequent instars the eyes are lost, and functional compound eyes are redeveloped only in the imago. Within a chamber just below the surface of the ground, or built up above the surface, the 17-year cicada at last goes through a period of reconstruction inside the nymphal cuticle, during which the adult structure of the insect is developed, including the compound eyes, the external genital organs, and the sound-producing organ of the male. When

the insect emerges from its transformation chamber it is an active adult, but it still wears the nymphal skin until it arrives at a suitable place for ecdysis.

As another example of simple specialization in a young homopteron we may cite the respiratory canal of the spittle bugs, Cercopidae. On the ventral surface of the tapering posterior segments of the nymph is a deep groove that expands anteriorly into a wide space covered on the sides by the extended abdominal terga, which protect the spiracles. This modification is a respiratory device necessary only to the nymph and is discarded at the moult to the imago. As further examples of juvenile aberration we might note the presence of large branched spines on the back of certain membracid nymphs, and of various minor nymphal characters in other homopterous families that are not retained by the adult. Juvenile specialization among the Homoptera, however, is carried progressively further in the Psyllidae, Aleyrodidae, and Coccidae, until in the last family the transformation to the imago attains the status of true holometabolism. In the Aleyrodidae and the Coccidae the young insects are so different from their parents that, following the definitions given in the introduction, we must call them larvae, but admittedly they are nymphs that have acquired the status of larvae by definition.

The Psyllidae go through five juvenile instars, which, except for the flattened form of the body, in general resemble the nymphal stages of ametabolous Hemiptera. The wings appear first in the third instar and increase in size during the fourth and fifth instars; the legs, however, undergo a metamorphosis, which has been fully described by Weber (1930, 1931) in *Psylla mali*. The first instar is active because the young psyllid newly hatched on the twig of an apple tree must find an opening bud on which to feed; the legs are relatively far apart on the under side of the body, and in their movements are fitted for walking. After the first moult the insect becomes sessile, the legs come closer together at their bases and are flexed transversely beneath the thorax in order now to function as clasping organs. From the beginning, however, the segmentation of the legs has been reduced by a suppression of the femoro-trochanteral and the tibio-tarsal joints. At the moult to the fifth instar the young insect takes on something of the form of the adult, the body becomes deeper, the antennae longer, and in the legs there appears a slightly marked division between the tibia and the tarsus and an indication of two tarsal subsegments. Finally, within the cuticle of the legs of the last juvenile instar the imaginal legs are developed, the trochanter being now separated from the base of the femur, the tarsus distinct from the tibia, and two

well-defined tarsomeres present. The first two pairs of clasping legs of the young become normal walking legs in the adult, but the hind legs are elongated and transformed into jumping organs by an enlargement of the coxae and a lengthening of the body muscles of the trochanters associated with a dorsal extension of the sternal apodeme on which they are attached. The general alteration of the body form at the last moult, Weber shows, involves changes and enlargements of muscles in the thorax that are destined to be motors of the wings. The mouth bristles are retracted into a crumenal pocket instead of being looped outside the head as in the immature stages.

While the degree of metamorphosis in the psyllids is thus not large, it is enough to show how a young nymphlike insect can be specifically modified in adaptation to its needs, even in a different way in successive instars. The transformation of the young psyllid into the adult, however, is complicated by the development of special imaginal characters along with the suppression of juvenile characters.

In the Aleyrodidae there is a juvenile metamorphosis somewhat similar to that of the psyllids because here also the first instar is active and the others are sessile. The young aleyrodid, however, is much flattened, the body being of a simple, oval, scalelike form and wingless in all immature instars; the spiracles are on the under surface, and a wide fringe of wax filaments forms a marginal palisade that encloses an air space beneath the body. There are four immature stages, the characteristics of which are described by Weber (1931, 1934) as follows. In the active first stage the antennae and the slender, tapering legs are relatively long; each leg has only three segments and bears a stalked apical adhesive disc, representing the unguitractor plate of the adult insect. In the second instar the antennae are much shortened, and the legs are reduced to small, unsegmented stumps useless for locomotion but retaining the adhesive discs. The same leg structure is carried over into the third instar, but in the fourth instar both the legs and the antennae become again larger, and the legs are now 2-segmented.

From the fourth instar the adult aleyrodid is produced directly, but by an unusual transformation process. As described by Weber (1931, 1934) in *Trialeyrodes vaporrariorum,* the body of the young insect in the fourth instar becomes deeper than that of the preceding instars, and the marginal wax palisade stands vertically below the edges. In the early transformation stage the long, slender legs of the imago grow beneath the larval cuticle, but for want of space they become much folded and looped. Above the bases of the legs deep infoldings of the body wall of the imago form large cavities, which separate the

median part of the body of the imago from the wide lateral extensions of the larval body. From the median walls of these cavities the wings are formed as outgrowths that finally extend back into the abdominal region. The lumina of the lateral body lobes of the larva are filled with fat cells, and at first are narrowly continuous above the wing cavities with the haemocoele of the central part of the body, but, as the wings push out, the lateral lobes become disconnected from the central body, and at ecdysis are shed with the larval cuticle. A cavity is similarly formed anteriorly that cuts off the precephalic margin of the nymph, while a third cavity at the posterior end of the body provides for the growth of the external genitalia. At ecdysis, therefore, all the superfluous marginal parts of the larval body are cast off, and the imago is formed from the central part only.

The metamorphic characters of the young aleyrodid are thus seen to include a flattening and simplification of the body and a suppression of the wings, together with modifications of the legs adaptive first to active and then to sessile habits. The characteristic feature of the final metamorphosis, however, is in the manner of transformation to the adult involving the discarding of parts of the larval body. The aleyrodid metamorphosis has been termed *allometabolism* (from *allo,* different), but the development of the wings beneath the cuticle of the last larval instar is entirely comparable to the simplest form of wing development in typical endopterygote insects; the term Endopterygota taken literally, therefore, would include the Aleyrodidae.

It is in the Coccidae that metamorphosis among the Homoptera reaches its highest degree of complexity. The young scale insect is a larva adapted to a parasitic life on plants, and in its external aspect it is quite different from the adult. The true form of an adult coccid, however, is known only from the winged male, since the female becomes sexually mature in a late larvalike stage and undergoes no further transformation.

On hatching from the eggs the simple, flattened first-instar coccid larvae are provided with eyes, antennae, mouth parts, and legs. They are active crawlers whose function it is to disperse themselves over the food plant. When the young larvae have settled down at a suitable feeding place, they moult and enter a second larval stage in which the legs in many species are reduced, or lost altogether, though in some forms the legs are fully retained. With typical species (diaspine scales) there are only two larval instars, but in some there are three or more, and generally during the larval period there is only a slight difference between the males and the females. At the last larval moult, however, the sexes are differentiated. The female looks like only

another and larger larval instar, since she has no vestiges of wings; in some species the legs and antennae are retained, but in many the legs are much reduced or suppressed. The female usually preserves her mouth parts and alimentary canal, though the external feeding organs may disappear. The ovaries, however, become functional and soon the body of the female is converted into a bag of eggs. In the reproductive stage the female scale insect thus appears to be a sexually precocious larva, but some coccidologists contend that she has attained a larval form secondarily by a process of reduction or degeneration from a winged adult. Perhaps the only way to settle the question would be to give the female a dose of the proper hormone and see what happens to her.

The male coccid, after the last larval moult, goes through usually two immobile transformation stages, and then becomes in most cases a winged insect. In the first transformation stage, know as a *propupa,* the male of winged species begins to take on the form of the adult; the antennae, legs, and wings appear, and the eyes are fully developed, but the mouth parts are reduced or suppressed. In the next stage, termed the *pupa,* the insect assumes more closely the form of the winged imago, the antennae and the legs increase in length, taking on the character of the adult appendages, and the wings lengthen. In the male of *Lepidosaphes ulmi,* according to Suter (1932), there is only one pupal stage, during which the wings and legs appear and increase in size until the moult to the adult. The adult male usually has a pair of well-developed wings, but is devoid of feeding organs. In some species, however, the male does not attain the typical winged structure; the wings may be absent, the antennae and the legs much reduced in length, while the body retains the larval form with no constriction between head, thorax, and abdomen. The redevelopment of the antennae and legs of the male scale has been shown by Berlese (1896) in the Diaspinae (*Mytilaspis*) to take place in the early pupa by evagination of the appendage rudiments from pouches of the integument beneath the cuticle of the propupa.

In addition to its external transformations the male coccid undergoes a very considerable degree of internal metamorphosis, which has been described particularly in *Pseudococcus* by Mäkel (1942). Along with the casting off of the mouth parts there is a great reduction of the alimentary canal, which retains its form in the pupa, but in the imago the mesenteron is reduced to a mass of cells without a lumen. The oesophagus remains as a slender tube, the proctodaeum is narrowed, though the rectum keeps its original dimensions, and the

Malpighian tubules increase in size. These changes are mostly retrogressive from the larval condition. On the other hand, the reproductive organs develop gradually to the definitive functional state, and there is a thoroughgoing reconstruction of the larval musculature into that of the adult.

In her account of the muscle transformation in the male of *Pseudococcus* Mäkel distinguishes five different groups of muscles, as follows: (1) Larval muscles that go over with little or no change into the imago; (2) larval muscles that undergo such changes as splitting, uniting, or a change of position; (3) larval muscles destroyed by histolysis and not regenerated; (4) transformation muscles formed by addition of imaginal elements to larval muscles; (5) muscles of the imago that arise as new muscles in the propupa. To this last group belong four muscles of the thorax, and seven oblique intersegmental muscles of the abdomen, together with two muscles connected with the external genital organs. The metamorphosis of the muscular system as given by Mäkel is based on a detailed comparative study of the musculature in the larva, pupa, and adult.

It is clear that the transformation of the male coccid is a true holometabolous metamorphosis, and that the larva is a specialized juvenile stage. It may be questioned, however, that the coccid pupa is comparable to the pupa of the higher holometabolous insects. The presence of two pupal stages having a general resemblance to the winged nymphal stages of other Hemiptera suggests that the so-called pupal instars of the male coccid pertain to the juvenile period of the life history and not to that of the imago. The work of Wigglesworth (1948, 1951a) on the hormonal control of transformation in the reduviid *Rhodnius* shows that the juvenile hormone controls the nymphal status up to the imago, and if this is true in other Hemiptera the coccid pupa is not a part of the imaginal stage. Holometabolism can be defined only as a type of metamorphosis; the fact that it occurs among the Hemiptera in the male coccid, and also in the Thysanoptera does not taxonomically relate these insects to each other or to such holometabolous insects as Coleoptera, Lepidoptera, Diptera, and Hymenoptera.

VIII. THYSANOPTERA

The Thysanoptera seem to contradict the principle that postembryonic metamorphosis is due to some structural aberration on the part of the young insect that fits it to a special environment or way of living. The active young thrips in appearance differs from the imago little more than a young aphis differs from a winged adult aphis, and

it would seem that in like manner it could grow into an adult thrips without any radical process of transformation. However, after two active, feeding nymplike stages (fig. 7 A,B) the young thrips becomes
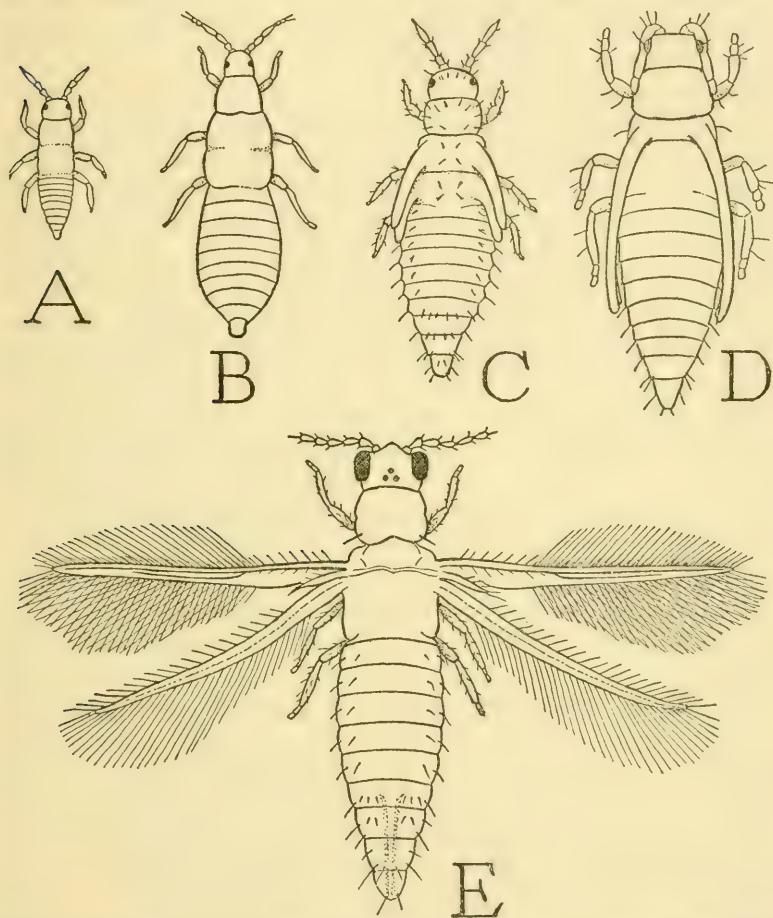

FIG. 7.—Life-history stages of a thysanopteron, *Scirtothrips citri* Moulton (outlines from Horton, 1918).

A, first instar. B, second instar. C, propupa. D, pupa. E, adult female.

inactive, ceases to feed, moults, and enters a quiescent stage known as a *propupa* (C). The propupa in turn is followed by a second resting stage termed the *pupa* (D), from which after a final moult the adult emerges (E). In the Terebrantia the wings appear in the propupal stage as straplike outgrowths, which become still more extended in the pupa. In the Tubulifera the propupa differs little in

external appearance from the second nymph, since in this suborder the wings do not appear until the pupal stage. In most of the Tubu- lifera, however, there is a second pupal stage separated from the first by a moult, making five immature instars in all, but according to Priesner (1926) a propupal stage is absent in some species and in others there is only one pupal stage.

The few external changes other than the growth of the wings that take place during the postembryonic development of the Thysanop- tera are of little consequence. In some forms the antennae are reduced in the propupa and their segmentation becomes indistinct. In the pupal stage the antennae elongate, their segmentation becomes distinct, the form of the head approaches that of the imago, the compound eyes increase in size, the ocelli appear, and the sexes are now distin- guishable. Most of these changes are merely those that any ametabo- lous nymph might go through in its development to maturity. The resting stages in the life history of a thrips, however, suggest that internal changes are going on, and, in fact, a reconstruction of some of the internal organs takes place during the propupal and pupal stages that is entirely comparable to the transformation processes of holometabolous insects. These changes in the thrips affect the alimen- tary canal, the salivary glands, the fat tissue, the muscular system, and in a lesser degree the nervous system.

The alimentary canal of *Liothrips oleae,* according to Melis (1935), does not differ essentially in external form during preimaginal stages from that of the adult, but the cellular structure of the mesenteron becomes highly unstable and is in a continuous state of reorganiza- tion. On the other hand, in *Parthenothrips dracaenae,* as described by Müller (1927), the alimentary canal undergoes changes in shape and size as well as cellular reconstruction during the propupal and pupal stages. In the two nymphal instars the long tubular ventriculus is looped forward upon itself and then turns back to join the intes- tine; in the propupa the whole canal becomes a simple straight tube with no ventricular loop; in the pupa the ventricular loop reappears but only as a short lateral fold from the middle of the tube; in the imago the ventriculus is again bent forward on itself as in the nymph, and there is a secondary small loop in the descending arm. Since the alimentary canal of the adult becomes practically the same as that of the young thrips the intervening changes might seem useless, except that, as the insect takes no food during the propupal and pupal instars, the ventricular changes may be simply economy adaptations to a lack of need for a digestive organ. In *Parthenopthrips,* Müller says, there is one renewal of the midgut epithelium. At the beginning of metamor-

phosis in the last part of the second larval stage the regenerative cells of the ventriculus actively multiply and later spread out to form a new epithelial layer while the old degenerating layer is cast off into the lumen. Elongation of the stomodaeum and the proctodaeum proceeds from cell proliferation by mitotic division in "imaginal rings" of cells at the inner ends of these two ectodermal parts of the canal.

The Malpighian tubules of *Liothrips oleae,* according to Melis (1935), undergo no appreciable transformation, being the same in all stages. The salivary glands degenerate in the propupa and pupa, and are reduced to long bodies crowded with large nuclei in a scant protoplasm, but they are restored in the adult to essentially the nymphal form. The cells of the fat body play the usual role in metamorphosis; they increase in size during nymphal life and store up nutritive products in their cytoplasm, which in the propupa and pupa are given out and consumed in the reconstruction of the muscles. The change in the nervous system involves principally a transposition of the brain from its nymphal position in the thorax into the head of the adult, accompanied by development of the cerebral nerves and their adaptation to the imaginal organs they innervate.

The reorganization of the muscular system is the most important feature of metamorphosis in the Thysanoptera. As described by Melis (1935) in *Liothrips oleae,* during the propupal stage the larval muscles of the head go into complete histolysis, in the thorax and in the last abdominal segment there is a partial myolysis, but most of the abdominal muscles do not undergo any appreciable change. During the pupal stage there follows a total regeneration of the intrinsic head muscles, and a reconstruction of the thoracic and abdominal muscles to fit the needs of the adult. The processes of histolysis and histogenesis as described in detail by Melis are the same as those in typical holometabolous insects; muscles that are to be reconstructed with new attachments undergo a partial dissolution, but the nuclei persist in small fragments of cytoplasm that reassemble to form new muscles, or attach themselves to remnants of old muscles to form reconstructed muscles.

The internal metamorphosis of the Thysanoptera is thus seen to be truly holometabolous, but the nymphlike form of the insects in all the immature stages, and the small degree of external change from nymph to pupa and from pupa to imago suggest that the so-called pupal stages are merely the usual third and fourth instars, which have become inactive because of the reconstructive process that takes place within them. The immature stages of the Thysanoptera thus appear to be comparable to the nymphal stages of ametabolous insects, with

the wings developed in the third or fourth instar. It is, therefore, difficult to account for an internal metamorphosis for which there is no apparent external reason.

IX. OLIGONEOPTERA, OR TYPICAL ENDOPTERYGOTA: NEUROPTERA TO HYMENOPTERA

Whether the orders here included constitute a monophyletic group of holometabolous insects or not will be a matter of opinion. Since holometabolism occurs in the unrelated Coccidae and Thysanoptera, some entomologists will contend that it may have arisen independently among other holometabolous orders. The modern larvae of the typical endopterygote insects differ from the nymphs of ametabolous insects and the larvae of hemimetabolous insects not only in being endopterous but also in several other respects. They lack eyes that are identical with the compound eyes of the adult, and usually they have independently developed simple larval eyes; the hypopharynx, when present, is more or less united with the labium; the body musculature differs from the typical adult musculature in varying degrees; and metamorphosis from larva to imago in all cases involves an intervening pupal stage.

Inasmuch as there can be little question that endopterygote insects have been evolved from exopterygote ancestors, the simplest and most reasonable view to take concerning the nature of the holometabolous endopterygote larva is that it represents in modified form the nymphal instars of ametabolous exopterygote insects. Both the larva and the nymph are the active juvenile stage of the insect during which the wings are developed. Whether the wings grow externally or internally, or may be retarded in their growth to a late instar, is a difference of no consequence. The larva as well as the nymph has wings in the course of development, and is not a "wingless" stage of ontogeny. If the legs also are developed beneath the cuticle, the larva for that reason is not "legless," and does not represent an apodous stage of ontogeny or phylogeny.

The principal problem concerning the origin of the endopterous holometabolous larva involves the question: For what way of life was the primary larva modified from an ordinary ametabolous nymph that led to the acquisition of its distinctive features and its holometabolous metamorphosis? The young cicada or the young stonefly clearly show how, by simple structural adaptations for environments different from those of the adult, a nymph might readily be converted into a hemimetabolous larva, but external modifications do not account for holometabolism.

The endopterous condition of the larva and the substitution of short-sighted simple eyes for long-sighted compound eyes were conceived by Lameere (1899) to have arisen as adaptations in a primary nymphlike juvenile form to boring into plant stems. The theory, however, does not take into consideration the facts that most present-day larvae of the boring type are specialized forms in their own orders, and that free-living forms give no evidence of having been reconstructed for life in the open from a primary boring type of larva. It is hard to believe, for example, that the antecedents of the aquatic *Corydalus* larva or the *Dytiscus* larva, or even those of terrestrial beetle larvae lived in plant stems. As for the change of eyes, it would seem that a boring larva would hardly need any eyes at all. Though the Lameere theory of larval origin is thus not convincing, it is the only theory that has been proposed to account specifically for the characteristic external features of modern endopterygote larvae.

We can readily imagine that the suppression of external wing pads during the nonfunctional period of their development would be a convenience to most any young insect regardless of its habitat. Wingless larvae, by comparison with winged nymphs, have certainly shown a great superiority in ability to adapt themselves to different environments and to different ways of living.

A theory concerning the nature of the endopterygote larva, elaborated by Jeschikov (1929), regards the larva as a free-living continuation of the embryo; the larva has even been defined as such (Henderson, 1949). First, we might ask, what animal is not a continuation of the embryo? The theory of Jeschikov, however, contends that the larva *is* an embryo, and that the nymphal stages of its ancestors are all condensed in the pupa. However, in no other insects are the wings developed in the embryo, at most they are represented only by differentiated groups of cells in the embryonic epidermis. The ametabolous and hemimetabolous Pterygota all show that wing development is a function of postembryonic life. Periodic moulting is common to both nymphs and larvae, but it would be quite exceptional in an embryo. If the larva is an embryo, cases of paedogenesis would really be embryogenesis, and larval heteromorphosis would be embryonic heteromorphosis; some embryos would take to the water on hatching, others would burrow into the ground, still others would climb trees, and finally we should have embryos spinning cocoons and transforming into pupae. These implications are rather too much for the theory. When the embryo comes out of the egg and takes on all the functions necessary for a free life, its embryonic stage is ended,

though of course what we now call it is merely a matter of conventional definition.

The endopterous condition of the larva very probably was not produced by a single mutation. In the simplest type of wing development among modern endopterygote insects, as shown by Tower (1903) in certain Coleoptera, the wing is first formed in the early pupa beneath the cuticle of the last larval instar, and is therefore exposed only at the moult to the pupa. If formed as a fold of the body wall at any earlier stage the wing rudiment would be exposed at the next larval moult. The first appearance of wing pads among exopterygote insects on different instars shows that the wing growth may be retarded. In the past history of those beetles in which the wing is not present as a fold until the early pupa, the external growth of the wing must have been first retarded and then suppressed until the end of larval life, and we may conclude, therefore, that the first step in attaining the endopterous condition was a retardation in the time of development of the wing rudiment. The formation of a wing fold is not the true beginning of the wing development; in earlier larval stages the alar rudiment is present in the form of a thickening or a differentiated group of cells in the epidermis, which is the wing in a state of suppressed growth.

On the other hand, in most of the endopterygote insects the development of the wings has been expedited by the early recession of the growing wing rudiments into pockets of the epidermis beneath the cuticle, which become closed and are thus not affected by the larval moults. Within these pockets the wings can grow without being exposed until they are everted at the moult to the pupa. According to Tower (1903) the wings develop in this manner among the Coleoptera in Scarabaeidae, Coccinellidae, and Chrysomelidae; Patay (1939) says the wings of *Leptinotarsa* develop in closed pockets toward the end of the third instar. A familiar example of the usual recessed type of wing development beginning in the second larval instar is that given by Mercer (1900) for *Pieris rapae*.

The endopterous condition in its evolution, therefore, has probably gone through two phases, both existing among modern insects. In the first phase the growth of the wings presumably was suppressed until the end of the juvenile period; in the second phase the wing rudiments developed again at an early larval stage, but now sank into the epidermis beneath the cuticle, thus still preserving the "wingless" state of the young insect. It must be evident, then, that there is no truly wingless larva of any winged insect; the wings exist in some

retarded stage of growth. The endopterygote larva, therefore, does not represent an apterous stage of ontogeny, and much less does it recapitulate an apterous stage of phylogeny.

Similarly, legless larvae are not truly apodous; the leg rudiments are present in some form, though they may be greatly reduced. In the honey bee, for example, Nelson (1915) has shown that external leg rudiments are present on the embryo, but at the time of hatching are reduced to discs in the epidermis, which later redevelop internally in the larva. The leg tissue, therefore, is continuously present, though it may not take the form of a leg bud until late in larval life.

The suppression of compound eyes during larval life, unlike the suppression of wing pads, would not seem to confer any advantage on a free-living young insect. The typical larval eyes are simple single eyes, usually only a few in a group on each side of the head. They are developed on the site of the future compound eyes and are connected with the same part of the brain; but generally at the end of larval life the larval eyes degenerate, and they never take any part in the formation of the definitive compound eyes. In the Culicidae and related Diptera it is shown by Constantineanu (1930) that the compound eyes begin their development in an early stage of the larva, and that the larval eyes, which are formed in the embryo, are retained in the adult. Yet the two remain as entirely distinct organs. In the larva of *Panorpa* there are 30 to 35 single eyes in a group on each side of the head, and, as described by Bierbrodt (1942), these panorpid larval eyes have attained the structure of ommatidia, and probably function as appositional compound eyes. However, the larval eyes and their nerves degenerate during the pupal metamorphosis and do not become the compound eyes of the adult. Here is a case, therefore, in which a larva has succeeded in reacquiring functional compound eyes, but these larval eyes, as those of other insects, give place to adult compound eyes newly developed in the pupa.

In discussing the origin and evolution of endopterygote larvae, Chen (1946) contends that the primary larva, derived from an exopterous nymph, was aquatic, and he cites the megalopterous larvae, particularly the larva of *Corydalus,* as being the closest modern representative of the primary larva. Though it may be conceded that the megalopterous larvae are relatively generalized modern forms, they are nevertheless superficially modified for aquatic life, and life in the water does not account for their more fundamental characters, which are those of endopterygote larvae in general. The stonefly, mayfly, and dragonfly larvae are all aquatic, and yet they have compound eyes and external wing pads, and they transform without a pupal stage.

If we assume that the primary endopterygote larva was a modified nymph, we might more reasonably expect it to be best represented among modern forms by some of the simpler terrestrial larvae, such as a raphidian larva (fig. 8 B), or coleopterous larvae in the families Carabidae, Staphylinidae (C), and Dermestidae (D). Such larvae live in the same general habitat as the adults, feed on the same kind
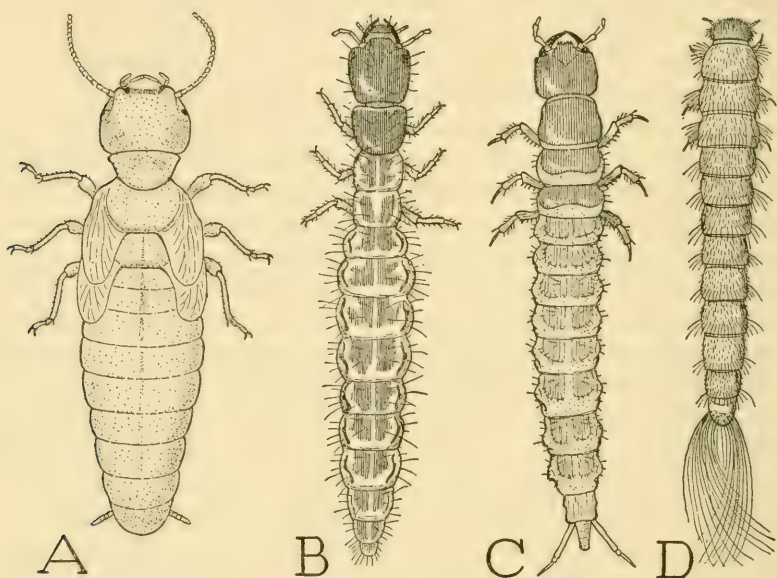

Fig. 8.—Examples of a generalized ametabolous nymph and of simple holometabolous larvae.

A, *Zootermopsis angusticollis* (Hagen), nymph of a winged termite. B, *Agulla adnixa* (Hagen), raphidian larva. C, *Creophilus maxillaris* Long, larva of a staphylinid beetle. D, *Attagenus piceus* Oliv., larva of a dermestid beetle.

of food with the same kind of mouth parts, and have no structural adaptations for any particular environment. Except for the lack of external wing pads and compound eyes they resemble an ametabolous nymph (A), and they differ least from the structure of the adults of their species.

The larvae of the lower endopterygote groups show their closer relation to the exopterygote insects in the possession of typical two-clawed pretarsi. Those with paired movable claws on the feet include the larvae of Megaloptera, Raphidioidea, most Neuroptera except Sisyridae, and the larvae of the coleopterous families Carabidae, Cicindellidae, Gyrinidae, Dytiscidae, Amphizoidae, and Noteridae. The two-clawed foot evidently is primitive among the winged insects;

the single claw of the larva in the higher orders, therefore, is a secondary larval modification, and does not represent a primitive one-clawed pretarsus, or dactylopodite.

It would seem, therefore, that an unspecialized modern larva should best represent the primary endopterygote larva, since from such a larva evolution could more readily produce various specialized forms. Yet even the simplest of modern larvae gives us no suggestion of how or why it acquired its distinctive larval characters. The endopterous holometabolous larva must, for the present, be accepted only as a fact; we have no evident explanation of its origin.

The reason for holometabolism, that is, for metamorphosis that involves the intervention of a pupal stage between the larva and the imago, is not to be found in the external characters of the larva. The young mayfly or the young dragonfly differ externally from their parents more than do the larvae of some endopterygote insects, but yet they transform without a pupal stage. The pupal transformation processes involve a variable degree of reconstruction of both external and internal larval tissues, but, so far as known, they always include at least a partial dissolution of the larval musculature accompanied by the formation of new muscles or of new muscle attachments for the imago. The cessation of muscular activity brings about the quiescence of the pupal stage. Since the lesser degrees of change in other internal organs might be accomplished direct from larva to imago, it appears to be the disparity in the muscular system between the young insect and the adult that constitutes the reason for holometabolism. As we have seen, this is true also for male Coccidae and the Thysanoptera. The external suppression of the wings, the absence of compound eyes, or the presence of abdominal appendages in the larva have nothing to do with the fact that the holometabolous larva has a muscular system that cannot go over entirely or directly into the adult musculature.

The somatic musculature of nearly all adult pterygote insects is built on the same fundamental plan, though some muscles may be reduced or eliminated in the thoracic segments of wingless species or in those having weak powers of flight. The musculature of exopterygote nymphs is essentially like that of the adults, but in holometabolous insects the musculature of the larva is usually very different from that of the adult. The pattern of the larval musculature is simpler in the less specialized larvae of each order, and it is least specialized in larvae that differ least from the adults. Hence, we may suppose that the simplification of the larval musculature in a primitive endopterygote

larva was an economy measure correlated with the reduction of the wings and the fewer abdominal movements that the larva had to make as compared with the adult. Whenever the difference between the larval musculature and the adult musculature reached a point where new attachments for imaginal muscles became necessary, a new moult had to intervene, and thus a pupal stage became interpolated between the larva and the imago. With the pupa once established as a reconstruction stage for the muscles, it served also increasingly for the transformation of other tissues.

In most of the major holometabolous orders the larval musculature becomes progressively more complex in the higher families. The wormlike form assumed by so many larvae, and the consequent necessity of a wormlike mechanism of movement readily accounts for the specialization of the musculature in all vermiform types of larvae. Since the insect larva, however, is not a worm, no matter how wormlike it may be, its musculature is never that of a worm, it merely serves mechanically to enable the larva to make wormlike movements.

Otherwise, the forms and structure of most modern specialized holometabolous larvae are clearly adaptations to specific environments or ways of living, usually different from those of the adult. Such larvae have thus taken on temporarily structures useful only to themselves, which must be discarded at the final transformation to the imago. The ordinary caterpillar with its short thoracic legs, its long abdomen supported on leglike props, its strong biting and chewing jaws and ample food tract is clearly made for feeding in the open and for the storage of food reserves. A boring larva, on the other hand, is unmistakably adapted to burrowing into wood or plant stems. The larvae of Diptera were probably in the first place aquatic, but their structure is readily adaptable to life in mud, fruit pulp, manure piles, and the bodies of other animals. The grubs of wasps and bees are incapable of self-support, but they are perfectly constructed for confinement in cells where they are furnished with food by their mothers or other adult attendants. Internal parasitic larvae are usually greatly simplified in structure because they have nothing to do but to feed on the food in which they are immersed.

The presence of paired appendicular organs on the abdomen of various endopterygote larvae has often been taken to be a retention from the embryo of a stage representing a primitive polypod condition in the ancestry of insects. Thus Chen (1946) says: "The primitive larvae are presumably of the campodeoid-polypod type, having three pairs of thoracic and ten pairs of abdominal legs; the latter bear each

a vesicle and a stylus." From this premise Chen concludes that the *Corydalus* larva is the closest modern representative of the primary larva, and that the latter was aquatic. In a former paper the writer (1931) reviewed the structure of the appendicular organs on the abdomen of endopterygote larvae, and suggested that these appendages represent the eversible vesicles and the styli of Thysanura.

Broad generalizations are always mentally comforting because they relieve the mind from the confusion of seemingly unrelated facts, for which reason also generalizations are prone to become wider than the evidence on which they are based. A closer comparison of the abdominal appendages of endopterygote larvae with the vesicles and styli of Thysanura shows that the two sets of organs are not identical in structure, which fact raises the suspicion that they may be in no way related. Furthermore, there is no valid reason for supposing that the primary endopterygote larva should have had thysanuran characters. Some exopterygote insects retain a single pair of styli on the abdomen, but none of them has abdominal vesicles or other abdominal appendages except cerci and the organs of copulation and egg laying, which are a common inheritance of Thysanura and both exopterous and endopterous Pterygota. Insects could not be encumbered with abdominal appendages after they acquired wings. The polypod progenitors of the insects are unknown; they probably became extinct when the primitive apterygotes became hexapods. As we have seen, even the Thysanura do not have true legs other than those of the thorax. Possible vestiges of abdominal legs are retained among the apterygotes only in the Protura and Collembola.

The adjectives "thysanuriform" and "campodeiform" as applied to the more simple types of endopterygote larva can have only a descriptive value. An endopterygote larva, no matter how thysanuriform it may be in appearance, is just as truly a winged insect as is an exopterygote nymph, and it is much farther removed than the nymph from its apterygote ancestors. Since it is hardly to be supposed that the exopterygote orders and the endopterygote orders represent two primary lines of divergence from primitive winged insects, the endopterygotes must have had a long line of exopterygote ancestry separating them from their apterygote progenitors. Exopterygote insects were already flourishing in Carboniferous times, endopterygotes appear in the Permian; the earliest apterygotes (Collembola) are known from the Devonian.

Larval abdominal appendages are most fully developed in the larva of *Corydalus* (fig. 9 A). Along each side of the abdomen on the first
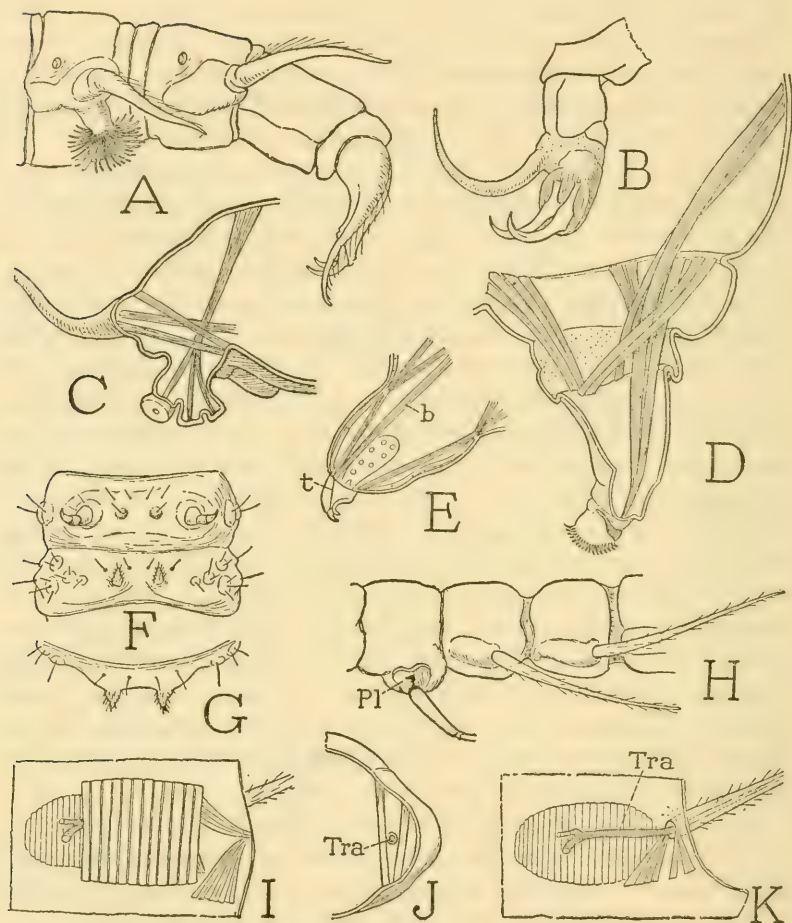
Fig. 9.—Abdominal appendicular organs of holometabolous larvae.

A, *Corydalus cornutus* (L.), posterior abdominal segments and appendages. B, same, terminal appendage of right side, mesal. C, same, cross section of gill-bearing segment. D, *Malacosoma americanum* (F.), a right abdominal leg cut open mesally to expose muscles. E, section of leg of a tardigrade, showing muscles (from Baumann, 1921). F, panorpid larva, under surface of meta-thorax and first abdominal segment. G, same, sternal arc of first abdominal segment, posterior. H, *Dineutes* sp., larva, metathorax and anterior abdominal segments. I, same, inner surface of an abdominal appendage-bearing lobe. J, same, section of left side of an abdominal segment. K, same as I with inner layer of muscles removed.

eight segments is a row of lobelike projections between the terga and sterna that fall in line with the bases of the thoracic legs. Each lobe bears a long, tapering lateral process, and each but the last a large ventral tubercle carrying a brush of gill filaments. On the tenth segment is a larger appendage (B) armed distally with a pair of strong claws, and bearing on its outer surface a slender process like that of the preceding appendages. In the larva of the related *Chauliodes* ventral tubercles are absent, but long, tapering lateral processes are present on the first eight abdominal segments, and the ninth segment bears a pair of appendages similar to those of *Corydalus*. Ventral tubercles are absent also in the *Sialis* larva (fig. 10 A), but long tapering lateral processes are present, each of which is distinctly divided into six segmentlike parts. The abdominal "legs" of caterpillars have a structure resembling so closely that of the gill tubercles of the *Corydalus* larva as to suggest that the two are homologous organs. The same is true of the abdominal "legs" of sawfly larvae, and of the apical appendages of trichopterous larvae, the structure of which has recently been reviewed by Pryor (1951).

The abdominal vesicles of Thysanura are retractile by short muscles arising on the supporting plates of the venter (fig. 2 C,D,E), and the styli are movable by muscles arising on these same plates (D,E). The plates are admittedly flattened remnants of abdominal limbs, and *Machilis* demonstrates that the styli are coxal appendages (B,*Sty*) acquired during postembryonic development. In the endopterygote larva the abdominal tubercles are likewise retractile, but the principal retractor is a long muscle taking its origin on the dorsal wall of the corresponding body segment (fig. 9 C,D). Whether this difference in the musculature of the thysanuran and larval organs is significant or not will be a matter of opinion, but the fact remains. On the other hand, the basal musculature of the tapering lateral processes of the megalopterous larvae (fig. 9 C) is quite comparable to that of a thysanuran stylus in that it arises from the supporting body lobe, which fact might therefore be taken as evidence that these processes truly represent styli.

When, however, we note the occurrence of similar abdominal processes in other unrelated larvae, the interpretation of any of them as primitive styli becomes doubtful. The aquatic larva of the gyrinid beetle *Dineutes* (fig. 10 B), for example, has a pair of long, tapering lateral filaments arising from each of the first eight abdominal segments and two pairs from the ninth segment. The single filaments are supported on lobes of the body (fig. 9 H) that lie in a line above

the level of the pleural plates (*Pl*) of the thorax. Each lobe is crossed internally by two layers of vertical muscle fibers (I) enclosing a large trachea between them (J,K,*Tra*) that runs out into the filament. The filament itself is movable by two antagonistic muscles, one mesal, the other lateral, attached on its base. Then there is the curious termitophilous tineid caterpillar, *Plastopolypus divisus* (fig. 10 C), first described by Silvestri (1920), which has long, slender, multiarticulate
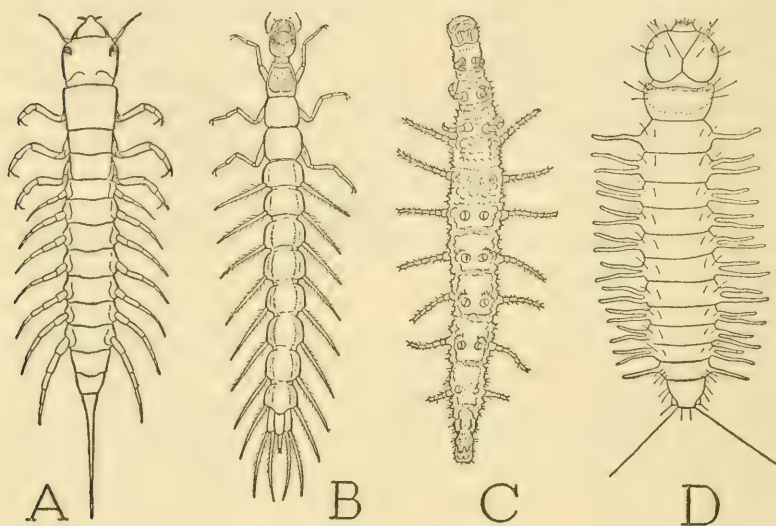

Fig. 10.—Examples of unrelated holometabolous larvae with lateral appendicular organs on the abdomen.

A, *Sialis* sp. Megaloptera. B, *Dineutes* sp. Coleoptera-Gyrinidae. C, *Plastopolypus divisus* Silv. Lepidoptera-Tineidae (from Hollande, Cachon, and Vaillant, 1951). D, *Nymphula maculalis* Clemens, Lepidoptera-Nymphulidae (from Welch, 1916).

processes projecting from the sides of the first seven segments of the abdomen. These appendicular structures have been shown by Hollande, Cachon, and Vaillant (1951) to be sensory and not exudatory organs, since they are covered with innervated setae and contain no glandular tissue; but these writers, and also Silvestri, find that each appendage is movable by a muscle inserted within its base. Must we, therefore, interpret all these structures as representative of thysanuran styli? Hollande, Cachon, and Vaillant contend that the abdominal appendages of the *Plastopolypus* caterpillar are merely secondary adaptations of the larva to life in the termite colony, as are also true exudatory lobes on the body of other termitophilous species.

Similar though nonmusculated processes are shown by Hollande, Cachon, and Vaillant to be present on a termitophilous fly larvae, but in this case two pairs are present on each body segment, one pair lateral, the other dorsal, and several other fly larvae associated with termites have simple nonarticulate lateral appendages, some very small, others large and club-shaped. Then there are the aquatic caterpillars with gill filaments along the sides of the abdomen (fig. 10 D), some of which are simple fingerlike processes and others elaborately branched filaments. The panorpid larva is sometimes cited as an example of a larva having abdominal leg rudiments, but an examination of this larva shows that the supposed "legs" on the abdomen (fig. 9 G) do not fall in line with the thoracic legs, and correspond exactly in position with seta-bearing papillae on the thoracic venter between the legs (F).

All such examples of the presence of segmental appendicular structures on the larval abdomen only go to show the facility with which the young insect can develop special organs for various purposes of its own. As Pryor (1951) has pointed out, similarity of structure in nonsegmented organs of locomotion is not necessarily a criterion of homology. With respect to the abdominal "legs," he says, "there is in fact as much resemblance between a caterpillar and an onychophoran or a tardigrade as between a caterpillar and *Corydalus*." The tardigrade leg (fig. 9 E) has a long muscle (*b*) from the body wall, which, according to Baumann (1921), is connected with each claw by a slender tendon (*t*). Likewise in the Onychophora the plantar discs and claws of the legs are retractile in the same manner by muscles, some of which have their origins in the leg and others on the body wall. Such cases of similarity in musculature, as noted by Pryor, are evidently independent adaptations to the functional needs of locomotor organs having the same type of structure and action.

Ideas that can be neither proved nor disproved have to depend on circumstantial evidence for support, but when circumstantial evidence is not conclusive they had better be dropped, or held for further investigation. This principle applies to the musculated abdominal appendages of endopterygote larvae. If these appendages are related to the vesicles and styli of Thysanura, they are appurtenances of abdominal legs and not legs themselves. On the other hand, many insect embryos do have leg buds on the abdomen which usually disappear, but it is certainly quite possible that embryonic remnants of primitive legs might be retained and redeveloped in a new form for postembryonic use. We have only to consider the extraordinary elab-

oration of pleuropodia in the embryos of some insects to see the extent to which appendages presumably equivalent to legs can be modified for a new purpose. Eastham (1930) has shown that rudiments of abdominal appendages appear on the embryo of *Pieris rapae* in line with the rudiments of the thoracic legs, and that there is no evident reason for not regarding all these appendages as serially homologous organs. Many cases might be cited from other arthropods in which a leg rudiment develops into a very unleglike structure, and perhaps a very good example of this is to be seen in the external genital organs of insects.

The idea usually deduced from the presence of paired movable appendages on the abdomen of endopterygote larvae is that such larvae are recapitulations of a polypod stage of insect ancestry. This idea, however, is not supported by other characters of these larvae. Take the caterpillar, for example; in no respect does it have a primitive organization. In the structure of its head, its mouth parts, and its muscular system the caterpillar is a highly specialized modern insect form, and, most important, it is a stage of postembryonic growth in which wings are in the course of development. The caterpillar has a polypod status because its abdominal appendages were not suppressed in the embryo, but it does not represent a primitive polypod stage of phylogeny. Wings certainly did not arise in a polypod ancestor of the insects; a winged centipede is hardly to be visualized as a reality.

The holometabolous larva is an independent organism. It can depart to any extent from the structure of its parents, and it is under no compulsion to recapitulate its ancestral history. The independence of the larva begins with the embryo, which develops directly into the larval form whatever this may be. From the experimental work of Hegner (1911) on the eggs of *Leptinotarsa,* of Reith (1925) and of Pauli (1927) on the eggs of muscoid flys, and of Smreczynski (1938) on eggs of the beetle *Agelastica alni,* it is known that in these insects the larval structure is fully determined in the preblastoderm stage of the egg. Probably the same is true for many other holometabolous insects. A few hours later, however, as shown by Geigy (1931) in *Drosophila,* injury to the blastoderm causes defects in the adult fly. In this very early stage, therefore, the egg has the potentiality of producing both a larva and an imago, but the larval development takes precedence over the imaginal development. The primary business of the holometabolous embryo is to produce a larva; in so doing it may entirely ignore its own phylogenetic history, and needs

only to conserve enough undifferentiated material for the reconstruction of the adult in the pupal stage. The embryo and the larva thus become a single independent phase in the life history of the insect, but this fact is not a vindication of the idea that the larva is simply a continuation of the embryo leading a free life instead of being confined to an egg shell. The reverse more nearly expresses the truth ; the specialized structure of the larva has been forced back on the embryo until the embryo becomes a preliminary larva. A phylogenetic significance, therefore, cannot be attributed either to the larva or the embryo of a holometabolous insect.

The insect larva owes its independence and its ability to take on characters of its own to its release from the necessity of inheriting special adult characters of its parents. The development of structures practical only to the winged imago must be inhibited throughout the embryonic and larval stages, and conversely, larval organs useful only to the larva may not be transmitted to the imago. In this way both the larva and the adult are free to become more and more specialized in different directions, but the greater their divergence, the greater becomes the degree of reconstruction required of the pupa. Yet the larva, no matter how divergent it may become from the line of adult phylogeny, must carry the adult inheritance as well as its own. The potency for redeveloping the parent form either resides in the ability of larval tissues to be transformed into imaginal tissues, or it is carried by undifferentiated embryonic cells of the larva, which resume the imaginal development in the pupa. In the more intense degrees of pupal metamorphosis, as Tiegs (1922) has said, the changes amount at times to an absolute death of the larva, the tissues of which go into almost complete dissolution, and if imaginal reconstruction cells were not present the larva would be left to decompose.

X. LARVAL HETEROMORPHOSIS

Heteromorphosis of the larva, commonly called hypermetamorphosis, is of frequent occurrence among predaceous and parasitic species of insects, examples being known in Neuroptera, Coleoptera, Strepsiptera, Lepidoptera, Hymenoptera, and Diptera. It seems remarkable that a larva can assume two or more distinct forms during its life history, and the fact that it may do so raises the question as to how the juvenile hormone is able to control a succession of different forms. However, since this hormone is nonspecific with regard to related species of insects, it should be nonspecific with regard to different larval forms of any one species. The hormone has nothing

to do with determining the structure of the young insect; this is the work of hereditary factors. The hormone simply maintains the integrity of the juvenile form, whatever this may be, against the forces of further development.

The ability of the embryo to develop into a larval form that has no relation to the form of its parents is strange enough, but it is passing strange that this same larva can change its form several times during its larval life and still finally revert to the adult structure. The fact of heteromorphosis appears to demonstrate the plasticity of larval tissues, which seemingly can be molded and remolded by the growth organizer to produce a succession of adaptive forms. The histological changes that may take place in larval metamorphosis, however, as well as the role of hormones remain yet to be investigated.

Two categories of heteromorphosis in parasitic larvae are to be distinguished according as the adult female lays her eggs in the open, or on or within the body or egg of the prospective host of the larva. In the first case the newly hatched larva must be able by its own activity either to find its appropriate host, or to attach itself to a carrier that will transport it to the nest wherein are the host eggs or larvae on which it is destined to feed. A first-instar larva of this type, therefore, is constructed for an active life, and has been termed a *planidium* (little wanderer), but its structure, of course, will depend on the insect order to which its parents belong. After entry into the nest or body of the host, however, the planidium transforms into a second-stage larva of much simplified form and structure adapted to a sedentary life of parasitism. With those species, on the other hand, in which the eggs are attached on, or inserted into, the body of the host, the young larva begins at once its parasitic existence; it has no need for an active stage, and develops directly from the embryo into a form adapted only for life and feeding usually within the host, and accordingly in many species it is greatly reduced and simplified in structure. During later instars, however, the simple larva takes on a form more typical of the usual larva of its order.

PARASITES WITH A PLANIDIAL STAGE

The term *planidium* has a functional rather than a structural significance, but it is remarkable how larvae in different orders have taken on similar characters in adaptation to the requirements of planidial life.

Coleoptera.—Larval heteromorphosis among the Coleoptera occurs in the Carabidae, Staphylinidae, Meloidae, and Rhipiphoridae. Most

familiar are the life histories of the blister beetles, Meloidae, some
of which feed on the eggs of grasshoppers, others infest the nests of
bees. The transformations of species of the American *Epicauta* are
well known from the early work of Riley (1876) and later papers by
Ingram and Douglas (1932) and Horsfall (1941). The European
Mylabris variabilis is described and fully illustrated by Paoli (1938).

The adult females of *Epicauta* and *Mylabris* deposit their eggs in
the ground where grasshoppers are likely to be, but not necessarily
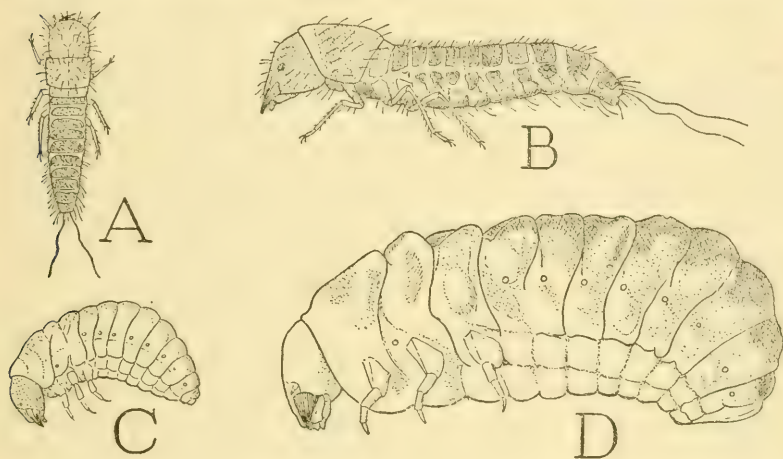
Fig. 11.—Three larval stages of a meloid beetle, *Mylabris variabilis* Pall. (from
Paoli, 1938).

A, first instar, planidium. B, same, more enlarged. C, second instar. D,
fourth instar, similar to third and fifth instars.

close to a grasshopper's nest. The first-stage larva is a planidium hav-
ing the form of an active generalized coleopterous larva with long
slender legs (fig. 11 A,B). It is commonly termed a "triungulin,"
though two of its pretarsal "claws" are merely strong spines. The
planidium runs actively about and burrows into the ground until it
finds the egg nest of an acridid. After feeding on a few eggs, it
moults and transforms into a more simple short-legged, soft-bodied
second instar (C). This larva resumes feeding, grows, and goes
through two more stages in which it becomes a thick scarabaeoid grub
(D). The next instar, which is the fifth, resembles the preceding, but
it comes out of the egg nest and burrows downward a short distance
into the ground. This larva in *Mylabris,* according to Paoli, does not
feed, and transforms into a sixth larva, in which the integument is
thick, rigid, and dark-colored, and the mandibles and legs are much

reduced. This sixth larva, the "ipnotica" of Paoli, is immobile and passes the winter in a dormant condition. In the spring it sheds its tough, protective integument. The seventh larva that emerges resembles the fourth and fifth instars; it is again active, though it does not feed, and burrows upward to near the surface of the ground, where it transforms into the pupa, from which finally the adult emerges.

The life history of *Epicauta* is essentially the same as that of *Mylabris*, though according to Horsfall (1941) the fifth larva of *E. pennsylvanica* feeds to repletion before it burrows down into the ground. Moreover, this fifth larva in species of *Epicauta* may transform directly into the pupa, thus eliminating the hibernating form and the seventh instar. Pupation following the fifth instar is said by Ingram and Douglas (1932) to take place with individuals of *Epicauta lemniscata* that complete the fifth stage in the spring, while those maturing in the fall or under unfavorable weather conditions go over into the hibernating stage, which is followed by the active seventh instar. Horsfall (1941) reports the same thing for *Epicauta pennsylvanica*. A notable feature in the metamorphosis of these meloid larvae is its reversibility, as shown by the transformation of the hibernating larva into an active burrowing form like that which preceded it, though geotropically one is positive and the other negative.

Other species of Meloidae are parasites in the nests of bees in the families Megachilidae and Andrenidae. The life history and larval stages of one of these, *Tricrania sanguinipennis*, infesting the underground nests of the andrenid *Colletes rufithorax* is fully described by Parker and Böving (1925). The female of *Tricrania* deposits her eggs under small objects lying on the ground in the vicinity of the nesting places of the bees. The newly hatched larvae are slender planidia, tapering at each end, with long legs and well-sclerotized body segments. It would appear that they might find their way directly into the nest of a prospective host, but observations show that generally they attach themselves to a male bee seeking a female and are thus carried into the nest. Within the brood cell the intruder first devours the egg of the bee, thus making sure of no competition from the bee larva that might otherwise hatch. At the first moult the planidium transforms into a soft, smooth larva having a boat-shaped form with the spiracles on the back, an adaptation that enables the larva to float on the food mass of honey and pollen in the cell, which constitutes its food from now on. At later stages, however, as the larva grows larger and the food mass shrinks, the larva becomes a fat scarabaeoid grub. In all, the *Tricrania* larva goes through six

instars, but, except for a shortening of the legs and other minor modifications, it makes no radical change of form after the second moult. There is no hibernating larval stage in the life of *Tricrania,* but the fifth and sixth instars remain within the unbroken fourth and fifth skins, which serve also as a covering for the pupa. The adult beetles are formed in the fall, but remain within the bee's nest until the following spring.

The metamorphosis of the carabid *Lebia scapularis,* which is predaceous on the larvae of the elm leaf beetle, *Galerucella luteola,* is described by Silvestri (1904) as follows. The young *Lebia* is a slender, elongate larva of the planidium type, having legs adapted to running, well-developed mandibles, and a pair of long, jointed apical processes on the abdomen. It attacks a *Galerucella* larva and feeds on the viscera until its growing body becomes so large and loaded with fat to such an extent that it can no longer move actively about. In this condition it might fall an easy prey to other insects, but the *Lebia* larva now encloses itself in a cocoon spun of silk threads from the Malpighian tubules, and finally includes its prey in the cocoon. When finished with feeding, and having attained its maximum development, this first larva moults into a second form having a general pale color, mouth parts unadapted to feeding, the legs and antennae reduced to small conical stumps, and the caudal processes suppressed. From this second, nonfeeding instar the larva goes into a prepupal stage, in which the head takes on adult characters, and wing rudiments are present on both the mesothorax and the metathorax. After another moult the prepupa becomes a pupa. Silvestri makes no comment on the unusual occurrence in the Coleoptera of a prepupa, which evidently belongs to the pupal stage of the insect. Heteromorphosis in *Lebia,* therefore, appears to affect the pupa as well as the larva.

Heteromorphosis again occurs in several genera of Staphylinidae in which the larvae are parasitic on the pupae of Diptera within the puparium. Wadsworth (1915) gives a good account of the life history and larval stages of *Aleochara bilineata,* a parasite of the cabbage fly, *Chortophila brassicae.* The newly hatched larva is an active thysanuriform planidium that must seek in the ground the puparium of the cabbage fly. Having found a puparium it gnaws a hole in the latter and feeds on the outside of the pupa from a puncture in the pupal integument until it becomes much swollen. The second instar of the larva is quite different from the first; the cuticle is soft and white, the antennae and mouth parts are altered, the legs reduced to vestiges, the claws are lost, and the caudal spines disappear. The third

larva resembles the second except for its larger size. Both the second and the third larvae lie lengthwise on the back of the thorax of the fly pupa, and obtain their food by suction. Pupation takes places in the fly puparium, and the adult beetle gnaws its way out.

The larval heteromorphosis of the Rhipiphoridae is too well known to need more than a brief notice. Species of *Rhipidius* are internal parasites in all larval stages on cockroaches. Other species attacking wasps and bees are endoparasitic in the first instar but take an external position in later instars. The first larva of one of these species is an active planidium which must find and attach itself to a carrier that will transport it to the nest of a prospective host. Here it enters the host larva as an internal parasite. When fully grown in the first instar, however, it leaves the body of the host through a puncture, moults, and in the second stage takes a position across the back of the host larva on the first or second thoracic segment. The external larva loses the features of the first instar and becomes a grublike parasite, some species being characterized by the presence of large tubercles on the back.

Neuroptera.—Among the Neuroptera the larvae of nearly all species are predaceous, their prey being mostly other insects which they attack in the open. The larvae of some Mantispidae, however, feed on spider eggs within the spider's cocoon. The mantispid eggs being laid on trees or bushes, the young larva must actively find its food. The life history of *Mantispa styriaca* has long been known from the work of Brauer (1869). The newly hatched *Mantispa* is a simple, slender neuropteroid larva with relatively small mandibles and no distinctive specialization. Hatched in the fall, it hibernates through the winter; in the spring it finds a spider's cocoon and cuts its way through the silken wall. With feeding in the first instar, the abdomen becomes greatly enlarged, but at the first moult the larva changes to a fat grub with a small head and greatly reduced legs. This change of the active first-stage mantispid larva to a sedentary grub is certainly not a reversion to any ancestral larval form among the Neuroptera; it is an individual secondary adaptation to the life of ease and plenty the larva is to lead from now on in the protection of the spider's cocoon, within which it finally pupates.

Strepsiptera.—The Strepsiptera are notable for the heteromorphosis of the parasitic larval stages of both sexes, and also for the fact that in most species the sexually mature female retains the larval form, though with a greatly modified reproductive system, and remains within the body of the host. In the genera *Eoxenos* and *Mengenilla*, however, the female leaves the host and in the adult stage is found

in the open, either free or enclosed in the last larval skin. The females of these species are much less modified in structure than are the females of species that remain in the hosts. The males of all species are free, fully winged insects.

The adult female of *Eoxenos laboulbenei,* as described by Parker and Smith (1933), is broadly oval, with a distinct head and thorax and a 10-segmented abdomen; wings are absent, but the legs are relatively long and segmented, mandibles are present though simple, and spiracles occur on each of the first seven abdominal segments. At the posterior border of the seventh abdominal segment is a genital aperture leading into a short, open, median oviduct, but otherwise nothing is to be seen of the reproductive system; in the mature female the entire abdominal cavity is full of eggs. Females of *Eoxenos* found within the last larval skin are enveloped also in a thin pupal cuticle, showing that, in this genus at least, the female is a true imago. In mating, as observed by Parker and Smith (1934), the male of *Eoxenos* curves his abdomen beneath that of the female, but the aedeagus pierces the integument of the female instead of entering the genital aperture. The eggs hatch within the body of the female and the young planidial larvae escape through the open inner end of the oviduct. The host of *Eoxenos laboulbenei* was for a long time unknown, but Carpentier (1939) finally discovered the parasitic stage of the larva in the body of a lepismatid, *Lepisma aurea.*

In other strepsipteran genera, parasitic in Orthoptera, Pentatomidae, Fulgoridae, Cicadellidae, and particularly in Hymenoptera of many families, both the female and the male develop to sexual maturity within the body of the host. The female remains within the host, and retains the form of the mature larva, having a large, soft abdomen and a short, cylindrical, darkly sclerotized cephalothorax (fig. 12 G), which latter alone is thrust out of the abdomen of the host. Mandibles are present in some species, absent in others, but the female is always wingless and legless. She remains enclosed in the last larval skin, and the parasitic females are not known to have a pupal stage. It is questionable, therefore, whether the egg-producing parasitic female is a true adult or a sexually precocious last-stage larva. As noted above, Parker and Smith found evidence of a pupal stage in the nonparasitic female of *Eoxenos laboulbenei.*

The reproductive organs of the parasitic females are greatly reduced, and the abdomen is filled with a great mass of eggs. The development of the eggs free in the body cavity is described by Brues (1903) in *Xenos peckii.* Between the ventral surface of the body of the female and the enveloping larval skin is a free space, or brood

chamber, which opens anteriorly at the base of the cephalothorax by a median slit, or in some species by a pair of apertures. The brood chamber is in communication with the body cavity of the female by several funnel-shaped tubes. During mating, according to Perkins (1918), the male of *Stylops aterrima* inserts the aedeagus into the anterior opening of the brood chamber; in *Acroschismus wheeleri*, Schrader (1924) says the spermatozoa, after being discharged into the brood chamber, find their way through the ventral ducts of the female's abdomen into the body cavity, where they disperse, penetrate the egg membranes, and effect fertilization. Silvestri (1940), however, has apparently demonstrated that the male of *Halictophagus tettigometrae*, in inserting the aedeagus through the ventral membrane between the head and thorax, penetrates the body wall of the female and discharges the spermatozoa directly into the haemocoele, whence they finally migrate to the posterior extremity of the abdomen. The young larvae on hatching from the eggs escape from the body of the female through the ventral funnels into the brood chamber, and gain the exterior by way of the anterior opening of the chamber.

The male strepsipteron develops also inside the body of the host, and before emergence as an adult he is enveloped by the last larval skin. Unlike the female, however, the male goes through a pupal stage before transforming into a free-winged insect, leaving the pupal cuticle behind within the larval skin.

For a good example of the larval stages of a typical strepsipteron we may refer to the well-illustrated account by Kirkpatrick (1937) of the life history of *Corioxenos antestiae*, a parasite of Pentatomidae infesting coffee plants in East Africa. The first-instar larva is a planidium (fig. 12 A) of coleopterous type of structure, and attaches itself (B) to an immature pentatomid of the genus *Antestia*. The parasite remains motionless on the host until the latter moults, when it bores into the body through the soft new skin. At its own first moult the planidium transforms into a simple, soft-bodied, legless scarabaeoid grub (C), in which even body segmentation is not visible. With succeeding moults the larva goes through four more instars (D,E,F), without any radical change of form except for the development of a row of eight processes along the back of the abdomen. The larva apparently feeds by the absorption of body liquids of the host through its skin, and the dorsal protuberances are supposed to increase the absorptive area. During the later larval stages (F) the body becomes differentiated into a slender cephalothorax and a large abdomen; extrusion of the cephalothorax from the host takes place in the

seventh instar, after which the female larva moults to the final form (G) within the last larval skin. The larval instars of the male resemble those of the female, but the male goes through a pupal stage before issuing as a winged adult.
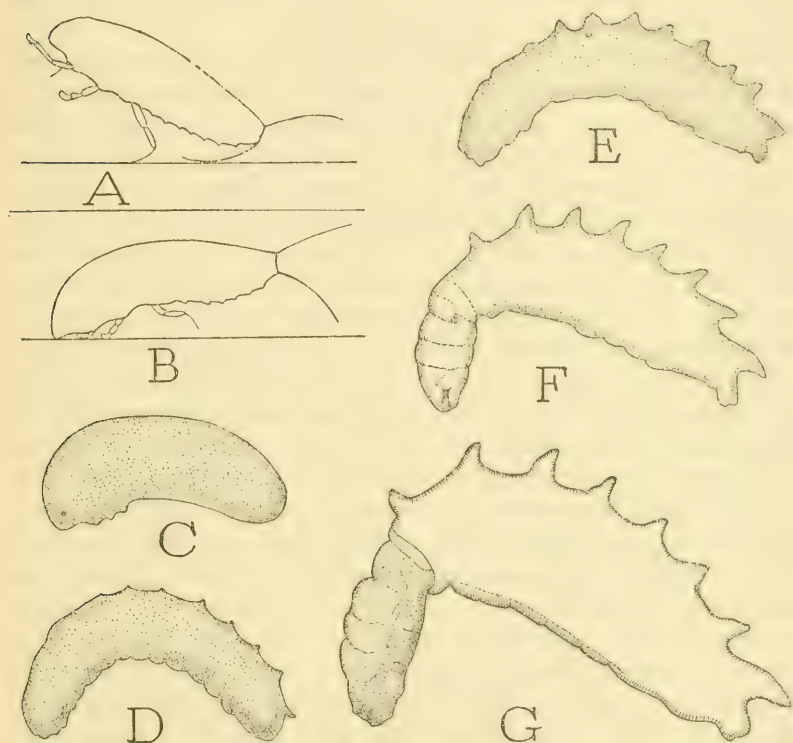

FIG. 12.—Developmental stages of a strepsipteron, *Corioxenos antestiae* Blair (from Kirkpatrick, 1937).

A, first instar, planidium in waiting attitude (length 0.25-0.27 mm.). B, same, in position of attachment on host. C, first parasitic instar (length 0.4 mm.). D, second parasitic instar, female. E, third parasitic instar, female. F, fifth parasitic instar, female. G, mature female, unfertilized (length 3 mm.).

Extrusion of the cephalothorax of *Corioxenos antestiae*, Kirkpatrick says, is always between the back plates of the third and fourth segments of the host, the male in the middle and the female on one side. In this species the female has a pair of openings into the brood pouch, one right, the other left, a provision to insure that one or the other will not be covered by a wing of the host. The body of the mature larva and also of the adult female lies in the body of the host with the ventral side of the abdomen uppermost and the cephalothorax

bent posteriorly, so that the dorsal surface of the exposed cephalothorax is uppermost when extruded. In this position of the female copulation with a free male takes place.

An even more detailed account of the biology, life history, and anatomy of a strepsipteron will be found in the paper by Silvestri (1940) on *Halictophagus tettigometrae* Silv.

Lepidoptera.—The caterpillar in its body form is the most conservative of all holometabolous larvae, even predaceous species in general preserve the eruciform type of structure. In the Epipyropidae, however, the larvae of which are external parasites on Homoptera, particularly Fulgoridae, there is a pronounced structural adaptation of the larva to parasitic life and even a heteromorphosis. Since the adult female deposits her eggs not on a prospective host but on vegetation, the first-stage larvae must attain a host by their own efforts, and they resemble, as much as a caterpillar might, the planidia of other parasites with similar habits. The newly hatched larva of *Agamopsyche threnodes* is described by Perkins (1905) as a minute, slender creature, tapering to the caudal extremity, and provided with legs unusually long for a caterpillar; it is clearly adapted for the active life of a young predaceous insect that must find a host for itself. The later instars, which feed on the back of the abdomen of the host, are very different from the first. In the mature stage the head is extremely small, the legs reduced, the mandibles minute; the body becomes contracted to an oval form, and the larva takes on a superficial resemblance to a mealy bug, accentuated by the presence of a waxy covering. A description of all the stages of *Epipyrops eurybrachydis* Fletcher is given by Krishnamurti (1933). Among the Lepidoptera various leaf-mining species also undergo a change of form during larval life, being at first flattened for feeding within the leaf, and later, on emergence from the mine, taking on the usual caterpillar form for cocoon spinning.

Diptera.—Parasitic dipterous larvae, of which the first instar is of planidium type, and which, therefore, are heteromorphic, are said by Clausen (1940) to occur generally in the Acroceridae (Cyrtidae), Bombyliidae, and Nemestrinidae, frequently in the Tachinidae, and in a few species of Sarcophagidae.

The Acroceridae (Cyrtidae, Oncodidae) are parasitic in their larval stages on spiders. The female deposits her eggs on bushes or trees, and the young larvae by their own efforts must attach themselves to spiders that chance to come their way, if they are to survive. The larval stages of *Oncodes pallipes* as described by Millot (1938) may be taken as typical of the family. The newly hatched planidium (fig.

13 I) is not over 0.4 mm. in length, slender and elongate, with a small head and 11 body segments. The body segments are sclerotized dorsally and ventrally and are armed with strong spines, a pair on the last segment being particularly long. The mouth armature includes a median sharp-pointed process and a pair of lateral hooks. The last abdominal segment terminates in an attachment apparatus consisting of three strong central hooks and a ventral semicircle of small spines. The larva at this stage is metapneustic, having a pair of spiracles only on the last segment. After hatching, the larva stands vertically by means of the attachment structure on the end of its abdomen, but it is capable of locomotion either by looping movements like those of a measuring worm, or by small leaps of a few millimeters made by suddenly straightening the curved body. If a young spider happens to pass close by, the planidium springs upon it and penetrates into its interior; otherwise the prospective parasite will die in the course of a few days. The parasite passes the winter without change in the body of the spider. In the spring it moults into a second instar and later again into a third instar (J). In these instars the larva is simply a small fly maggot; the body is indistinctly segmented, tapering anteriorly, enlarged posteriorly, and ends with a small apical cone. There are now two pairs of spiracles but those of the prothorax are not functional. The infested spider remains alive and normally active almost to the end, but at last the parasite consumes the vital organs of its host and comes out to pupate, leaving nothing of the spider but the empty skin.

The planidium of *Pterodontia flavipes* (fig. 13 H), another acrocerid parasite of spiders, described by King (1916), resembles that of *Oncodes,* but the body ends with a small adhesive disc between the bases of a pair of long, slender spines. This larva, according to King, progresses either by looping in the manner of a leech, or by jumping. Preparatory to making a leap, the larva stands erect on the attachment disc with the caudal spines extended backward; by a sudden downward pressure of the spines the larva then throws itself a distance of five or six millimeters. When on moist surfaces, however, King says, the larva progresses by extending and contracting its body. This last observation is of particular interest because it shows that the planidium still retains the common mode of locomotion of a fly maggot. In its subsequent stages the *Pterodontia* larva returns to the form of a simple, smooth-skinned maggot, which, when mature, emerges from the body of the spider.

For another example of larval heteromorphosis among the Diptera, we may refer to the paper by Clausen (1928) on *Hyperalonia oeno-*

maus, a bombyliid larval parasite of the scoliid *Tiphia,* which itself is parasitic on grubs of the scarabaeid genus *Anomala.* The eggs of *Hyperalonia* are deposited on the ground or dropped there by the female in flight. The first larva (fig. 13 G) on hatching is a slender, vermiform planidium 0.9 mm. in length, with a strongly sclerotized head and 12 uniform body segments; the thoracic segments bear each a pair of long, slender lateral spines, and on the apical segment of the abdomen is a pair of similar but longer spines directed posteriorly. This larva has to search through the ground for the buried cocoons of *Tiphia;* after entering a cocoon it feeds on the thoracic region of the *Tiphia* larva. At the first moult the planidium changes into a much simpler larval form, which lacks the body spines and the strong sclerotization of the head, and is characterized by deep intersegmental constrictions. In the third stage (F) the larva becomes thick-bodied and grublike, but is not essentially different from the second larva; it passes the winter in the cocoon of the host, and pupates the following spring. The same species attacks also other scoliid genera, and the Bombyliidae in general, according to Clausen, are parasitic on Orthoptera (egg cases), Coleoptera, Lepidoptera, Diptera, and Hymenoptera.

Hymenoptera.—Among the Hymenoptera, larval heteromorphosis following a first-stage planidium occurs in the parasitic Perilampidae and Eucharidae. The females in these families lay the eggs apart from the host, and the young larvae are provided with a strongly sclerotized integument which allows them to live a relatively long time without desiccating and without feeding. By means of a caudal sucker and long tail bristles the planidium is able to stand erect and to spring at a prospective host.

The following account of the planidium of a species of *Perilampus* parasitic on larvae of *Chrysopa* is given by H. S. Smith (1917). The eggs are laid on the leaves of plants where the *Chrysopa* larvae are looking for aphids. From the egg hatches an active planidium (fig. 13 A), which at first crawls rapidly about, but soon attaches itself to the leaf by its caudal sucker and stands up at a right angle to the leaf surface. In this position it may remain motionless for days at a time until some insect comes within its reach. Then suddenly the planidium becomes "frantically active, reaching and swaying back and forth in its attempt to attach itself to the prospective host." If a *Chrysopa* larva comes too near, "the planidium attaches itself with lightning-like quickness to a hair or bristle of the host. It then leisurely crawls down the hair to the host's body and attaches itself by its mouth hooks." When the *Chrysopa* larva spins its cocoon and pupates, the
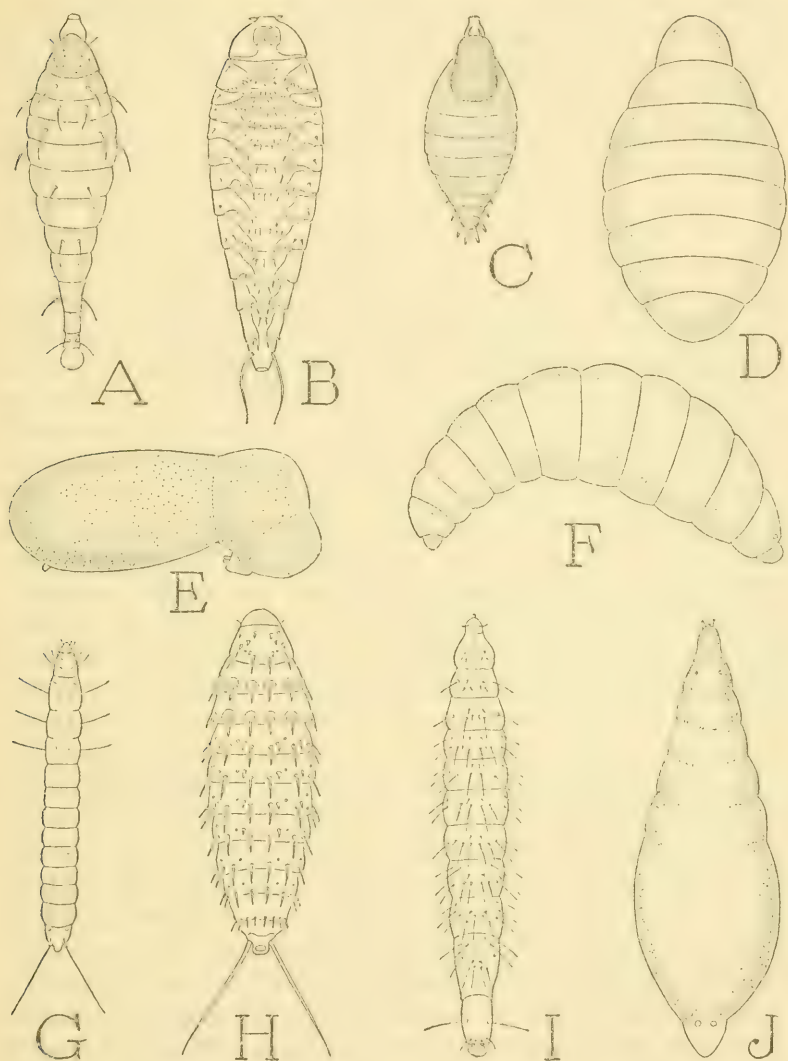
Fig. 13.—Examples of hymenopterous and dipterous parasitic larvae with a planidial first instar.

A, *Perilampus chrysopae* Crawford, planidium (from Smith, 1912). B, *Perilampus hyalinus* Say, planidium (from Smith, 1912). C, *Schizaspidia tenuicornis* Ashm., planidium (from Clausen, 1923). D, same, second instar (from Clausen, 1923). E, same, third instar (from Clausen, 1923). F, *Hyperolonia oenomaus* Rond., third instar (from Clausen, 1928). G, same, first instar (from Clausen, 1928). H, *Pterodontia flavipes* Say, first instar (from King, 1916). I, *Oncodes pallipes* Latr., first instar (from Millot, 1938). J, same, third instar (from Millot, 1938).

planidium feeds as an external parasite on the pupa. Often, however, the parasite attaches itself to the stalk of a *Chrysopa* egg, in which case the young chrysopid falls a sure victim to the *Perilampus* planidium in wait for it.

Another species of *Perilampus* described by H. S. Smith (1912) is a secondary parasite on the fall webworm, *Hyphantria cunea*. The planidium (fig. 13 B) enters the body of the caterpillar through the skin and searches for the larva of a primary parasite, including both dipterous and hymenopterous species. At the first moult the perilampid larva loses the characteristic features of the planidium and changes into an ordinary hymenopterous grub, in which form it remains through subsequent instars with only slight modifications.

The description by Clausen (1923) of the life history of a Japanese eucharid, *Schizaspidia tenuicornis* Ashm., parasitic on ant larvae, will serve as a good example of the nature of the planidium and the heteromorphosis of the larva in the Eucharidae. The eggs of this species are laid by the females during the later part of summer in the buds of trees and hatch the following spring. The newly emerged larva (fig. 13 C) is a planidium scarcely more than one-tenth of a millimeter in length, having suctorial mouth parts and a pair of sharp mandibles, and is provided with a small adhesive disc at the posterior end of the abdomen, which is armed with strong spines. Locomotion is accomplished by successive loopings and extensions of the body as the latter is held to the support alternately by the mouth and the caudal disc. When awaiting the chance arrival of a prospective host, however, the planidium stands up at an angle of 45 degrees on its caudal sucker, and then, when opportunity offers, it attaches itself by its mandibles to a passing ant, and is thus transported to the ant's nest. Here the parasite is brushed off from its carrier and now attaches itself by its jaws to an ant larva. At the first moult the special characters of the planidium, together with the mandibles, are cast off with the exuviae.

The second instar of the parasite is a simple, thick, grublike larva (fig. 13 D) having only suctorial mouth parts; it maintains its hold on the host by the mandibles of its own cast skin. When now the ant larva becomes a pupa, the parasite frees itself from the larval exuviae of the ant and by means of its oral sucker attaches itself to the pupa. It then moults to its third instar (E), in which the body segmentation is lost and the mouth is armed with a short stiletto for puncturing the skin of the pupa. The ant pupa is now sucked dry and soon dies, after which the fully fed parasite pupates. Though the *Schizaspidia* larva assumes a characteristically different form in each of its three instars, the pupa is typically hymenopteran.

The larval history of *Schizaspidia tenuicornis* shows how complex the life of a parasite may be, and how both in its structure and its instincts the young insect must become adapted in each instar to conform with the particular conditions that confront it. As noted by Clausen, the *Schizaspidia* larva, in losing its mandibles, breaks with all other hymenopterous parasites, in which the mandibles are retained in all stages.

PARASITES WITHOUT A PLANIDIAL STAGE

Finally we come to those dipterous and hymenopterous parasites of which the female deposits her eggs directly on or in the body of the host or in the host egg. In these species the young larva on hatching finds itself in immediate contact with its food supply, and there is hence no need of an active stage in its life history. The larva is structurally adapted during its embryonic development for life in the body of the host, and in many cases, especially with hymenopterous parasites, the adaptive modifications result in a greatly simplified larval form.

Diptera.—Among the Diptera, modifications or special structural developments of endoparasitic larvae appear to be related principally to the function of respiration, but they may be superposed on a state of simplification in which most of the usual vital organs are not yet developed.

An extreme case of reduction or of delayed development accompanied by specialization in the first-stage larva of Diptera is seen in the agromyzid *Cryptochaetum,* parasitic in scale insects, described by Thorpe (1931, 1941). The eggs of the fly are inserted into the body of a half-grown scale before the body wall has become hardened. The first-stage larva of *C. iceryae,* according to Thorpe (1931), is little more than a transparent cylindrical sac (fig. 14A), 0.3 to 0.4 of a millimeter in length. There is no mouth or sclerotized mouth parts, no somatic muscles, no spiracles, tracheal system, or heart. The alimentary canal is complete, but the stomodaeum and the proctodaeum are not open into the mesenteron, and no food is present in the tract; the parasite evidently absorbs nutriment through its integument from the body liquid of the host. A special feature of the larva is the presence of a pair of large, fingerlike diverticula containing blood projecting from the posterior end of the body. In the second-stage larva (B) the body becomes distinctly segmented, and the posterior segments are ringed with short spines; the mouth is open and strongly sclerotized mouth parts are present; there is a tracheal system but no

spiracles, and a few longitudinal muscles have been developed. The caudal diverticula of the first instar have lengthened into a pair of tails nearly half the length of the body, and fine tracheal branches later penetrate into their open basal parts. In the third stage the body preserves the general form and structure of the second stage, but the tails have increased greatly in length, being one and a half times or more the length of the body. In its fourth stage (C) the larva
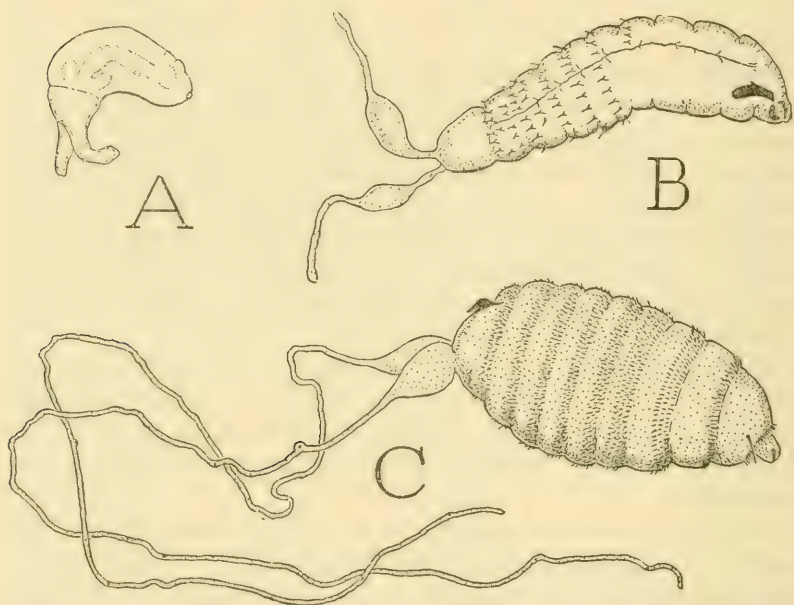

FIG. 14.—Three larval stages of an agromyzid dipteron, *Cryptochaetum iceryae* (Will.), parasitic in the coccid *Icerya purchasi* Maskell (from Thorpe, 1931).

A, first instar. B, second instar. C, fourth instar.

becomes an ovoid, yellowish-white maggot composed of a head and 10 body segments; the tails are greatly lengthened, slender filaments, but have become brittle and are easily broken. Each body segment has a belt of minute spines around its anterior end, anterior and posterior spiracles are now present, but the hooklike posterior spiracles are still closed, the alimentary canal is open, the muscular system is fully developed.

In *Cryptochaetum striatum* (Thorpe, 1941) the larval stages are said to be much the same as in *C. iceryae,* but in the third stage the respiratory tails are 10 times the length of the body and are filled for at least two-thirds of their length with fine tracheal branches.

In contemplating a larva of such incomplete structure as that of

the first instar of *Cryptochaetum*, the question comes up as to how it got that way. The usual answer to the question is that the embryo hatched at an early immature stage. Concerning the "early hatching" idea, Thorpe (1931) says: "The theory obviously cannot be pushed too far, for there are many truly adaptive characters which arise *de novo* in insect larvae, and cannot in any way be described as embryonic." There is no question that "adaptive characters" may include the suppression of structures that are temporarily useless, as well as the development of new structures that are only temporarily useful. Nature is always economical where there is no need of prodigality. A larva living in the midst of liquid food which it absorbs through its skin has no use for a mouth, feeding organs, or a functional alimentary canal, and no need of a locomotor muscular system. If also it can get sufficient oxygen by absorption from the medium in which it lives, there is no immediate need of a tracheal system. All these negative conditions might be supposed to have been acquired by the simple expedient of early hatching, but the larva, if so produced, is not a normal early-stage embryo. The retarded state of development very probably was early determined in the egg, and the larva must then be what it is regardless of when it hatches. The principal *new* structures of the *Cryptochaetum* larva, Thorpe points out, are the respiratory tails. Otherwise the larva simply develops the other organs when they are needed. The delay in development is a mere economy, and numerous examples of various degrees of economy might be cited from other species.

Hymenoptera.—In the Hymenoptera endoparasitic first-stage larvae often have such strange forms that they would hardly be known for young insects if their development had not been followed. Clausen (1940) distinguishes, describes, and illustrates 14 different types of first-stage parasitic larvae in the Hymenoptera, nearly all of which but the planidium are endoparasitic. The eggs of some species are deposited on the outside of the host, of others in the body cavity of the host, and of still others in the host egg. The so-called "egg parasites," however, Clausen observes, are truly larval parasites, since they feed on the larva and "their development is primarily at the expense of that stage." In the present discussion we are concerned entirely with the forms of these first-instar larvae, which later take on the more conservative structure of typical hymenopterous grubs. The species are therefore heteromorphic, though their heteromorphism affects principally the first instar. The change to the final form may take place at the first moult, but often the second instar is intermediate in form between the first and the following instars. As with

the parasitic larvae of Diptera, these aberrant hymenopterous parasites present various special developments in combination with different degrees of undevelopment of usual organs. Whatever their form or structure may be, however, we must assume that in some way it is fitting to the life these larvae live.

As an example of greatly simplified and specialized first-stage larval structure in the Hymenoptera we may take the braconid *Helorimorpha antestiae,* an internal parasite of the pentatomid *Antestia,* described by Kirkpatrick (1937), or the similar larva of the ichneumonid *Limnerium validum,* endoparasitic in the fall webworm, described by Timberlake (1912). In each of these species the first-instar larva (fig. 15 C) has an enormous "head" on a relatively small, simple, unsegmented body ending in a long tapering tail. The only appendages present are a pair of slender, incurved, sharp-pointed mandibles. An even simpler larva of the same type is that of *Platygaster marchali* (E).

In the second stage the *Limnerium* larva takes on a vermiform type of structure with a small head and 12 body segments, the tail of the first instar being greatly shortened. The third instar, as also that of *Helorimorpha antestiae* (fig. 15 D), is a typical hymenopterous larva. The heteromorphosis of these species, therefore, results from the extreme modification of the first instar; in its subsequent changes the larva merely returns to the usual form.

A somewhat more specialized type of first-instar larva occurs among the Platygasteridae, examples of which are here illustrated at A,B,F, and I of figure 15. The large anterior part of the body carries the mandibles, antennal rudiments, and a pair of simple posterior appendages. This headlike part of the larva has been shown by Marchal (1906) to be a cephalothorax bearing the antennae, mouth parts, and the prothoracic legs. The body region behind the cephalothorax is partly or entirely segmented, and may end with tail appendages of various patterns. In their development these larvae eventually attain the form and structure of an ordinary hymenopterous grub.

A curious type of first instar larva is characteristic of the Scelionida; it is classed by Clausen (1940) as the "teleaform" type of larva, but in form it suggests the embryo of a mouse (fig. 15 J). *Hadronotus ajax,* an egg parasite of the squash bug, *Anasa tristis,* furnishes a good example. The newly hatched larva (J) as described by Schell (1943) is a slender creature with a sharp, tail-like caudal horn curved anteriorly. The body is constricted between a large anterior part, probably a cephalothorax, and an elongate posterior part,

but is unsegmented. The cephalothorax bears anteriorly a pair of large, soft mandibles, and posteriorly a "labial projection." The caudal horn is a feeding accessory. This larva grows by a great increase in the size of the abdomen only. In the second stage the larva takes on an oval saclike form, still without segmentation. The third instar, however, is a fully segmented, typical hymenopterous larva (K).

Finally, we must note that not all parasitic hymenopterous larvae take on queer forms in the first instar. Among the Proctotrypoidea the larva of *Phaenoserphus viator,* parasitic on a carabid beetle larva, as described by Eastham (1929), hatches in the form of a simple grub (fig. 15 H), in which the abdomen becomes fully segmented during the first instar. The only special character of this larva is the presence of small paired ventral papillae on the eight body segments following the prothorax. On the head, according to Eastham, are a labrum, a pair of antennal papillae, a pair of sickle-shaped mandibles, a pair of simple maxillary lobes, a small labium, and a sclerotized ring supporting the mouth parts.

Advocates of the Berlese "early hatching" theory would explain the simplicity of these first-instar parasitic larvae as products of immature eclosion of the embryo. Thus Chen (1946), who discredits the theory as applied to other larvae, says: "The precocious types are confined to parasitic Hymenoptera and appear to have been independently acquired by the different groups." He then distinguishes among these first-stage larvae a "vermiform polypod" type (fig. 15 H), an "oligomerous protopod" type (A), and a "polymerous protopod" type (F), supposedly representing successively earlier stages of embryonic development. The usual implication of this theory is that the different types of larvae correspond with phylogenetic stages presumed to be recapitulated in embryonic development.

The presence of apparent abdominal appendages on the first-instar larva of *Phaenoserphus viator* (fig. 15 H) gives this larva a polypod appearance, but Eastham (1929) says the abdominal papillae may be merely adaptive structures. He notes that the difficulty of ascribing such a larva to a primitive embryonic stage "lies in comparing the whole larva at any one stage in its life with any single embryonic state." The presence on the head of fully developed, typical hymenopterous larval mouth parts does not harmonize with the idea that the larva respresents an early polypod stage of the embryo. The presence of mandibles on such a simplified larva as that of *Helorimorpha* (C) likewise shows that the form of this larva has no embryonic or phylo-
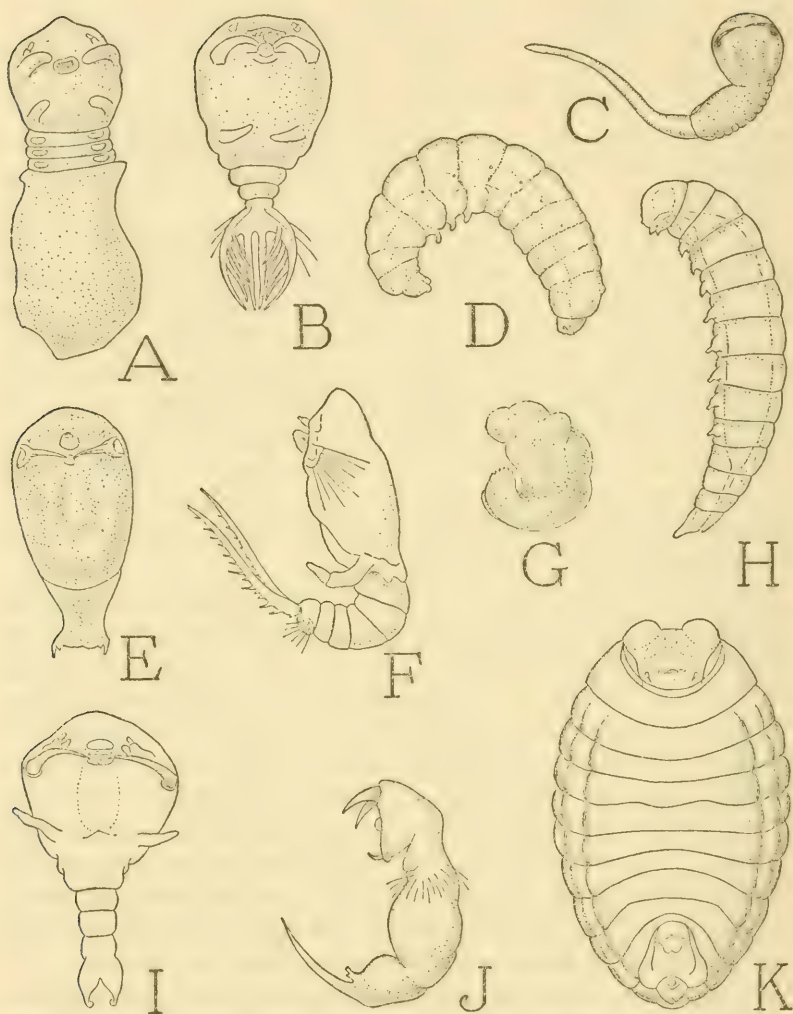
FIG. 15.—Examples of hymenopterous parasitic larvae without a planidial first instar.

A, *Platygaster herrickii* Packard, first instar (from Kulagin, 1898). B, *Platygaster instricator* Kulagin, first instar (from Kulagin, 1898). C, *Helorimorpha* sp., first instar (from Kirkpatrick, 1937). D, same, mature larva (from Kirkpatrick, 1937). E, *Platygaster marchali* Kieffer, first instar (from Marchal, 1906). F, *Synopeas* sp., first instar (from Marchal, 1906). G, same, embryo (from Marchal, 1906). H, *Phaenoserphus viator* Hal., first instar (from Eastham, 1929). I, *Tricacus remulus* (Walker), first instar (outline from Marchal, 1906). J, *Hadronotus ajax* Girault, first instar (from Schell, 1943). K, same, third instar (from Schell, 1943).

genetic significance. The other appendages have simply been suppressed as needless.

The same may be said of the so-called "oligomerous" and "polymerous protopod" larvae (fig. 15 A,B,F,I). They do not *as a whole* have the structure of any one stage in ordinary embryonic development, and none of them is suggestive of being a primitive embryo. An embryo develops continuously, but these larvae maintain the form and structure they have at hatching until the first moult, as does any ordinary larva. In short, there is no reason for regarding them as embryos. Just as a free, active, first-stage larva, or planidium, is adapted to the predatory life it must lead, so these internal parasitic larvae are adapted to an endoparasitic life. They are specialized both in the forms they have, and in the developmental retardation of organs they do not have and do not need. The principle of economy is invoked here just as with the simplified dipterous larvae.

In the first-stage *Hadronotus* larva (fig. 15 J) we see again an example of early specialization in form accompanied by retardation in the development of organs not immediately needed. If we consider the numerous other forms of first-instar larva among the parasitic Platygasteridae and Scelionidae, illustrations of which are assembled by Clausen (1940, figs. 108-111, 113), it is clear there is no evident logic in picking out any one form as representing a particular stage of ordinary embryonic development. The development of *Synopeus rhanis* within the egg from the blastula to the first larva (F), as illustrated by Marchal (1906, pl. 17), shows that the embryo (G) develops directly from the beginning into the platygasterid larval form, without going through any stages suggestive of those of an embryo that develops into a typical free-living larva. Evidently the larval form is determined in the egg, and the embryo, thus relieved from phylogenetic influences, develops into a larva of the platygaster type. The time of hatching has nothing to do with it.

An example of heteromorphosis affecting the first larval stage very similar to that in the parasitic Hymenoptera occurs in the pseudoscorpion (Barrois, 1896; Vachon, 1938). The eggs at an early stage of development are discharged into a brood pouch suspended below the genital aperture of the female and are here nourished on a secretion from the ovaries. On hatching, the larva breaks through both the chorion and the wall of the brood pouch, but remains attached to the outside of the latter by its ventral surface and the mouth region. It is now nourished, as were the eggs, by the ovarial secretion discharged into the brood pouch. At this stage the young pseudoscorpion is a simple saclike creature with rudimentary appendages, but without

body segmentation or internal organs. A deep musculated invagination on its ventral surface was regraded by Barrois as a sucking organ, but Vachon has questioned this function. However, in some manner the larva absorbs the ovarial secretion from the brood pouch and completes its development in one instar. At the next moult it takes on at once the adult structure in miniature. The so-called larva might be regarded as a second embryo, but clearly it is an adaptive form quite unlike any early stage in ordinary arachnid development.

The frequency with which larval heteromorphosis occurs among unrelated insects shows that the larval organization is highly unstable and that mutations make it readily responsive to the need of environmental adaptation. A case of heteromorphosis among the vertebrates would be most astonishing; with the insects heteromorphosis is commonplace. The adaptational changes in the structure of heteromorphic larvae from one instar to the next is good evidence that homomorphic larvae are themselves merely juvenile adaptations to their various modes of living. The ease with which the insect larva assumes a form compatible with its living conditions is well illustrated by the difference between a free-living planidium of one parasitic species and the endoparasitic first larva of another related species. The planidium is equipped for activity, for finding and attacking its prospective host; the endoparasite is reduced to the bare essentials needed for feeding on an ambient food supply and for mere existence otherwise. It may be noted here, also, that simplification of structure often occurs in the second or following instars, as with species having a planidial first larva, in which case "early hatching" cannot be invoked to account for it. Whatever form the early larva may take on, however, it is incumbent on the larva eventually to return to its parental form, and this it does by first reverting in its later stages to the larval form typical of its order or family.

XI. THE PUPAL TRANSFORMATION

The insect pupa is one of the most remarkable things in animate nature; within it are intimately mingled the processes of both life and death. With the shedding of the last larval skin the fully formed pupa appears as a rough sketch of the future adult. The visible pupa, however, is only an external shell; inside of it the larval tissues and organs are being replaced by those of the imago. The juvenile hormone no longer maintains the larval organization, and in consequence the tissues of the larva have either gone into a state of dissolution, or, under the influence of the developmental hormones, are being recon-

structed into imaginal organs, while other organs of the imago are being formed anew from undifferentiated living cells whose development had been repressed by the juvenile hormone. Though hormones control or regulate the transformation processes, there resides in the pupa some mysterious organizing force that builds up the imago from the larval material or from special cells that have been carried by the larva from the embryo. When the imaginal structure is accomplished, the pupal skin is shed and the insect now reappears in the parental form that produced the fertilized egg from which the larva was hatched. The life cycle is thus completed, only to be indefinitely repeated.

Various investigators have observed that the cells of tissues, particularly the epidermis, undergoing metamorphosis discharge dark-staining globules from the nuclei. These globules are commonly termed *chromatic droplets*. Earlier writers, as Pérez (1910) and Poyarkoff (1910), regarded their discharge as a sign of "rejuvenation" in the larval cells; by the rejection of the droplets the cells were supposed to discard their larval ingredients and to be thus prepared for a new growth. The same globules, however, are observed to result from the dissolution of nuclei, and Wigglesworth (1942), from a review of the evidence, concluded that the droplets are always formed in this way. He noted that they are present in the epidermis during the moults of *Rhodnius,* and in greatest numbers where nuclei appeared to be formed in excess of the need for new cells. Nuclei become superfluous, he says, "either because they belong to specialized larval structures that are being discarded, or because the exuberance of cell division has led to their production in greater numbers than are needed." Several writers have observed chromatic droplets also in the growing tissues of the embryo.

The epidermis.—Since the newly exposed pupa appears to be already perfectly formed and does not thereafter change externally, it is the ectoderm that undergoes the first reconstruction. The change to the pupal form, however, is not as sudden as it appears to be, since long before the larval skin is cast off the transformation processes had begun in the so-called prepupal stage of the larva, just as each larval stage begins within the unbroken cuticle of the preceding instar. Moulting and ecdysis, therefore, are not synchronous, and the two terms are not synonymous.

The method by which the pupal epidermis is formed is not the same in all insects. In various families of the Coleoptera in particular it appears that the cells of the larval epidermis retain a faculty for renewed and differential growth, and that in these insects most of the

larval epidermis goes over, with changes, directly into the pupal epidermis. At the other extreme, in the higher orders the larval cells enter a state of degeneration and are thrown into the body cavity, while the entire pupal epidermis is generated anew from small groups of cells, the imaginal discs, that have remained undifferentiated from the embryo. Imaginal discs of undeveloped appendages, however, are present in all cases, and represent adult structures whose growth is continued during the larval life.

In the beetle *Sitophilus* (*Calandra*) *oryza* Murray and Tiegs (1935) say it is usually possible to distinguish in the epidermis even of the very young larva groups of small, more basophile cells that will form the appendages, rostrum, and copulatory organs of the adult, but that there is no distinct imaginal tissue to form the main part of the body wall. Also in *Leptinotarsa,* according to Patay (1939), the larval epidermis simply undergoes a renewal of developmental activity by which it is transformed into the pupal epidermis without any process of dissolution of its cells. Again, in the chrysomelid *Galerucella,* Poyarkoff (1910) finds little evidence of destruction of larval cells in the transformation of the epidermis from the larva to the pupa.

On the other hand, in Hymenoptera and Diptera there may be a complete renewal of the epidermis from imaginal discs of the larva, accompanied by a destruction of the larval cells. In the thorax the imaginal discs of the appendages not only form the appendages themselves, but they spread outward on all sides to furnish new epidermis for the thorax, and in the abdomen the pupal epidermis is likewise proliferated from abdominal discs. As the new epithelium spreads from the regeneration centers, the old cells of the larval epidermis go into a state of dissolution and are forced into the body cavity where they dissolve or are consumed by phagocytes.

According to Anglas (1901), in *Vespa* and *Apis* as the pupal epidermis spreads from the proliferation centers, the old epidermis becomes vacuolated and separated from the basement membrane. The new tissue advances by incorporating what remains of the larval cells, the protoplasm of which is absorbed, digested, and assimilated by the multiplying imaginal cells. The new epidermis is at first plastic, allowing the modeling of the pupal form, but later it becomes fixed by the hardening of the new cuticle. Anglas reports there is no phagocytosis of the disintegrating larval cells, such as described in some other insects.

In the chalcid *Nasonia,* Tiegs (1922) says that in the newly hatched larva the ectoderm consists of large cells which constitute the greater part of the integument, and of strips of small embryonic

cells which are the imaginal discs of the future pupal integument. In the last part of the final larval instar the larval cells go into a state of cytoplasmic disintegration, which is partly chemical and partly due to the action of phagocytes. At the same time the cells of the imaginal discs of the epidermis multiply and spread out, replacing the disintegrating larval cells, until they re-form the entire body wall, including such internal parts of it as the tendons of muscles, the tentorium, and the thoracic phragmata.

The regeneration of the integument in Diptera from imaginal discs has been described by various writers. Wahl (1901) gives a full account of the epidermal regeneration centers in the larva of *Eristalis,* which on the thorax include the discs of the pupal respiratory trumpets, the wings, the halteres, and the legs, and on the abdomen epithelial thickenings formed of embryonic cells. Pérez (1910) says the newly generated epidermis of *Calliphora* on the thorax grows over the larval epidermis, the cells of which are thus rejected into the body cavity and phagocytized. In the abdomen the epidermal renovation is progressive and slow, but here also the old cells are thrown into the body cavity where they become the prey of phagocytes.

Finally, we may quote from the more recent paper by Robertson (1936) on the epidermal regeneration in *Drosophila.* At an early larval period the rudiments of the legs, wings, and halteres, Robertson says, are masses of embryonic cells sunken into pockets of the ectoderm, which remain open through hollow stalks. These pockets are the imaginal discs which will regenerate the thoracic epidermis. As development proceeds, the mouths of the stalks become wider and the peripheral parts of the discs expand into the surrounding epidermis, the cells of which gradually retreat and are sloughed off into the body cavity, where they are taken up by phagocytes. The imaginal discs continue to expand by cells multiplication until finally they unite and thus replace the entire larval epidermis of the thorax with a new epidermal epithelium, which is that of the pupa and the adult. On the abdomen likewise the larval epithelium is replaced by a new epidermis generated from islands of undifferentiated cells. On most of the abdominal segments there are two pairs of these imaginal discs, one pair dorsal, the other ventral, but the spiracles also are centers of regeneration, making thus six discs on each spiracle-bearing segment. On the last segment, however, there is only a single, ventral histoblast. During the early part of the pupal stage the cells of the abdominal discs multiply and spread out, displacing the larval cells, which are rejected into the body cavity and there phagocytized. At

about the thirty-sixth hour of pupal development in *Drosophila* the imaginal epidermis is complete.

That the body setae may also undergo a metamorphosis is shown by the studies of Krumins (1952) on *Galleria mellonella,* the wax moth. The setal apparatus consists of the three usual cells, the trichogen, the tormogen, and a sense cell. In all larval instars except the first, the setae are slender and hairlike and are re-formed at each moult, but in some cases the sense cell is subepidermal and in others it is intraepidermal. At the moult to the pupa only those larval setae having intraepidermal sense cells are re-formed on the pupa, and these pupal setae are replaced on the imago by conical setae. The adult, however, acquires also smaller conical setae not represented on the pupa.

The appendages.—In the lower orders of holometabolous insects in which the adult mouth parts are not essentially different from those of the larva, and the larval legs are functional external organs, the corresponding pupal appendages are formed simply within the cuticle of the larval appendages. If the adult appendages are to be much longer than the larval appendages, the growing organs become folded beneath the larval cuticle until they can straighten out at the pupal ecdysis. In some cases, however, the lengthening organs push back into pockets of the pupal integument, but if the imaginal organ begins its growth during larval stages it will be accommodated in a pocket of the larval integument. Eassa (1953) very precisely describes the growth of the imaginal antennae of *Pieris brassicae,* which have their inception in the first larval stage. Each imaginal antennal rudiment is differentiated around the sense cells and trichogenes at the base of the corresponding short larval antenna; as it increases in size it recedes into a pocket of the head wall, and becomes folded upon itself. During the fifth (last) instar the antennal pocket of the forming pupal head is open by a long slit under the yet unshed larval cuticle, from which the antenna will be everted at the ecdysis of the pupa. On the pupal head, however, the antenna has taken a much higher position than that of the larval antenna. The intervening part of the head wall, Eassa shows, is newly generated from the unfolding wall of the antennal pocket.

The growth of the antenna and the reconstruction of the head in *Pieris* is very similar to that which takes place in lower Diptera, except that in the latter the antennal pouches may include the rudiments of the compound eyes. In the cyclorrhaphous flies the antennae and eyes are developed in pouches of the larval head commonly known as the "frontal sacs," which are ingrowths behind the frons (not "in-

vaginations of the pharynx" as they are often said to be). With the formation of the pupa the two postfrontal pouches unite, and when everted their walls form a large part of the imaginal head bearing the eyes and the antennae (see Snodgrass, 1953).

The imaginal legs of holometabolous insects, in which the larva has external legs, are formed in the usual manner within the larval legs and find space to grow beneath the larval cuticle. If the larva is externally legless, however, the rudiments of the adult legs, which may appear early in larval life, grow within peripodial pockets of the larval epidermis, and are not everted until the moulting of the last larval skin. In the same manner are developed the wings of all endopterous insects. In the higher orders the everting leg and wing pouches contribute to the formation of the thoracic wall of the pupa.

The alimentary canal.—Of the three constituent parts of the alimentary tract of an insect, the stomodaeum and the proctodaeum are unquestionably ectodermal since they are formed in the embryo as ingrowths of the body wall. The embryonic mesenteron, however, is ordinarily generated from cells proliferated at the inner ends of the stomodaeum and proctodaeum, which, growing respectively rearward and forward, envelop the yolk in a sac, which is the definitive mesenteron, or functional stomach of the insect known as the ventriculus. Because of the mode of its embryonic origin, some writers have insisted that the insect stomach also must be ectodermal. That this interpretation is entirely unnecessary and evidently erroneous, however, has been shown by Henson (1946), who points out that the tissue at the inner ends of the stomodaeum and the proctodaeum represents the anterior and the posterior lips of the closed blastopore, which, according to the rules of embryogeny, should normally generate ectoderm outwardly and endoderm inwardly. The writer (1935) has explained the matter in essentially the same way in showing that the anterior and posterior mesenteron rudiments are remnants of an originally invaginated endoderm that regenerate the mesenteron. As already noted in the introduction, the embryonic method of forming the stomach is an adaptation to life in the egg. Inasmuch as the embryo cannot take its food into its stomach in the manner of its free-living ancestors, the embryonic stomach grows around the food stored as yolk in the egg. The insect stomach, therefore, begins its history with a metamorphic process, but it does not violate the germ-layer theory.

Since the diet of an adult insect is often very different from that of the larva, the alimentary canal in most holometabolous insects undergoes a very considerable alteration during the pupal transforma-

tion, the change affecting not only the form and relative size of its several parts, but also the nature of the epithelial wall. The degree of reconstruction that takes place in the stomodaeum and proctodaeum varies in different insects, but the mesenteron epithelium is probably always renewed from the larva to the pupa, and in some cases it undergoes a second renewal from the pupa to the adult. An interesting feature in the metamorphosis of the alimentary canal, however, is that the reconstructive changes do not proceed in the same manner in all insects.

The stomodaeum and proctodaeum being of ectodermal origin, their changes in the pupal metamorphosis are similar to those of the epidermis. They may be merely remodeled by a renewal of activity in their cells without any cell destruction, or they may be partly or wholly regenerated from proliferation centers, accompanied by a degeneration and elimination of the old larval cells, which are thrown off into the body cavity. Where the proliferation centers are best differentiated they take the form of circular bands of cells at the inner end of the stomodaeum and the proctodaeum, termed the anterior and posterior *imaginal rings*.

Reconstruction of the stomodaeal and proctodaeal epithelium by a general renewal of developmental activity of the larval cells, without accompanying cell destruction, has been described in some Coleoptera, as in *Galerucella* by Poyarkoff (1910), *Leptinotarsa* by Patay (1939), and *Sitophilus* by Murray and Tiegs (1935). In *Tenebrio,* according to Rengel (1897), the remodeling of the stomodaeum and proctodaeum proceeds from their inner ends, but there are no specific imaginal rings clearly differentiated. The old larval epithelium appears to be absorbed by the advancing newly formed cells. Dobrovsky (1951) follows in great detail the anatomical alterations that take place in the digestive tract of the honey bee during postembryonic development. The stomodaeum and proctodaeum apparently are remodeled into the adult structure by a new growth of the larval cells. In the wasp, according to Anglas (1901), the cells at the posterior end of the stomodaeum and the anterior end of the proctodaeum begin at the time of pupation an active proliferation extending respectively backward and forward; the advancing new cells absorb the old and thus renew the epithelium.

In Trichoptera, Lübben (1907) describes the remodeling of the stomodaeum and proctodaeum by new growth of the larval cells. Russ (1908), however, says that in *Anabolia laevis* imaginal rings are present, though of little importance. The anterior ring serves only for the lengthening of the stomodaeum and the formation of the

stomodaeal valve; the posterior ring is but weakly developed and plays no important role in the reconstruction of the proctodaeum. A part of the rectal region is regenerated from a circumanal zone of proliferation.

The regeneration of the stomodaeum and proctodaeum from imaginal rings is said by Tiegs (1922) to take place in the hymenopteron *Nasonia,* but it is particularly in Lepidoptera and Diptera that these proliferation centers have been observed. In the silkworm, according to Verson (1905), the cells of the imaginal rings become active at the change to the pupa, but they are merely centers of enlargement of the stomodaeum and proctodaeum. Newly formed cells are added to the larval cells already present, pushing the latter farther away without replacing them. Otherwise the stomodaeum and proctodaeum, though they undergo great changes in form, are remodeled by renewed activity of the larval cells. Likewise in *Malacosoma,* Deegener (1908) says the imaginal rings form only small additions to the larval stomodaeum and proctodaeum, and there is no degeneration or emission of larval cells. The larval cells remain, forming the pupal epithelium by reconstructive growth.

The imaginal rings of *Calliphora erythrocephala* are very precisely described by Pérez (1910). The anterior ring is a circle of small cells in the alimentary epithelium surrounding the base of the stomodaeal valve, and therefore on the dividing line between stomodaeum and mesenteron. The posterior ring is a narrow circle of cells in the intestinal wall just behind the bases of the Malpighian tubules. Cellular proliferation from the imaginal rings is said by Pérez to regenerate most of the stomodaeal and proctodaeal epithelium in *Calliphora,* but the terminal parts are formed from anterior and posterior centers of ectodermal proliferation. The degenerating replaced larval cells are thrown off into the body cavity. In *Calliphora vomitoria,* according to Van Rees (1889), there is only a partial regeneration of the stomodaeum and proctodaeum from imaginal rings; the anterior part of the stomodaeum is remodeled by transformation of the larval cells, and in the proctodaeum the rectum is regenerated from behind forward. In *Drosophila* the stomodaeal epithelium is described by Robertson (1936) as being mostly regenerated from the anterior imaginal ring, but regeneration in the pharyngeal region proceeds from the buds of the labium. "As the new epithelium forms, the old larval cells are displaced into the body cavity where they are devoured by phagocytes." The proctodaeal epithelium of *Drosophila* is likewise regenerated in its anterior part from the posterior imaginal ring, and

posteriorly by forward proliferation from the ectodermal imaginal disc of the last body segment.

From these samples of the reconstruction processes that convert the stomodaeum and the proctodaeum of the larva into the corresponding parts of the adult, we may conclude that in the majority of insects the larval cells of the ectodermal parts of the alimentary canal retain the potentiality of rejuvenation. When released from the inhibition of the juvenile hormone they proceed by renewed division and differentiation with the formation of the adult organs. As with the epidermis, however, there is a tendency for certain groups of cells to assume more and more of the work of reconstruction, and these cells finally take the form of specific regeneration centers, the so-called imaginal rings. It is to be noted that the degenerating larval cells of the stomodaeal and proctodaeal epithelia are thrown out into the body cavity, as are those of the epidermis; the discarded epithelium of the mesenteron, on the other hand, is ejected into the stomach lumen.

The mesenteron in its function is more specifically physiological than are the ectodermal parts of the food tract, since it is the seat of digestion and absorption, while the stomodaeum and proctodaeum serve rather in a mechanical way for ingestion, storage, and elimination. The mesenteron, therefore, undergoes a more thorough renovation during the pupal metamorphosis, since it must radically alter its functional activities in response to the usual change of diet from larva to adult. Probably in all holometabolous insects there is a complete renewal of the mesenteron epithelium, but here again, as with the epidermis, the stomodaeum and the proctodaeum, we find that the method of renewal is not the same in all insects.

The larval epithelium of the mesenteron consists typically of two sets of cells. Those of one set are the functional cells concerned with secretion and absorption; those of the other are small cells next to the basement membrane between the bases of the functional cells, known as *replacement cells* because by multiplying they form new functional cells to take the place of those that have become exhausted and which in a degenerating condition are thrown out into the lumen of the stomach. In the majority of insects it is these replacement cells that form also the entire epithelium of the pupal mesenteron, but some Coleoptera appear to repeat the embryonic method of forming the stomach, since they regenerate the mesenteron epithelium from cells at the inner end of the stomodaeum.

According to Mansour (1934) the mesenteron epithelium is regenerated from the posterior end of the stomodaeum in representatives of the following coleopterous families: Cucujidae, Chrysomelidae,

Curculionidae, and Scolytidae. In *Galerucella* Poyarkoff (1910) says the larval epithelium of the mesenteron is rejected in toto, including the basement membrane, and that there is then formed a provisional pupal epithelium derived from cells of the posterior face of the stomodaeal valve. The cells of the new pupal epithelium become differentiated into ordinary epithelial cells and small replacement cells. The pupal epithelium, however, is in turn replaced by an imaginal epithelium formed by the pupal replacement cells, but the imaginal epithelium is thus also derived primarily from the stomodaeum. In *Sitophilus* (*Calandra*) *oryza* Mansour (1927) says that about three days before the pupal moult, the larval epithelium of the mesenteron collapses and degenerates, and together with the replacement cells is thrown off into the lumen. The adult epithelium is then derived in *S. oryza* and in other rhynchophorous species from the posterior end of the transforming stomodaeum. According to Murray and Tiegs (1935), however, the larval replacement cells of *S. oryza* are not discharged with the old epithelium, but remain as a layer of scattered cells on the outer surface of the new epithelium and eventually form the mesenteron caeca.

The regeneration of the mesenteron of *Leptinotarsa decimlineata* is described by Patay (1939) as follows. When the larva is ready for transformation, the stomodaeal valve becomes the seat of an intense proliferation, forming numerous fusiform cells of an embryonic character. The basement membrane behind the valve soon breaks, and the larval epithelium turns inward and rearward while the newly formed cells from the valve extend over its outer surface. The larval epithelium, including the replacement cells, is then soon rejected into the lumen. The valve cells construct an entire new epithelium, including islands of replacement cells and a basement membrane. Thus is formed the pupal epithelium, but again at the moult to the imago the pupal epithelium is rejected and the replacement cells reconstruct an imaginal epithelium. The metamorphosis of the mesenteron of *Leptinotarsa* as given by Patay is thus the same as that in *Galerucella* as described by Poyarkoff.

Statements that the mesenteron is formed from cells of the posterior end of the stomodaeum are not to be understood to mean that these cells are ectodermal; as already noted, Henson (1946) has shown that corresponding cells in the embryo represent the anterior end of the blastopore, and therefore properly generate endoderm inward. The imaginal ring of the larva, as said by Henson, "is not an imaginal rudiment but a reactivated blastopore."

The formation of the pupal mesenteron epithelium from replacement cells of the larva is widespread among the insects, and is too well known to need an extensive review here. According to Mansour (1927) this method of epithelial regeneration is known to occur among Coleoptera in Tenebrionidae, Histeridae, Hydrophilidae, Bostrychidae, Elateridae, Scarabidae, Buprestidae, Anoboliidae, Dytiscidae, and Lucanidae. It is the only method of replacement that has been observed in Trichoptera, Lepidoptera, Hymenoptera, and Diptera. At the beginning of metamorphosis in these insects, the digestive cells of the larval epithelium go into a state of degeneration, while the replacement cells enter a phase of active division, proliferating new cells that spread out under the old epithelium and eventually replace it. The degenerating larval cells are cast off into the stomach lumen, where they form a disintegrating mass of material known as the "yellow body."

Of particular interest are those cases in which the pupal epithelium of the mesenteron is said to be replaced by a special imaginal epithelium. However, without any renewal of the pupal epithelium, the imaginal mesenteron may undergo changes of form and relative size. Deegener (1904) described in *Cybister* the formation of a separate epithelium for the pupa differing from that both of the larva and the imago, the function of which he said is to digest the yellow body resulting from the dissolution of the larval epithelium. Both the pupal epithelium and the imaginal epithelium are generated from replacement cells. We have already noted that Poyarkoff (1910) reports the formation of a provisional pupal epithelium in *Galerucella,* which is replaced by an imaginal epithelium generated from the replacement cells of the pupal epithelium. Poyarkoff, however, contends that the pupal epithelium of *Galerucella* is never functional because in the pupal stage the mesenteron is closed at both ends. In the same way in *Leptinotarsa,* according to Patay (1939), the pupal epithelium of the mesenteron derived from the inner end of the stomodaeum is replaced by an imaginal epithelium regenerated from the pupal replacement cells. In the coleopteron *Acanthoscelides obtectus* as described by Bushnell (1936), the pupal epithelium formed from the larval replacement cells is later cast off into the stomach lumen, leaving only a basal layer of cytoplasm containing the smaller nuclei, from which there is then regenerated the definitive imaginal epithelium. The degenerating material from the larval epithelium, Bushnell says, is probably digested and absorbed by the pupal epithelium, which is then itself cast off and gives place to the imaginal epithelium. Lastly, we may note that Tiegs (1922) says the pupal epithelium of the chalcid

Nasonia, which is formed from larval replacement cells, proceeds to digest and absorb the detritus from the rejected larval epithelium, after which it degenerates, but from its posterior part is formed the definitive mesenteron of the adult.

Deegener (1904) contended that the presence of separate pupal and imaginal epithelia in the mesenteron of many insects is evidence that the pupa represents a former actively feeding stage in the life history of holometabolous insects. Most students of insect metamorphosis, however, have seen a physiological reason for the formation of a specific pupal mesenteron epithelium in the fact that the pupal stomach must digest the disintegrating tissue of the larval mesenteron thrown into it, in order that this material may be reutilized by the developing imaginal organs. In this case the physiological requirements of the adult stomach will be very different from those of the pupal stomach, and it is therefore but a physiological necessity that the epithelium should be renewed for the purposes of the adult. Deegener (1908) himself notes that there is no formation of a new imaginal epithelium in *Malacosoma;* the pupal epithelium persists and goes over directly into the epithelium of the imaginal mesenteron, but with many changes in its cytological structure.

That there is a complete regeneration of the mesenteron epithelium at the moults of the larva, as described by Möbusz (1897) in *Anthrenus,* has not generally been observed, but there is nothing improbable in Möbusz's claim, since the replacement cells are active at all times in renewing the depleted functional epithelium. According to Henson (1929) the mesenteron epithelium of *Vanessa* is renovated at each larval moult by the addition of new cells. It would be of interest to know if any such change takes place in the successive forms of heteromorphic larvae.

The Malpighian tubules.—In some insects the Malpighian tubules go over from the larva to the adult without any essential change, in others their walls are regenerated from replacement cells while the old cells degenerate, in still others the larval tubes completely disappear and the imaginal organs grow out in their place as a new set of tubes.

It is still an open question, or at least a disputed one, as to whether the Malpighian tubules of insects are ectodermal or endodermal in origin. Most investigators claim that they arise from the inner end of the proctodaeum, others state as positively that they are outgrowths of the posterior part of the mesenteron. In the embryo of the honey bee Nelson (1915) says the rudiments of the tubules are formed prior to the ingrowth of the proctodaeum as invaginations of the ectoderm

around the point where the proctodaeum is to appear. For a short time, therefore, the tubules "open directly on the external surface of the embryo." A similar condition, according to Nelson, is known otherwise only in *Chalicodoma*. If it occurred more widely we might suspect that the Malpighian tubules were originally circumanal glands of the integument, and that they have secondarily been carried inward with the ingrowing proctodaeum.

The larval tubes of Hymenoptera that have been studied degenerate and disappear, the imaginal tubes are formed anew. In the honey bee Oertel (1930) says the larval tubes disappear apparently by chemical means, not by phagocytosis. The imaginal tubes are then formed as budlike outgrowths from the extreme anterior end of the proctodaeum. According to Dobrovsky (1951) the ring of buds of the imaginal tubes of the bee appear on the surface of the pylorus a short distance behind the inner fold, or "diaphragm," that separates the lumen of the larval mesenteron from that of the proctodaeum. These observations agree with those of Anglas (1901) that the larval tubes of the wasp and bee arise from the front end of the procto-daeum, disappear at metamorphosis, and are replaced by imaginal tubes that grow out just behind their bases. In the same manner, according to Tiegs (1922), are formed the imaginal tubules of the chalcid *Nasonia*, though there are no larval tubules.

The developing imaginal Malpighian tubules of the beetle *Leptino-tarsa* are described and distinctly illustrated by Patay (1939) as diverticula from the anterior end of the proctodaeum. At the beginning of pupation their cells take on an appearance of degeneration, the cytoplasm becoming vacuolated and the nuclei irregular, but after the moult to the imago they soon again assume the aspect of normal functional cells, and without destruction or cell division the persisting larval tubules become the organs of the imago. In some other Coleoptera, however, the imaginal tubules are said to be regenerated from small replacement cells in the walls of the larval organs. Poyarkoff (1910) describes the imaginal tubules of *Galerucella* as being formed in this manner, and Murray and Tiegs (1935) say the cells of the larval tubules in *Sitophilus* (*Calandra*) degenerate in the pupa, while new imaginal cells are proliferated by active mitosis of the replacement cells until they form a new tube. The detritus of the larval cells is not discharged but slowly absorbed.

A detailed account of the transformation of the Malpighian tubules from the larva to the adult without dissolution or cell destruction is given by Samson (1908) for the lepidopteron *Heterogenea limacodes*. During the long prepupal stage of this species the Malpighian tubules

go into a degenerative state to such an extent that they appear to be on their way to complete dissolution; at the moult to the pupa, however, reconstructive changes begin that lead to the reformation of the tubules into the organs of the imago. The imaginal tubules retain the form of the larval tubules, but they have undergone an entire change in their histological structure, which, Samson suggests, is correlated with the change of food from the larva to the moth.

In the Diptera the Malpighian tubules, so far as observed, undergo no essential change from larva to adult. Pérez (1910) says that the cells of the tubules in Muscidae simply go into a resting condition during the pupal period, and then again resume functional activity in the imago. Robertson (1936) notes simply that the cell structure of the tubules in *Drosophila* appears to be the same in the larva and the imago. The tubules of *Drosophila,* Robertson says, open into the digestive tract just *in front* of the posterior imaginal ring that regenerates the proctodaeum, from which fact it would appear "that the Malpighian tubules of *Drosophila* belong to the mesenteron." Henson (1946) finds likewise in *Calliphora* that the Malpighian tubules grow out in front of the posterior imaginal ring, so that not only the tubules but also the pyloric region from which they arise are of endodermal origin, and he believes that the same condition prevails in other insects.

The fat body.—The so-called fat body of the insect is a physiological tissue; the changes its cells undergo from larva to imago are merely the accompaniments or results of functional activities and are not of the nature of a true metamorphosis. In the larva the fat cells elaborate and store nutritive materials in the form of fat, albuminoids, and glycogen, which are utilized mostly in the pupal reconstruction, but may be carried over into the adult. In some insects there is little or no destruction of the fat cells during metamorphosis, in others most of the cells disintegrate in the pupa to liberate their stored products, while a few are carried over intact to generate the fat body of the adult. Insects such as most Coleoptera in which the pupal transformation is less intense, and which feed amply in the adult stage, have less need of larval food reserves, and show the least change in the larval fat cells during metamorphosis. On the other hand, with insects in which there is an extensive breakdown of larval tissues and an almost complete reconstruction of adult tissues in the pupa, the food material stored in the larval fat cells is of vital importance for the reconstruction of new imaginal tissues. It is in such insects that the fat cells most abundantly give up their contents to the pupal blood, and perish in so doing, leaving only a few to go over into the adult to form the imaginal fat body.

In the Muscidae, it is said by Pérez (1910), the larval fat cells disintegrate completely in the pupa and their remains are devoured by phagocytes. The imaginal fat body, according to Pérez, is then redeveloped from mesenchymatous cells on the inner surface of the epidermis, the abdominal fat tissue being derived from mesenchyme on the inner surfaces of the imaginal discs of the epidermis. If the imaginal fat body is renewed in this manner in the higher Diptera, its formation from mesenchyme is paralleled by the renewal of the muscles from free myoblasts in the same insects.

The oenocytes.—The oenocytes are specialized ectodermal cells developed from the epidermis in the neighborhood of the spiracles, mostly in the abdomen. In some insects the oenocytes remain in the epidermis, but usually they are liberated into the body cavity, where they occur either in groups connected with the spiracular tracheae, or freely scattered in association with the fat cells. Most students of insect metamorphosis report that the oenocytes are renewed at the pupal transformation, and Wigglesworth (1933) says there is in the hemipteron *Rhodnius* a new generation of oenocytes formed at each nymphal moult, though some of the old oenocytes persist. According to Albro (1930) the larval oenocytes of the beetle *Galeruclla nymphaeae* persist very definitely up to the pupal period, but then they undergo degeneration and histolysis. The smaller imaginal oenocytes appear later newly proliferated from the epidermis. In *Sitophilus* (*Calandra*) the larval oenocytes are said by Murray and Tiegs (1935) to begin a slow distintegration in the prepupal stage, some being attacked by leucocytes, but the majority later disappear without phagocytosis. The imaginal oenocytes are independently developed from the epidermis of the abdomen close to the spiracles, but in the imago they are mostly dispersed among the cells of the fat body. No budding of imaginal oenocytes from larval oenocytes was observed by Murray and Tiegs, such as described by some earlier writers. In *Leptinotarsa,* Patay (1939) observes that the imaginal oenocytes scatter in the body cavity by amoeboid movements.

The function of the oenocytes is still not exactly known, though the cells are now thought to be secretory organs of some kind. It has commonly been observed that the appearance of secretional activity in the cells is greatest at the times of moulting, and Albro (1930) expressed a common opinion in her statement that secretion by the oenocytes "is in some way, directly or indirectly, correlated with the phenomenon of moulting seems highly probable." Wigglesworth (1933), however, finds that the oenocytes of *Rhodnius* show their greatest activity *after* the new epidermis is complete. He concludes, therefore, that the oeno-

cytes are concerned with the formation of the new cuticle, "that they synthesize, and secrete into the blood, materials which go to form a part of the cuticle." This conclusion receives support also from the fact that the oenocytes are specialized epidermal cells. For a good, well-documented review of the present status of the oenocyte question, see Richards (1951).

The tracheal system.—In most holometabolous insects the tracheal system of the larva is carried over to the adult with little change other than the development of new branches to accommodate the particular needs of the imago, and the elimination of tracheae needed only by the larva. As with other parts of the ectoderm, however, more complex reconstructive processes take place in the tracheal tubes of some insects, involving a dissolution of the larval epithelium and the regeneration of a new imaginal epithelium. According to Anglas (1901) the tracheal system of the bee undergoes no true metamorphosis, the only change being one of growth and extension by proliferation from the ends of branches, and the enlargement of certain tubes to form the air sacs of the adult. In the curculionid beetle *Sitophilus* (*Calandra*), Murray and Tiegs (1935) say that the tracheal system of the adult differs from that of the larva principally in the elaboration of the thoracic tracheae. The larval tracheae are directly converted into the adult tracheae, accompanied by cell division in the epithelium, but only rarely is there any disintegration of the cells. Even terminal branches within the metamorphosing larval muscles remain intact and become reassociated with the newly forming imaginal fibers.

On the other hand, in the chalcid *Nasonia,* Tiegs (1922) finds that there is an extensive reconstruction of imaginal tracheae from replacement cells in the basal parts of the larval spiracle trunks. Partly by disintegration and partly by phagocytosis, he says, the entire larval tracheal system disappears, but regeneration of the imaginal epithelium keeps pace with the destruction of the larval cells, so that there is no discontinuity in the tracheal system itself. Pérez (1910) gives a detailed account of the tracheal metamorphosis in *Calliphora erythrocephala.* Though the greater part of the larval system of the fly persists into the imago with more or less extensive remodeling, certain parts of it are destined to be totally destroyed by phagocytes, and to be replaced by newly generated tissue. The tracheal regeneration centers, or histoblasts, are groups of small cells distributed through the walls of the larval tubes; they give rise to new branching trunks, and replace the larval epithelial cells of those parts that have been destroyed by phagocytes. The presence of histoblastic centers of regeneration in the tracheal system, as in other parts of the ectoderm,

thus appears to be a specialized condition developed in only certain groups of insects.

The dorsal blood vessel.—From the descriptions of most writers on the internal metamorphosis of insects it would appear that the heart and aorta undergo little change from larva to adult during the pupal transformation, and it has been observed in various insects that the heart continues to beat throughout the pupal stage. In the wasp, Anglas (1901) says the dorsal vessel undergoes no metamorphosis except a change of form. According to Murray and Tiegs (1935) the cells of the heart and aorta of *Sitophilus* increase in size during the larval stage, but they do not divide, and they survive the period of metamorphosis intact; the alary muscles of the heart go over with little change into the imago. In *Leptinotarsa* about the only change in the heart described by Patay (1939) is the formation during the pupal stage of the pulsatile vesicle in the mesothorax of the imago. Robertson (1936) says of *Drosophila* that "the dorsal vessel of the larva seems to pass over directly into the adult," and that "the alar muscles either disappear and are re-formed in the late pupa, or they are somewhat altered, being much more delicate in the imago than in the prepupa."

In contrast to these accounts, Tiegs (1922) reports that the heart of *Nasonia* undergoes a profound metamorphosis, beginning at the time of larval defaecation. Just prior to this the cells of the heart and the pericardium undergo a granular degeneration. The imaginal heart is then regenerated mainly from scattered embryonic cells in the heart wall. A new pericardium is formed from a mass of embryonic cells lying below the larval pericardium, from which proliferating cells extend forward, absorbing the elements of the larval pericardium as they grow. Eight hours after defaecation, Tiegs says, the heart tube of *Nasonia* has been completely regenerated, and below it is the regenerated pericardium.

It seems probable that further studies on the heart of other insects during metamorphosis will reveal greater changes than have heretofore been reported, unless there is some special reason for the renovation of the organ in *Nasonia*. On the other hand, if reorganization in the structure of the heart is of common occurrence, it is difficult to explain how a regular heartbeat is maintained during the pupal stage. In the larva the heart beats continuously in a forward direction, but it has been shown by Gerould (1924) and other investigators that during the pupal and adult life in many insects there is a periodic reversal in the direction of the beat. Gerould (1933) records the occurrence of periodic heartbeat reversal in the pupa and imago of representatives

of Coleoptera, Lepidoptera, Hymenoptera, and Diptera. "In general," he says, "normal reversal occurs independently of the central nervous system and is essentially myogenic." For a bibliography of the subject, and a description of the structure and action of the heart in the pupa and imago of *Bombyx mori,* see Gerould (1938).

The nervous system.—It is well known that changes in the gross structure of the central nervous system commonly take place between the larva and the adult. Ganglia are drawn forward or condensed by a shortening of the connectives in both the thorax and the abdomen, with the result that ganglionic masses on the nerve cords are fewer and individual ganglia are displaced from their proper segments. On the other hand, condensation of ganglia may be present in the larva, as in the higher Diptera, in which all the body ganglia are united in a large thoracic nerve mass closely connected with the brain. The significance of these gross changes in the nervous system is not clear, but concentration and anterior displacement of ganglia is always found in the more specialized insects.

The internal reorganization of the nervous system during the pupal transformation has been less studied than that of other tissues. Bauer (1904) has shown that a reconstruction of the brain and the development of the optic lobes of the adult proceeds from neuroblasts in the larval brain, and, though he apparently made no special study of reorganization in the other ganglia, he says that scarcely any other organ system of the insects undergoes such a thorough metamorphosis as does the central nervous system.

In their account of the metamorphosis of *Sitophilus* (*Calandra*) *oryza,* Murray and Tiegs (1935) say that "no direct observations have been made on the manner in which the nervous system of an insect like *Calandra* becomes readjusted during metamorphosis to meet the needs of the highly specialized imaginal musculature," but they add that "many new motor neurons doubtless develop from neuroblasts." However, "disintegration of larval cells occurs but rarely, and consequently degenerating nerve trunks are never found, as in many other insects." In contrast to this Tiegs (1922) finds in the chalcid *Nasonia* that the larval cells of the nerve cord degenerate, while the imaginal neuroblasts begin to divide and multiply, growing at the expense of the larval cells on which they nourish themselves. In the larval brain there is a distinct layer of nonfunctioning neuroblasts outside the central mass of functional cells. At the time of defaecation by the larva the larval brain cells go into dissolution as do the nerve fibers, while the neuroblasts become active and give rise particularly to the complex

optic lobes of the compound eyes and to the centers of the imaginal ocelli and antennae.

A study of the developing innervation of the pupal legs of *Tenebrio molitor* has been made by Sorokina-Agafonowa (1924), who describes an elaborate definitive branching of motor and sensory nerves growing out from the main leg nerve of the larva. The sensory branches go to the epidermis and end in bipolar nerve cells. In a later part of the pupal stage these end cells divide each into several cells until there are hundreds of them which become connected with small setae of the cuticle. The author points out that the connection between the nerve cells and the receptor organs thus appears to be secondary and not primary. It is generally said, however, that the sense cell of a setal sense organ is a division product of a cell in the epidermis, and that the sensory axon grows centrally from it (see Wigglesworth, 1953b).

A complete analysis of insect metamorphosis certainly should include a study of differences in the neuromuscular mechanisms between larva and adult that form the basis of difference in sensory reactions and instincts. It would seem that in many cases there must take place in the pupa an extensive rearrangement of both sensory and motor nerves and an almost complete reorganization of the neuron associations in the central nervous system to account for the behavioristic differences between the larva and the adult. Since we cannot attribute any degree of intelligence to a larva, the common act of spinning a cocoon must be supposed to depend on some special pattern of structure in the larval nervous system that would be entirely useless to the adult. Van der Kloot and Williams (1953a, 1953b) have made an interesting analysis of the role of both external and internal stimuli in the spinning of the cocoon by the Cecropia caterpillar.

A good example of a complex larval instinct is seen in the manner by which the caterpillar of the bagworm moth, *Thyridopteryx ephemeraeformis* constructs its portable bag. Several hundred tiny larvae may hatch out at the same time from the eggs of a single female moth. After a period of dispersal they all settle down and proceed by identical methods to enclose themselves in conical bags. Each little caterpillar first with its mandibles cuts out a number of small oval pieces of leaf epidermis (cork or blotting paper will do just as well), and then strings them together in a band with threads of its silk attached to the leaf at each end (fig. 16 A). This done, instead of crawling beneath the band, the caterpillar turns a complete somersault, going head first over and under the band (B), landing on its back in reversed direction (C). Then, righting itself (D), it cuts out more leaf bits and makes a ventral band (E) continuous with the one over its back. It now has a

complete girdle about its thorax. Next, elevating its abdomen (F) it lengthens the girdle downward until only its head and feet are exposed below (G). Finally, when the bag encloses the whole body, the anchoring threads break loose and the now fully clothed young caterpillar walks away (H) to take its first meal on the leaf. As the cater-
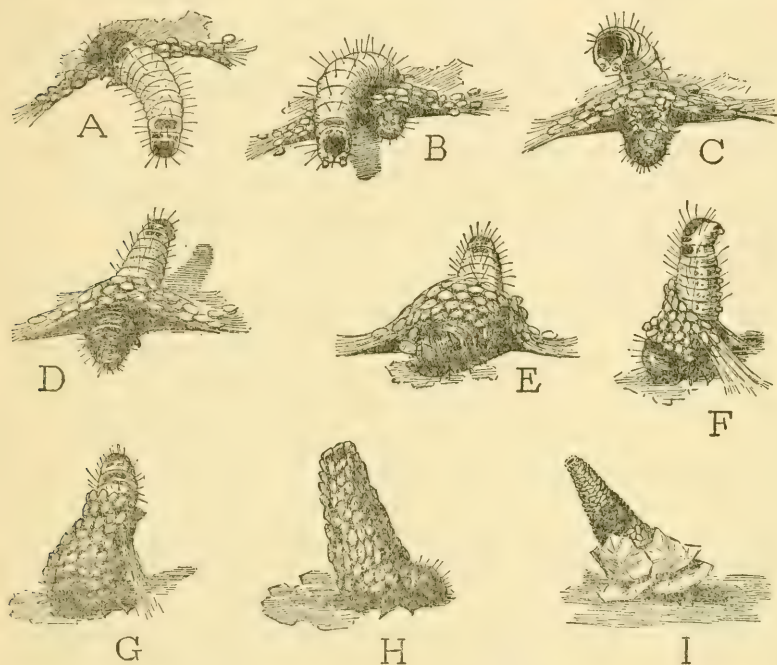
Fig. 16.—Construction of a bag by a newly hatched bagworm, *Thyridopteryx ephemeraeformis* (Haw.).

A–H, consecutive acts of an individual larva making its bag from bits of leaf epidermis cut out with its mandibles. I, an older specimen with later additions to the bag, less enlarged.

pillar grows it merely enlarges the bag by leafy additions to the lower edge (I). Such instinctive skill and methodical procedure as this of the newly hatched bagworm must depend on the presence of a highly developed mechanism for coordinated sensory and motor chain reactions in the central nervous system.

The muscular system.—In considering the metamorphosis of the muscular system it must first be noted that all the muscles of all holometabolous insects do not undergo the same degree of change. Five categories may be distinguished: (1) Larval muscles that go over unchanged into the adult, (2) larval muscles that are reconstructed into

imaginal muscles, (3) larval muscles that are destroyed and not re-placed, (4) muscles newly formed for the imago replacing larval muscles that have been completely destroyed, (5) newly formed muscles not represented in the larva or which are as yet undeveloped in the larval stage.

The histolysis and histogenesis of the muscles have been described by many writers for various insects. The accounts are not all in entire agreement as to the details of the processes, but a chief point of difference relates to the part that phagocytes may play in the destruction of the larval muscles, a question which is of no concern to us in the present discussion, and is fully reviewed by Oertel (1930). The most important matter is the apparently well-established fact that in different insects the muscles are regenerated in different ways. In the more generalized orders, such as Coleoptera, the histogenesis of a re-organized muscle or of a replacement muscle is said to proceed from small nuclei *within* the tissue of the larval muscle itself. On the other hand, in the more specialized orders, particularly in the higher Diptera, such muscles are remodeled or replaced by myoblasts originating *out-side* the larval muscles, probably generated from mesoderm in the embryo. Muscles of appendages that are undeveloped in the larva are in all cases derived from free myoblasts.

The degenerative processes in larval muscles are always pretty much the same. The complete histolysis of a thoracic muscle of *Ephestia kühniella* is described as follows by Blaustein (1935). The advent of degeneration appears at the beginning of the prepupal period with the disappearance of cross striation in the muscle fibers. Lymphocytes now enter the muscle through the sarcolemma and penetrate between the fiber bundles, which lose their connections and separate from one another. The sarcolemma is next broken, admitting increasing numbers of lymphocytes, and is finally ruptured on all sides. The lymphocytes, however, Blaustein says, probably do not at this time have a phagocytic action on the muscle tissue. At the end of the third day of pupal life the muscle nuclei begin to degenerate in large numbers, and dissolve as the nuclear membranes disappear. The degenerating muscle tissue is now attacked by phagocytic lymphocytes that penetrate between the dissociated fibrillae. By the end of the fourth day of the pupa the histolysis of the muscle is complete, and there remains in the place of the muscle only a great number of phagocytes engorged with muscle fragments.

Essentially the same process of muscle degeneration has been described by other writers for other insects. Some earlier writers regarded the lymphocytes penetrating the muscles as phagocytes, but it

is now generally agreed that phagocytes do not initiate the destruction of the muscles. They devour the products of the muscle disintegration, and the greatly enlarged, engorged phagocytes may become extremely numerous throughout the body cavity of the pupa, as in higher Diptera, in which they have been called "spherules of granules," or "Körnchenkügeln."

The reconstruction of the muscular system was thought by Berlese (1902) to proceed from the nuclei of the larval muscles, which, being set free in small masses of cytoplasm, became myocytes and were carried to the places where imaginal muscles were to be formed. More recent writers, however, find that in those insects in which the muscles are reconstructed from intrinsic elements, the larval muscles contain two sets of nuclei. Those of one set are the functional larval nuclei, which are destroyed; those of the other set are converted into myocytes, which form the new muscle in place of the degenerated larval muscle. In the beetle *Galerucella,* for example, Poyarkoff (1910) says that the larval muscles contain large nuclei that multiply by amitosis, and small nuclei that multiply by mitosis. The first are the larval nuclei, and will disappear; the small nuclei are the regenerative elements of the imaginal muscles. These mitotic nuclei become enclosed in small masses of sarcoplasm to form myocytes, which associate in long strands that eventually become the fibers of the new or reconstructed imaginal muscle. The regeneration of muscles in *Sitophilus (Calandra)* is similarly described by Murray and Tiegs (1935). The small nuclei are at first scattered in the sarcoplasm of the larval fibers, but as the muscle degenerates they migrate into the body of the muscle, which becomes crowded with them. Here these nuclei form myocytes, which unite into columns of cells that finally become the imaginal fibers. Likewise the formation of adult muscles that replace degenerating larval muscles is said by Patay (1939) in *Leptinotarsa* to proceed from small peripheral nuclei within the tissue of the larval muscles.

In the honey bee, Terre (1899) very concisely describes two sets of nuclei in the larval muscles; those of one set are large nuclei in the body of the muscle, the others are small nuclei mostly arranged in longitudinal rows at the surfaces of the fibers. After the larva has finished spinning its cocoon, the muscle substance degenerates and is penetrated by the small nuclei, while the large nuclei dissolve and disappear. The small nuclei become surrounded by masses of myoplasm and thus become the myocytes that reconstruct the muscle for the imago. On the other hand, in the account of the metamorphosis of the muscles of the honey bee given by Oertel (1930) it would appear that

the myoblasts invade the muscle from the outside. Oertel does not discuss the genesis of the free myoblasts, but he says "it is commonly believed that the myoblasts are of mesodermal origin." In the regenerating abdominal muscles he notes that the fibers in some cases are completely covered by myoblasts, and, in connection with the thoracic muscles, that nuclei present in the larva before sealing of the comb cell become incorporated into the new muscles. In the wasp *Polistes,* according to Pérez (1912), the larval muscles have two sets of nuclei, large larval nuclei in the body of the muscle, and small embryonic nuclei attached to the *outside* of the muscles. The muscles undergo a degeneration and reconstruction without being entirely destroyed, but the larval nuclei are mostly eliminated as the imaginal nuclei take their places in the regenerating muscle. In comparing the muscle metamorphosis of the vespids with that of the muscid flies Pérez says the only difference is that in the muscids the imaginal myoblasts are at first exterior to the muscles, while in the wasps the myoblasts are attached on the muscles they are to reconstruct and later become free in order to proliferate outside the muscle.

In the chalcid *Nasonia,* according to Tiegs (1922), the adult muscles are all formed from free mesodermal myoblasts, which are present in the earliest larva. During the larval period the myoblasts are small embryonic cells scattered in the body cavity close to the muscles. As the larval muscles degenerate the neighboring myoblasts become active, multiply by mitosis, penetrate the sarcolemma, and move about in the disintegrating myoplasm by amoeboid movements. Eventually the whole larval fiber, including the sarcolemma, disappears and the invading myocytes take its place, becoming arranged in rows that finally form the new imaginal fibers.

The description by Blaustein (1935) of the muscle transformation in the lepidopteron *Ephestia kühniella* is not explicit as to the origin of the myoblasts, but this author says that where a prospective muscle is to be formed very small embryonic cells are first laid down. By mitotic division they multiply, and by fusion with one another they form long strands that become the imaginal muscle fibers.

The histogenesis of the muscles of the dipteron *Psychoda alternata* is described by Schmidt (1929), but here again it is not clear whether the myoblasts are intrinsic or extrinsic with relation to the larval muscles. The dorsal longitudinal muscles of the metathorax of the larva while undergoing degeneration lose their cross striation and the sarcolemma disappears, the contractile substance and the plasma blend into a homogeneous mass in which are imbedded many small nuclei, which are the myoblast nuclei that will regenerate the imaginal muscles.

In the higher Diptera there appears to be no doubt that the imaginal myoblasts are primitive embryonic cells at first *free* in the body cavity of the larva. As examples of the process of muscle formation in the higher Diptera we may cite from the paper by Pérez (1910) on the metamorphosis of Muscidae, and from that by Robertson (1936) on *Drosophila*. Both authors describe the myoblasts of the imaginal muscles as originating *outside* the larval muscles. According to Pérez the myocytes are mesodermal cells preexisting in the body cavity, more or less in the vicinity of the epidermal histoblasts, but they are not of ectodermal origin. They represent the precocious rudiments of the imaginal musculature in a state of dissociation. These free myocytes, Pérez asserts, are the homologues of the small regenerative nuclei in the larval muscles of those insects in which the muscles are re-formed from intrinsic elements. However, he does not suggest how the free myocytes became dissociated from the larval muscles. Robertson does not discuss the origin of the free myocytes in *Drosophila*.

The adult muscles of Muscidae, according to Pérez, excepting those that are exclusively imaginal, are mostly muscles that have been reconstructed in the pupa from larval muscles. The larval muscle degenerates into a homogeneous mass, which is then penetrated from the outside by the myoblasts, which reconstruct the larval muscle tissue into a muscle for the adult. The imaginal muscles of the muscids, Pérez says, are thus formed from two different sources, the remains of the larval muscles, and the embryonic myoblasts, the two being combined in different proportions in different muscles. On the other hand, Robertson says, "Practically all muscles of *Drosophila* are destroyed by histolysis and consumed by phagocytes during the prepupal and early pupal instars." Thoracic muscles, which in *Calliphora* Pérez believed were remodeled into imaginal muscles, according to Robertson simply undergo a long-delayed histolysis. Myocytes of the longitudinal thoracic muscles appear in the dorsal part of the pupa of *Drosophila* as early as the fifth hour of the pupal period. They surround the persisting larval muscles and increase greatly in numbers. The larval muscles degenerate completely and disappear, leaving in their place the myocytes, which spread out in the position of the future imaginal muscles. Differentiation then proceeds anteriorly and posteriorly from the central mass of myocytes until a new muscle is fully formed.

Muscles newly generated in the pupa, having no representatives in the larval musculature, are for the most part the muscles of appendages that are undeveloped in the larva, including the mouth parts, the antennae, the legs, and the external reproductive organs. These mus-

cles necessarily are generated from unorganized groups of myoblasts of mesodermal origin that are adventitious on the inner surfaces of the ectodermal histoblasts of the appendages. If, however, an appendage is functionally developed in the larva, it has its own normal larval muscles, and these muscles will undergo a metamorphosis of the type characteristic of the species. In the larva of the beetle *Thymalus*, for example, Breed (1903) says the leg muscles go into a state of degeneration until they reach a structureless condition, but this condition is of short duration and is followed by a phase of reconstruction.

The reason for the metamorphosis of the muscular system is not hard to see; it is the difference between the musculature of the larva and that of the imago. Breed (1903) argued that the larval musculature must undergo a reconstruction because of the specialized condition of the adult musculature in winged insects. The truth, however, is clearly just the reverse. The adult musculature is essentially the same in all insects from Ephemeroptera to Diptera, except that the thoracic musculature is uniquely specialized in Odonata and is simplified in Blattidae, Mantidae, and Isoptera. The musculature of an adult holometabolous insect, therefore, is in general no more specialized than that of a winged adult ametabolous or hemimetabolous insect. It is the musculature of the holometabolous larva that has become specialized for purposes of the larva. Its specialization was at first perhaps one of simplification, but with the larval evolution the larval musculature increases in complexity along patterns that have little or no relation to the imaginal musculature because it becomes adapted to the entirely different mechanism of movement in the larva. The more different a larva becomes from the adult of its species, the more specialized its musculature must be, and, therefore, it is in such insects as Lepidoptera, Hymenoptera, and Diptera that the greatest degree of muscle reconstruction occurs between larva and imago.

It is evident that the pupal transformation of the muscles is not entirely comparable to the regeneration of any of the other tissues. The formation of imaginal muscles from special nuclei within the larval muscles might be likened to the regeneration of ectodermal parts from histoblasts within the ectoderm, but the construction of muscles from myoblasts scattered in the larval body has no counterpart in the regeneration of other tissues. Furthermore, it is difficult to understand how the free myocytes in one case, as Pérez contends, can be homologues of the regenerative nuclei in the other, and it is quite mysterious how mesodermal cells lying idle throughout embryonic and larval life can be assembled in the pupa and induced to form new muscles for

the imago. Yet there seems to be no doubt that they do this very thing. The essence of holometabolism is the muscle transformation.

XII. MUSCLE ATTACHMENTS AND THE NATURE OF THE PUPA

The somatic muscles of arthropods for mechanical reasons are necessarily attached on the cuticle of the integument. The attachment is by means of fine fibrils called tonofibrillae, which traverse the epidermis from the cuticle and are attached to the muscle fibrillae; their outer ends in some cases appear to be embedded in the inner part of the endocuticle. The nature of the tonofibrillae and the manner of their formation have been discussed for half a century, and are still not definitely known; a review of opinion is given by Richards (1951) and need not be repeated here. Probably the best explanation of the tonofibrillae is that they are cuticular filaments formed by the epidermal cells where a muscle comes into contact with the integument; if their outer ends are embedded in the cuticle we may assume that the inner layer of the endocuticle was laid down subsequent to the formation of the tonofibrillae. The connection with the muscle fibrillae is said to be formed by a splitting of the inner ends of the cuticular fibers, which are thus "spliced" to the muscle fibrillae so that the two become mechanically continuous.

It is well known that homologous muscles may have their attachments at different places on the body wall in different insects. The shift is generally attributed to "migration" of the muscles in the phylogenetic history of the insects; but in embryonic development and in metamorphosis the muscles become attached where their ends come in contact with the epidermis. It seems probable, therefore, that the formation of tonofibrillae by the epidermis is evoked by the muscle contact. A necessary condition for muscle attachments on the cuticle is that the latter must be established when the epidermal cells are physiologically active and thus able to produce tonofibrillae while the cuticle is in a formative state. Since most of the adult muscles of holometabolous insects undergo a prolonged period of reconstruction in the pupa, they do not make their final attachments until the end of the pupal period when the imaginal cuticle is being formed. On the other hand, if a muscle is ready for attachment at an early stage, as in hemimetabolous insects, it can be attached at once on the imaginal cuticle at the end of the larval stage.

The nature of the pupa has been a subject of much difference of opinion. Perhaps the most common interpretation is that the holometabolous pupa represents the last nymphal stage of insects without

metamorphosis, which would mean either that the pupa is simply a modified last larval instar, or that the juvenile specialization that produced the larva stopped at the penultimate moult, so that the pupa is a reversion to a nymphal stage with incompletely developed external wings. The nymphal theory of the pupa is carried still further by Jeschikov (1929), who contends that the larva is merely a free-living stage of the embryo and that the pupa represents the whole period of ancestral postembryonic development, "sie erscheint als Resultat des Zusammenfliessens aller nymphalen Altersstufen." The pupa itself sufficiently refutes this theory; it gives no evidence of being a composite stadium since its external structure once formed remains unchanged. (See also p. 49.)

A more reasonable theory concerning the nature of the pupa is that of Poyarkoff (1914), which holds that the pupa is a preliminary imaginal stage that has been separated from the final adult by an extra moult in order to furnish a new cuticle for the attachment of muscles reconstructed or newly formed in the pupa. Furthermore, Poyarkoff adds, the pupa as a preliminary adult serves as a necessary mold for the muscles forming within it, since in the larva these muscles could not attain the size and the points of attachment appropriate for the adult. It is only after the insect has assumed the external imaginal form in the pupal stage that new muscles can be completed, but even then they are still incapable of functioning because of the lack of attachments. They cannot be attached at the beginning of pupation since they are not yet formed, and they are not able to attach on the pupal cuticle after the latter is hardened. Hence a new moult is necessary to furnish the only condition in which tonofibrillae can be formed for anchoring the muscles on the cuticle. Hinton (1948) strongly advocates the views of Poyarkoff concerning the nature of the holometabolous pupa. If the larval muscles had not departed from the plan of the adult musculature, the larva might go over directly into the adult. The pupal moult is the solution on the part of the insect to the problem of attaching new or reconstructed muscles. The only evidence against this interpretation of the pupa that might arise would be the discovery in some insect with a pupal stage that no new muscle attachments are formed. At present no such condition is known.

There can be no question that in its general form and structure the pupa is an unfinished adult. The likeness to the adult is strikingly seen in the relatively generalized raphidian pupa (fig. 17 B), which has distinctly imaginal characters in the shape of the head, the long, slender legs, the subsegmented tarsi, and the large, paired movable

claws on each foot (D). When this pupa is ready to transform it leaves the winter nest of the larva and crawls to a suitable place on the bark of twigs of the tree, to which it tightly clings with its claws
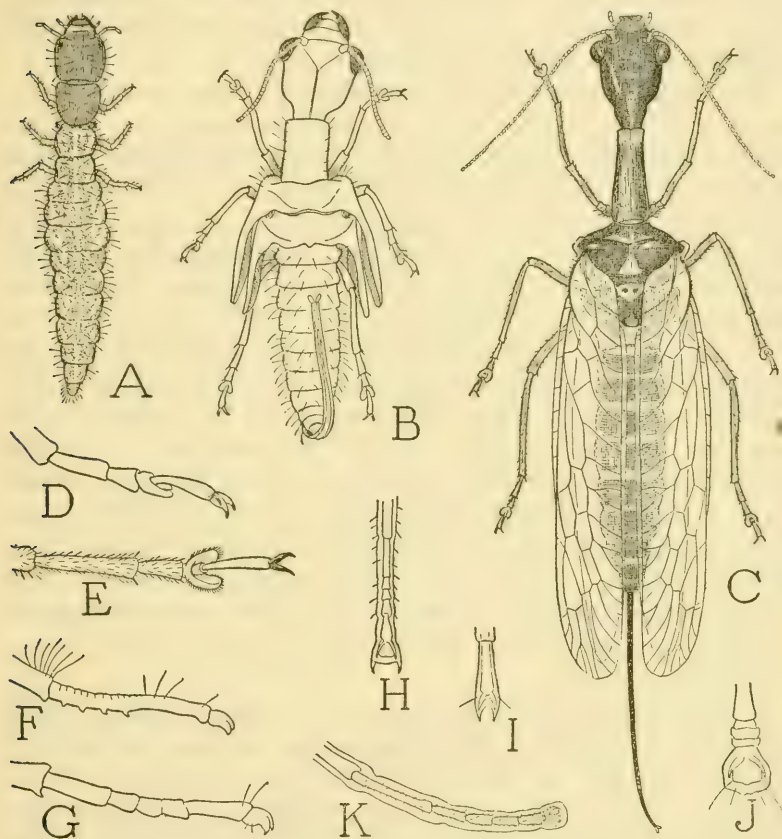
FIG. 17.—Larva, pupa, and adult of a raphidian, and examples of pupal tarsi.

A, *Agulla adnixa* (Hagen), larva. B, same, pupa. C, same, adult female. D, same, pupal tarsus. E, same, tarsus of adult. F, myrmelionid pupal tarsus. G, *Corydalus cornutus* (L.), pupal tarsus. H, chrysopid pupal tarsus. I, *Boreus* sp., pupal tarsus. J, *Mantispa* sp., pupal tarsus. K, *Musca domestica* (L.), pupal tarsus.

(see Stein, 1838, Kästner, 1934). The pupa of the megalopteron *Nigronia serricornis* (Say) also has paired claws, but in most of the other neuropteroid families the end segment of the pupal leg is merely split into two apical points (F, G), or it bears two small clawlike teeth (H, I) within which the paired claws of the adult are formed. In a

mantispid (J), however, the pupal tarsus ends with a simple expansion, and in the higher insect orders, whether the larval leg is one-clawed or two-clawed, the end of the pupal leg (K) is a simple lobe ensheathing the pretarsus of the adult. The clawless pupal leg in the higher orders, therefore, is a result of secondary simplification in an appendage not yet needed for locomotion.

That the pupa is a part of the imaginal phase of the insect can be deduced from other lines of evidence. In the ametabolous or hemimetabolous insects the juvenile hormone maintains the nymphal or larval status up to the transformation to the imago; in the holometabolous insects the same hormone carries the larval form only up to the pupa. Furthermore, the histoblasts of the larva, or imaginal discs, form directly not the organs of the adult but those of the pupa. The dividing line that separates the holometabolous pupa from the larva, therefore, is the same as that which separates the ametabolous imago from the nymph. The holometabolous pupa and adult thus equate as a unit with the ametabolous imago. Williams (1952) has shown that the same hormone system, namely, that of the brain and the thoracic glands, controls both pupation of the larva and the adult development of the pupa. Finally, when we consider that all the internal organs of the pupa are the adult organs in a state of being completed, the pupa can hardly be regarded as anything else than a preliminary adult. At the last larval moult, as Poyarkoff has said, the insect changes into an imago, but the state of its internal organs does not permit it to become at once an adult.

The occurrence of a moult in the imaginal stage, as Hinton (1948) points out, is not limited to the holometabolous insects; it regularly takes place in most Ephemeroptera, while in the apterygote insects and the other arthropods moulting is usual throughout life. Hinton suggests, therefore, that the pupa is equivalent to the ephemeropterid subimago. However, it would hardly seem that there can be any real relation between the imaginal moult of the mayfly and the moult of the pupa in the very distantly related holometabolous insects. More probably the pupal moult was a secondary, independently developed moult in the ancestors of the present holometabolous insects, rather than a "throwback" to a time when adult moulting was a regular event. It has been shown by Burks (1953) that the subimagines of Ephemeroptera are sexually mature; their sperm and eggs mixed in normal saline solution produce fertilized eggs, from which larvae may be hatched. Some species, therefore, have simply eliminated the second moult.

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Research Fund

TWO SILICIFIED CARBONIFEROUS TRILOBITES FROM WEST TEXAS

(With 3 Plates)

BY

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(WITH THREE PLATES)

The specimens of silicified trilobites described in the following pages were collected and prepared by Dr. Arthur L. Bowsher, of the United States National Museum (hereafter abbreviated as U.S.N.M.). I am indebted to Dr. Bowsher for suggesting that I study this material and to Dr. G. Arthur Cooper for permitting the loan of it to me. All the specimens are in the National Museum collections and are from the following localities:

U.S.N.M. locality 3070.—Helms formation, El Paso quadrangle, Hueco Mountains, Tex., 2½ miles west of Powwow Tanks, latitude approximately 31°50′17″ N., longitude 106°04′40″ W. This locality is stop 13 (p. 40), West Texas Geological Society Guidebook, Field Trip No. 5, November 1949, and stop 1 on the map accompanying West Texas Geological Society Field Trip of May-June 1946. No. 3070-2 is from a limestone thought to be the same as bed 9, section "C" of 1946 Field Trip Guidebook, and No. 3070-4 is from a limestone thought to be the same as bed 11 of the same section.

U.S.N.M. locality 3069.—Helms formation, El Paso quadrangle, Hueco Mountains, Tex., 1.1 miles west of Powwow Tanks, latitude approximately 31°50′17″ N., longitude 106°03′38″ W. No. 3069-2 is from about 10 feet above the base of the Helms in the saddle, from an oolitic limestone lens, and approximately equivalent to the horizon of No. 3070-2. No. 3069-4 is from about 25-30 feet above the base of the Helms in the saddle, from an oolitic limestone with *Archimedes,* and approximately equivalent to the horizon of No. 3070-4.

The numbers of these localities are used in subsequent references to the specimens. The Helms formation in west Texas and adjacent New Mexico has been described briefly by Laudon and Bowsher (1949, pp. 19-20, 31-34), and the term is used here in the restricted

sense of these authors. The Helms formation is stated by Laudon and Bowsher to be of Chester (Upper Mississippian) age, and it is of interest that the commonest trilobite in the formation, described here as *Paladin (Paladin) helmsensis,* new species, is very much like the type species of the genus from the Morrow Series (Lower Pennsylvanian) of Oklahoma.

The silicified specimens show the morphology of the exoskeleton in unusual detail and perfection; hence in the next section significant features of morphology and development are described and discussed, and these comments are not repeated in the ensuing detailed descriptions. The terminology employed follows that of previous papers (Whittington, 1950, p. 533), except that I have used *pleural region* of the pygidium rather than pleural lobes or side lobes of Warburg (1925), and *interpleural grooves* rather than furrows. The additional terms used in describing the articulation of the thorax, and the hypostome, are explained on plates 2 and 3.

In order to avoid ambiguity in the terms "length" and "breadth" in descriptions, I have used (in the abbreviated form indicated in parentheses) sagittal (sag.) to describe a measurement in the median line; exsagittal (exs.), parallel to, but outside of, the median line; and transverse (tr.), at right angles to the median line.

MORPHOLOGY AND DEVELOPMENT OF THE SILICIFIED SPECIES

An unusual feature of the silicified exoskeletons is the relatively great thickness, as compared, for example, to those of silicified Ordovician trilobites. I consider the thickness to be original and not a result of the process of silicification. Plate 2, figures 5 and 6, and plate 3, figures 3, 5, and 6, show the thickness of the exoskeleton at the suture lines and along selected sections. The doublure of both pygidium and cephalon is thicker than the immediately overlying dorsal exoskeleton (pl. 3, figs. 3, 5), nowhere more so than at, and adjacent to, the rostrum. The inner part of the thoracic pleurae is also thick, at a maximum at the posterior edge, the inner surface flat and sloping forward to the much thinner anterior edge. The thickness is such that there is no ridge on the inner surface corresponding to the pleural furrows on the outer surface (pl. 3, figs. 10, 13).

Four pairs of glabellar furrows have been observed in some Carboniferous trilobites (e.g., Stubblefield, 1948, p. 99; R. and E. Richter, 1951, pl. 5). On the inner surface of the exoskeleton (pl. 3, fig. 2) these furrows form inwardly projecting platforms with a well-defined edge (cf. R. and E. Richter, 1951, p. 225). These are areas of muscle

attachment, as is also the thickened and projecting outer one-third of the occipital furrow. On the outer surface (pl. 3, fig. 1) only the first (basal) furrow appears as a depression, the second, third, and fourth furrows as smooth areas, in larger specimens appearing as conspicuous dark patches, dark perhaps because the exoskeleton is thicker here. The articulating furrows of the thoracic axis are slightly thickened at the extremity, and presumably are areas of muscle attachment. On the pygidial axis (pl. 3, fig. 5), however, the outer parts of the ring furrows become shallower, and the ovate areas between them, appearing darker in some specimens, are areas of muscle attachment.

The eye surface (pl. 3, figs. 4, 6) is externally almost smooth, the facets faintly convex. On the inner surface each circular facet is strongly convex, and the facets are close-spaced and arranged in vertical and diagonal rows. The course of the cephalic sutures is revealed in detail (pl. 2, figs. 1, 5, 6; text fig. 1), and I am not aware of any previous descriptions of the rostrum of a Carboniferous trilobite. The edge of the exoskeleton at the sutures is thick and flat, and the hypostome fits against both the posterior edge of the rostrum and the adjacent inner edge of the doublure. The wing process (at the tip of the large anterior wing) evidently rested in the conspicuous circular pit in the anterior boss on the inner surface of the cranidium (pl. 3, fig. 17). Thus the hypostome was attached to the rest of the cephalon in the same manner as in calymenids, cheirurids, and other trilobites.

Articulation between the segments of the thorax and the cephalon and pygidium is effected by a series of devices (see pl. 3, figs. 7-13, 15, 16, and compare Whittington and Evitt, 1954, pp. 21-24). The ring process is a large boss situated at the outer, posterior edge of the axial ring, and fits into a ring socket at the anterior, outer edge. Above the ring socket, in line with the axial furrow, is a tiny, round axial process, which fits into the axial socket in the posterior edge of the segment at the base of the ring process. A narrow (exs.) strip along the anterior edge of the inner part of the pleura is defined by a shallow furrow, and the leading edge is thin and bluntly rounded. It fits into a groove in the thick posterior edge of the inner part of the pleura, this groove being beneath the upper, outer margin of the pleura. This "tongue and groove" articulation extends out to the fulcrum, where it dies out, and there are no articulation processes and sockets at the fulcrum. The posterior edge of the cephalon inside the branches of the facial suture, and the anterior margin of the pygidium inside the fulcra, are shaped like the corresponding edges of the thoracic segments. The outer parts of the thoracic pleurae, and the pygidium, are faceted to facilitate overlap in enrollment. In the doublure of each

segment is a broad V-shaped notch (pl. 3, fig. 14), the Panderian opening, and the anterior edge of this notch is raised (inwardly projecting), and acts to limit the amount of overlap between segments.

Only what are probably the later meraspid stages of the development are known (pls. 1, 2). The cranidium shows a general reduction in convexity with increasing size. The glabella in the smallest specimens is almost parallel-sided, and with increasing size the lateral expansion of the anterior lobe takes place, the posterior part widens between the eye lobes, and the relative convexity of the posterocentral glabellar region, and of the basal glabellar lobes, is reduced. The eye lobe becomes relatively shorter. The pygidium shows a considerable reduction in convexity with increasing size, and the shallow median notch in the posterior margin of small specimens soon disappears. The meraspid development of *Ditomopyge* was described by Weller (1935), and the smallest cranidium, 1 mm. in length, has the subparallel-sided glabella, long (sag.) anterior border and eye lobe seen in *Paladin*. However, the glabellar lobation is absent, in contrast to the presence of well-marked basal lobes and furrows in *Paladin*. Small pygidia of *Ditomopyge* show a median notch in the posterior border (Newell, 1931, pl. 31, fig. 31; Weller, 1935, p. 508) like that seen in *Paladin*. While the development of the pygidium in the two genera has some features in common, a notable difference is that in *Ditomopyge* the pleural regions increase in convexity (Weller, 1935, figs. 4c, 5c, 7c, 8c), in contrast to the decrease in *Paladin*.

The meraspid specimens of *Paladin* do not resemble any geologically older adult Carboniferous trilobite, and Weller (1935, p. 513) likewise found that the meraspid specimens of *Ditomopyge* resembled no known geologically older adult trilobite. One may take these observations as further evidence of the untruth of the so-called "law" of recapitulation, in the strict sense of Haeckel (cf. de Beer, 1951).

SYSTEMATIC DESCRIPTIONS

Family PROETIDAE (Hawle and Corda, 1847), Salter, 1864

Subfamily PHILLIPSIINAE (Oehlert, 1886), Přibyl, 1946

A characterization of this subfamily has recently been given by Přibyl (1946, pp. 33-34). The present material of *Paladin* shows that up to four pairs of glabellar furrows may be present. Few illustrations have been published of phillipsiinid hypostomes, but those available (e.g., Woodward, 1883-1884; Weber, 1937) suggest that they are similar to each other and like that of *Paladin* (pl. 1, figs. 29, 30, 35; pl. 2, figs. 21, 26, 27, 32, 33). Characteristic are the large anterior

wings, lack of distinct anterior border, narrow lateral, but wider (sag.) posterior, border, and short (sag.), crescentic, inflated posterior lobe of the middle body. This type of hypostome is not like known examples of hypostomes (Přibyl, 1947, figs. 12-15, 17-19) of proetid genera in other subfamilies, and may be typical of the Phillipsiinae. The shape of the rostrum may equally well be characteristic of the subfamily, but little information is available.

Genus PALADIN Weller, 1936

Type species.—*Griffithides morrowensis* Mather, 1915, by original designation of Weller, 1936, p. 707.

Discussion.—The most abundant of the two species of silicified trilobites described below has been compared with the holotype of *Paladin morrowensis,* and belongs in this genus. The second species differs from the first notably in the greater convexity of the cephalon and pygidium, the shorter anterior cephalic border, and the outline of the glabella, which is less expanded between the eye lobes but more strongly expanded anteriorly. These relatively minor differences ally it with *Kaskia chesterensis* (Weller, 1936, pp. 708-711, pl. 95, figs. 4a-6), the type of the genus *Kaskia* Weller, 1936. *K. chesterensis* has an even shorter (sag.), steeper anterior border. Weller admitted (1936, p. 708) that *Paladin* and *Kaskia* were closely similar, and that there were species intermediate between typical species of the two genera. The second silicified species here described is one of these intermediates. In view of these facts, it seems to me preferable to regard *Kaskia* as a subgenus of *Paladin,* with *P. morrowensis* representing the typical subgenus *Paladin (Paladin),* and this procedure has been followed below.

Reed (1942, pp. 653, 660-667, pl. 10, figs. 4-5b, pl. 11, figs. 1-5a; 1943, pp. 179-184, pl. 2, figs. 6, 7, pl. 3, figs. 1-8) considered that the forms he referred to his genus *Weberides* included most of, if not all, the originals of Woodward's (1883-1884) plate 4, and were similar to the Russian species described by Weber (1933, pp. 33-35, 37-41, pl. 2, figs. 2-11, 17-33, 36-41, text figs. 14-17, 19-21; 1937, pp. 74-75, pl. 8, figs. 31-34, 36, 39-44, 48) under the names *Griffithides lutugini* and varieties and *G. transilis* and varieties. Weller (1936, pp. 707-708), however, had previously placed these Russian species and varieties in his genera *Paladin* and *Kaskia.* Reed recognized this (1943, p. 180) but did not say how *Weberides* differed from *Paladin.* It seems that some of the species referred to above may be congeneric, and if so ought to be placed in *Paladin.* Before it is concluded that

Weberides Reed, 1942, is a synonym of *Paladin,* however, the diplo-type of *Weberides* should be reexamined, for Reed (1942, p. 663) admits that he did not see it. The specimen in question (original of M'Coy, 1844, pl. 4, fig. 5) is a pygidium, with a short, blunt spine on the posterior border.

The genus *Ditomopyge* Newell, 1931 (as emended by Weller, 1935) is related to *Paladin* (*Kaskia*), as Weller pointed out (1936, p. 711). The inflation of the central region of the glabella in front of the occi-pital ring seen in *P.* (*K.*) *rarus,* new species, could give rise to the preoccipital lobe of *Ditomopyge.* The free check of *P.* (*K.*) *rarus,* new species, is much more like that of *Ditomopyge* than that of *P.* (*P.*) *helmsensis,* new species, which lacks the flattened upper surface of the border. Contrary to the opinion of Weller (1936, pp. 713-714), I regard *Ameura* as related to *Paladin.* I have examined the holotype of *Ameura sangamonensis* (Meek and Worthen, 1865) and the gla-bella is only slightly wider between the eye lobes than across the an-terior lobe. The basal glabellar lobes do have independent convexity. The pygidium, of length (sag.) about equal to width, recalls the original of Woodward's (1883-1884) plate 4, fig. 9, and the elongated appearance is distinctive.

The aforementioned four genera, together with *Sevillia* (Weller, 1935, p. 506, explanation of text fig. 9, *nomen nudum;* Weller, 1936) and *Linguaphillipsia* Stubblefield, 1948, probably form a related group ranging from Lower Carboniferous to Lower Permian in age, wide-spread in North America and Eurasia.

PALADIN (PALADIN) MORROWENSIS (Mather, 1915)

Plate 1, figures 1-6, 9

Holotype.—Walker Museum No. 16174, incomplete cephalon, from Brentwood limestone, Morrow Series, lower Pennsylvanian, Sawney Hollow, head of Indian Creek, Okla., and 3½ miles south of Evansville, Ark.

Description.—The holotype is refigured here, and the following notes are added to supplement Mather's (1915, pp. 244-246, pl. 16, figs. 13, 13a) original description. Basal glabellar furrow deepest at about the midlength, disappearing before reaching axial furrow. Ad-ditional furrows not represented by depressions in outer surface. An-terior branch of facial suture running at first outward at about 50° to the sagittal line, then on the border, opposite the maximum width of the anterior glabellar lobe, curving to run inward straight to the mar-gin. The angle between the two sections is about 100°. The doublure

of the cephalon is convex and slopes steeply laterally, but is flattened and slopes gently anteriorly. The rostral suture runs close to the outer edge, the connective sutures curve inward, and the hypostomal suture runs in a curve convex forward. The rostrum is thus similar in outline to that of *P. (P.) helmsensis,* new species.

The associated pygidium is also refigured, and the border is gently convex, not concave as stated by Mather (1915, p. 245).

PALADIN (PALADIN) HELMSENSIS Whittington, new species

Plates 2, 3; text figure 1

Holotype.—U.S.N.M. No. 116513, cranidium, original of plate 2, figures 1, 2, 5, 6; locality 3070-2.

Paratypes.—U.S.N.M. Nos. 116514a-h; free cheek, rostrum, and hypostome from locality 3070-2; two segments from locality 3069-4; two segments from locality 3070-4; pygidium from locality 3069-2.

Description.—Dimensions of holotype in millimeters: Length (sag.) 7.0, height 2.7; length of glabella (sag.) 6.3, width across anterior lobe 3.9, at third furrows 3.1, of occipital ring 3.9. Length of paratype pygidium (sag.) 6.3, width 7.8, height 2.8. Cephalon subsemicircular in outline, gently convex. Glabella gently convex (sag. and tr.), outlined by shallow axial and preglabellar furrows; narrowing slightly immediately in front of the occipital ring, expanding between the eye lobes, then narrowing again forward to the minimum width opposite the third furrows, and then expanding forward again until width across anterior lobe is the same as, or slightly greater than, that of occipital ring. Latter moderately convex, highest point near posterior margin, from which it slopes down to the shallow, sinuous occipital furrow; faint median tubercle. Four pairs of glabellar furrows (pl. 3, figs. 1, 2), the first (basal) appearing as shallow depressions, gently curved, directed inward and backward to isolate triangular, gently convex basal lobes. The basal furrows are deepest at midlength, becoming poorly defined at the outer extremity, faint at the inner ends as they meet the occipital furrow. The maximum width of the basal lobes is one-third the glabellar width in front of the occipital furrow. Between the basal lobes the central glabellar region is slightly inflated and posteriorly slopes steeply. The second and third glabellar furrows are progressively shorter and directed less strongly backward, the fourth short, ovate, directed slightly forward and commencing a short distance inside the axial furrows. Cheeks sloping gently outward and forward, with a broad (tr.) lateral border defined by the slight change in slope at the faint border furrow, the anterior border nar-

rower (sag.). Posterior border defined by a deep border furrow, and with independent convexity. Genal spine broad at base, relatively long. Eye lobe large, length (exs.) more than one-third that of cephalon, situated with the anterior edge about opposite the glabellar midpoint, and close to the axial furrow, the highest point lower than the glabellar midline between the eye lobes. Palpebral lobe without rim, outer part horizontal, inner part sloping down to axial furrow. Eye surface (pl. 3, figs. 4, 6) with numerous small, gently convex facets. Anterior branch of suture runs straight outward and forward from the eye lobe onto the border, then curves and runs straight inward and forward to reach the anterior margin at a point in line (exs.) with the inner margin of the eye lobe. The posterior branch runs outward and backward to the border furrow, then curves, at first more strongly outward, over the posterior border to reach the margin just inside the base of the genal spine. Doublure laterally of less width (tr.) than the border, gently convex and sloping steeply outward. Anteriorly doublure becomes flattened, horizontal, and narrower (sag.). The rostral suture runs along the outer edge of the doublure, the connective suture in a curve convex outward. The anterior and posterior margins of the rostrum are thus forwardly curved, the lateral margins outwardly so. The rostrum (pl. 2, figs. 40-42) is also thickest along a line midway between the anterior and posterior margins, so that while the outer surface is flat, the inner is convex. The doublure of the free cheek adjacent to the rostrum shows a corresponding thickening, which fades out laterally. Certain features displayed by the inner surface of the cephalon have been discussed above. Plate 3, figure 2, shows the doublure of the occipital ring. In the inner edge of the doublure of the free cheek (pl. 3, fig. 6) is a shallow notch, in line with the posterior border. I interpret this notch as the Panderian opening, and as corresponding with the larger notches in the thoracic pleural doublures.

Length of hypostome (pl. 2, figs. 21, 26, 27, 32, 33) (sag.) slightly greater than maximum width across anterior wings. Middle body gently convex longitudinally, more strongly so transversely, not defined anteriorly or separated from the anterior wings by a furrow, but laterally and posteriorly outlined by the change in slope at the borders. The crescentic posterior lobe, the tips at about two-thirds the length of the middle body and opposite the lateral shoulders, has a faint independent convexity, most marked at the tips. The anterior sutural edge of the hypostome is thick, extending between the bases of the wings, and fits against both the inner edge of the rostrum and the doublure of the free cheeks (text fig. 1). The anterior wings are

broad (exs.) at the base, slope steeply upward, with a small articulating boss at the outer, anterior corner. The lateral borders narrow, gently convex, shoulder well marked, posterior border broader, margin sinuous, posterolateral corners rounded. The interior view shows that the doublure is narrow along the lateral borders, wider along the posterior border, and the furrow dividing the middle body more evident. In lateral view the notch between shoulder and anterior wing is seen, and posterior wings seem not to be developed.
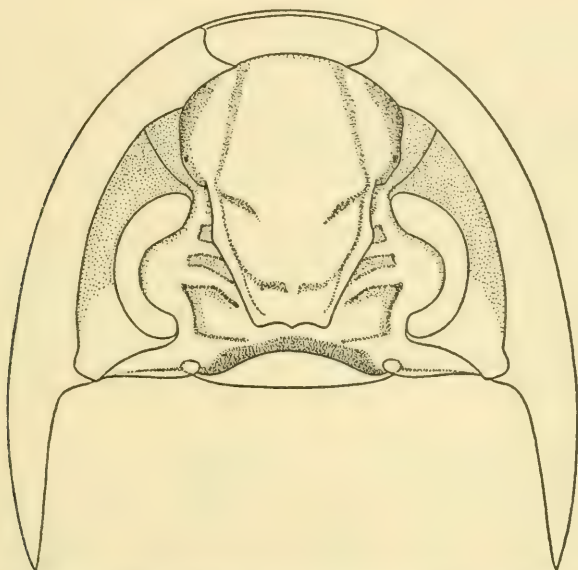
Fig. 1.—*Paladin* (*Paladin*) *helmsensis,* new species. Outline reconstruction of the exoskeleton of the cephalon in ventral view, approximately ✕ 7.

Number of thoracic segments unknown. Axis moderately convex, each ring subdivided into a short (sag.) anterior part that disappears laterally, and a longer (sag. and exs.) posterior part. The articulating furrow narrow and deep, the half-ring short (sag. and exs.). Inner part of pleura horizontal, outer part bent steeply down, faceted, the facet of the anterior segments (pl. 3, figs. 10-13) abruptly cutting off the narrow (tr.) outer pleural part. The narrowness of these latter enables these segments to fit between and under the genal spines of the cephalon. Succeeding segments (pl. 3, figs. 7-9, 15, 16) have the outer pleural parts wider (tr.). Pleural furrow narrow and deep, situated at about half the length (exs.) at the fulcrum, and extending to the inner edge of the facet. The interior view (pl. 3, fig. 10) shows

the doublure of the axial ring and the low ridge, the area of muscle attachment, formed by the outer part of the articulating furrow. The devices which facilitate articulation between the segments have been described above. In the doublure of the outer pleural part (pl. 3, fig. 14) is the broad notch of the Panderian opening. The doublure in front of, and outside, this notch is gently convex.

Pygidium moderately convex, axis moderately convex and gently tapering. In largest specimens 17 ring furrows, the inner part straight, deep, the outer shallow, turning slightly back. Inner, anterior part of pleural region horizontal, outer part gently convex, steeply sloping, border distinctly separated by change in convexity, and sloping outward. Ten deep pleural furrows in largest specimens, progressively more strongly backwardly directed, ending at inner edge of border. Interpleural grooves faint, sometimes absent, sometimes first five visible, not extending on to border. Doublure of same width as border, inner part bent steeply up.

External surface of glabella and palpebral lobes with shallow, irregular pits (pl. 3, fig. 1), largest near the median line. Small tubercles occur along the posterior edge of the occipital and axial rings. Raised lines, parallel to each other and the margin, on the outer part of the cephalic and pygidial borders and the outer surface of the doublures. Hypostome with similar lines on the middle body and borders, and tiny, shallow, scattered pits on the middle body.

Discussion.—Comparison of the cephalon of *Paladin* (*Paladin*) *morrowensis* with the type of *P.* (*P.*) *helmsensis* shows that the latter differs from the former principally in characters of the glabella. That of *P.* (*P.*) *helmsensis* is less inflated (as seen in longitudinal profile), has the basal glabellar lobes and posterior part of the central glabellar region less inflated, and has the anterior lobe less expanded transversely, though between the eye lobes the glabella of *P.* (*P.*) *helmsensis* is more markedly expanded than that of *P.* (*P.*) *morrowensis.* The external surface of the glabella and palpebral lobes is tuberculate in *P.* (*P.*) *morrowensis,* pitted in *P.* (*P.*) *helmsensis.* The lateral cephalic border of *P.* (*P.*) *morrowensis* slopes more steeply than that of the Texas species. The pygidia of the two species (pl. 1, figs. 4-6; pl. 2, figs. 9, 10, 14, 15) are similar, that of *P.* (*P.*) *helmsensis* being distinguished by the axis showing more rings and being more inflated posteriorly, and by the border being relatively broader (sag.) posteriorly. The axial rings of *P.* (*P.*) *morrowensis* are apparently without the row of tubercles on the posterior margin. Evidently *P.* (*P.*) *helmsensis* and *P.* (*P.*) *morrowensis* are closely related species, though they differ considerably in age.

DEVELOPMENT OF *Paladin* (*Paladin*) *helmsensis,* NEW SPECIES

Cranidium.—Length of smallest cranidium (pl. 2, figs. 34-36) (sag.) 1.5 mm., glabella narrowest between the anterior end of the eye lobes, but since it lacks the anterior and posterior expansions of larger forms it appears almost parallel-sided. Basal glabellar furrows deep and broad, so that the basal lobes are prominent, and the posterior part of the central glabellar region is quite strongly inflated. The second and third glabellar furrows are ill-defined patches on the exoskeleton. Length of anterior border of the cranidium (sag.) about one-eighth that of the glabella. Length of palpebral lobes (exs.) more than one-third that of cranidium. In cranidia of increasing size that part of the glabella in front of the third furrow becomes relatively wider (compare figs. 1 and 34, pl. 2). The palpebral lobes become relatively smaller, the length (exs.) being reduced to less than one-third that of the cranidium. The basal glabellar furrows become shallower, and the convexity of the basal lobes and posterior part of the central glabellar region is reduced. Small cranidia with close-spaced tubercles on the glabella and palpebral lobes, the tubercles on the frontomedian glabellar lobe close-spaced and arranged in lines subparallel to the anterior margin. With increasing size of the cranidium these tubercles become less prominent, and in the largest cranidia only the reticulate pattern of pits remains.

The smallest hypostome known (pl. 2, figs. 39, 44) is little different from the largest—the shoulders are rather more prominent, and the tips of the crescentic posterior lobe of the middle body are more strongly inflated. The smallest pygidium known (pl. 2, figs. 37, 38, 43) is 1.6 mm. in length (sag.), 2.2 mm. in width. Axis of 15 rings. Pleural region convex, inner, anterior part horizontal, outer part steeply sloping, the border sloping outward but less steeply. Eleven pleural furrows visible, terminating at the inner margin of the border. First three interpleural grooves shallow, situated close to the succeeding pleural furrows, and extending on to the inner part of the border. Border broad (sag.) posterolaterally, narrow (tr.) anterolaterally, with a shallow median notch in the posterior margin. With increasing size the pygidium maintains about the same ratio between length and width, and the original of plate 2, figures 30, 31, is 2.2 mm. in length (sag.), 3.3 mm. in width. The convexity of the pleural regions is markedly reduced, the notch in the posterior margin disappears and the difference in the width of the border laterally and posteriorly is reduced. In a pygidium (sag.) 3.2 mm. long only the first interpleural groove is visible. The tubercles on the median part of the axial rings are visible in this and larger specimens.

PALADIN (KASKIA) RARUS Whittington, new species

Plate 1, figures 7, 8, 10-35

Holotype.—U.S.N.M. No. 116511, cranidium, original of plate 1, figure 7, 8, 10, 11, locality 3070-4.

Paratypes.—U.S.N.M. Nos. 116512a-c, free cheek and pygidium from locality 3070-2, hypostome from locality 3069-4.

Description.—Length of holotype cranidium 5.6 mm., height 3.2 mm.; length (sag.) of glabella 5.1 mm., width across anterior lobe 3.6 mm., between anterior ends of palpebral lobes 2.9 mm., of occipital ring 3.2 mm.

The cephalon of this species is similar to that of *Paladin* (*Paladin*) *helmsensis,* new species, but is distinguished by (1) the greater convexity; (2) the glabella being slightly expanded between the eye lobes, but more strongly expanded across the anterior lobe; (3) the sharper angle in the course of the anterior branch of the facial suture on the border (compare the antero-lateral margins of the cranidia in pl. 1, fig. 7, and pl. 2, fig. 1); (4) the relatively shorter (sag. and exs.) anterior border; (5) the much greater change in slope at the border furrow of the free cheek, resulting from the inner part of the border being flattened. Additional ways in which the cephalon of *P.* (*K.*) *rarus* differs from that of *P.* (*P.*) *helmsensis* are: (6) the basal glabellar furrows are deeper, the basal lobes more inflated; (7) the palpebral lobes are narrower (tr.); (8) the middle body of the hypostome is more convex, with deeper middle furrows, and tiny maculae are present. There is a sharper angle in the anterior margin between where the hypostome fits against the rostrum and the doublure of the free cheek, the shoulders are more prominent, and the posterior border has the three blunt spines; (9) the external surface of the glabella and palpebral lobes is tuberculate rather than pitted.

Rostrum and thorax unknown.

Length of paratype pygidium (sag.) 5.0 mm., width 6.9 mm., height 3.0 mm. This pygidium is distinguished from that of *P.* (*P.*) *helmsensis* by the greater convexity and consequent height. Both the axis and the pleural regions inside the border are more convex in *P.* (*K.*) *rarus,* and the border slopes more steeply outward. The number of axial rings and pleural furrows is the same in the two species, but the ribs between the furrows in *P.* (*K.*) *rarus* are much more convex.

Discussion.—Paladin (*Kaskia*) *rarus* is distinguished from the type species *P.* (*K.*) *chesterensis* (Weller, 1936, pp. 708-711, pl. 95, figs. 4a-6), also of Chester age, by the less steep slope of the anterior part of the glabella and the longer (sag.) projecting anterior border (com-

pare pl. 1, fig. 10, with Weller, 1936, pl. 95, fig. 4c). The pleural regions of the pygidium of the Texas species appear to be more convex than those of *P. (K.) chesterensis.* Four pairs of glabellar furrows are present in *P. (K.) rarus,* but only three are described as present in *P. (K.) chesterensis.*

Weller (1936, pp. 708-710) pointed out that forms intermediate between the type species of *Paladin (Paladin)* and *Paladin (Kaskia)* occur. In the outline and convexity of the glabella, *P. (K.) rarus* is more like *P. (P.) morrowensis* than is *P. (P.) helmsensis,* a further illustration of the close relationship between these species.

DEVELOPMENT OF *Paladin (Kaskia) rarus,* NEW SPECIES

The smallest cranidium (pl. 1, figs. 23, 24) is 3.2 mm. in length (sag.). Compared with the largest cranidium it is more convex as a whole, as well as considering the frontomedian and basal glabellar lobes separately; the glabella is less expanded anteriorly, and the palpebral lobes are longer. The development thus parallels that of *Paladin (Paladin) helmsensis,* with an expansion of the glabella anteriorly, a general reduction in convexity, and decrease in size of the palpebral lobes. The smallest pygidium (pl. 1, figs. 26-28) is 1.7 mm. in length (sag.), strongly convex, the outer parts of the pleural regions overhanging the border. There are 13 or 14 axial rings, 10 pleural furrows, no interpleural grooves. There is no median notch in the posterior margin of the border. The chief change with increasing size of the pygidium is the reduction in convexity, so that the outer parts of the pleural regions slope steeply but do not overhang the border.

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EXPLANATION OF PLATES

PLATE 1

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PLATES

PALADIN (PALADIN) MORROWENSIS AND PALADIN (KASKIA) RARUS

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

PALADIN (PALADIN) HELMSENSIS

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

PALADIN (PALADIN) HELMSENSIS

(SEE EXPLANATION OF PLATES AT END OF TEXT.)

A REVISION OF THE SEA-STARS OF THE GENUS TETHYASTER

(WITH 12 PLATES)

BY

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British Museum (Natural History)

AND

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The interrelationships of the sea-stars that we regard as constituting the genus *Tethyaster* have never been satisfactorily worked out. All the species are rare—at least few specimens have been collected—and no one museum has been able to secure a fully representative series either of the included species or of the growth stages of any single species. The growth stages in this genus are especially important, for the young may present an aspect quite different from that of fully developed individuals, and the adult characters are often late in making their appearance.

In the preparation of this revision we have studied all the specimens in the U. S. National Museum, in the British Museum (Natural History), and in the Museum of Comparative Zoology at Cambridge, Mass., for the loan of which we are greatly indebted to our friend Dr. Elisabeth Deichmann.

Two of the species (*canaliculatus* and *vestitus*) have not previously been figured, the type specimen of another (*magnificus*) has not been figured, and of one (*grandis*) only a few details have been illustrated. Of the others, two (*subinermis* and *aulophora*) have been illustrated in satisfactory detail, and the last (*pacei*) has been figured sufficiently for purposes of identification.

Thomas Say in 1825 (p. 143) described a very large sea-star from New Jersey under the name of *Asterias vestita,* as follows:

5. *A. vestita.* Disk broad, surface reticulated, covered by cylindrical prominences, margin articulated; rays depressed.

The whole surface is covered by cylindrical prominences, which are placed near each other, truncated at their summits, and each summit crowned by from ten to eighteen small, equal, cylindrical fimbriae; wart-like tubercle [madre-

porite] large, radiated, very conspicuous; *margin* articulated; each articulation with about four very much compressed, subquadrate, truncated spines or moveable processes, which are vertically adpressed to the surface of the segment, and are imbricated with respect to each other.

Diameter 1 foot 2 inches.

The locality was given as Cape May, N. J. Say said that it is "Allied to *A. aranciaca* Linn., but distinct by many characters, and particularly by the form and number of the lateral spines. It is very rare on this coast." The type and only known specimen disappeared, and the species has since remained an enigma.

Dr. A. Philippi in 1837 (p. 193) briefly described *Asterias subinermis* from a specimen 14 inches in diameter from the coast of Sicily. This well-known but rare species has been recorded from both coasts of the Mediterranean as far east as Rhodes and from the Bay of Biscay southward to the Gulf of Guinea. It has never been confused with any other species and has no synonyms, but it has been assigned to various genera—*Astropecten* (Müller and Troschel, 1842), *Archaster* (Perrier, 1875), *Goniopecten* (Perrier, 1885), *Plutonaster* (*Tethyaster*) (Sladen, 1889), and *Tethyaster* (Perrier, 1894), almost all these dispositions being followed by other authors. A detailed account of this species, under the name *Plutonaster subinermis,* with figures and bibliographic references, was given by Ludwig in 1897 (p. 105).

Say's *Asterias vestita* was listed, without description, as *Astropecten vestitus* by Lütken in 1859 (pp. 27, 54). Verrill in 1866 (p. 339) under *Astropecten vestitus* Lütken said "Say's specimen was from Cape May, collected by Mr. J. Robbins. I am not aware of any other being found."

In 1882 (p. 440) Prof. F. Jeffrey Bell described *Archaster magnificus* from two specimens with R=207 and 138 mm., and r=50 and 37 mm., which had been presented to the British Museum some years before by J. C. Melliss who had obtained them at St. Helena.

W. Percy Sladen in 1889 established, under *Plutonaster,* the subgenus *Tethyaster* (p. 101) in which he placed Philippi's *Asterias subinermis* and Düben and Koren's *Astropecten parelii.* He also (p. 192) diagnosed the genus *Moiraster* for the reception of *Archaster magnificus* Bell.

In 1895 Verrill (p. 133) listed *Astropecten vestitus* Lütken and said "B. range, shallow water. Cape May (Say). It is not uncommon farther south." [1] In 1899 Verrill (p. 210) proposed the new genus *Sideriaster,* based upon a new species, *S. grandis,* from *Albatross* station 2378. The description was brief, but he figured the actinal side

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[1] Possibly here confused by Verrill with *Astropecten cingulatus* Sladen.

of a part of the middle of a ray, an adambulacral plate, and an abactinal paxilla.

In 1908 Dr. René Koehler described in detail and figured a small specimen of *Moiraster magnificus* with R = 62 mm. from Pointe Pyramid, Ascension, in 40 fathoms.

In 1914 (p. 21) Verrill discussed *Sideriaster*(?) *vestitus* (Say). He said that the type of *Sideriaster, S. grandis,* does not agree sufficiently well with *vestitus* to be identified as the same species, but it seems almost certain that it is congeneric. He added that when more specimens can be obtained it may prove to be the same species.

In 1915 (p. 191) Verrill republished his diagnosis of *Sideriaster* and (p. 192) his description of *S. grandis,* also republishing the figures of details previously given. He also discussed (pp. 193-195) *Sideriaster* (?) *vestitus* (Say) Verrill at considerable length. He noted that "Probably the type is lost. It is probably not an *Astropecten.* In having a large disk, and especially in having four appressed spines in a transverse row on the inferomarginal plates, the *Sideriaster grandis* V. agrees, perhaps, with Say's species. But he gives too little, as to other characters, to enable me to say whether they are related."

In 1916 (p. 52) A. H. Clark described in detail, but did not figure, *Sideriaster canaliculata* from *Albatross* station 2998, Gulf of California, in 40 fathoms.

Dr. Walter K. Fisher in 1911 (p. 417) published a diagnosis of a new genus, *Anthosticte,* based upon a new species, *A. aulophora,* described from a single specimen from *Albatross* station 5420 in the Philippines. In 1919 (p. 140) he republished the diagnosis of *Anthosticte,* redescribed and figured *A. aulophora,* and discussed the relationships of the new genus.

Dr. Th. Mortensen in 1925 (b, p. 147) described and figured *Anthosticte pacei* from South Africa. He wrote that "from the type species *A. aulophora,* the only species hitherto known of the genus *Anthosticte,* the present species is easily distinguished through the lower paxillae and the complete lack of pedicellariae." In 1933 (p. 422) Mortensen recorded three specimens of *Moiraster magnificus* that he dredged off Egg Island, St. Helena. In these R = 160-179 mm. He gave various details of the specimens.

In 1947 Señorita María Elena Caso described and figured *Moiraster gigas* from a very large specimen with R = 205-245 mm. from Santa Rosalia, Baja California, on the western shore of the Gulf of California.

In 1950 (p. 302) A. H. Clark recorded under the name of *Moiraster magnificus* a specimen with R = 168 mm. from off the western coast

of Puerto Rico. This specimen we now consider as representing *vestitus*.

As for the interrelationships of these genera, they were discussed in some detail by Fisher in 1919 (p. 143). He said that *Moiraster, Tethyaster, Sideriaster,* and *Anthosticte* agree in having unarmed supermarginals, inferomarginals with a few small enlarged spines, naked madreporite, large actinal interradial areas, and intermediate plates far along the ray, marginal and actinal fascioles, true paxillae, stellate abactinal plates, an astropectinid adambulacral armature, and probably also in having the single papulae uninterrupted all over the dorsal surface. He said that the first two seem to be a little more closely related than either is to the last two, while *Sideriaster* and *Anthosticte* are possibly also nearly related. He noted that unfortunately there is but one species in each genus, and it is difficult to ascertain what characters are of generic importance. He remarked that, according to the standards used in other larger genera, *Anthosticte* differs from *Tethyaster* chiefly in having very deep marginal fascioles, gonads to the end of the ray, and no midradial series of enlarged paxillae. *Anthosticte* has taller and more delicate paxillae, but this may not be of generic importance. Its special points of agreement in addition to the characters listed are the deposits in the tube feet (not recorded for *Moiraster* and *Sideriaster*) and shallow interambulacral fascioles, and an incipient interradial series of actinal intermediate plates, less prominent and regular than in *Tethyaster*.

He said that *Anthosticte* differs from *Sideriaster* in having very deep marginal fascioles and no distally enlarged subambulacral spines. Neither the deposits in the tube feet nor the gonads of *Sideriaster* are described. He considered that the fascioles between the adambulacral plates which he examined in the type specimen of *Sideriaster grandis* form one of the most striking features of the genus. They are densely lined with small, delicate spinelets, and are therefore similar to marginal fascioles. Such is not the case, he said, in *Anthosticte, Tethyaster,* or *Moiraster*.

Mortensen in 1933 (p. 424) also discussed these four genera. He wrote that the knowledge now acquired of the characters of *Moiraster* (from his three specimens from St. Helena) makes it clear that the four genera are even more closely related than Fisher thought them to be—so closely, indeed, that it seems scarcely possible to maintain them all. He said that *Tethyaster* is well characterized by its midradial row of enlarged paxillae, the shallow marginal fascioles, and the low paxillae, so it may justly be maintained as a separate genus. He noted that Fisher's statement that its gonads do not extend to the

ends of the rays is a curious mistake, "in flat contradiction to the description given by Ludwig." As for *Anthosticte,* he said that it is now seen that the only character by which it differs from *Moiraster* is the absence of enlarged spines on the ventrolateral plates. In regard to fascioles between the adambulacral plates he said there seems to be a very gradual passage from *Anthosticte* to *Moiraster* and *Sideriaster.* He noted that *Sideriaster,* which is still imperfectly known, would likewise seem to differ from *Moiraster* only in lacking enlarged spines on the ventrolateral plates. He said that it is, of course, a matter of taste whether this character, the presence or absence of enlarged spines on the ventrolateral plates, affords sufficient reason for generic distinction. But, he added, this is all the difference there is.

In 1950 the question of the identity of a specimen taken by the M.V. *Rosaura* off the mouth of the Orinoco in 75 meters was raised between the two present authors. Dr. Dilwyn John has provisionally attributed the specimen to *Sideriaster,* but investigation seemed to show that it also had some affinity with Bell's *Moiraster magnificus* from St. Helena. At about the same time the M.V. *Oregon* dredged 10 specimens of *Sideriaster grandis* off Corpus Christi, Tex., another was dredged by the yacht *Triton* off Sombrero Key, Fla., and still another was received by the U. S. National Museum from off the coast of Tamaulipas, Mexico. Furthermore, the Museum acquired a very large sea-star from the coast of North Carolina that agrees completely with the meager description of Say's *Asterias vestita,* but is slightly larger. There seems to be no doubt that it represents Say's long-lost species.

With this additional material available it has seemed advisable to review the status of *Tethyaster, Moiraster, Sideriaster,* and *Anthosticte.* We have personally examined specimens of all the species described in these genera except *Anthosticte pacei,* which was briefly, though sufficiently, described and figured by Mortensen.

We can see no valid reason for not considering all these species congeneric and we therefore unite them all in the genus *Tethyaster,* of which we regard *Moiraster, Sideriaster,* and *Anthosticte* as synonyms.

Genus TETHYASTER Sladen

Asterias (part) SAY, 1825, p. 143.—PHILIPPI, 1837, p. 193.
Astropecten (part) MÜLLER and TROSCHEL, 1842, p. 74, following authors.
Archaster (part) PERRIER, 1875, p. 369, and following authors.
Goniopecten (part) PERRIER, 1885, p. 71.
Plutonaster (subgenus *Tethyaster*) (part) SLADEN, 1889, p. 101 (diagnosis; genotype *Asterias subinermis* Philippi).

Moiraster SLADEN, 1889, p. 192 (diagnosis; genotype *Archaster magnificus* Bell).
—FISHER, 1919, pp. 143, 144 (discussion).—MORTENSEN, 1933, p. 424
(discussion).

Tethyaster PERRIER, 1894, p. 322; 1896, p. 50.—KOEHLER, 1896a, pp. 56, 57; 1896b,
pp. 450, 451.—GREGORY, 1900, p. 251.—FISHER, 1919, p. 143.—KOEHLER, 1921,
p. 53; 1924, p. 199.—RIVERA, 1930, p. 105.—MORTENSEN, 1933, p. 424.

Plutonaster (part) LUDWIG, 1897, p. 105.—CUÉNOT, 1927, p. 295.—NOBRE, 1931,
figs. 42, 43.

Sideriaster VERRILL, 1899, p. 210 (diagnosis; genotype *Sideriaster grandis,* sp.
nov.); 1914, p. 21; 1915, p. 191.—FISHER, 1919, p. 143.—MORTENSEN, 1933,
p. 424.

Anthosticte FISHER, 1911, p. 417 (diagnosis; genotype *Anthosticte aulophora,* sp.
nov.).—MORTENSEN, 1933, p. 424.

Thetyaster NOBRE, 1931, p. 62.

Thethyaster NOBRE, 1931, p. 176.

Diagnosis.—A genus of Astropectinidae with both series of marginal plates large and conspicuous, equally developed, the superomarginals granulated or with numerous short spinelets, the inferomarginals with a median row of usually about five enlarged and flattened appressed spines; actinal intermediate areas large with numerous intermediate plates arranged in definite series with an incomplete unpaired median row; the inferomarginals separated from the adambulacrals by a series of actinal intermediate plates for most of the ray; fascioles between the marginals, adambulacrals, and actinal intermediate plates; madreporite large and bare; adambulacral armature astropectinid; abactinal plates with paxillae having high columns; gonads extending far along ray.

Geographical range.—From New Jersey south to the mouth of the Orinoco; Gulf of Mexico; St. Helena and Ascension; Bay of Biscay south to the Gulf of Guinea; Mediterranean east to the Aegean Sea; South Africa; Philippines; Gulf of California.

Bathymetrical range.—From 44 to about 1,400 (?1,425) meters.

Remarks.—Presumably the most specialized species of *Tethyaster* are those with the spines on the inferomarginal and actinal intermediate plates wide, rectangular, and broadly truncated, as these depart most widely from the generalized astropectinid type. Although our knowledge of this genus is admittedly meager, these species appear to be primarily American, ranging from New Jersey to Venezuela (*vestitus*), occurring at St. Helena and Ascension (*magnificus*), and found also in the Gulf of California (*canaliculatus*). This group in its distribution would parallel roughly the genera *Encope, Mellita,* and *Leodia* among the echinoids, the *Marginatus* group of *Astropecten,* and *Astrocaneum* in the Gorgonocephalidae. It should be noted that

the crinoid genus *Crinometra* so very characteristic of the Caribbean area is also represented at St. Helena.

A more generalized type with less strongly modified spines on the inferomarginals, which only very rarely extend on to the actinal intermediate plates, is widely distributed, occurring in the Gulf of Mexico (*grandis*), in the Mediterranean and east Atlantic from the Bay of Biscay to the Gulf of Guinea (*subinermis*), off South Africa (*pacei*), and in the Philippines (*aulophora*). At the same time *aulophora* is distinguished from the other members of this group by the relatively tall and slender dorsal paxillar columns, such as are found also in *vestitus* and *magnificus*. However, this character is probably less fundamental than the shape of the inferomarginal spines.

Other differences between the species are shown in the key.

KEY TO THE SPECIES OF TETHYASTER

(This key is adapted for fully developed specimens with R = 100 mm. or more.)

a^1. Actinal intermediate plates each with an enlarged, broad, flattened, and broadly truncated procumbent spine directed outward (if these are undeveloped the inferomarginal spines are broadly truncated) ; enlarged and flattened spines on the inferomarginals broad, usually approximately rectangular or scoop-shaped with broadly truncated ends, rarely tapering; R = 200-250 mm. in fully grown individuals.

  b^1. Enlarged spines on actinal intermediate plates fan-shaped or scoop-shaped with divergent sides and broadly truncated ends; spines on the inferomarginals similar (may be tapering in young individuals: pl. 3; fig. 1, *c*) (Gulf of California) .... *canaliculatus*

  b^2. Enlarged spines on actinal intermediate and inferomarginal plates rectangular, rarely scoop-shaped.

    c^1. Enlarged and flattened spines in fully grown individuals 6-7 mm. long, first appearing when R = about 70 mm. (pl. 10) (St. Helena and Ascension).................... *magnificus*

    c^2. Enlarged and flattened spines in fully grown individuals reaching only 4 mm., first appearing when R = about 150 mm. (pl. 6; fig. 1, *d*) (New Jersey south to off the Orinoco River).. *vestitus*

a^2. Actinal intermediate plates without a central enlarged spine (there may be a very few pointed spines in some specimens of *grandis*) ; enlarged and flattened spines on inferomarginals sharp-pointed.

  b^1. Columns of paxillae slender, high, about 4 times as high as thick ; most of paxillae with a pedicellaria of 2-4 valves (Philippines) .... *aulophora*

  b^2. Columns of paxillae stout, low, not over twice as high as thick ; no abactinal pedicellariae, so far as known.

c^1. Marginals short, 68-85 in number; rays fairly broad, width of rays at base = r; paxillae of median row on rays sometimes larger than others (Bay of Biscay to Gulf of Guinea and most of Mediterranean).................... *subinermis*

c^2. Marginals longer, up to 65 in number; rays narrow, width at base less than r; paxillae of median row on rays not larger than others.

    d^1. Rays very narrow, R = 4.3 r; first series of actinal intermediate plates reaching to about outer third of ray, second only in proximal third; intermarginal fascioles deep, extending inward for about two-thirds the proximal and distal sides of marginals (South Africa)........... *pacei*

    d^2. Rays broader basally, R = 3.2 to 3.5 r; first series of actinal intermediate plates reaching to about outer fourth of ray, second to well beyond middle; intermarginal fascioles shallow, extending inward for less than one-third the proximal and distal sides of marginals (pls. 11, 12) (Gulf of Mexico) ....*grandis*

TETHYASTER CANALICULATUS (A. H. Clark)

Plates 1-4; text figure 1, *c*

Sideriaster canaliculata A. H. CLARK, 1916, p. 52 (description; *Albatross* station 2998).—ZIESENHENNE, 1937, p. 212 (notes; *Zaca* stations 136, D-19; 142, D-3; 146, D-1; 147, D-2; 150, D-9).—CASO, 1947, p. 225 (listed).
Moiraster canaliculata CASO, 1947, p. 225 (listed).
Moiraster gigas CASO, 1947, p. 225, fig. 1, p. 226, fig. 2, p. 227, fig. 3, p. 228, fig. 4, p. 229 (description; Santa Rosalia, Baja California).

Diagnosis.—Enlarged spines on the inferomarginals and actinal intermediate plates scoop-shaped with divergent and convex sides, broadly truncate, the outer portion commonly with a broad, shallow groove and the distal end slightly notched; size large, R up to 250 mm.

Type.—In the U. S. National Museum (No. 36951).

Type locality.—*Albatross* station 2998, Gulf of California west of Culiacán, Sinaloa (lat. 24°51′00″ N., long. 110°39′00″ W.); 73 meters; bottom temperature 64° F.; March 16, 1889.

Additional localities.—Santa Rosalia, Baja California (Caso, 1947).

Zaca station 136, D-14; Arena Bank, Gulf of California (lat. 23°29′30″ N., long. 109°25′ W.); 82 meters; April 20, 1936 (Ziesenhenne, 1937).

Zaca station 142, D-3; Santa Inez Bay, Gulf of California (lat. 27°04′ N., long. 111°53′ W.); 73 meters; April 11, 1936 (Ziesenhenne, 1937).

Zaca station 146, D-1; Santa Inez Bay (lat. 26°52′ N., long 111°53′ W.); 64 meters; April 16, 1936 (Ziesenhenne, 1937).

Zaca station 147, D-2; Santa Inez Bay (26°57′30″ N., long. 111°48′30″ W.) ; 110 meters ; April 17, 1936 (Ziesenhenne, 1937).

Zaca station 150, D-9; Gorda Banks, Gulf of California (lat. 23°04′ N., long. 109°30′30″ W.) ; 91-109 meters; April 22, 1936 (Ziesenhenne, 1937).

Geographical range.—Central and southern part of the Gulf of California.
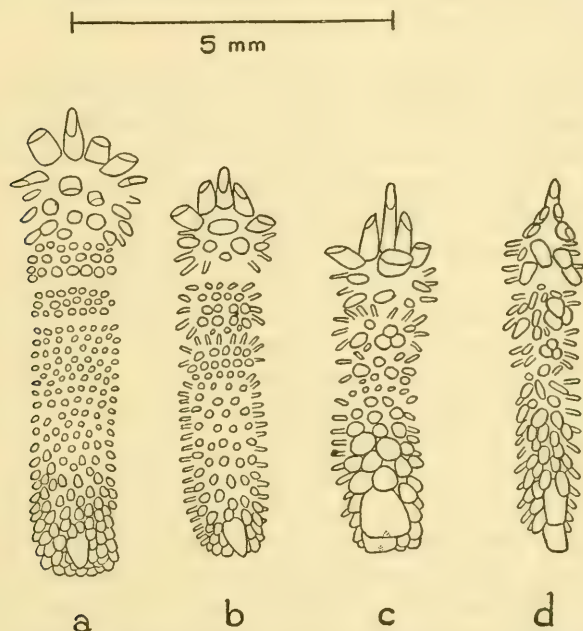
FIG. 1.—Adambulacrals, intermediate plates, and inferomarginals of *a, Tethyaster subinermis* (R = 86 mm.) ; *b, T. grandis* (R = 59 mm.) ; *c, T. canaliculatus* (R = 64 mm.) ; *d, T. vestitus* (R = 70 mm.). The adambulacral plate is at the top in each case and is about the tenth, while the inferomarginal corresponding is about the seventh.

Bathymetrical range.—From 64 to 110 meters.

Remarks.—Our reasons for considering Señorita Caso's *Moiraster gigas* a synonym of the previously described but much smaller *Sideriaster canaliculatus* are the following. The supermarginals of the type of *canaliculatus* (R = 64 mm.) number 45, those of the type of *gigas* (R = 205-245 mm.) 58-62. Considering the discrepancy in size this difference is negligible. In *canaliculatus* R : r = 3.4 : 1, in *gigas* (average) 3.6 : 1. This difference is not significant.

The paxillae on the rays in *canaliculatus* are in three regular alternating rows in the midradial region, and from these central rows diago-

nal rows run out at an angle of 45° to the superomarginals. Judging from Señorita Caso's figure (fig. 3) there is the same arrangement in *gigas,* though here the lateral rows make a larger angle with the median.

In *canaliculatus* the enlarged and flattened spines in the inferomarginals are broad, broadly truncate, about half as broad as long, or even shorter, with convex sides, the outer half commonly deepened in the middle or broadly grooved. In *gigas* these spines are "espatuladas, truncadas, aplanadas, ligeramente henidas en sus extremos libres."

In the type of *canaliculatus* most of the actinal intermediate plates carry one or two enlarged tubercles somewhat swollen in the outer half and frequently somewhat flattened. These resemble the less-developed of the corresponding spines on the actinal intermediate plates in the young specimen of *vestitus* from Puerto Rico.

In the type of *canaliculatus* all the plates bordering the adambulacrals and mouth plates, and a few of the other actinal intermediate plates, bear pedicellariae with three or four valves. In *gigas* also "Todas las placas que limitan a las placas adambulacrales y las placas bucales y alguna que otra placa intermediaria, están provistas de pedicelarios espiniformis, trivalvados, de forma irregular; en general, unos son pequeños y otros grandes."

In the largest specimen collected by the *Zaca* (M.C.Z. No. 36232; pl. 3) R = 95 mm., r = 26 mm.; R : r = 3.6 : 1. The paxillae have cylindrical columns which are about half again as high as thick and rather slender. The crown consists of 8-10 subcapitate peripheral spinelets, mostly about twice as high as thick at the base, with one or two usually much more slender than the others, and most frequently a single central spinelet which resembles the larger peripheral.

There are 54-58 marginals. The superomarginals resemble those of the smaller type specimen (R = 64 mm., r = 19 mm.). The inferomarginals have usually two flattened, tapering, and pointed spines which at the base of the rays are 3-4 mm. long and about 0.75 mm. broad at the base.

Each actinal intermediate plate carries in the middle a strongly flattened wedge-shaped or narrowly fan-shaped spine with straight sides and a gently convex tip which is usually about twice as broad as the base. These flattened spines, which are mostly 1-1.5 mm. long, lie parallel with the surface of the plate, directed toward the inferomarginals. In addition to these central spines the plates bear a few much smaller subcapitate spines and numerous fine lateral spinelets.

The enlarged spines on the actinal surface of the adambulacral

plates are somewhat flaring, abruptly truncated, and broadly grooved or chisel-shaped.

A number of the plates in the inner part of the interradial areas, especially those adjoining the adambulacrals, bear pedicellariae of three, sometimes four, valves which resemble stout subcapitate spines, one of which is commonly smaller than the others.

This specimen is intermediate between the smaller type specimen and Señorita Caso's much larger type of *gigas*, resembling the latter in having enlarged and flattened spines on all the actinal intermediate plates. So far as can be judged from the published figure, these spines resemble those of *gigas*. The spines on the inferomarginals, however, are tapered and pointed and resemble those of *grandis* more nearly than those of the type of *gigas*.

In a specimen from Arena Bank in 40 fathoms (M.C.Z. No. 3447; pl. 4, upper) with R = 41 mm., r = 15 mm., R : r = 2.7 : 1, the paxillae are very low, the thick columns being about as high as broad. The crown consists of 6-7 peripheral granules and one central elongated capitate granule, all similar.

There are 39 marginals. The inferomarginals are mostly on the actinal surface, the outer ends curving upward to meet the superomarginals. In lateral view they are at the arm bases about half as high as the superomarginals, but the height of the superomarginals decreases so that in the outer half of the ray the two series are, in lateral view, of about the same height.

The marginals and the actinal intermediate plates have a similar covering of granules with swollen tips which are not higher than thick, largest and lowest in the center of the plates, becoming more slender along the edges. The spines on the adambulacral plates resemble those of the larger specimen. The very few pedicellariae are in the inner part of the interradial areas.

A specimen from Santa Inez Bay in 35 fathoms (M.C.Z. No. 3448; pl. 4, lower) with R = 32 mm., r = 11 mm., R : r = 2.9 : 1, and 34 marginals, resembles the preceding, but there are no pedicellariae and the adambulacral spines, though similar, are not so stout.

A specimen (M.C.Z. No. 36251) with R = 30 mm., r = 11 mm., R : r = 2.7 : 1, and 30 marginals, resembles the preceding, as does another (M.C.Z. No. 36251) with R = 18 mm., r = 7 mm., R : r = 2.6 : 1, and 27 marginals.

In five small specimens from Gorda Bank (M.C.Z. No. 3449) R = 7-10 mm., r = 3.5-4.5 mm. The spines on the adambulacral plates are slender, cylindrical or slightly swollen in the outer part, and little if at all flattened; they bear numerous fine serrations. All the granules on

both surfaces are more slender, relatively higher, and less crowded than in the larger specimens, and bear very numerous fine serrations.

In a specimen from Santa Inez Bay (M.C.Z. No. 3450) with R = 4 mm., r = 2.7 mm., there are 8 marginals. The terminal plate is very large. All the spines and the slender elongate granules are spinulose.

With decrease in size the madreporite decreases in relative size and in the smaller specimens cannot be distinguished.

In nearly all the specimens we have seen the rays differ somewhat in length, as was the case in Señorita Caso's type of *gigas*.

Specimens examined.—All known specimens except the type of *gigas*.

TETHYASTER VESTITUS (Say)

Plates 5-8; text figure 1, *d*

Asterias vestita SAY, 1825, p. 143 (description; Cape May, N. J.).

Astropecten vestitus LÜTKEN, 1859, pp. 27, 54 (listed).—VERRILL, 1866, p. 339 (Say's record) ; 1895, p. 133 (Say's record ; "not uncommon farther south.")

Sideriaster (?) *vestitus* VERRILL, 1914, p. 21 (identity of Say's species) ; 1915, pp. 193-195 (discussion).

Moiraster magnificus A. H. CLARK, 1950, p. 302 (off Puerto Rico) (not *magnificus* Bell, 1882).

Diagnosis.—Enlarged spines on the inferomarginal and actinal intermediate plates rectangular, sometimes tapering distally, broadly truncate, in fully grown individuals up to 4 mm. long, first appearing when R is about 150 mm. ; size large, R up to 250 mm.

Description.—The paxillae are compact and in contact, with a slender tall pedicel 3-4 mm. high and four or five times as high as broad, crowned by a floriform group of usually 20-30 peripheral and 5-15 or more central, terete, slightly tapering, blunt spinelets 0.5 to 1 mm. long and 3-5 times as long as broad at the base. On the disk and arms they are arranged in rows at an angle of approximately 75° to the midradial line ; in the middle of the interradial areas of the disk there are 4 or 5 usually irregular rows that do not reach the interradial border. The paxillae are largest on the disk, slowly and gradually becoming slightly smaller with more slender, more pointed, and relatively longer spinules toward the interradial margins and on the rays. The madreporite is very large, 17 by 16 mm., slightly sunken below the summits of the surrounding paxillae, slightly concave with very numerous and fine, regularly radiating striae.

The marginal plates correspond throughout the ray. They are high and narrow with very deep fasciolar channels between them, the chan-

nels being roughly twice as deep as the width of the summits of the marginals or even deeper. The superomarginals, 78 in number, are in the interradial arcs flat and 13 mm. high, decreasing in height to 6 mm. and becoming slightly convex on about the sixth, then remaining similar to near the arm tips. They bear about four rows of elongated granules or short spinelets. The two outer rows are regular and are composed of slightly tapering spinelets, resembling those of the paxillae in the center of the disk, and about three times as long as broad at the base; the two median rows are irregular and are composed of shorter and stouter spinelets. On the high, narrow superomarginals in the interradial arcs there are only two rows of spinelets, or an irregular single row, these spinelets resembling those of the outer rows of the outer superomarginals. The inner rows first appear on about the eighth superomarginal. The superomarginals are bordered on each side by an irregular double row of from 30 to 40 slender tapering spinelets which just meet those of the neighboring superomarginals. The lower end of the superomarginals is bordered by a row of about 6 stout spinelets directed diagonally outward.

The inferomarginals are about the same size as the superomarginals in the interradial angles but, being more uniform in size, are slightly larger elsewhere. In the interradial arcs they are flat and make a considerable angle with the superomarginals, but they soon become convex, continuing the curve of the superomarginals to the flat actinal surface. They bear a median row of usually four broad, flat, truncated, appressed spines 3 to 4 mm. long and 1.25 to 1.50 mm. wide, which overlap the bases of those succeeding. These are flanked by much smaller flattened and truncated spines mixed with more or less terete spinelets. The plates are bordered laterally by very numerous fine, laterally directed spinules resembling those bordering the superomarginals. Toward the ends of the rays the enlarged spines become very short, not much longer than broad.

The terminal plate is rather large, swollen, heart-shaped, with the distal end deeply notched and the proximal end broadly truncated. It overlies about 4 superomarginals.

The actinal intermediate areas are large. One series of plates extends to within about 20 mm. of the end of the ray, a second to within about 40 mm., and a third to about the middle. An incomplete and usually irregular row extends from a pair just beyond the mouth plates to about one-third the distance to the inferomarginals. Between the first inferomarginal and the second adambulacral the series contains 9 or 10 plates. Deep channels lead from the marginal fascioles to the fascioles between the adambulacrals, these being separated by single

regular rows of actinal intermediate plates. Each of these intermediate plates bears a tall, stout, laterally compressed column somewhat broadened at the summit, which bears a large, flattened, truncated spine 4 mm. long and about 1.3 mm. broad resembling the large spines on the inferomarginals. This spine lies parallel with the surface of the plate and is directed toward the inferomarginals. Occasional plates may carry two or even three of these spines. The median spine is accompanied by a few much smaller, flattened spines or stout spinelets, and the border of the summit of the plate carries a large number of fine, laterally directed slender spinelets directed laterally and arranged in an irregular double row. In a single interradius seven of the actinal intermediate plates carry a fine, somewhat scattered granulation instead of the large flattened spine and the accompanying smaller ones. Many of the actinal intermediate plates adjoining the adambulacrals carry spiniform pedicellariae with usually two, sometimes three, blades.

The adambulacral plates are broader than long. The inner half forms an acute angle of roughly 60° and the outer half has parallel sides. At the apex of the furrow angle there is a stout, sharp, prismatic, slightly recurved spine which in the basal part of the ray is 7 or 8 mm. long. On the sides of the angle are two, sometimes three, similar but much flattened sharp spines of about the same dimensions. The actinal surface of the plate carries usually 4 or 5 spines as stout as the marginal spines but slightly shorter, flattened, broadly truncate, and fluted in the outer half. Each adambulacral plate therefore carries a more or less compact group of usually 9 or 10 generally similar conspicuously large and stout spines. The plates are bordered laterally by an irregular double row of fine spinules similar to those on the actinal intermediate plates.

The mouth plates are densely covered with spines, larger on the inner third (toward the mouth) than elsewhere. There are about 6 enlarged and strongly flattened marginal spines which are placed far down on the side of the plate, with a second series parallel with them along the edge of the plate. Beyond the marginal spines the mouth plates carry along their border very numerous, very fine, laterally directed spinules arranged in about three rows.

Type.—Lost; the specimen described above, from the coast of North Carolina, may be regarded as a neotype.

Type locality.—Cape May, N. J.; the type was collected by J. Robbins.

Additional localities.—Twelve miles west-southwest of Diamond Shoal, N. C.; 44 meters; February 6, 1951 (U.S.N.M. No. E.8000).

Caroline station 35; off the west coast of Puerto Rico (lat. 18°24′45″ N., long. 67°14′15″ W.); 146-329 meters; 1933 (U.S.N.M. No. E.3963).

Rosaura station 35; off the mouth of the Orinoco River; 86 meters (B.M. No. 1949.1.19.18).

Geographical range.—From New Jersey south to the mouth of the Orinoco River.

Bathymetrical range.—From 44 to 146 (?329) meters.

Remarks.—We have no hesitation in identifying the specimen from North Carolina with Say's *Asterias vestita* for the following reasons. The distinctive features in Say's brief description are (1) the paxillae on the abactinal surface; (2) the large and very conspicuous madreporite; (3) the occurrence of about four very much compressed, subquadrate, truncated, and imbricated spines on the marginals; (4) the size; and (5) the comparison with [*Astropecten*] *aranciaca*. All these features are equally distinctive of the specimen from North Carolina, but of no other species known from the western Atlantic. The only species that might be considered in this connection is Verrill's *Sideriaster grandis,* but this is smaller and the spines on the marginals are tapering and pointed, not subquadrate and truncated.

In the specimen from Puerto Rico (pls. 7, 8) R = 160 mm., r = 45 mm.; R = 3.6 r (R = 3.9 r in the large specimen from North Carolina). The abactinal paxillae have short, stout, cylindrical columns 1.25 mm. high and 0.75 mm. in diameter.

The marginals are 75 in number. The superomarginals are densely covered with low, somewhat flattened granules, largest in the middle, and resemble those near the tip of the rays in the large specimen in which, however, the granules are higher. The enlarged spines on the inferomarginals are small, mostly 1.5 to 2 mm. long by 1 mm. wide.

Many of the actinal intermediate plates, in some interradii more than half, in others fewer, show the enlarged and flattened spines in various stages of development; most of them are about two-thirds the size of those on the inferomarginals and of the same shape.

A few scattered paxillae on the disk and arm bases carry pedicellariae with usually 3, occasionally 2 or 4, blades which are scarcely more than slightly modified spines. A number of the actinal intermediate plates of the inner row, especially in the second fourth of the ray, carry a pedicellaria, sometimes two, consisting of scarcely modified spines.

The specimen taken by the *Rosaura* has R = 75 mm. It has not yet developed the enlarged spines on the actinal intermediate plates, but the inferomarginal spines (see text fig. 1, *d*) are broadly truncated

or spatulate in shape. There are some actinal pedicellariae. The columns of the midradial proximal dorsal paxillae are about 0.35 mm. in maximum thickness, measuring 0.75 mm. in height, or 1-2 mm. including the basal part. The paxillar spinelets are about 0.45 mm. long. The marginals are 52 in number.

Specimens examined.—All those known.

TETHYASTER MAGNIFICUS (Bell)

Plates 9, 10; text figure 2, *e-g*

Archaster magnificus BELL, 1882, p. 440 (description; St. Helena).
Moiraster magnificus SLADEN, 1889, p. 193 (reassignment of Bell's species).—
    KOEHLER, 1908, p. 630, pl. 12, figs. 107-110 (Ascension; notes).—MORTEN-
    SEN, 1933, p. 422, text figure 6, pl. 21, figs. 1, 2, pl. 22, fig. 1 (Egg Island,
    St. Helena; notes).—CASO, 1947, p. 225 (listed).

Diagnosis.—Enlarged spines on the inferomarginal and actinal intermediate plates rectangular or even with divergent sides, rarely somewhat tapering distally, broadly truncate, in fully grown individuals 6-7 mm. long, first appearing when R = about 70 mm.; size large, R up to 220 mm. at least.

Types (2).—In the British Museum (Nos. 68.6.15.1 and 68.6.15.2).

Type locality.—St. Helena, collected by J. C. Melliss; no further details.

Additional localities.—St. Helena, Egg Island; about 73 meters (Mortensen, 1933). Ascension, Pyramid Point; 73 meters (Koehler, 1908).

Geographical range.—St. Helena and Ascension.
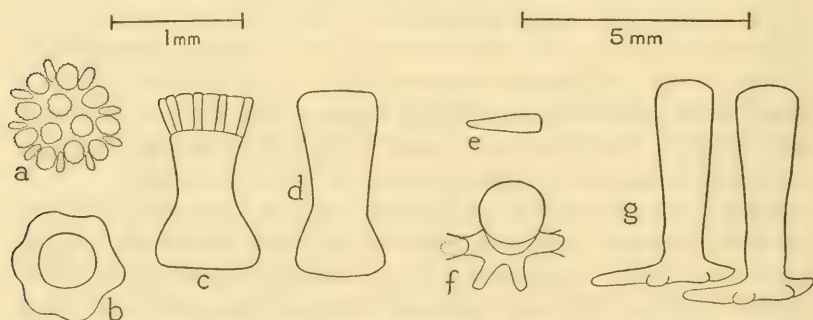
FIG. 2.—*a-d, Tethyaster subinermis. a-c,* specimen from Naples with R = 55 mm.; *a* and *b,* dorsal views of proximal midradial paxillae with and without spinelets; *c,* side view of a complete paxilla; *d,* side view of a paxilla without spinelets from a specimen from Senegambia with R = 72 mm.

e-g, Tethyaster magnificus, alcoholic specimen from St. Helena with R = 215 mm. *e,* paxillar spinelet; *f,* dorsolateral view of a paxilla without spinelets, and single lobes of two adjacent ones; *g,* lateral view of two adjacent paxillae without spinelets, showing their position in the skin. Drawings by A. M. Clark.

Bathymetrical range.—The only definite records are 73 meters.

Remarks.—There are three specimens of this species in the British Museum, all collected at St. Helena by J. C. Melliss, although Bell mentioned only two. The third (B.M. No. 67.12.30.1) is preserved in alcohol but possibly spent some time in formalin since it is in a very flaccid state. The two types are both dry.

The larger of the types has R = 215, 213, 222, and 214 mm. on the four entire arms (Bell gives 207 mm.). In the alcoholic specimen R = about 215 mm.

Mortensen and Koehler have added considerably to Bell's original description and the only further points to be made here concern the paxillae and the relative size of the actinal intermediate spines.

A strip of the dorsal skin with paxillae from the midradial base of a ray of the alcoholic specimen shows considerable overlapping of the bases of consecutive dorsal plates, although this may have been exaggerated by the contraction under preservation. In dorsal view the bases of the plates are seen to have much more prolonged lobes than in *T. subinermis.* The height of the columns relative to their minimum width (4 or 5 : 1) is also greater than in *T. subinermis,* but comparable to the proportions found in *T. vestitus.*

The smaller type, with R = 138 mm., has the paxillar columns only two-and-a-half times as high as wide. Its actinal intermediate spines are already large and overlapping, averaging 3.5 mm. in length. The two larger specimens have these spines 5 to 7 mm. long. In Koehler's specimen from Ascension and Mortensen's from St. Helena with R about 65 mm. the spines are just beginning to make their appearance but do not much, if at all, exceed their breadth in length.

It therefore seems that in *T. magnificus* the development of the actinal intermediate spines is accelerated so that they first appear when R is about 60 mm., whereas in *T. vestitus* they begin to develop only when R is about 150 mm.

Specimens examined.—The type and paratype and a third specimen also collected by J. C. Melliss at St. Helena.

TETHYASTER GRANDIS (Verrill)

Plates 11, 12; text figure 1, *b*

Sideriaster grandis VERRILL, 1899, p. 220, pl. 30, figs. 8, 8*a*, 8*b* (description; *Albatross* station 2378) ; 1914, p. 21 (discussion) ; 1915, p. 192, pl. 12, figs. 5-5*b* (redescription, with the original figures republished).

Diagnosis.—Enlarged spines on the inferomarginals narrow and sharp-pointed, in some specimens a few also on the actinal inter-

mediate plates; columns of the paxillae low, not over twice as high as thick; no abactinal pedicellariae (on any of the specimens examined) ; rays broad at the base, tapering, the width at base equal to, or greater than, r; first series of actinal intermediate plates reaching to outer fourth of the ray, second to about the middle; superomarginals up to 65 in number; paxillae with coarse, elongated granules; granulation of actinal intermediate plates coarse, coarsest in the center; conspicuous fascioles present; R up to 160 mm.

Description.—The paxillae are compact and in contact, with a low, stout pedicel about 1.5 mm. high, less than twice as high as thick, having a rather strongly concave profile, crowned by a group of slightly elongated, well-separated granules, usually 15-20 peripheral which are about twice as long as thick, cylindrical with broadly rounded tips, and usually 7 stouter and shorter central granules, one in the middle surrounded by 6 others. The paxillae are largest on the disk, gradually decreasing in size and with fewer and smaller central granules outwardly along the rays and toward the superomarginals. In the central part of the rays they are arranged in regular longitudinal rows, on the sides in rows at right angles to the superomarginals, three rows to each two superomarginals. The median row on the rays is sometimes slightly larger than the others.

The madreporic body is large, approximately circular, 10 mm. in diameter, wholly exposed, flat, with numerous fine prominent radiating ridges. It is situated somewhat nearer the interradial border than the center of the disk.

The marginal plates correspond throughout the ray. They are high and narrow with shallow fasciolar channels between them which at the base are about half as deep as the exterior face of the plates, becoming shallower distally. The superomarginals, 65 in the specimen described, are high and narrow in the interradial arcs, 6 mm. high and 1.5 mm. wide, but gradually become wider, after the tenth being 6 mm. high and 2.5 mm. wide, the relation of height to width then remaining essentially the same to the arm tips. The superomarginals in the interradial angles bear about 5 irregular columns of granules, those in the middle of the plate the largest, the lateral about half as large; on succeeding superomarginals the granules become smaller and usually more uniform, in 6-8 irregular columns, though often the central granules are enlarged. The superomarginals are bordered on each side by a somewhat irregular row of very fine, closely set spinelets extending laterally over the fasciolar grooves.

The inferomarginals are confined to the actinal surface. They are

everywhere of about the same size and shape as the superomarginals. They bear a dorsoventrally median row of usually 4, sometimes 5, tapering, pointed, and flattened spines about 4 mm. long which increase slightly in length from the lowest to the uppermost and are appressed to the surface of the plate, each overlapping the base of the one next above. On either side of this median row of spines, and also between them, there are numerous much shorter, more or less flattened, truncated spinules. The outer edges of the inferomarginals, like those of the superomarginals, are bordered with an irregular row of very fine, closely set spinules extending outward over the fascioles.

The terminal plate is of moderate size, heart-shaped, with the distal end deeply notched and the proximal end slightly truncated.

The actinal intermediate areas are large. The innermost series of plates extends to about the outer fourth of the ray (to about 25 mm. from the tip), the second to well beyond the middle (to about 45 mm. from the tip), and the third to about the tenth inferomarginal. Between the first inferomarginal and the second adambulacral the series contains about 10 plates. In each interradius there is a median unpaired row of 1-5, commonly 3, plates. The actinal intermediate plates bear 6-12 well-spaced, coarse, elongated granules, which are cylindrical with broadly rounded ends, not over twice as high as thick, and are bordered with an irregular row of fine spinules extending laterally over the rather deep fascioles. On the interradial areas the elongated granules are irregularly arranged, but on the rays they become aligned in two or three irregular rows parallel to the axis of the ray. In some specimens some of the actinal intermediate plates in the outer part of the interradial areas may bear an enlarged, flattened, outwardly directed appressed spine similar to those on the inferomarginals but smaller.

The adambulacrals are at first broader than long, later becoming squarish or even slightly longer than broad; the inner end forms an obtuse angle; in the middle of the inner edge there is a broad, strongly flattened, recurved spine with a broadly rounded tip; on each side of this, on the edge of the plate, are two flattened but straight and slightly smaller spines. Behind these, on the actinal surface of the plate, there is a row of usually 3 similar spines, and behind these two more, slightly smaller. In the outer part of the ray the median spine in the row of three gradually enlarges, and toward the tip of the ray the median spine becomes long, stout, and conspicuous. The adambulacrals are bordered with numerous fine spinules extending laterally.

Each mouth plate bears about a dozen short, stout, somewhat flattened spines resembling those on the adambulacrals which they adjoin;

on the border abutting on the adambulacrals the mouth plates are bordered with numerous very fine spinules.

The gonads extend almost to the tips of the rays.

The occurrence of pedicellariae in this species is very erratic. None of the specimens have any pedicellariae on the abactinal surface, and some have no pedicellariae at all. The one described has a few pedicellariae consisting of three blades of slightly modified spines situated on some of the interactinal plates from about the tenth adambulacral to about the middle of the ray.

Type.—Presumably in the Yale University Museum.

Type locality.—*Albatross* station 2378, off Mobile, Ala. (lat. 29°14'30" N., long. 88°09'30" W.) ; 124 meters; gray mud; February 11, 1885.

Additional localities.—Off Sombrero Light, Fla.; 110-128 meters; yacht *Triton,* 1951 (1 specimen).

M.V. *Pelican,* between Pensacola and Mobile; March 1, 1939 (1 specimen).

M.V. *Oregon,* southeast of Corpus Christi, Texas (lat. 27°25' N., long. 96°13' W.) ; 139 meters; bottom temperature 60.5° F.; November 27, 1950 (10 specimens).

Off Tamaulipas, Mexico (lat. 24°10' N.) ; 64-67 meters; Hildebrand, March 1951 (1 specimen).

Geographical range.—Known only from the Gulf of Mexico.

Bathymetrical range.—From 67 (?64) to 139 meters.

Remarks.—In a specimen with R = 145 mm. some of the superomarginals in the second quarter of the rays carry small pedicellariae at one or both of the lower angles. The inferomarginals from about the fifth outward carry mostly two pedicellariae, one at each upper angle, occasionally three or only one. The intermediate plates of the inner row from about the eleventh to about the middle of the ray carry usually two pedicellariae, one at each outer angle, occasionally only one. The pedicellariae have usually three, rarely two or four, subequal valves which resemble short spines with a swollen tip.

A small specimen from off Tamaulipas, Mexico, with R = 58 mm. and r = 18 mm., is in general similar to the one described. The enlarged spines on the inferomarginals are apparently just beginning to appear. They are mostly about twice as high as the maximum diameter, which is usually halfway to the tip, and are stumpy, subconical, slightly flattened, with a subacute tip; a few have acute tips; some are circular in cross section, and some are simply much enlarged granules. There are no pedicellariae.

Specimens examined.—All known specimens except the type.

TETHYASTER SUBINERMIS (Philippi)

Text figures 1, *a*, 2, *a-c*

Asterias subinermis PHILIPPI, 1837, p. 193 (description; Sicily).—LAMARCK, 1840, p. 258 (from Philippi).—MÜLLER and TROSCHEL, 1840, p. 324 (listed). —PREYER, 1886, p. 32 (Naples; rare in about 100 fathoms).

Astropecten subinermis MÜLLER and TROSCHEL, 1842, pp. 74-75 (Sicily).—SARS, 1859, p. 48 (Messina; 100 fathoms).—DUJARDIN and HUPÉ, 1862, p. 425 (coasts of Sicily).—PERRIER, 1875, p. 369; 1876, p. 289 (Nice; Algeria; Mediterranean).—STUDER, 1884, p. 46 (off Liberia, lat. 4°40′ N., long. 9°10′06″ W., 59 fathoms).—CARUS, 1885, pp. 90-91 (summary of localities). —PREYER, 1886, p. 32 (Naples; rare in about 100 fathoms).—CUÉNOT, 1888, p. 134 (Banyuls).—COLOMBO, 1888, pp. 47, 66 (Naples).—STUDER, 1889, p. 28 (lat. 4°40.1′ N., long. 9°10.6′ W., 108 meters).—VON MARENZELLER, 1895, pp. 125, 127, 145 (Adriatic Sea, east of Pelagosa, lat. 42°23′00″ N., long. 16°21′59″ E., 131 meters, sand and mud).—NOBRE, 1903, p. 155 (Setubal); 1904, p. 133 (Setubal).

Astropecten crenaster (part) DUJARDIN and HUPÉ, 1862, p. 414 (according to Cuénot, 1912).—?FISCHER, 1869, p. 364.

Astropecten aranciaca FISCHER, 1869, p. 363 (not of Linné = *subinermis* according to Cuénot, 1912) (Bassin d'Arcachon).

Archaster subinermis PERRIER, 1878, pp. 33, 57, 88 (Mediterranean).

Goniopecten subinermis PERRIER, 1885, p. 71.

Plutonaster (Tethyaster) subinermis SLADEN, 1889, pp. 82, 83, 101, 102, 722.

Tethyaster subinermis PERRIER, 1894, p. 323; (*Talisman* station 5, Baie de Cadix, lat. 36°26′ N., long. 8°47′ W., 60 meters, mud and shells; station 15, coast of Morocco, lat. 33°57′ N., long. 10°47′ W., 1,283-1,425 meters, mud, coral; station 66, off Cape Bojador, Morocco, lat. 26°13′ N., long. 17°10′ W., 175 meters, mud, coral).—KOEHLER, 1896b, pp. 450, 451 (*Caudan,* lat. 45°18′ N., long. 5°23′ W., 180 meters; lat. 45°52′ N., long. 6°03′ W., 250 meters; lat. 46°40′ N., long. 6°30′ W., 300 meters; *Talisman,* Baie de Cadix and coast of Morocco, 60-1,425 meters); 1896a, pp. 56, 124 (*Caudan* station 17, lat. 45°18′ N., long. 5°23′ W., 180 meters, gravel and sand; station 20, lat. 45°52′ N., long. 6°03′ W., 250 meters, mud; station 27, lat. 46°40′ N., long. 6°30′ W., 300 meters, mud).—PERRIER, 1896, p. 50 (Bay of Biscay, station 44, 166 meters; station 46, 155 meters).—KOEHLER, 1921, p. 54, fig. 40 (range); 1924, p. 200, pl. 7, fig. 4 (range).—MORTENSEN, 1925a, p. 178 (Atlantic coast of Morocco).—CUÉNOT, 1927, p. 295 (from Cuénot, 1912).— KOEHLER, 1930, figs. 1-3 (principally Mediterranean; Portugal; Cadix; coasts of Morocco and Liberia).—RIVERA, 1930, p. 105, fig. 4, p. 106 (Cádiz). —CUMANO, 1934, p. 138 (north of Berlengas).—NOBRE, 1938, p. 55 (Leixões, Bacia do Tejo, Sezimbra), pl. 30 (apparently from Ludwig, 1897), p. 195 (west of Sezimbra); TORTONESE, 1947a, p. 18 (Rodi [Rhodes]).—MADSEN, 1950, p. 186 (*Atlantide* station 120, lat. 2°09′ N., long. 9°27′ E., 650-260 meters; station 163, lat. 13°43′ N., long. 17°23′ W., 65-89 meters; about lat. 30°30′ N., long. 10° W., 100 to 120-500 meters).

Plutonaster subinermis LUDWIG, 1897, pp. 105-118, pl. 1, figs. 1, 2, pl. 6, figs. 10-24 (detailed description; range).—LO BIANCO, 1899, p. 473 (Gulf of Naples, very rare, on muddy bottoms, rarely on bottoms of other types).—KOEHLER, 1909a, p. 7; 1909b, p. 22 (*Princesse-Alice* station 1447, lat. 45°21′ N., long.

2°39′ W., 130 meters, fine sand, July 23, 1903).—Cuénot, 1912, pp. 28, 109 (range).—Goto, 1914, p. 359.—Cuénot, 1927, p. 295.—Nobre, 1931, figs. 42, 43, p. 62 (probably from Ludwig).

Thetyaster subinermis Nobre, 1931, p. 62 (west coast of Portugal).

Tethyaster Tortonese, 1947b, p. 888 (Rhodes).

Diagnosis.—Enlarged spines on the inferomarginals narrow and sharp-pointed, none on the actinal intermediate plates; columns of the paxillae low, not over twice as high as thick; no abactinal pedicellariae; rays broad at the base, tapering, width at base equal to, or greater than, r; first series of actinal intermediate plates to outer fourth of ray, second to about the middle; superomarginals short, 68-85 in fully developed individuals; granulation of superomarginals and actinal intermediate plates fine, uniform, and crowded; size large, R up to 275 mm.

Description.—This species was described and figured in detail by Ludwig (1897, p. 105).

Type.—We have no information regarding the type.

Type locality.—Sicily.

Geographical range.—From the Bay of Biscay (lat. 46°40′ N.) south to the Gulf of Guinea, off Spanish Guinea (lat. 2°09′ N., long. 9°27′ E.); Mediterranean, east to Rhodes in the Aegean Sea.

Bathymetrical range.—From about 50 to about 1,400 (possibly 1,425) meters.

Remarks.—In a specimen from Algiers (B.M. No. 1947.6.24.1) with R = 110 mm. there are 73 superomarginals. In a specimen from Naples (U.S.N.M. No. E.8001) with R = 86 mm., r = 21 mm., there are 72 superomarginals; in this specimen the mouth plates are followed by 1 pair of plates in three interradii, and by 2 pairs in two; these are followed by a midinterradial unpaired row of 5 plates in three interradii, of 4 in two, that reach to the suture between the interradial pair of inferomarginals. In Ludwig's figure this unpaired median row consists of 5 plates, but reaches only to about two-thirds the distance to the inferomarginals.

In a specimen from off Gambia (*Atlantide* station 163, lat. 13°43′ N., long. 17°23′ W., 69-89 meters) (B.M. No. 1950.3.18) with R = 72 mm. there are 62 superomarginals. In a specimen from off Spanish Guinea (*Atlantide* station 120, lat. 2°09′ N., long. 9°27′ E., 650-260 meters) (B.M. No. 1950.7.3.26) with R = 71 mm. there are 68 superomarginals. In a specimen from Naples (B.M. No. 98.5.3.105-6) with R = 50-57 mm. there are 48 superomarginals.

In individuals of this species the rays may be of slightly different lengths.

In some specimens from Naples the paxillae of the midradial row on the rays gradually become enlarged in the outer part of the ray, but this does not seem to be the case in specimens from Algiers or from the Atlantic.

Specimens examined.—Five, listed above.

TETHYASTER PACEI (Mortensen)

Anthosticte pacei MORTENSEN, 1925b, p. 147, fig. 1, p. 148, pl. 8, fig. 3 (description; "Off South African Coast").

Diagnosis.—Enlarged spines on the inferomarginals narrow and sharp-pointed, none on the actinal intermediate plates; columns of the paxillae low, not over twice as high as thick; no abactinal pedicellariae (in the single known specimen); rays narrow, width at base markedly less than r; first series of actinal intermediate plates to about the outer third of the ray, second only in the proximal third; R = 120 mm.

Type.—In the Zoological Museum, Copenhagen, Denmark.

Type locality.—"Off South African Coast."

Remarks.—This species is known only from the type specimen, which we have not seen.

TETHYASTER AULOPHORA (Fisher)

Anthosticte aulophora FISHER, 1911, p. 417 (description; *Albatross* station 5420); 1919, p. 140, pl. 17, fig. 1, pl. 18, fig. 2, pl. 19, fig. 2, pl. 38, fig. 3, pl. 39, figs. 1, 1a-d (redescription).—MORTENSEN, 1925b, p. 148 (comparison with *A. pacei*).

Diagnosis.—Enlarged spines on the inferomarginals narrow and sharp-pointed, none on the actinal intermediate plates; columns of the paxillae slender, high, about four times as high as thick; most of the paxillae with a pedicellaria of 2-4 valves; R = 162 mm.

Type.—In the U. S. National Museum (No. 28656).

Type locality.—*Albatross* station 5420, between Cebu and Bohol, Philippines (lat. 9°49′35″ N., long. 123°45′00″ E.); 232 meters; bottom temperature 59° F.; March 25, 1909.

Remarks.—This species is known only from the type specimen which we have examined.

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PLATES
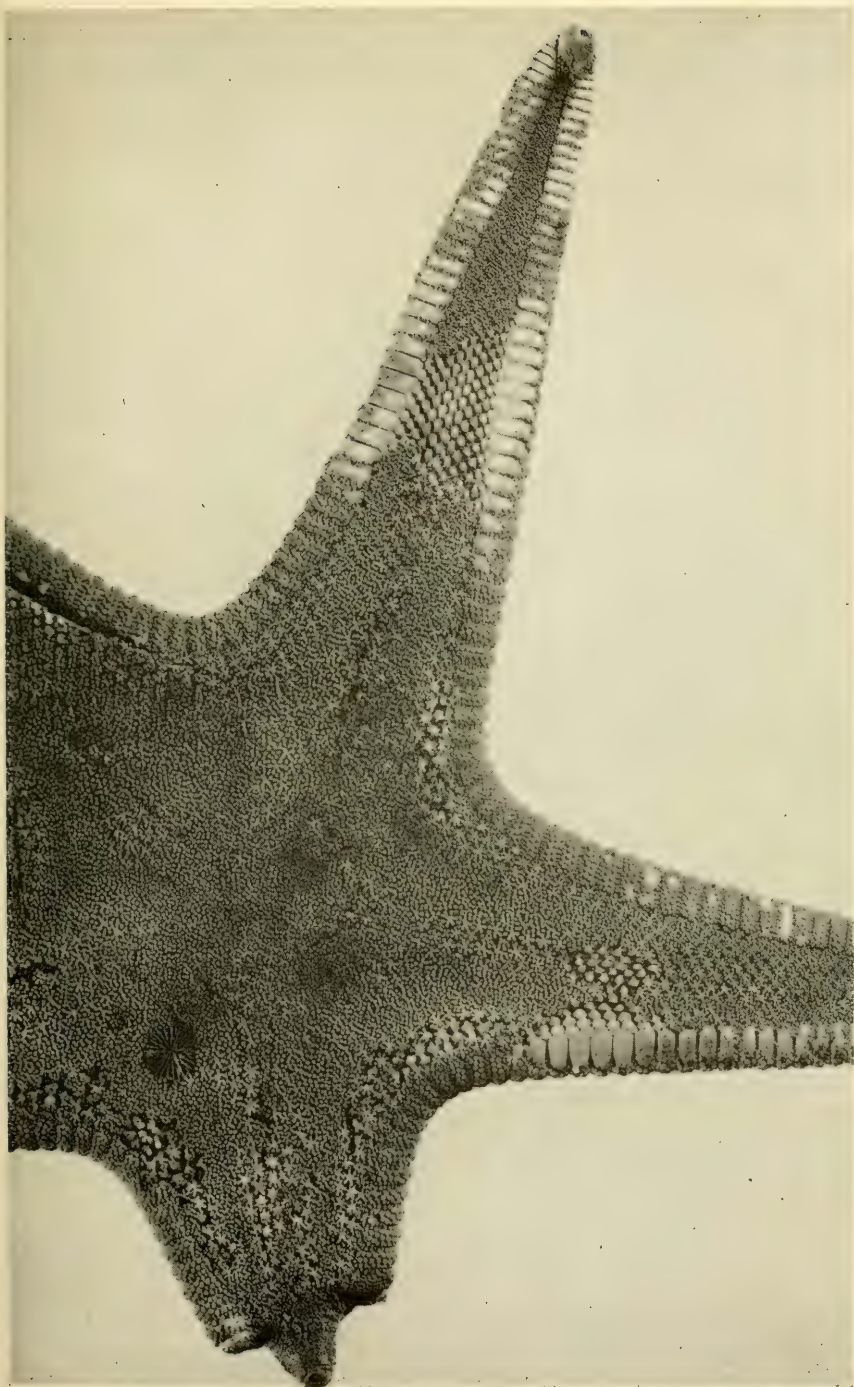
Tethyaster canaliculatus (A. H. Clark), the type specimen from *Albatross* station 2998, Gulf of California, in 73 meters; abactinal view, × 2. (U.S.N.M. No. 36951.)
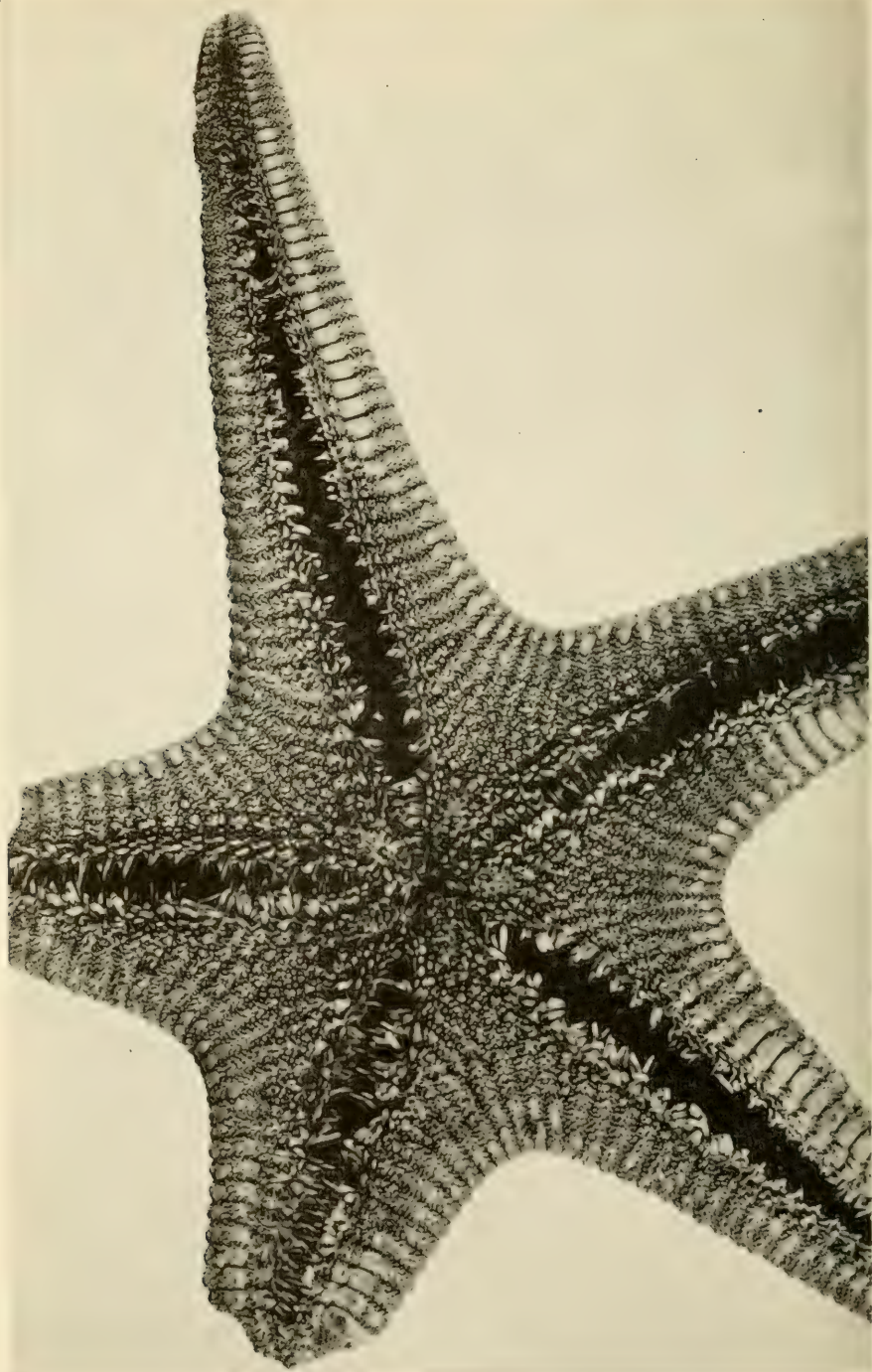
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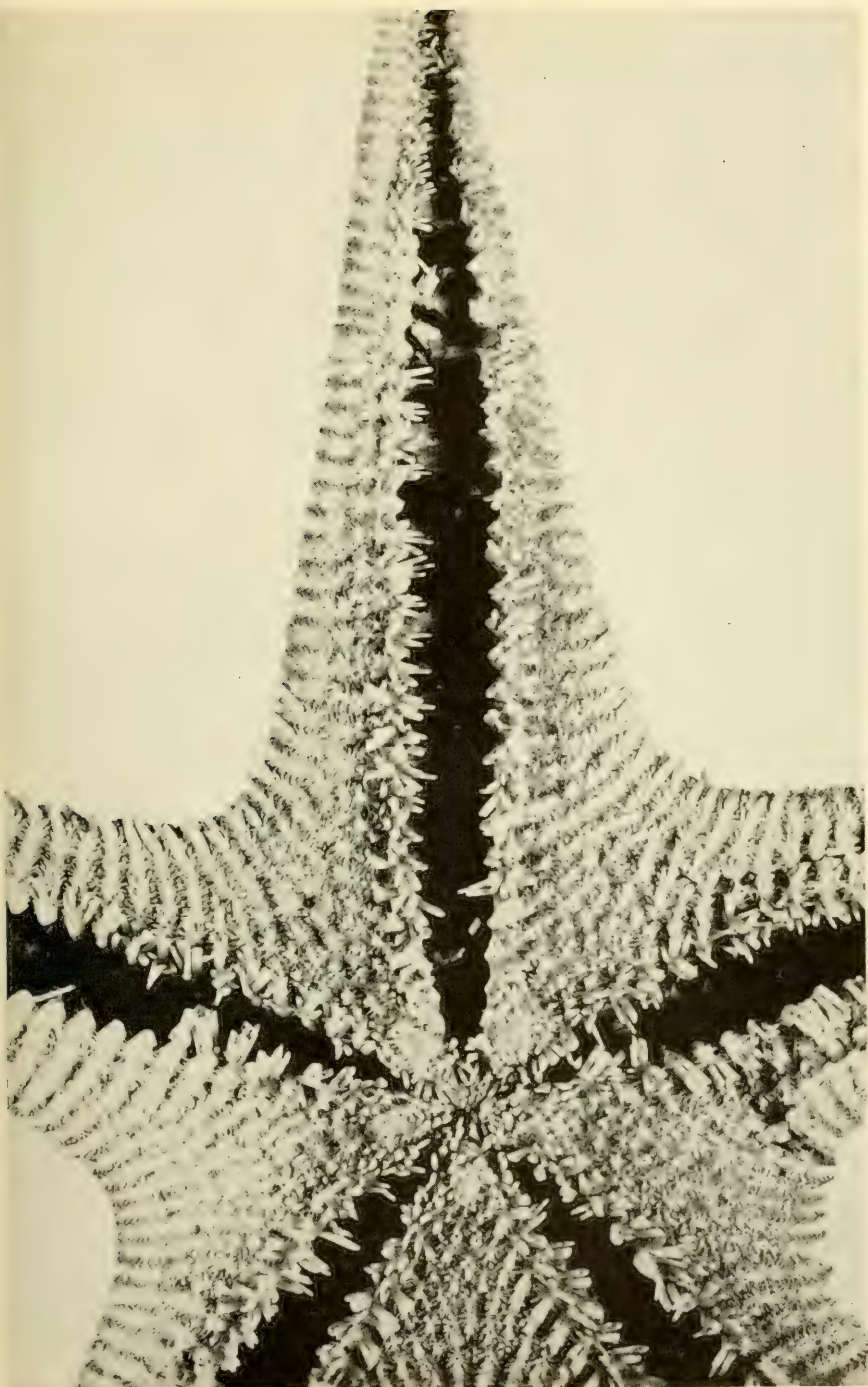
Tethyaster canaliculatus (A. H. Clark), the specimen with R = 95 mm. from *Zaca* station 142, D-3, Santa Inez Bay, Gulf of California, in 73 meters; actinal view, × 2. (M.C.Z. No. 36232.)
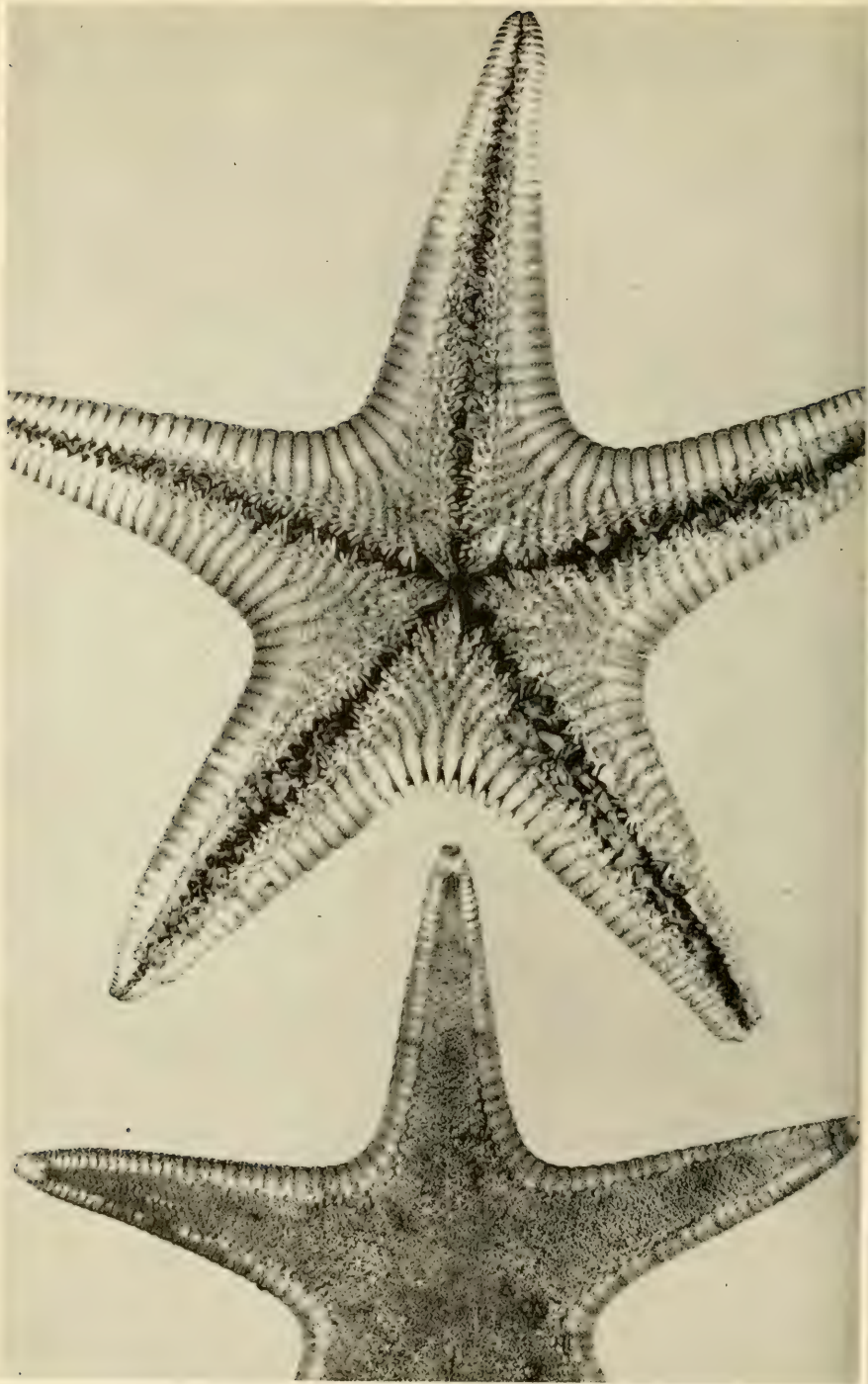
Tethyaster canaliculatus (A. H. Clark): *Upper,* the specimen with R = 41 mm. from *Zaca* station 136, D-14, Arena Bank, Gulf of California, in 82 meters; actinal view. (M.C.Z. No. 3447.) *Lower,* the specimen from *Zaca* station 146, D-1, Santa Inez Bay, Gulf of California, in 73 meters; abactinal view. (M.C.Z. No. 3448.) Both figures × 2.
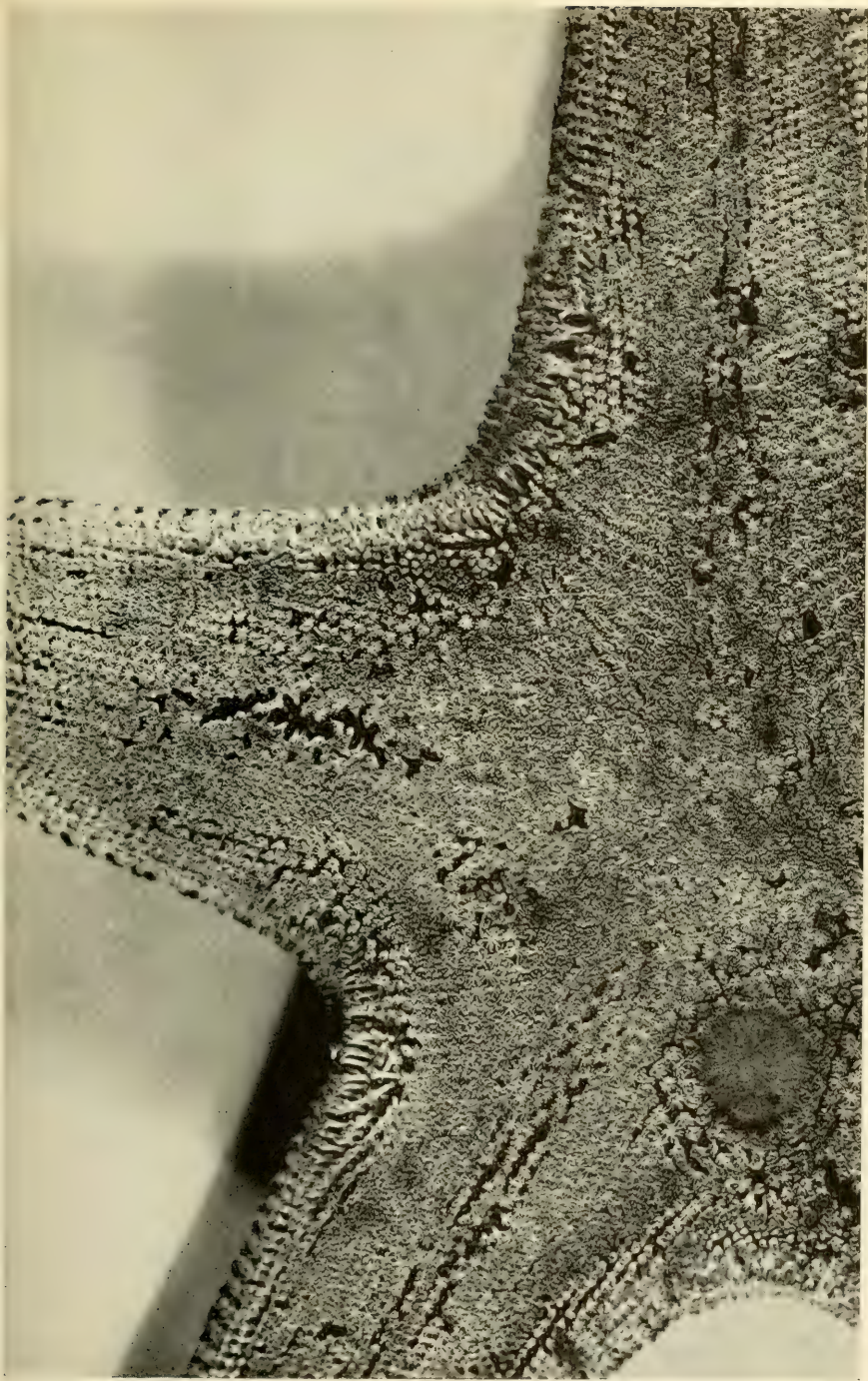
Tethyaster vestitus (Say), specimen from off Diamond Shoal, North Carolina, in 44 meters; abactinal view, natural size. (U.S.N.M. No. E.8000.)
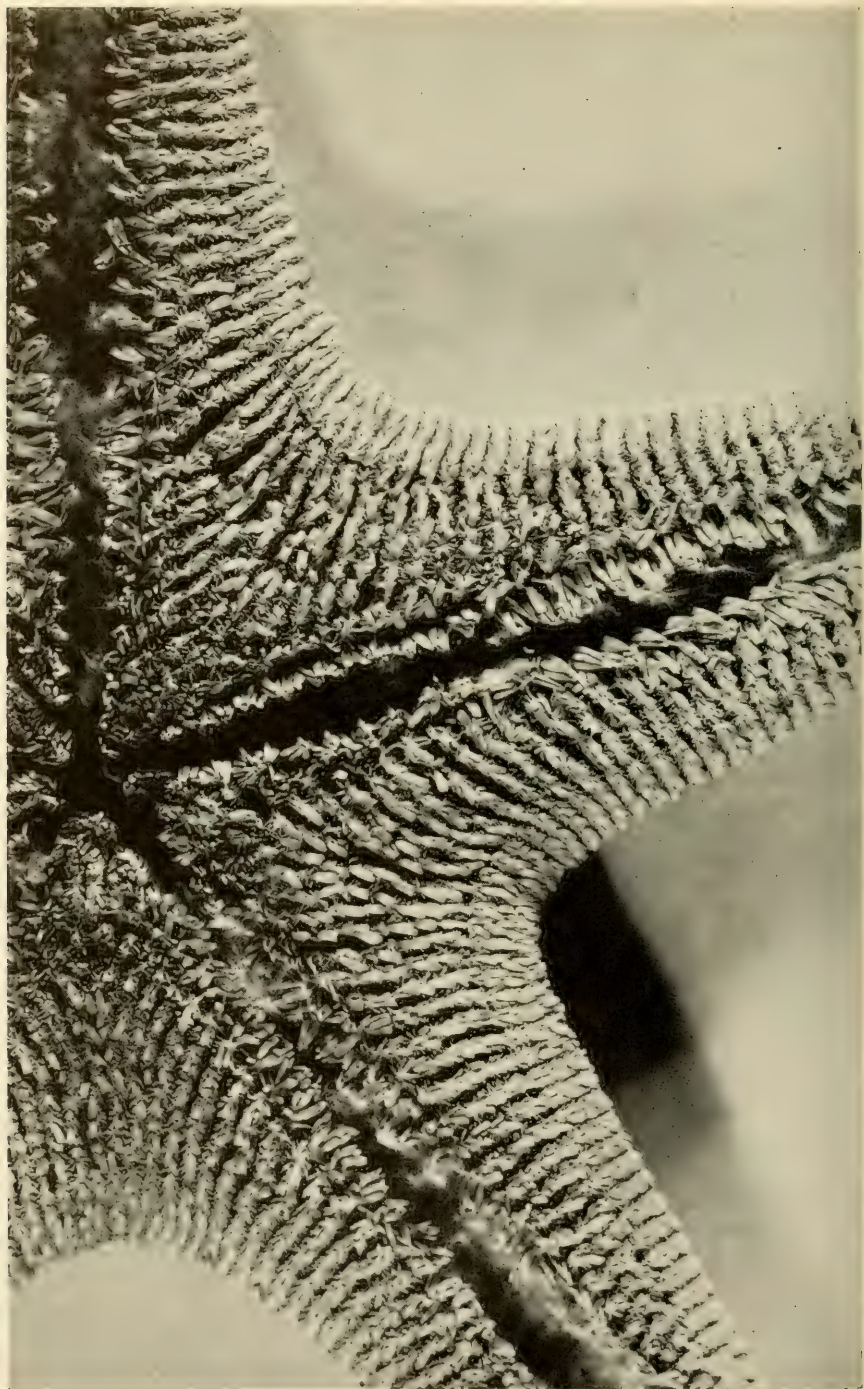
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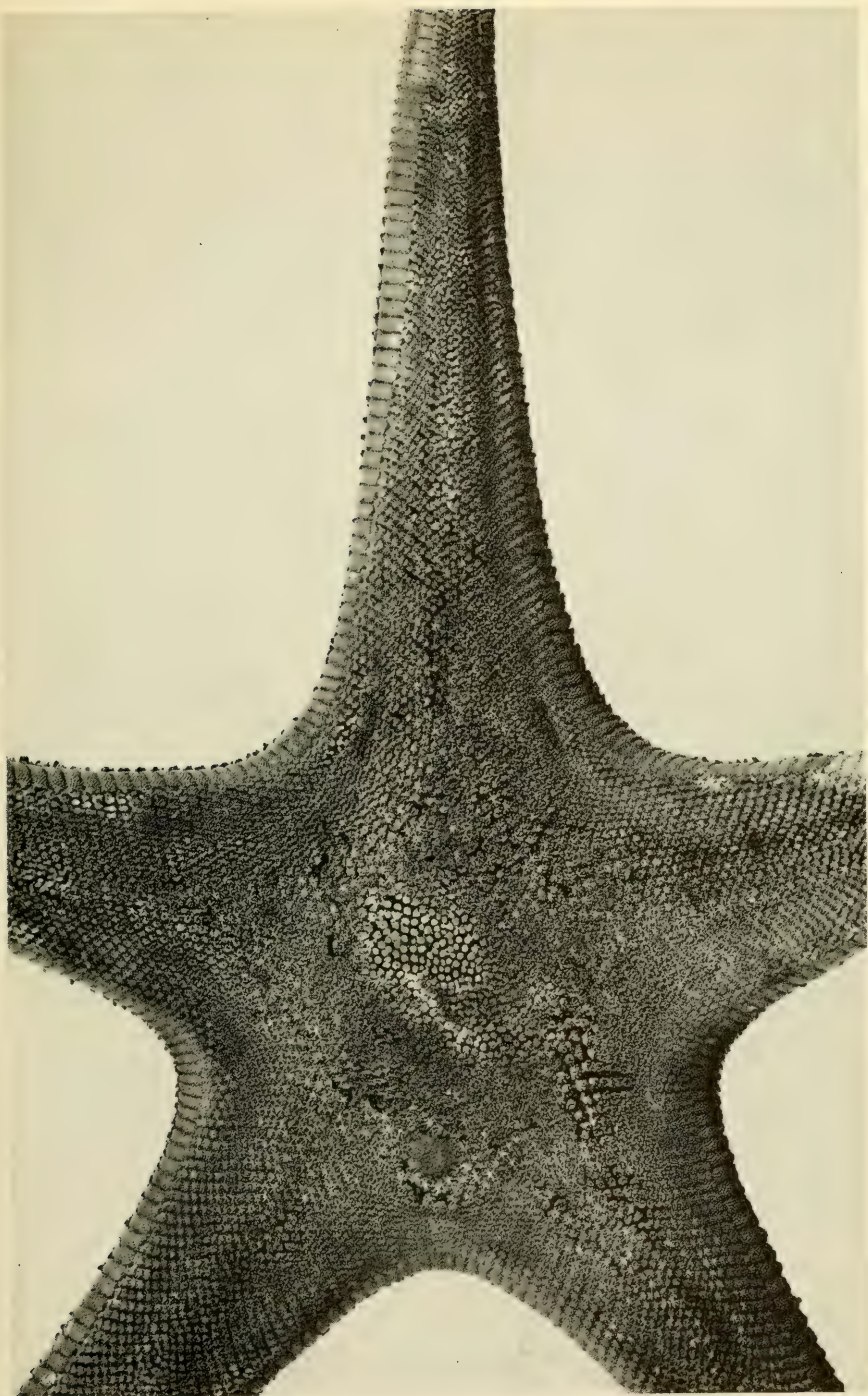
Tethyaster vestitus (Say), specimen from off Puerto Rico in 146-329 meters; abactinal view, natural size. (U.S.N.M. No. E.3963.)
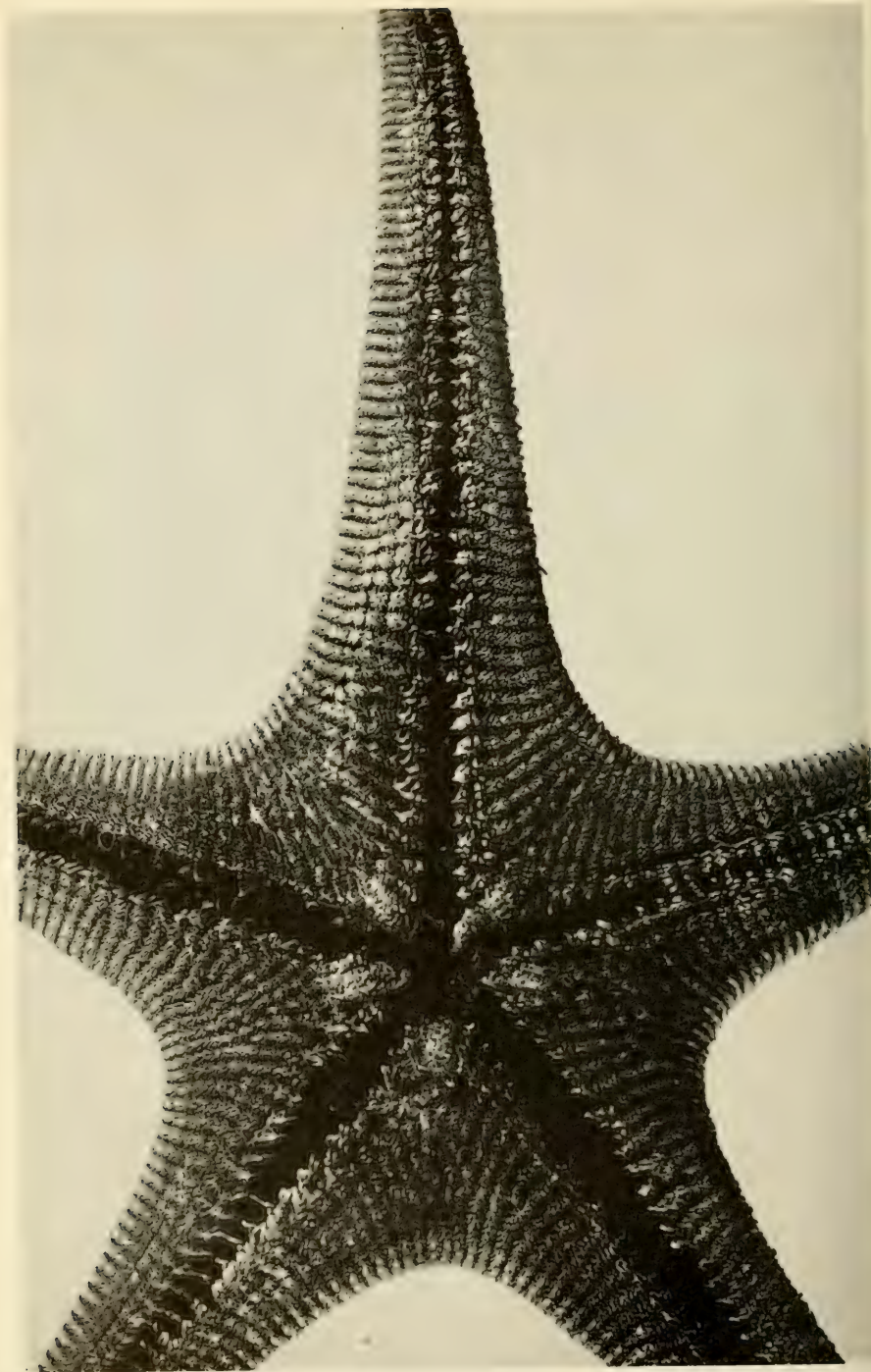
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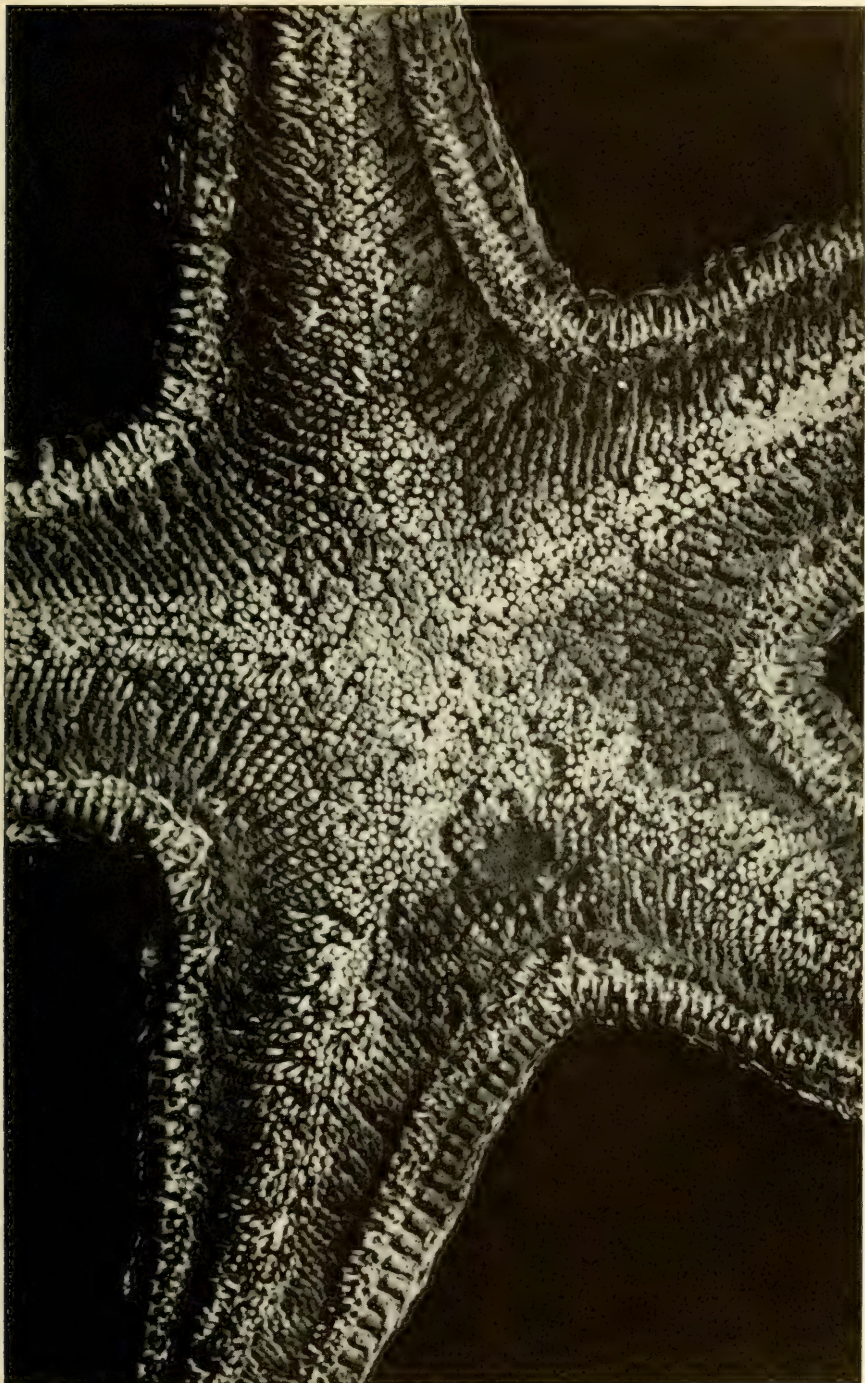
Tethyaster magnificus (Bell), the larger cotype from St. Helena; abactinal view, natural size. (B.M. No. 68.6.15.1.)

Tethyaster magnificus (Bell), the larger cotype from St. Helena; actinal view, natural size. (B.M. No. 68.6.15.1.)
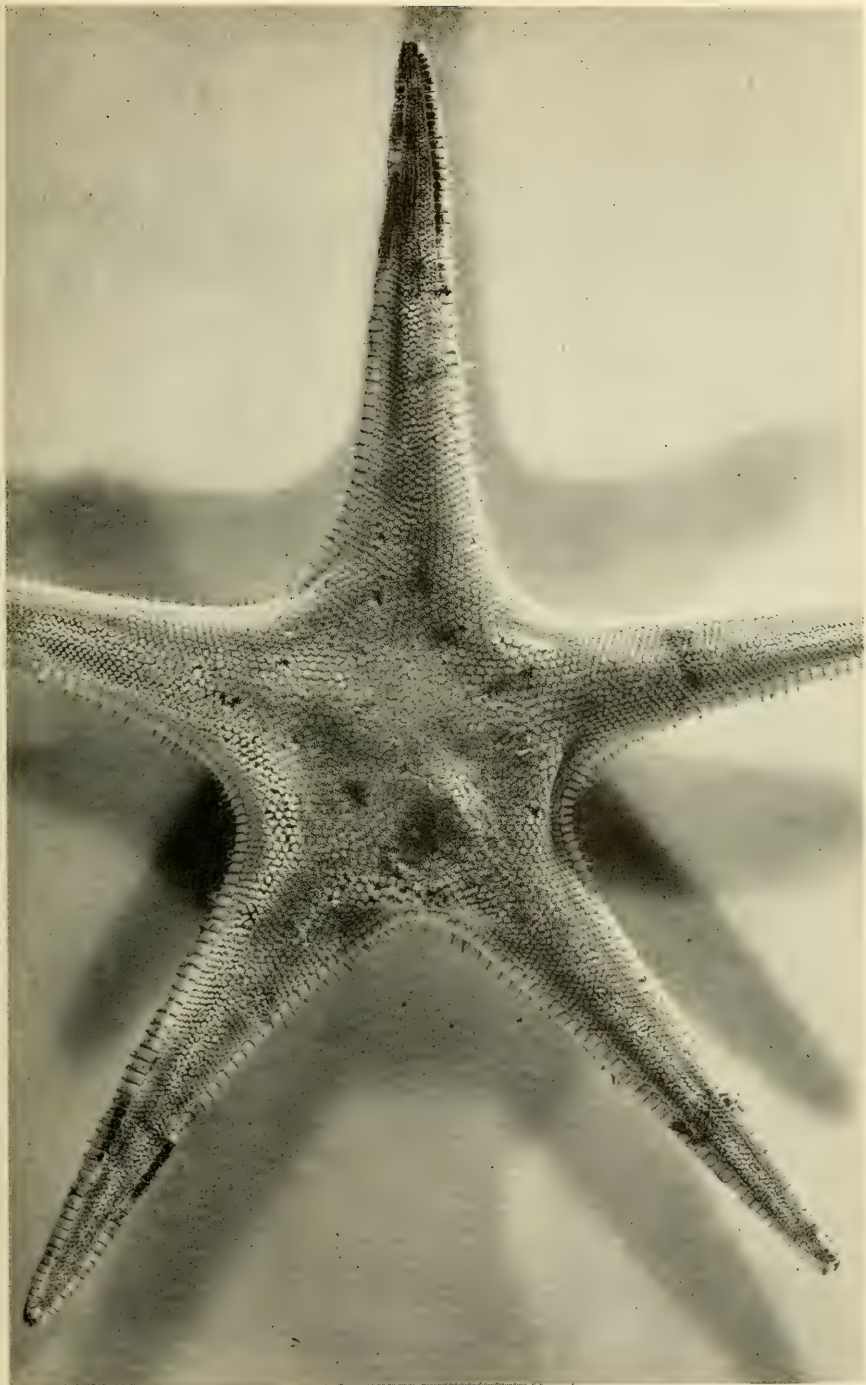
Tethyaster grandis (Verrill), from off Corpus Christi, Tex., in 139 meters; abactinal view, natural size. (U.S.N.M.)
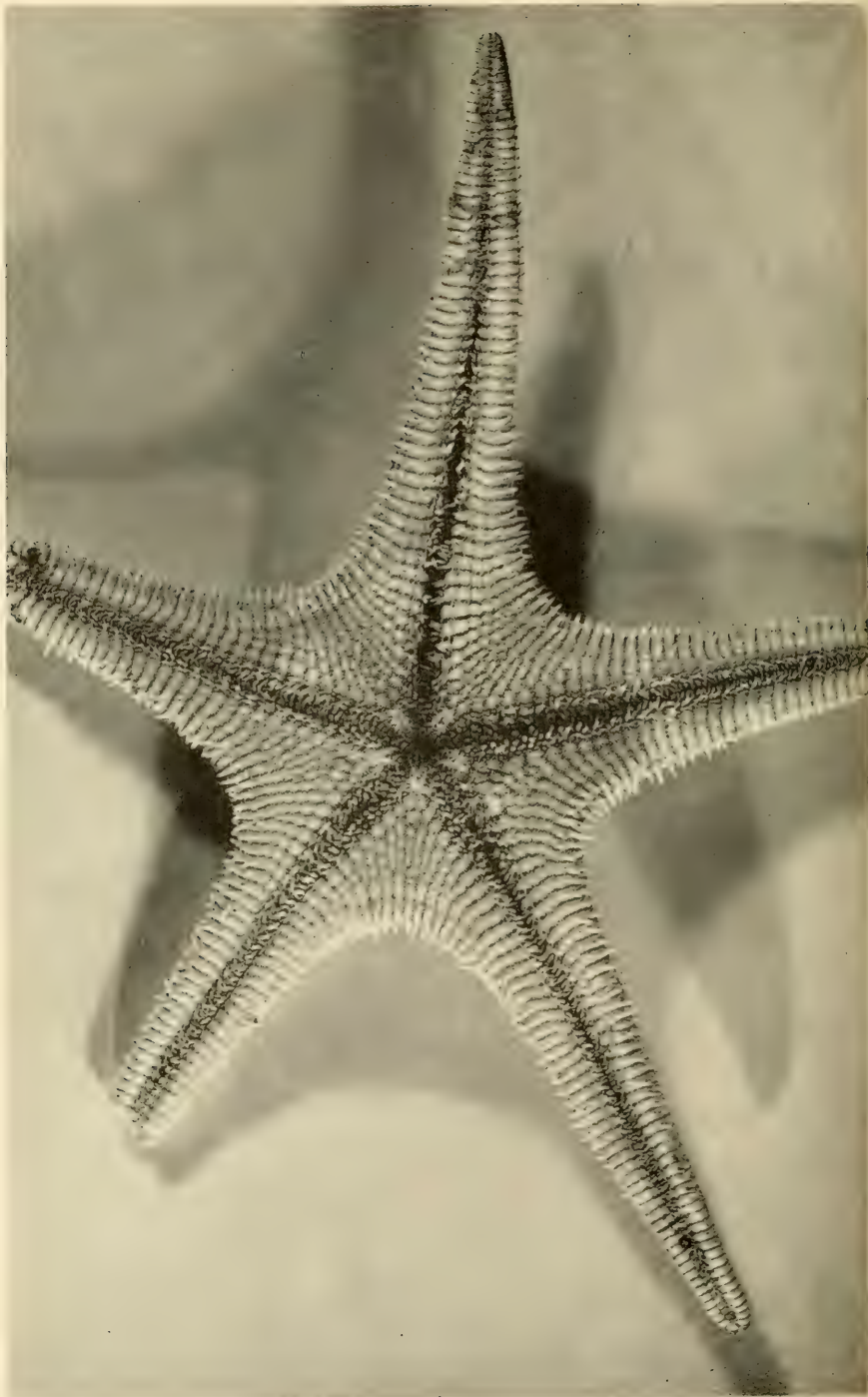
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THE REPRODUCTION OF COCKROACHES

(With 12 Plates)

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INTRODUCTION

Cockroaches are important for several reasons. As pests, many are omnivorous, feeding on and defiling our foodstuffs, books, and other possessions. What is perhaps less well known is their relation to the spreading of disease. Several species of cockroaches closely associated with man have been shown to be capable of carrying and transmitting various microorganisms (Cao, 1898; Morrell, 1911; Herms and Nelson, 1913; and others). Recently there has been a resurgence of interest in this subject, and some workers have definitely implicated cockroaches in outbreaks of gastroenteritis.

Antonelli (1930) recovered typhoid bacilli from the feet and bodies of *Blatta orientalis* Linnaeus which he found in open latrines during two small outbreaks of typhoid fever. Mackerras and Mackerras (1948), studying gastroenteritis in children in a Brisbane hospital, isolated two strains of *Salmonella* from *Periplaneta americana* (Linnaeus) and *Nauphoeta cinerea* (Olivier) that were caught in the hospital wards. Graffar and Mertens (1950) isolated *Salmonella typhimurium* from *Blattella germanica* (Linnaeus) captured in a hospital in Brussels. These latter workers were only able to check the epidemic of gastroenteritis among children by ridding the hospital nursery of cockroaches. Bitter and Williams (1949) have isolated three species of *Salmonella* from the hind gut of *P. americana* captured in a hospital, private home, and sewer manholes.

It is significant that four strains of poliomyelitis virus have recently been isolated from *Periplaneta americana*, *Supella supellectilium* (Serville), and *Blattella germanica,* which were collected on the prem-

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ises of paralytic poliomyelitis patients (Syverton et al., 1952). In addition to harboring bacteria and viruses, cockroaches also harbor pathogenic protozoans and nematodes. The Surinam cockroach, *Pycnoscelus surinamensis* (Linnaeus), is the vector of the eyeworm of poultry (Fielding, 1926), and the American cockroach can carry, mechanically, hookworm of man (Porter, 1930) ; the latter species can also transmit, experimentally, intestinal flagellates such as *Giardia* from man to rat (Porter, 1918). Although these examples could be multiplied, it is apparent that, as Bitter and Williams (1949) have stated, tolerance of cockroaches around man's habitations is unwarranted ; it may even be dangerous.

There are about 450 genera and more than 3,500 species of cockroaches (Rehn, J. W. H., 1951). Practically nothing is known of the biology of most species. Very little is known of the biologies of the cockroaches associated with man, except for the more common pests such as the German, American, and oriental cockroaches. Yet less than 1 percent of the known species are domiciliary pests (Rehn, J. A. G., 1945). This is a fertile field for future work.

Reproduction, enabling the individual to increase its kind many times, is a vital factor in the biology of an insect species. Only rarely do swarms of insects invade a locality from a distant point ; each community usually raises its own insect pests (Metcalf and Flint, 1939). Cockroaches illustrate this principle perfectly. Hence the reproduction of cockroaches is a subject of more than academic interest. Reproduction is a phase of cockroach biology that demonstrates the diversity of behavior that has evolved in this relatively ancient group. In the following pages we shall describe, among several species of cockroaches, these aspects of reproduction : courtship, copulation, reproductive organs and fertilization, parthenogenesis, the oötheca, oviposition and hatching, and egg parasites.

COURTSHIP

In general the courting behaviors of the species of cockroaches that have been studied appear to be similar in many respects ; characteristic differences, however, lend interest to the study of each additional species. The writers (1952) have studied *Blattella germanica, Blatta orientalis,* and *Periplaneta americana* and have analyzed the stimuli involved in the courting behavior of the German cockroach. We could not demonstrate distance attraction between males and females of *B. germanica;* yet, when a sexually active male comes in physical contact with the female he responds with a characteristic courting behav-

ior. The male turns around so that his terminal abdominal segments are toward the female, and he raises both front and hind wings to an angle of 45° to 90° (pl. 1, fig. 1). In this way he exposes glandular areas on his abdominal terga which emit a secretion that attracts the female when she is close to him. A responsive female will feed (pl. 1, fig. 2) on the male tergal-gland secretion, and as she does, the male pushes backward and grasps the female genitalia. In *B. germanica* the male must make contact with the female before he will court. Mutual sparring with the antennae between the sexes and movement by the female are important actions in stimulating the male to court. The male courting response (i.e., raising the wings) is the overt expression of male sexual stimulation; it can also be induced by stroking or touching a receptive male's antennae with antennae (pl. 1, fig. 1), legs, abdomen, or wings, which have been removed from a female.

The raising of the male's wings during courtship, or just prior to copulation, apparently is characteristic of those species of cockroaches in which the males have wings. Raising of the wings has been observed in the three domestic species previously mentioned and also in *Leucophaea maderae* (F.) (Sein, 1923); *Blaberus craniifer* Burm. [= *B. fusca* Brunner (Rehn and Hebard, 1927)] (Saupe, 1928; Nutting, 1953); *Supella supellectilium* (Roth, 1952); *Blattella vaga* Heb. and *Nauphoeta cinerea* (Roth and Willis, unpublished data).

Chemical as well as mechanical stimuli are involved in the courting behavior of *Blattella germanica*. This is shown by the fact that a substance that is sexually stimulating to males can be isolated from females. The cuticular surface of the cockroach is covered with a freely exposed grease (Ramsay, 1935; Kramer and Wigglesworth, 1950). Presumably the sex substance is present in the cuticular grease, because this material can easily be rubbed off from females onto males to make the latter sexually stimulating to other males. The available evidence indicates that sex discrimination by the male German cockroach is mainly effected by contact chemoreception.

The sexual behavior of *Blattella germanica*, in terms of stimulus response and releaser mechanisms, may be summarized as follows:

Male makes antennal contact with the female $\longrightarrow$ Male courts = raises wings (releaser = mutual antennal fencing between sexes; chemical stimulus on the female; movement of the female) $\longrightarrow$

Female feeds on the tergal-gland secretion of the male (releaser = tergal-gland secretion) $\longrightarrow$ Copulation (releaser = feeding by the female on the male's tergal-gland secretion)
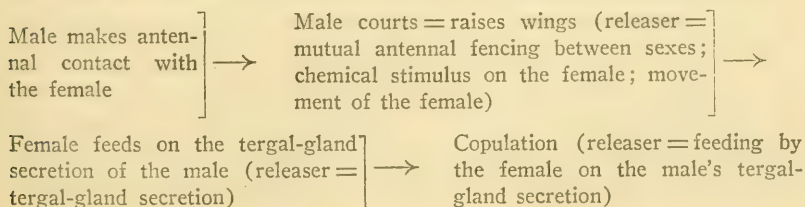
The male receives the female sex stimulus by means of receptors that are present on his antennae and probably on his mouthparts.

It is highly probable that in those species of cockroaches in which *only* the males have a distinctive, externally visible tergal gland, the function of this gland is to entice the female into a position in which mating can occur. Feeding by the female on the glandular secretion or over the dorsal abdominal surface of the male cockroach has been observed in *Blattella germanica* (Sikora, 1918; Wille, 1920; Roth and Willis, 1952) ; *Blatta orientalis* (Roth and Willis, 1952) ; *Ectobius lapponicus* Linnaeus and *Ectobius sylvestris* (Poda) (Konček, 1924) ; *Supella supellectilium* (Roth, 1952) ; *Blattella vaga, Eurycotis floridana* (Walker), *Nauphoeta cinerea,* and *Leucophaea maderae* (Roth and Willis, unpublished data). The external appearance of the tergal gland may vary considerably between species and genera (cf. pl. 2, figs. 6-8) ; this structure has considerable taxonomic value (Hebard, 1917; Rehn, J. A. G., 1931; Ramme, 1951). Frequently the glandular area is a depression in one (pl. 2, figs. 7, 8) or sometimes two (pl. 2, fig. 6) of the abdominal tergites and has a mass of secretory cells lying beneath the epidermis. Groups of setae or hairs are often present (pl. 2, fig. 8). In *B. orientalis* the female moves her mouthparts actively over the male's dorsum; yet the source of the male's secretion (if any) is still unknown. Tergal glands are found on the dorsum of the male, female, and nymphs of the oriental cockroach (Minchin, 1888), but they apparently have nothing to do with sex behavior. The contents of these glands have the distinctive odor of the oriental cockroach (Haase, 1889).

In Hawaii, Bridwell (1921), while walking in Palolo Valley at night, saw 50 to 75 *Periplaneta americana* performing their "mating dance" in the middle of the road. In this species the male sexual behavior is released by an odorous material secreted by the female. The source of the sex attractant in the female is unknown, but it is a material that readily rubs off from the female and can be perceived by the male at a considerable distance. By keeping unmated females in containers lined with filter paper, we have collected the attractant on the paper from which the active material was extracted in crude form with petroleum ether. The attractive female odor alone suffices to stimulate the male of *P. americana* to overt sexual activity. Males will even attempt to mate with pieces of paper or glassware that have been in contact with virgin females. Paper taken from jars containing old, nonvirgin females did not stimulate males, indicating that the sex attractant is produced chiefly by unmated females (Roth and Willis,

1952). However, it is possible that a mated female may again become attractive (i.e., secrete the attractant) sometime during her lifetime. Neither we nor Gupta (1947) have observed males of the American cockroach courting the female prior to copulation, as is done by the German and oriental males. The male American cockroach is much more direct in his approach, and the female appears to be relatively passive; movement of the female's mouthparts over the male's dorsum is not a necessary stimulus for the male to attempt to copulate, as in the other two species.

Summarized, the sexual behavior of *Periplaneta americana* is as follows:

Male in the vicinity of the female → Male searches for female (releaser = sex-odor from female) → Male raises wings and attempts to clasp female's genitalia (releaser = sex-odor from female) → Copulation (releaser = sex-odor from female)
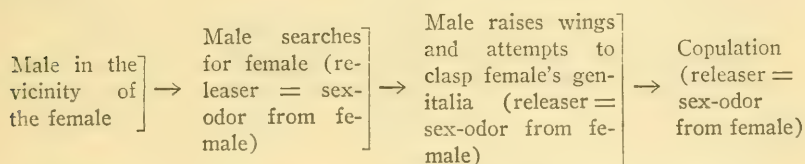
In the behavior of *Blattella germanica* there was a succession of releasers that alternately brought forth responses from both partners before culmination of the sexual act. In contrast the sex odor from the female seems to be the only mechanism involved in releasing a chain of responses by the male of *P. americana* that ends in copulation. However, the female of *P. americana* may or may not be receptive to the male's advances. Perhaps there is an as-yet-undetermined releaser that regulates the female's response.

The males of some species of cockroaches perform characteristic body movements during courting behavior. The male of *Leucophaea maderae* stands near the female and rapidly moves his body up and down. According to Sein (1923) the male raises the anterior section of his body and strikes his abdomen against the ground producing a prolonged tapping sound. However, we have seen males of this species move the anterior parts of their bodies up and down rather than their abdomens. The male of *Blaberus craniifer* raises himself on his legs and makes trembling movements with the abdomen (Saupe, 1928); we have observed the male of this species behave in a similar manner and also butt the female with his head or pronotum. The wingless male of *Eurycotis floridana* stands near the female, repeatedly vibrates his body from side to side, and extends his abdomen slightly revealing the light-colored, intersegmental membrane between the sixth and seventh tergites (pl. 1, fig. 3); the female then behaves as described earlier for the other species, applying her mouthparts to the male's dorsum starting near the end of the abdomen (pl. 1, fig. 4) and

working up to the first abdominal tergite (pl. 1, fig. 5), on which is located a small glandular area bearing a patch of setae.

COPULATION

The terminal abdominal segments are modified to form the male external genitalia, which consist of genital lobes or phallomeres that are associated with the opening of the ejaculatory duct. These structures are described by Snodgrass (1937) and van Wyk (1952). Certain phallomeres of the adult cockroach form highly complex structures with horny processes or hooks. In the female the external genitalia include the ovipositor and associated sclerites and the openings of the oviduct, accessory glands, and spermathecae (Snodgrass, 1937).

As we mentioned earlier, while the female *Blattella germanica* feeds on the male's glandular secretion, he pushes his abdomen backward so that the female is directly above him. This is the position (pl. 1, fig. 5) just prior to copulation, and it is assumed by most, if not all, species of cockroaches. We have seen this method of initiating copulation, in the female superior pose, in these genera: *Blattella, Blatta, Periplaneta, Eurycotis, Nauphoeta, Supella,* and *Leucophaea.* Saupe (1928) and Nutting (1953) observed that the female of *Blaberus craniifer* also straddles the abdomen of the male just prior to successful copulation. Because this behavior is so similar among different genera, we are convinced that it is a regular feature in the copulation of *Leucophaea* although we have seen it only once. However, Pessoa and Correa (1928) state that the male of *L. maderae* "draws near [the female] and turns his body in an opposite direction, to that of the female, placing the posterior extremity of his abdomen against [the] posterior extremity of the abdomen of the female." We cannot reconcile their statement with our observations and those of van Wyk (1952) who saw "that the male carries the female on his back at the beginning of copulation with their heads in the same direction and the venter of the female resting on the dorsum of the male and that they later assume an end to end position."

The relationships of the external genitalia during copulation have been studied in *Blattella germanica* (Khalifa, 1950), *Periplaneta americana* (Gupta, 1947), and *Polyzosteria limbata* Burm. (Chopard, 1919). As the male German cockroach pushes backward under the female, he extends his hooked left phallomere. This appendage clasps a large sclerite located near the female's ovipositor. If a hold is secured on the sclerite, the male moves out from under the female, and the couple assume the opposed position in which their heads face in

opposite directions. This is the copulating position (pl. 3, figs. 9-14) assumed by all species of cockroaches in which the act has been observed; we have also seen *Nauphoeta cinerea* in this position, and it has been observed in *Polyzosteria limbata* (Chopard, 1919) and *Parcoblatta pensylvanica* (Rau, 1940b). Once in the final opposed position, two lateral hooks lying on either side of the anus of the male hold the ovipositor near its base. A small crescentic sclerite, which lies on one side near the right phallomere, grips the ovipositor firmly in a medial position (Khalifa, 1950). In successful matings cockroaches remain in copula in the end-to-end position for at least 30 minutes. Usually copulation lasts more than an hour, and Nutting (1953) noted many pairs of *Blaberus craniifer* that remained joined for 4 hours or more. Statements in the literature to the effect that copulation is rapid, lasting only a few seconds or less, were based on observations of unsuccessful matings.

INTERNAL REPRODUCTIVE ORGANS AND FERTILIZATION

The internal genital organs of male cockroaches consist of a pair of testes, genital ducts, accessory genital glands, seminal vesicles, and a phallic gland (Snodgrass, 1937). In *Blattella germanica* each testis consists of four rounded sacs or vesicles which open into a common genital duct. Each vesicle is divided into several zones which contain sex cells in various stages of development; the spermatozoa are contained in the zone nearest the genital duct (Wassilieff, 1907). The testes of *Blatta orientalis* mature at the end of nymphal development and atrophy in the adult; hence the spermatozoa must be stored in the seminal vesicles before the testes degenerate (Snodgrass, 1937). The diploid number of chromosomes (including the X chromosome) has been determined during spermatogenesis for several species of cockroaches; *Loboptera decipiens* Germ. has 34, *Blattella germanica* 24, *Periplaneta americana* 34, *Periplaneta australasiae* (Fabricius) 28, *Blatta orientalis* 48, and *Blaberus fusca* [=*B. craniifer*] 74 (Suomalainen, 1946). All species of cockroaches that have been investigated are XO in the male (White, 1951).

The sperm of cockroaches is transferred to the female by means of a capsule or spermatophore (pl. 4, fig. 17) formed from the secretions of the male accessory sex glands. Spermatophores have been found in males of *Blatta orientalis* (Zabinski, 1933); *Blattella germanica* (Khalifa, 1950; Roth and Willis, 1952); *Periplaneta americana* (Gupta, 1947; Roth and Willis, 1952); *Leucophaea maderae* (van Wyk, 1952); *Eurycotis floridana* and *Nauphoeta cinerea* (Roth

and Willis, unpublished data); and *Blaberus craniifer* (Nutting, 1953). Presumably spermatophores are produced by other blattids as well. Nutting (1953) observed that the spermatophore of *B. craniifer* may be retained in the female's genital pouch for several days, one female carrying her spermatophore intact for 5 days, whereas most of the cockroaches previously noted retain the spermatophore for a shorter period.

The accessory glands ("mushroom-shaped gland") in the oriental cockroach consist of 350 to 450 small, intermediate, and large-sized tubes. Based on their staining reactions, Jurecka (1950) distinguished 6 types of tubes in males of *Blatta orientalis*; their period of most active secretion occurs for several hours following metamorphosis into the adult. This is followed by a resting period from the time secretion ceases until copulation, at which time the secretions and the spermatozoa are ejected and molded into a spermatophore. The spermatophore consists of a number of capsules full of spermatozoa (Qadri, 1938); the female carries it 2 or 3 days then drops it (Zabinski, 1933).

Van Wyk (1952) described the male accessory glands in *Leucophaea maderae*. These are composed of approximately 30 to 40 tubules arranged in three groups. He assumes that each group of glands is responsible for one of the three layers of the spermatophore. The spermatophore of *L. maderae* remains in the genital chamber of the female for about a day before it dries and drops from the female.

If the males of *Blattella germanica* are prevented from mating, the larger accessory gland tubes ("utriculi majores") become so distended with their chalk-white secretion (pl. 4, fig. 15) that they may fill most of the abdominal cavity. After copulation the tubes of the accessory glands are almost emptied of secretion (pl. 4, fig. 16) (Roth and Willis, 1952). The following description of spermatophore formation is taken from Khalifa (1950). The spermatophore in *B. germanica* begins to form in the male as soon as the copulating pair are securely hooked together. In this species the layers of the spermatophore are formed from three protein secretions produced by distinctly different groups of accessory gland tubules. The walls of the tubules consist of a layer of glandular cells surrounded by a muscular layer. The accessory glands open into the ejaculatory duct. The secretions from the various accessory glands pour into the pouch of the ejaculatory duct, and when the spermatophore is completely developed, it distends the pouch. At one point in the formation of the spermatophore, sperm flow from each seminal vesicle into a milky middle layer within the spermatophore; each of the two sperm masses forms

a separate sac. Following formation, the completed spermatophore descends the ejaculatory duct and is pressed by the male's endophallus against three sclerites lying on the left-hand side of the spermathecal groove in the female serve for holding the spermatophore. The tip surround the opening of the common oviduct, and the spermathecal groove in the female serve for holding the spermatophore. The tip of the spermatophore, which contains the openings of the sperm sacs, is inserted into the spermathecal groove so that the two spermathecal pores of the female come in direct contact with the two openings of the sperm sacs. The spermatophore remains in the genital chamber of the female for about 12 hours, during which time the sperm migrate to the spermathecae. In *B. germanica* the sperm have to be chemically activated before they leave the spermatophore; probably the activating chemical originates from a pair of spermathecal glands which are associated with the spermathecae of the female. The empty spermatophore dries and shrinks and is eventually dropped by the female. During her lifetime a female may copulate and receive a spermatophore more than once (Khalifa, 1950), and a male may also copulate and produce a spermatophore more than once (Cros, 1942; Roth and Willis, 1952). The work of the male is now done.

The internal reproductive organs of the female cockroach consist of a pair of ovaries, oviducts, spermathecae, and specialized accessory (colleterial) glands which produce the various secretions that go to make up the oötheca or egg case (Snodgrass, 1937, 1952). In *Periplaneta americana* each ovary usually consists of eight ovarioles. Each ovariole is made up of an elongated egg tube and a short pedicel which connects the basal end of the egg tube to the oviduct. The anterior part of the egg tube consists of a germarium made up of oöcytes or incompletely formed eggs in the early stages of differentiation, and the remainder or vitellarium contains oöcytes in various stages of growth. In the newly emerged adult female all of the oöcytes are relatively small, although a gradation in size is noticeable, the largest being at the base (pl. 4, fig. 18). About 8 days after copulation the basal oöcyte reaches a final size of about 3 mm. in length; it is now encased in a chorion, and is ready for deposition (pl. 4, fig. 19). After oviposition of the basal oöcyte (pl. 4, fig. 20), the next oöcyte in line completes its growth; this cycle results in a succession of mature eggs about every 8 days (Gier, 1936). Actually by the time an oötheca is completely formed and deposited, the basal oöcytes of the ovary are already well developed (pl. 4, fig. 21). Scharrer (1943, 1946) found that the development of the eggs of *Leucophaea maderae,* at least for a certain period of time, is under the hormonal control of the corpora

allata, endocrine glands situated near the brain. Apparently the hormone from these glands is not required for the reproductive activity of the male (Scharrer, 1946).

The external genital structures of the female cockroach lie concealed within a cavity at the end of the abdomen that is closed posteriorly by the apical lobes of the seventh sternum (Snodgrass, 1952). This cavity is divided into a genital chamber, which lies proximal to the base of the ovipositor, and the oöthecal chamber, or vestibulum, which is the posterior part of the cavity. The ovipositor is composed of three pairs of fingerlike valvulae and two pairs of valvifers (Brunet, 1951). The relation of the external genitalia to the formation of the oötheca is discussed below.

Dewitz (1885, 1886) described how sperm enter the eggs of *Blatta orientalis*. The eggs become bent in the oviducts and pass singly into the genital chamber where they approach the spermathecal opening. As the egg passes over the sensory hairs that are found mainly around the spermathecal pore, muscles of the spermatheca contract and force out the sperm. The numerous micropyles, through which the sperm enter, are found at the anterior pole of the egg and come in contact with most of the sperm. The sperm appear to be attracted to the surface of the egg and move clockwise rather than in a straight line. The eggs are fertilized as they pass along the vestibulum.

PARTHENOGENESIS

Parthenogenesis is considered to be a rare occurrence among cockroaches. The best-known example of this type of reproduction in blattids is the Surinam cockroach *Pycnoscelus surinamensis*, which in the Indo-Malaysia area is bisexual; but in North America and Europe, where it has been introduced, it is parthenogenetic, producing only females (Màtthey, 1948). It is generally believed by most observers that parthenogenesis does not occur in our domiciliary species or at most is a rare occurrence in the American cockroach. However, only recently we have found that some unfertilized eggs of four species of our common domestic cockroaches may complete their development, and that in two of the species some of the eggs may hatch.

Normally, none of the unfertilized eggs of *Supella supellectilium* or *Blattella germanica* hatch, and only a small number of the eggs in an oötheca sometimes complete development (pl. 6, figs. 36-40). However, we dissected an egg case of *S. supellectilium* and removed a fully developed parthenogenetic embryo; this individual shed its embryonic membrane while we photographed it (pl. 6, figs. 41-45); the nymph

was successfully reared, eventually becoming an adult female. On the other hand, some unfertilized eggs of *Blatta orientalis* and *Periplaneta americana* do hatch normally. In fact in *P. americana,* which has been claimed to be a species in which parthenogenesis is a possible but infrequent phenomenon (Griffiths and Tauber, 1942), we have found that hatching of unfertilized eggs is not uncommon; of 110 unfertilized females, 94 (85 percent) have produced oöthecae from which some eggs hatched (pl. 6, figs. 46-48).

In our experiments, which are still in progress, we have obtained a total of 2,433 undamaged oöthecae from unfertilized *P. americana* females; from these oöthecae at least some of the unfertilized eggs in 1,030 (42 percent) hatched and the nymphs left the oötheca; in 779 (32 percent) some of the embryos developed until their pigmented eyes were visible, or to an older stage, but failed to hatch; and the eggs in 624 oöthecae (26 percent) failed to develop. More than 500 adult females have been reared from parthenogenetically developed eggs; no males have resulted from the unfertilized eggs. These parthenogenetically produced females lay relatively few eggs and these eggs usually fail to hatch. However, if mated, these females frequently produce eggs that hatch. Parthenogenesis in *P. americana* is certainly less important than bisexual reproduction in the preservation of this species in nature. However, parthenogenesis could operate among the wild population, and in a temporary absence of males an unfertilized female could transmit some of her germ plasm beyond the end of her own life span.

THE OÖTHECA

FORMATION

Kadyi (1879) and others have described the formation of the oötheca of *Blatta orientalis.* The secretions from the colleterial glands flow out over the inner surface of the vestibulum or oöthecal chamber in a sheet that surrounds and is stretched by the incoming eggs. The vestibulum is closed posteriorly by the apical lobes of the seventh sternum. As the forming oötheca presses against these lobes, a characteristic pattern (pl. 7, fig. 52) is imparted to the distal end of the oötheca (Wheeler, 1889). After a certain number of eggs have entered the vestibulum, the distal end of the oötheca emerges beyond the end of the abdomen. Pryor (1940a) has described the color changes: At first the projecting portion is an opaque white; within 3 or 4 hours it becomes transparent, changes first to pink, and then to reddish chestnut; the oötheca continues to darken after it is laid,

becoming almost black in about 3 weeks. During formation the anterior part of the oötheca remains soft and white, eggs still entering and being pushed to the rear. The similar formation of the oötheca by *Blattella germanica* has been well described by Wheeler (1889).

The organic axis of the egg when it is still within the ovary and oviduct of the female is oriented with the cephalic pole directed toward the head of the mother; the egg then emerges from the oviduct caudal end first and falls into the genital armature caudal end down (Hallez, 1885). Because the oötheca of the viviparous cockroach *Diploptera dytiscoides* Serville lies on its side within the brood sac, with the micropylar ends of the eggs directed toward the left wall of the brood sac, Hagan (1951) stated, "This fact is of considerable historic interest since it causes the embryos to develop with an orientation contrary to the principles of Hallez's law." However, Hallez postulated the orientation of the eggs within the ovarioles and oviducts, en route, so to speak, to the oötheca; hence Hallez's law is not applicable to a secondary orientation of the eggs which depends on any future position of the oötheca. Wheeler (1889) demonstrated this clearly with oöthecae of *Blattella germanica* in which embryos developed normally when the oöthecae were oriented in five different positions; he concluded that gravitation has no perceptible effect on the development of the eggs of this species, and that these eggs have their constituents prearranged and completely conform to Hallez's "loi de l'orientation de l'oeuf."

As the eggs move posteriorly, the valvulae of the ovipositor move them into the oöthecal chamber and in some way set them on end with their heads upward (Snodgrass, 1952). The eggs from the right ovary pass into the left side of the oötheca and vice versa (Kadyi, 1879; Wheeler, 1889; Wille, 1920). Gier (1947) found that some of the eggs of *Periplaneta americana* are placed wrong end up in the oötheca, and though development occurs normally, the nymphs cannot emerge from the egg case. We have seen this in *Supella* also. In the completed oötheca, the eggs are placed vertically and, except at the ends of the egg case, arranged in two rows with the axis of each egg in one row opposite the interval between adjacent eggs in the other row (pl. 4, fig. 24; pl. 6, fig. 35). Figures 25 to 34 (pl. 5) show the external appearance of an oötheca of *Eurycotis* as it was being formed.

From what we have seen of oötheca formation in so-called viviparous cockroaches (see pp. 25-28), it is similar to that described above. The eggs of *Pycnoscelus surinamensis, Nauphoeta cinerea,* and *Leucophaea maderae* are erected vertically in two rows in the oötheca

which stretches around them (pl. 11, figs. 74, 75; pl. 12, fig. 86) as in the oviparous species. In these three species the wall of the oötheca is relatively thin and membranous. The color varies from pale straw to amber. These oöthecae do not darken and remain quite transparent as does the oötheca of *Blaberus craniifer* (pl. 4, figs. 23, 24; pl. 11, fig. 82; pl. 12, fig. 94). The oötheca of *P. surinamensis* is complete, and although there is no differential keel, such as occurs in the oviparous species, there is a narrow, longitudinal slit between the thickened edges of the wall of the oötheca along its dorsal surface. The oötheca of *N. cinerea* is incomplete, similar to that of *B. craniifer,* and usually does not cover the micropylar ends of the eggs or parts of the sides of the last three eggs deposited. We have seen some egg cases of *N. cinerea* with eggs attached along the outside, apparently rolled back by the walls of the brood sac from the imperfectly covered anterior end of the egg case, as the female retracted the oötheca into the brood sac.

Shelford (1906) found that the oötheca of the viviparous cockroach *Panchlora virescens* is represented by a complete, thin, transparent membrane. However, the membrane forming the oötheca of *B. craniifer* is incomplete; as Saupe (1928) and Nutting (1953) point out, the edges of the oötheca are separated by the micropylar ends of the eggs (pl. 4, fig. 24). In *Diploptera dytiscoides* the oötheca is reduced to a thin membrane that covers no more than half of the egg mass (Hagan, 1951). Riley (1891a) dissected an "egg cluster" of *Panchlora viridis* and reported that the oötheca was only a membranous sheath enclosing about half the length of the eggs. He reported that in some egg cases of this species the eggs were arranged in a double row side by side, with no visible enveloping membrane. This latter condition seems doubtful; the membrane may have been so thin and colorless as to be nearly invisible. Or perhaps this was an abnormal condition; Gould and Deay (1940) and we have seen egg masses of *Periplaneta americana* deposited without an oötheca (pl. 7, fig. 58).

Among cockroaches that do not carry the oötheca internally during embryonic development, the hardened oötheca resembles insect cuticle. Both have been shown to be scleroproteins which are very similar if not identical chemically (Pryor, 1940a, b). However, the oöthecae of *Periplaneta americana* and *Blatta orientalis* contain no chitin (Campbell, 1929; Pryor, 1940a), a compound found in varying amounts in insect cuticles. Most of the materials which go to make up the oötheca are secreted by the colleterial glands (Pryor, 1940a; Brunet, 1952). The left colleterial gland secretes a water-soluble protein (Pryor, 1940a) and an oxidase (Brunet, 1952); the right gland produces a

fluid containing a dihydroxyphenol, specifically protocatechuic acid (3, 4-dihydroxy-benzoic acid) (Pryor et al., 1946). When the secretions from the right and left glands mix, the phenolic substance is oxidized, producing a quinonoid tanning agent; interaction of the tanning agent with the protein gradually hardens and darkens the oötheca (Pryor, 1940a). The oötheca also contains crystals of calcium oxalate (Kadyi, 1879); these crystals occur mixed with protein in the lumen of the left colleterial gland. When the diphenolic substances of the right gland mix with the protein of the left, the calcium oxalate may play a part in maintaining an optimum pH for the oxidation of the phenol (Brunet, 1952).

Certain valvulae of the ovipositor of oviparous species are modified to mold the oötheca, especially the crista or keel. Wigglesworth and Beament (1950) have shown this clearly in *Blattella germanica*. The chorion along the upper pole of each egg is expanded and forms a vacuolated ridge which lies below the crista of the oötheca of this species. In the keel above each egg, overlying the vacuolated ridge of the chorion, is a small, oval, air-filled cavity which has two lateral expansions that pierce the crista and thus connect with the outer air. These cavities are respiratory chambers which, with associated ducts, convey air to the membranes around the eggs. From the roof of the genital chamber of the female, elongated fingerlike genital appendages project downward into the soft part of the forming oötheca and hold the latest egg in place. Near the base of these fingerlike appendages is a pair of thumblike projections directed backward, which serve to mold the upper cavity of the oötheca and to orient the egg within it. At the base of the thumblike lobes is a small median lobe with a tiny sclerotized horn projecting on either side, which has the exact form of the respiratory chambers and is the die on which they are molded. The colleterial glands discharge their secretions at the base of the genital appendages, and the "horned die" molds the material providing a respiratory chamber and respiratory duct for each egg. In *Periplaneta americana* the third valvulae of the ovipositor are modified to form the "horned die" which molds the inner surface of the keel of the oötheca (Brunet, 1951).

These respiratory structures in the oöthecae of oviparous cockroaches, because of their relatively small connections with the outer air, retard loss of water by the eggs. The importance of this function is emphasized when part or all of the keel has been eaten by the cockroaches themselves (pl. 7, figs. 56, 57); the eggs in these damaged oöthecae usually fail to develop at room humidities, or if they do, rarely hatch. Under these conditions death undoubtedly follows ab-

normal loss of water. We have found that the rate of water loss from American cockroach eggs at low humidities is greatly accelerated after removal of the keel. Sometimes abnormal oöthecae are deposited in which the respiratory chambers are not differentiated in the keel (pl. 7, fig. 60).

The oöthecae of different species of cockroaches are quite distinctive as they may vary in size, shape, and the number of enclosed eggs (cf. pl. 4, fig. 23; pl. 6, figs. 36, 39; pl. 7, figs. 49, 59; pl. 12, fig. 87). Lawson (1951, 1952, 1953) has studied the structural features of the oöthecae of several species of oviparous cockroaches. Each egg cell in the oötheca is indicated externally by an evagination (forming half of the respiratory chamber) on each side of the upper part of the keel (Lawson, 1951). Thus the number of respiratory chambers and their corresponding canals (pl. 7, fig. 53), which show clearly in the keels of certain oöthecae (e.g., *Periplaneta americana, Blatta orientalis,* pl. 7, figs. 49, 59, and *Eurycotis floridana*), is often a good criterion for the number of eggs in the oötheca. This relationship was recognized by some early workers. For example Sells (1842) described an oötheca of *B. orientalis* with 22 to 24 teeth along the serrated edge, which corresponded with the number of eggs contained within. This is rather a large number of eggs for the oriental cockroach, and Sells may have been dealing with another species. We have found that in abnormally small oöthecae of *P. americana,* usually those containing fewer than eight eggs, the number of respiratory chambers and ducts is frequently not the same as the number of eggs in the oötheca (pl. 7, figs. 54, 55). Wille (1920) also found that the number of egg cells in the oötheca of *Blattella germanica* did not always correspond to the number of teeth in the keel. Occasionally, eggs may be deposited without the formation of a protective oötheca (pl. 7, fig. 58), or an oötheca may be formed which contains no eggs.

REPRODUCTIVE POTENTIAL

The maximum number of eggs deposited at one time by a cockroach is largely dependent on the number of ovarioles comprising the ovaries. The number of eggs per oötheca varies with the species. In the oriental cockroach, a species which normally has 8 ovarioles per ovary, the normal number of eggs per oötheca has been stated to be 16 (Seiss, 1896; Rau, 1924; Gould and Deay, 1940). Because there are usually 8 ovarioles in each ovary, it is often stated that *Periplaneta americana* normally deposits 16 eggs. However, the oöthecae of this species frequently contain fewer than 16 eggs. Disease or some ab-

normality of one or more of the ovarioles will reduce the number of eggs produced in an oötheca (Gier, 1947). We have records of one female American cockroach which consistently deposited six to eight fertile eggs per oötheca; dissection revealed that she had one normal ovary, whereas the other had degenerated; several eggs had been liberated into her body cavity. The number of eggs per oötheca that have been reported for various species of cockroaches are given in table 1. However, because this information is not available for many species, we have included some data on the number of nymphs hatching per oötheca. Counts of nymphs are usually smaller than egg counts because the undeveloped eggs or unhatched eggs left in the oötheca are not included.

Among the domiciliary oviparous cockroaches at least, the number of egg cases produced by a female during her lifetime is even more variable than the number of eggs per egg case. There is comparatively little information about the egg-laying potential of other cockroaches. Table 2 summarizes the more comprehensive data. Certain unique values have been included because they extend the range of observations.

Temperature, fecundation, and age of the female influence the rhythm of egg and oötheca production of *Blatta orientalis* (Ricci, 1950); the rhythm accelerates with an increase in temperature, resulting in more oöthecae in a given period of time. Diet may also affect the reproductive ability of blattids. Chauvin (1949) found that the fecundity of *Blattella germanica* decreased considerably on a diet deficient in sterols, and the reproductive ability of these insects disappeared almost entirely after two or three generations had been reared on the experimental diet. Noland et al. (1949) also found that the oöthecae produced by German cockroaches reared on certain synthetic diets were often small, deformed, or shriveled, and only a small proportion of the eggs hatched. This nutritional effect on reproduction could not be traced to any known deficiency in the diet, and these workers suggested that a "reproduction factor" was lacking from the diets. In *Periplaneta americana* specific diets such as peptone or dextrose reduced the frequency of oötheca production as well as the number of eggs in the oötheca (Gier, 1947). However, female adults of *Blatta orientalis* maintained on a diet containing only 2.5 percent protein deposit normal oöthecae (Lafon, 1951). The lack of vitamin E in the diet for periods of 4 to 8 months does not influence the vitality of mature sperm of *B. orientalis* (Kudrjaschow and Petrowskaja, 1937).

TABLE 1.—*Number of eggs per oötheca, or nymphs hatched per oötheca, of various species of cockroaches*

NUMBER OF EGGS OR NYMPHS PER OÖTHECA

SPECIES	Mean	Minimum	Maximum	No. of oöthecae	Stage	SOURCE
Blaberus craniifer Burmeister	23.3	11	38	8	Nymphs	Saupe, 1928
Do	36.4	23	45	14	Eggs	Nutting, 1953
Blatta orientalis Linnaeus	16[a]	..	..	..	Eggs	Rau, 1924
Do	13.8[b,c]	5	15	27	Nymphs	Gould and Deay, 1940
Do	..	8	16	..	Eggs	Cros, 1942
Do	14	1	18	249	Eggs	Roth and Willis, unpublished data
Blattella germanica (Linnaeus)	40	28	58	34	Eggs	Wheeler, 1889
Do	41	34	48	20	Eggs	Girault, 1911
Do	37	18	50	40	Eggs	Ross, 1929
Blattella humbertiana (Saussure)	..	..	40	..	Eggs	Takahashi, 1940
Blattella vaga Hebard	31	15	39	150	Eggs	Roth and Willis, unpublished data
Ectobius panzeri Stephens	12[b]	9	13	11	Eggs	Brown, 1952
Epilampra wheeleri Rehn	..	35	50	..	Nymphs	Sein, 1923
Eurycotis floridana (Walker)	23	15	25	100	Eggs	Roth and Willis, 1954a
Ischnoptera deropeltiformis (Brunner)	39[b]	38	40	2	Nymphs	Rau, 1947
Leucophaea maderae (Fabricius)		30	35	..	Nymphs	Scharrer, 1951
Do	40[a]	..	..	..	Eggs	van Wyk, 1952
Nauphoeta cinerea (Olivier)	32.4	26	40	20	Eggs	Roth and Willis, unpublished data
Parcoblatta pensylvanica (Degeer)	32[a]	..	..	..	Eggs	Gould and Deay, 1940
Do	24.6[b]	18	30	29	Nymphs	Rau, 1940b
Periplaneta americana (Linnaeus)	16	12	18	7	Eggs	Lefroy, 1909

(*continued*)

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TABLE 1.—*Concluded*

NUMBER OF EGGS OR NYMPHS PER OÖTHECA

SPECIES	Mean	Minimum	Maximum	No. of oöthecae	Stage	SOURCE
Periplaneta americana (Linnaeus)	16[a]	..	24[d]	100+	Eggs	Gould and Deay, 1940
Do	11.9[b]	6	16	40	Eggs	Rau, 1940a
Periplaneta australasiae (Fabricius)	26	22	28	20	Eggs	Girault, 1914
Periplaneta fuliginosa (Serville)	24[a]	..	..	..	Eggs	Gould and Deay, 1940
Do	24[b]	22	26	4	Nymphs	Rau, 1945
Pycnoscelus surinamensis (Linnaeus)	24	14	42	..	Eggs	Zappe, 1918
Do	..	..	48	1	Eggs	Caudell, 1925
Do	23.8[b]	11	32	6	Nymphs	Saupe, 1928
Do	18.2[b]	3	34	36	Nymphs	Roeser, 1940
Do	..	30	36	..	Eggs	Schwabe, 1949
Do	25.8	17	34	20	Eggs	Roth and Willis, unpublished data
Supella supellectilium (Serville)	12	..	..	..	Nymphs	Cottam, 1922
Do	13.7	..	..	224	Nymphs	Gould and Deay, 1940
Do	16	11	18	27	Eggs	Roth and Willis, unpublished data
Symploce hospes (Perkins)	19.5[b]	18	20	4	Nymphs	Illingworth, 1915

[a] Stated to be the normal or usual number, or number in a perfect capsule.
[b] Calculated from source data.
[c] Gould and Deay (1940) give a mean of 14.4 nymphs hatched from all (number not stated) fertile capsules in their experiment. Rosenfeld (1910) gives an average of 24 eggs per oötheca (10 capsules) with a range from 10 to 28; this high value may have resulted from a misidentification of *P. fuliginosa* as *P. americana.*
[d] Maximum based on one capsule only.

TABLE 2.—*Production of oöthecae by various species of cockroaches*

NUMBER OF OÖTHECAE PER FEMALE

SPECIES	Mean	Minimum	Maximum	No. ♀♀	Temp. °C.	SOURCE
Blatta orientalis Linnaeus..........	2.5[a]	1	4	55	..	Rau, 1924
Do	9[a]	1	18	5	Room	Gould and Deay, 1940
Do	6[a]	4	9	3	28°[b]	do.
Do	..	..	22[c]	1	22-24°	Ricci, 1950
Do	11.5	0	27	30	29-37°	Roth and Willis, unpublished data
Blattella germanica (Linnaeus).......	..	..	4	..	22°	Wille, 1920
Do	1.7[a]	1	2	16	35°	Ross, 1929
Do	5.5[a]	4	8	6	Room	Gould and Deay, 1940
Do	7.3[a]	2	12	26		Morisset, 1946
Do	5.1[a]	3	9	14	21-30°[b]	Gerber, 1950
Do	4.5	0	7	58[d]	29-37°	Roth and Willis, unpublished data
Parcoblatta pensylvanica (Degeer)......	7.8	4	11	5	Room	Rau, 1940b
Periplaneta americana (Linnaeus)......	..	..	22[e]	1	Room	Gould and Deay, 1940
Do	21.5	5	46	10	..	Klein, 1933
Do	55.8[a]	16	90	16	Room	Gould and Deay, 1940
Do	50.8[a]	13	76	5[f]	28°[b]	do.
Do	28.9	10	52	20[f]	17-28°	Griffiths and Tauber, 1942
Do	10.6	3	21	15[g]	17-28°	do.
Periplaneta australasiae (Fabricius)......	17	..	17[h]	1[i]	..	Spencer, 1943
Periplaneta fuliginosa (Serville)........	17	..	..	4	Room	Gould and Deay, 1940
Pycnoscelus surinamensis (Linnaeus).....	1.4[a]	1	3	26	..	Roeser, 1940
Supella supellectilium (Serville)........	7.5[a]	5	9	4	..	Cottam, 1922
Do	13.7	6	22	7	Room	Gould and Deay, 1940
Do	11.5	1	27	8	Constant	do.
Symploce hospes (Perkins)............	..	..	38[j]	1	..	Illingworth, 1915

a Calculated from source data.
b Source data, given as °F., converted to nearest °C.
c During a period of 202 days, not the entire adult life of female.
d Virgin females which produced infertile eggs.
e During a period of 150 days, not the entire adult life of female.
f Females kept in 1,000 cc. containers.
g Females kept in 250 cc. containers.
h During a period of 100 days, not the entire adult life of female.
i Unfertilized.
j During a period of 210 days, not the entire adult life of female.

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OVIPOSITION AND HATCHING

As we shall show below, cockroaches exhibit, or have exhibited at some time during their phylogeny, a variety of ovipositional behaviors from single-egg oviparity through multiple-egg oviparity and ovoviviparity to viviparity. Unfortunately these descriptive terms have been used so diversely in the literature that their use creates confusion (see Hagan, 1951). We shall make no attempt to redefine these terms, but shall point out their limitations with respect to cockroaches, as they appear to us.

Birth in insects is characterized as *oviparous,* in which the birth product is an egg covered by a chorion or shell, or *viviparous,* in which the egg hatches within the mother and the birth product is an embryo devoid of a chorion (Hagan, 1951). Viviparity may be further divided, with respect to cockroaches, into *ovoviviparity,* in which the egg contains enough yolk to nourish the embryo until hatching, and *pseudoplacental viviparity,* in which the embryo possibly derives a part of its nutriment from the mother by means of a pseudoplacenta (Hagan, 1951).

THE OVIPAROUS COCKROACHES

In marked contrast to the viviparous species, which carry the oötheca internally, the oviparous species of cockroaches always carry the oötheca externally (pl. 5, figs. 32-34; pl. 8, figs. 63, 64). The period during which the oviparous female carries the oötheca before dropping it depends on the habits of the genus and external factors such as temperature, etc. Most genera, the ovipositional habits of which are known, deposit the oötheca on the substratum shortly after its formation, within a few days or less. Genera in which this habit has been observed are *Periplaneta* (Sein, 1923); *Blatta* (Miall and Denny, 1886; Moore, 1900); *Supella, Parcoblatta, Cariblatta, Eurycotis* (Roth and Willis, unpublished data); and others. Many species carry the oötheca with the keel upward, as it was formed, until deposition. This condition may be observed in *Blatta orientalis, Periplaneta americana, P. australasiae, P. fuliginosa, Supella supellectilium, Cariblatta lutea minima* Hebard, *Eurycotis floridana,* and undoubtedly others.

On the other hand, certain genera of cockroaches rotate the oötheca 90° to the left or right and carry it until, or shortly before, the eggs hatch. This habit has been described in *Blattella germanica* (Wheeler, 1889; Wille, 1920; Ross, 1929; Woodruff, 1938; Gould and Deay, 1940; Pettit, 1944; Rau, 1944). It has also been observed in other

species of this genus: *B. lituricollis* (Walker) (Zimmerman, 1948) ; *B. humbertiana* Saussure (Takahashi, 1940) ; *B. vaga* (we have observed the young hatching from an oötheca that was still being carried by the female; see pl. 8, fig. 65). The direction of rotation of the egg case of *B. germanica* has been reported to be toward the right (Wheeler, 1889; Wille, 1920; Ross, 1929) or toward the left (Gould and Deay, 1940). Possibly the direction of rotation is of genetic origin and is relatively constant within a particular laboratory colony. The oötheca seems to be held in position by pressure of the encircling genital armature (Ross, 1929). Rarely *B. germanica* may form a new oötheca before the empty one is discarded, and the empty oötheca remains attached to the fresh one (pl. 7, fig. 62). We have also seen instances of *Periplaneta americana* depositing two oöthecae attached to each other by their ends; formation of the second was started before the first was dropped, and the soft end of the new oötheca curved around the hard end of the old one.

The oviposition behavior of *Ectobius panzeri* Stephens combines aspects of both the *Blatta* and *Blattella* types just described. Brown (1952) reported that *E. panzeri* usually rotates the oötheca through 90° and most often to the left. Some females carry the egg case for as long as 16 days, but the majority deposit it in less than 10 days. This species winters in the egg, and the nymphs hatch out the next spring (Brown, 1952). Lucas (1928) found a female of *Ectobius lapponicus* Linnaeus that carried her egg case at least 12 days. In this species the egg case is deposited in the summer and the eggs hatch quite soon.

Some of the species that deposit the oötheca shortly after it is formed frequently conceal it and cement it to the substrate. The female may cover the oötheca with bits of debris which she chews from the substrate (Latreille, [1803/1804] ; Sampson, *in* Shelford, 1912) and mixes with saliva (Haber, 1920). The habit of concealing the oötheca, or covering it with debris, is practiced by *Periplaneta americana* (Haber, 1920; Adair, 1923; Rau, 1943) ; *P. australasiae* (Girault, 1915; Spencer, 1943) ; *Blatta orientalis* (Qadri, 1938; Rau, 1943) ; *Loboptera decipiens* (Berland, 1924) ; *Supella supellectilium* (Flock, 1941) ; *Cryptocercus punctulatus* Scudder (Cleveland et al., 1934) ; and *Eurycotis floridana* (Roth and Willis, 1954a). The habit of covering the oötheca with debris is not equally developed in all the domiciliary species. In the laboratory, the eggs of *P. americana* are covered most frequently; those of *B. orientalis* are usually dropped free, uncovered and not cemented to the substrate (Gould and Deay, 1940; and our own observations) ; those of *Supella* are usually ce-

mented to the substrate but are only sometimes partly covered with bits of feces or other debris which is cemented to the oötheca. These females show no further care for the oötheca after it has been deposited, leaving the eggs to hatch, which often requires several weeks.

As mentioned earlier, with few exceptions the embryos are arranged in the oötheca with their heads directed toward the keel (pl. 9, fig. 66) or dorsal side of the oötheca. Generally at hatching the two halves of the keel separate, and most of the young of *Periplaneta americana* emerge almost simultaneously in less than 10 minutes (Gould and Deay, 1938) or at the most within the hour (Klein, 1933). Goeze (1782) stated that the hatching cockroaches produce a material which softens the cement between the halves of the serrated crista enabling the young nymphs to escape from the egg case. This view has been repeated in many publications, but there seems to be no experimental evidence for the statement. Internal pressure exerted by the fully developed nymphs causes the oötheca to split along the keel (Wheeler, 1889; Gould and Deay, 1938; Gier, 1947). If some of the young are late in hatching, they cannot escape from the capsule (which tends to snap shut after the young have emerged), or they may be trapped between the two lips of the keel (Fischer, 1928) (pl. 6, figs. 46-48). Pettit (1944) found that the oötheca of *Blattella germanica* splits apart more readily as the development of the embryo nears completion. As soon as the crista opens, the young cockroaches swallow air bubbles at the rate of two or three a second. These unite to form a large bubble in the alimentary canal that almost doubles the volume of the insect. By squirming and waving the upper parts of their bodies, the young cockroaches worm their way out. We have also observed the hatching nymphs of *Periplaneta americana* swallow air. The emerging insects are covered by thin, transparent embryonic membranes which are quickly shed, usually during emergence (pl. 6, figs. 44, 47), and often eaten. Sometimes in *P. americana* these membranes remain caught between the lips of the keel. In *Ectobius panzeri*, the oöthecae of which are buried in sand, this first nymphal skin is shed after the nymphs reach the surface (Brown, 1952). Brown did not observe these exuviae to be eaten.

Numerous writers have repeated the statement that the female German cockroach assists her young to hatch by slitting the oötheca along the seam with her mandibles. This belief originated with a statement by Hummel (1821); he misinterpreted the behavior of a female which apparently was only "exploring," with her antennae and palpi, a recently dropped oötheca when the nymphs coincidentally began to emerge. This egg case, incidentally, had been dropped by another fe-

male, and the female in question was still carrying her own oötheca. Wheeler (1889), Ross (1929), and Pettit (1944) have thoroughly discredited this midwifery.

Although the usual method of emergence among oviparous cockroaches is to split the keel of the oötheca, Terry (1910) states that the young of *Euthyrrhapha pacifica* (Coquebert) gnaw an exit hole through the capsule; a similar method for emergence of the young is said to occur in *Nyctibora lutzi* Rehn and Hebard (Wolcott, 1950).

THE VIVIPAROUS COCKROACHES

For our use viviparity as defined by Hagan (1951; see above) may be too restrictive, in that different individuals of the same cockroach species (e.g., *Pycnoscelus surinamensis*) may give birth either to nymphs, which emerge as such from the mother, or to eggs, still enclosed in the oötheca, which hatch immediately or shortly after the egg case has been dropped. Hence the species may be considered ovoviviparous or oviparous depending upon the behavior of the individual insect. Snodgrass's (1935) broader definition would include both types of behavior in viviparity, as in both, the eggs complete development within the body of the female. By accepting a broader definition of viviparity we avoid the anomaly of having oviparous behavior, by definition, in species that logically would be considered ovoviviparous. Such facultative oviparity, in typically ovoviviparous species, differs greatly from the obligate oviparity of the common domiciliary cockroaches, certainly much more than it differs from viviparity.

Viviparity among the so-called ovoviviparous cockroaches, as we shall show below, differs fundamentally from viviparity in other insects. Among the insects considered by Hagan (1951), viviparity is the birth of embryos from eggs retained in the mother's genital tract. The ovoviviparous cockroaches, however, oviposit into an oötheca, and the eggs actually pass out of the female's body. This fact has only recently been elucidated (Chopard, 1950; Nutting, 1953; and original observations below) and perhaps is not generally known. Oviposition among the ovoviviparous cockroaches is very similar to that of oviparous forms, except that the completed oötheca is retracted by the ovoviviparous female and deposited in her brood sac instead of on the substrate. Viviparity among ovoviviparous cockroaches is, therefore, a secondary condition. The birth product is first an egg enclosed in a chorion, and as such satisfies the criteria for oviparity. After the female retracts the oötheca into her brood sac, the eggs may hatch

within her body and the secondary birth product is an embryo devoid of a chorion, thus satisfying the criteria for viviparity. However, eschewing all theological implications, can an individual once born be born again? If not, the so-called ovoviviparous cockroaches of which we have the greatest knowledge are, strictly speaking, oviparous. Yet it is a decided convenience to use the term viviparous for those species of cockroaches which incubate the eggs in the brood sac, as opposed to oviparous species which do not incubate the eggs within the body.

Viviparity has been reported for several cockroach genera and species (Chopard, 1938). It has been assumed by some observers that a species is viviparous when, upon dissection, embryos are found developing in a brood sac, even though hatching was not observed (e.g., *Panesthia javanica,* Wood-Mason, 1878; *Eustegaster micans* Saussure, and *Oxyhaloa saussurei* Borgmeier, Holmgren, 1903-1904). Recently emerged nymphs found associated with a female, with no evidence of an oötheca, have also been cited as evidence of viviparity (e.g., *Panchlora,* Scudder, 1890; Davis, 1930). Newly hatched nymphs of viviparous cockroaches frequently eat the oötheca (Nutting, 1953; our own observations), so its absence is not surprising.

A number of workers have observed that the females of apparently viviparous species produce oöthecae that protrude externally. This event may occur as the oötheca is formed (see below) or later on when the oötheca is expelled either prior to or at the time of hatching. Frequently, expulsion of the oötheca does not coincide with completion of embryonic development. If the female deposits the oötheca prematurely, the eggs usually fail to hatch. This has been reported for *Blaberus craniifer* (Nutting, 1953), *Pycnoscelus surinamensis* (Saupe, 1928; Roeser, 1940), *Nauphoeta cinerea* (Illingworth, 1942), *Gromphadorhina laevigata* (Chopard, 1950), and *Leucophaea maderae* (Scharrer, personal communication). Karny (1924) described a female of *Pseudophoraspis nebulosa* Burmeister carrying a weakly "chitinized," pale-yellow oötheca which contracted on drying; this description together with the fact that this species has a brood sac, and has been found with young clinging to the underside of the abdomen (Shelford, 1906), would lead us to believe Karny was dealing with a species similar in oviposition behavior to the above viviparous forms.

The observations of Chopard (1950) first served to explain the carrying of oöthecae by the above cockroaches. He found that *Gromphadorhina laevigata* extrudes an oötheca which after several hours extends about 25 mm. beyond the end of the abdomen. Then when the oötheca is held only by its end, it is slowly drawn back into a large brood sac that extends into the metathorax. In the gravid female the

ovipositor is completely inverted; Chopard states that the inversion probably occurs at the moment the oötheca penetrates the brood sac. Snodgrass (1952) thinks that the ovipositor of *Gromphadorhina* probably inserts the fully formed oötheca into the brood sac. The eggs are incubated within this pouch for about 70 days at the end of which time the young are born. Nutting (1953) observed a similar behavior in *Blaberus craniifer*. Gurney (1953) suggested that this method of transference of the oötheca into the brood sac may occur in other viviparous genera which have been seen with protruding oöthecae.

We have observed the extrusion of the oötheca during its formation and its subsequent retraction into the brood sac in *Pycnoscelus surinamensis, Nauphoeta cinerea,* and *Leucophaea maderae;* it is apparent that the formation and retraction of the oötheca in these species is quite similar to that of *Gromphadorhina* and *Blaberus*. The oviposition behavior of the three former species is described below:

Pycnoscelus surinamensis.—Ten females have been observed during various stages of extruding and retracting their oöthecae (pl. 11, figs. 74-79). One female completed the entire process in 2 hours and 15 minutes from the time the first eggs were extruded to the time they disappeared back into her abdomen. She took 1 hour and 25 minutes to extrude the oötheca to its fullest extent; the oötheca then remained more or less unchanged in this position for 40 minutes, and then the female began to retract the oötheca into the brood sac. Retraction time took only 10 minutes. The retraction time for the oöthecae of two other females was also about 10 minutes. When the egg case is extruded (pl. 11, figs. 74, 75), the abdomen of the female is much contracted, the segments being tightly telescoped. The axes of the eggs are vertical at this time and remain so until the egg case is fully extruded. As the female begins to retract the oötheca, the axes of the eggs incline more and more to the left (pl. 11, figs. 76, 77), so that as the last eggs disappear from view they are horizontal. When the oötheca is finally retracted, the abdominal segments return to the normal position. Saupe (1928) was incorrect in his assumption that the oötheca was formed and rotates 90° *inside* the brood sac.

Nymphs hatched from the eggs of three of the observed females 31, 33, and 35 days after formation of their oöthecae. We did not observe the hatching process. One of these females which we dissected after the young had hatched had ovaries in which none of the eggs were well developed. A female dissected 37 days after she had formed an oötheca had no egg case in her brood sac; but her ovaries contained well-developed eggs which were apparently ready to be deposited in an oötheca. It is likely that this female had expelled and eaten the

oötheca which we had seen her retract. Another female dissected 36 days after forming an oötheca had a recently formed egg case containing undeveloped eggs in her brood sac. Apparently this female had also expelled and eaten the egg case we had seen formed, and then formed a new one unobserved. Obviously in determining the time required for the embryonic development of cockroaches which are incubated in a brood sac, one must be certain that the oötheca which is seen being retracted is not subsequently dropped, eaten, and replaced by a new one without the knowledge of the observer.

Nauphoeta cinerea.—More than 20 females have been observed with oöthecae in various stages of extrusion and retraction (pl. 12, figs. 86-90). Complete extrusion of the eggs takes about $1\frac{1}{2}$ hours or less. As the eggs are extruded, the female invests them with a thin, straw-colored oötheca. During the early stages of formation the oötheca frequently projects upward at a slight angle. Usually by the time the oötheca is half formed it bends slightly downward, and when completely extruded it assumes a curve of rather short radius (pl. 12, fig. 87). Except for the first egg, which lies with its axis on an angle to the others, the eggs are extruded with their axes vertical; they remain in this position until the oötheca has been completed. The female then rotates the egg case to the left rather rapidly so that within about 5 to 10 minutes the axes of the eggs are horizontal; the female then retracts the oötheca, in about 1 to 2 hours or sometimes much longer. One female carried her egg case with about three eggs exposed for 22 hours before complete retraction occurred. Sometimes retraction is incomplete and several eggs remain protruding from the end of the abdomen. These exposed eggs dry up and shrivel. One female which had failed to retract her oötheca completely (about 15 eggs had remained exposed) gave birth to 12 nymphs 34 days later. Inasmuch as the genital opening is blocked when dead eggs protrude from the abdomen, the female must drop the oötheca or extrude it at least partially to allow the developed nymphs to hatch. Hatching of the eggs of four females occurred from 33.5 to 41 days after they formed their oöthecae. The oötheca in the brood sac fills almost the whole abdominal cavity (pl. 12, figs. 91-94).

Leucophaea maderae.—Two females were observed as they extruded and retracted their egg cases. As a result of an accident, the egg case of the first female broke incompletely into two halves which were held together by a thin portion of the delicate membrane forming the oötheca. This female could not retract all the eggs into her abdomen. The eggs that protruded became dry and shrunken after 3

days' exposure, but remained attached to the female. She died on the fourth day; the eggs within the brood sac appeared normal.

When the second female was first observed, four eggs were already visible beyond the end of her abdomen. As more eggs were extruded, their axes, which were originally vertical, began to tilt toward the left side of the female. After 3 hours and 20 minutes the oötheca was fully extruded; it contained about 38 eggs and extended three-quarters of an inch or more beyond the posterior end of her abdomen. After another 10 minutes the axes of the eggs were horizontal, and the female began to maneuver the oötheca into the brood sac. When fully extruded, the oötheca was curved so that the terminal eggs farthest from the body were far to the left of the midline of the body of the female. While being retracted, the oötheca stuck out straight behind the female. After 45 minutes only one egg (the first laid) was visible. But this egg projected for 1 hour and 25 minutes more before it disappeared. Total retraction time was 2 hours and 10 minutes, and the whole process took more than $5\frac{1}{2}$ hours.

In all species of viviparous cockroaches in which oviposition has been observed, including *Leucophaea maderae,* the last eggs deposited in the oötheca are the first to enter the brood sac as the oötheca is retracted. This action places the most recently laid eggs in the anterior end of the brood sac and the oldest eggs in the posterior end of the brood sac. Yet van Wyk (1952) stated that in *Leucophaea maderae* "The oötheca is contained in the vestibulum [2] and the latter extends cephalad as the former increases in size. The oldest eggs are therefore situated at the anterior end of the vestibulum." Obviously this description was not based on direct observation of the transfer of the oötheca into the brood sac.

Though the formation of the oötheca is very similar in the above three species, certain differences should be noted. In *Pycnoscelus* the axes of the eggs remain vertical until the oötheca is fully extruded and then they gradually incline toward the left as the egg case is retracted into the brood sac; retraction itself is very rapid requiring only about 10 minutes. In *Nauphoeta* the axes of the eggs are also vertical until the oötheca is fully extruded. However, unlike *Pycnoscelus,* the oötheca is completely rotated in about 5 or 10 minutes and is then retracted in about an hour or more. In *Leucophaea,* as in *Nauphoeta,* the axes of the eggs are horizontal when the retraction process begins.

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[2] The vestibulum or oöthecal chamber is the portion of the genital cavity lying above the 7th sternum (Snodgrass, 1937, 1952). Van Wyk (1952) considers the brood sac to be an anterior expansion of the vestibulum.

The time required for the formation and retraction of the oötheca is quite variable; we may have induced some variation by disturbing the females. However, the complete formation and extrusion of the oötheca (not including retraction) by the above species occurs more rapidly than among species in which the oöthecae remain exposed after they are formed. For example, *Eurycotis floridana* (Walker) forms its egg case in about 6 hours (Roth and Willis, 1954a), and *P. americana, B. orientalis, B. vaga,* and *B. germanica* require about the same length of time or longer for oötheca formation; Wille (1920) reported 16 to 24 hours for complete oötheca formation in *B. germanica.* Brown (1952) reported 6 hours for oötheca formation by *Ectobius panzeri.* The longer period taken by oviparous cockroaches to form their oöthecae may be related to the fact that in these species the toothed keel of the oötheca is a complicated structure containing respiratory chambers and ducts. Obviously a certain amount of time is necessary to form each of the respiratory chambers; the protein substance of the oötheca must harden around the "horned die" before the next chamber is formed. The oöthecae of *Pycnoscelus, Nauphoeta,* and *Leucophaea* have no respiratory chambers in a specialized crista; this may account for the comparative rapidity with which these species form their egg cases.

It is very difficult to ascertain just how birth occurs in the cockroaches that retain their eggs within a brood sac; the young may hatch as the oötheca is extruded from the brood sac into the vestibulum or oöthecal chamber, and the nymphs then issue from the body of the female; they may hatch as the oötheca is extruded beyond the oöthecal chamber; or the oötheca may be dropped completely, the young hatching shortly afterward. Only direct observation can determine the method, and inasmuch as it is practically impossible to tell the exact moment when birth will occur, the insects have to be watched closely and at times continuously.

Actual observations of the hatching of viviparous cockroaches are few in number. Hatching has been observed in *Panchlora viridis* (Riley, 1890, 1891a, b); *Pycnoscelus surinamensis* (Thomas, 1949; Schwabe, 1949); *Diploptera dytiscoides* (Hagan, 1939); *Blaberus craniifer* (Nutting, 1953); *Gromphadorhina laevigata* (Chopard, 1950); *Leucophaea maderae* (Scharrer, 1951; van Wyk, 1952); and *Nauphoeta cinerea* (Roth and Willis, unpublished data).

We have observed birth twice in *Nauphoeta cinerea.* The first time, we saw a female extrude an oötheca containing fully developed embryos; while it was still attached to the female, two other cockroaches seized the egg case, and one, managing to free the oötheca from the

mother, carried it off. We retrieved this oötheca; four eggs hatched immediately, and the nymphs commenced feeding on the oötheca. About 23 well-developed embryos failed to hatch. The second time we observed birth, most of the nymphs had hatched before we noticed the event. The young cockroaches, still invested with their embryonic membranes, dropped from the female's oöthecal cavity as she extruded the oötheca. When we isolated the female in a vial, she seized and ate two nymphs immediately after they had dropped free and before they shed their embryonic membranes. The remainder of the oötheca, which had been extruded as far backward as the oöthecal cavity, was removed from this female when further hatching ceased. There were six live embryos in this fragment of oötheca; these did not hatch.

Some reports about hatching in viviparous cockroaches are conflicting. For example, Scharrer (1951) states that the young of *Leucophaea maderae* hatch from their eggs the moment they leave the mother. Van Wyk (1952) says the eggs of this species "hatch in pairs in the oötheca while it is still in the vestibulum [3] and the young immediately leave the mother. . . . The remains of the oötheca and the chorion of each egg are thrown out by the mother after all the eggs have hatched." Yet Pessoa and Correa (1928) state that this species deposited the egg case, and the young hatched from the capsule 20 days after laying.

Saupe (1928) argued that the oötheca of *Blaberus craniifer* fills the brood sac so completely that the nymphs have no room to hatch within the sac. Although he did not observe the act, Saupe believed that hatching occurred in *B. craniifer* as the oötheca was extruded or shortly after it had been dropped. Nutting (1953) also believes that it is impossible for the young to hatch in the brood sac of *B. craniifer*; he observed the hatching of nymphs from an oötheca that was being extruded by the female and also from recently dropped oöthecae of this species. In *Pycnoscelus surinamensis* the oötheca completely fills the brood sac which is stretched tightly against the egg case. Thomas (1949) observed that in this species the nymphs were delivered alive and individually. Schwabe (1949) stated that the nymphs of *P. surinamensis* hatch within the body of the female. Even in *P. surinamensis,* however, the female may expel the oötheca, and then the

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[3] As van Wyk (1952) considers the vestibulum to include the brood sac, we do not know from his description whether or not hatching occurred within the brood sac proper or within the posterior part of the vestibulum. After the oötheca has been released from the brood sac, hatching most probably occurs as the oötheca is extruded beyond the vestibulum.

young hatch outside the female; we have observed this several times. According to Zappe (1918) hatching of *P. surinamensis* may occur within the mother, or the oöthecae containing well-developed embryos are laid in the soil, the young hatching within 24 hours. Later Zappe (Hagan, 1951) claimed that in Connecticut this species is oviparous. The two females of *Nauphoeta cinerea* that we observed giving birth expelled their oöthecae, at least partially, before the eggs started to hatch.

The site in which the eggs of viviparous cockroaches hatch would seem to depend upon the rapidity with which the embryos respond to a stimulus to hatch. The site might be anywhere from the vestibulum to a position outside of the body of the female. Presumably hatching does not occur within the tightly investing brood sac because of spatial limitations and the pressure exerted by the wall of the brood sac. This pressure undoubtedly increases between the time the oötheca is retracted and the time of hatching, as the eggs of viviparous cockroaches increase in size during embryonic development (Hagan, 1951; Nutting, 1953), thereby stretching the brood sac even more. Nutting (1953) believes that pressure exerted by the female on the oötheca during extrusion may supply the necessary hatching stimulus. His evidence is not convincing: he secured hatching from oöthecae, that had been extruded 2 to 6 days earlier, after manipulating the oöthecae with his fingers. Yet these same oöthecae had been subjected to whatever pressure the female might apply prior to and during extrusion, and the eggs had not hatched. These oöthecae might have been dropped prematurely before the embryos were ready to hatch. On the other hand, the release of the oötheca from the tightly stretched brood sac during extrusion might be a hatching stimulus—at least this seems to be true in *Pycnoscelus surinamensis* (see below).

Pycnoscelus will drop its oötheca when exposed to temperatures above 35° C. or below 5° C., and after being poisoned, injured, or decapitated (Roeser, 1940). Roeser observed that seldom is an oötheca found inside a dead female; shortly before or after death due to natural causes the female expels the oötheca from the brood sac. We decapitated five females 33 to 35 days after they had retracted their oöthecae. Each female extruded her oötheca, and nymphs began hatching as soon as the egg case was released from the brood sac (pl. 11, figs. 80-85). The nymphs swallowed air, swelled up, and emerged from the oötheca, shedding the embryonic membranes which had surrounded them (pl. 11, figs. 83, 85, arrows). Some of these eggs were obviously ready to hatch before the females were killed, and release

from the pressure of the brood sac was followed by immediate hatching. Just what the stimulus is for the female to extrude the oötheca at the end of the gestation period is unknown. Some eggs were completely undeveloped and others not far enough developed to hatch; these remained in the oötheca. Apparently some of the eggs may develop at different rates. Schwabe (1949) recorded one instance in which 36 hours elapsed between the birth of the first and last nymphs of the brood. The oötheca is sufficiently developed to prevent hatching if only a few individuals in the egg case have reached the hatching stage and the egg case is dropped prematurely. Yet we noticed two nymphs which hatched from one dropped egg case in which only five embryos had developed; two of the others were only able to free part of their heads from the oötheca.

Injury or death causes the extrusion of the oötheca by females of other species of viviparous cockroaches. From the number of genera in which this reaction has been observed, we think that the phenomenon is probably general among cockroaches that carry their oöthecae in brood sacs. Beebe (1925) saw a giant "woodroach," which was being eaten by a spider, give birth to 51 young which "had burst from their mother." Shelford (1906) recorded a specimen of *Epilampra burmeisteri* Guerin from Brazil that was preserved with two nymphs (still partly surrounded by their embryonic membranes) emerging from the tip of the female's abdomen; these nymphs may have been expelled by the female as she died. Gissler (Riley, 1891b) observed 24 young emerge from the genital orifice of a female *Panchlora viridis* which had died. Stewart (1925) killed a female of *Blabera cubensis* [= *Blaberus discoidalis* Serville (Rehn and Hebard, 1927)] in a cyanide bottle; during the few seconds the female survived she partly extruded an oötheca containing 44 eggs. Heal (personal communication) observed *Leucophaea maderae* females with creamy-white, fragile egg cases protruding from the ends of their abdomens; these females had been killed either with cyanide or pyrethrum during disinfestation of buildings. We have seen *Blaberus craniifer* partially expel an oötheca after decapitation prior to dissection (pl. 4, fig. 22); a pin placed against the posterior end of this oötheca prevented further extrusion. We have also seen a female of *Nauphoeta cinerea* expel its oötheca on being dropped into boiling water. Insecticidal sprays may cause the German cockroach female to drop its oötheca prematurely (Woodbury, 1938; Parker and Campbell, 1940). A similar occurrence of oviposition by injured or dying mosquitoes, *Aedes sollicitans* (Walker), and the phenomenon of "death stress" have been studied by DeCoursey and Webster (1952).

Hagan (1939, 1941, 1951) has worked extensively with the vivipa-rous cockroach *Diploptera dytiscoides*. He has described evanescent embryonic structures, the pleuropodia, to which, tentatively, he ascribes nutritional or respiratory functions, or both. The pleuropodia arise as a part of the swelling of the first abdominal segment. With embryological development they increase greatly in length, becoming thin-walled tubes which end near the micropyle. They are bound to the inner surface of the chorion by the yellow serosal cuticle. Because of this modification Hagan cites *D. dytiscoides* as the one example of pseudoplacental viviparity among cockroaches.

Hagan (1951) described oviposition in *Diploptera dytiscoides:* On reaching the lower end of the common oviduct the eggs "are directed by the ovipositor from the genital chamber ventrally into the open end of the uterus." The implication here, which has subsequently been confirmed by Hagan (personal communication), is that the first-laid eggs are the first to enter the brood sac and the last-laid eggs are the most posterior in the brood sac. A pronounced central dome in the roof of the genital pouch is presumed to facilitate "tilting of the eggs as they pass into the uterus" (Hagan, 1941). This method of oviposition contrasts markedly with what has been observed in other viviparous cockroaches, as Snodgrass (1952) has noted. For this reason we are re-evaluating oviposition in *D. dytiscoides* in the light of what is now known of oviposition in other viviparous cockroaches.

Hagan (personal communication) had not observed protrusion of the oötheca by *Diploptera dytiscoides,* in the field or in rearing cages. Other entomologists in Hawaii whom he questioned had not observed this species with the oötheca extruded. Apparently Hagan based his account of oviposition in *D. dytiscoides* on an interpretation of the anatomical relationships in dissected specimens. *D. dytiscoides* is a small insect three-quarters inch in length (Hagan, 1941); the eggs it produces are also small, being 1.20 mm. long and 0.43 mm. in the greatest dorsoventral dimension (Hagan, 1951). As only 12 oöcytes are usually matured at one time, the oötheca is very short, with a computed length of about 3 mm. Possibly the posterior end of the forming oötheca does not protrude far enough from the oöthecal cavity to be easily seen. As the complete process of formation and retraction can be very rapid with much larger oöthecae containing many more eggs (e.g., *Pycnoscelus surinamensis, Nauphoeta cinerea,* above), the transfer of the egg case by *D. dytiscoides* into the brood sac might pass unnoticed by anyone not specifically looking for it.

It is difficult for us to visualize the formation of the oötheca of *D. dytiscoides* during a direct passage of the eggs from the oviducts

into the brood sac. The oötheca of this species is apparently comparable to those of *Pycnoscelus surinamensis, Blaberus craniifer, Nauphoeta cinerea,* and *Leucophaea maderae,* except that it may possibly be less extensive than those of the first two species. The delicate oötheca of *D. dytiscoides* encloses the lower ends and sides of the eggs, the micropylar ends remaining free (Hagan, 1951). This is very similar to the condition that we have found in *N. cinerea,* in which, at times, the oötheca seems to be merely a thin film of varnish applied over the sides of the eggs. There are other close similarities between the oötheca of *D. dytiscoides* and the oöthecae of other viviparous cockroaches. For example, the eggs are disposed in the oötheca in two parallel rows, the eggs of one row fitting opposite the intervals in the other row; the ventral surfaces of the eggs in one row face the venters of the eggs in the opposite row; and at the ends of the oötheca the first and last eggs lie in the midline (Hagan, 1951). These features of the oötheca of *D. dytiscoides* apply to blattid oöthecae in general; hence we would expect the mode of formation of the oötheca in this species to be similar to what has been found in other viviparous cockroaches.

Probably the oötheca of *Diploptera dytiscoides* is formed around the eggs as they are aligned in a double row in the oöthecal cavity with their axes vertical, as has been observed in other species of cockroaches. Then, after the last egg is deposited, the female presumably rotates the oötheca and retracts it into her brood sac with the last-laid eggs coming to lie in the anterior end of the brood sac. This procedure would place the oötheca in the brood sac with the axes of the eggs rotated 90° to the left as Hagan (1951) found in his specimens. Until direct observation proves the above interpretation to be wrong, it seems logical to identify oviposition in *D. dytiscoides* with that in other viviparous cockroaches.

VARIATION IN OVIPOSITION

Wood-Mason (1878) suggested that the habit of certain species of blattids of carrying the oötheca for a week or more before deposition represents the retention of a vestige of a lost viviparity. However, Shelford (1909, 1912) believed that the method of depositing eggs in an oötheca onto a substrate is probably a more primitive behavior than incubating the eggs in a brood sac. Not only have fossil oöthecae been found, but also fossil cockroaches which possessed elongated ovipositors, indicating that during the Permo-Carboniferous period there were two categories of cockroaches; the more primitive had a

long external ovipositor and laid eggs not united in an oötheca; the other had a much reduced internal ovipositor and made oöthecae like recent blattids (Laurentiaux, 1951).

Various adaptations of oviposition behavior and oöthecal structure serve to some extent to protect the cockroach eggs. Two general methods of protection have evolved; the eggs are either retained within the mother as long as possible, or the eggs are surrounded by a hard cover (Shelford, 1912). The method of incubating the eggs in a brood sac within the mother possibly affords greater protection to the species than does the deposition of a hardened oötheca; certainly the danger from insect parasites of the eggs would be largely eliminated in this way. Sells (1842) reported that an oötheca of *Blaberus maderae* [= *Leucophaea maderae*], which he received from Jamaica, contained 96 specimens of a small chalcid wasp; some oöthecae had a round hole through the side of the capsule from which the wasps had emerged. His statement that the oötheca had a keel with 16 dentations indicates that he was dealing with an oviparous species rather than a specimen of *L. maderae*. Bordage (1896) was undoubtedly incorrect in stating that *Blatta maderae* [= *L. maderae*] was a host of the egg parasite *Evania desjardinsii* [= *E. appendigaster*], because the oötheca is protected from the parasite within the body of the cockroach.

However, the egg-laying rate is decreased among viviparous species because the female cannot produce more egg cases during the gestation period, which usually takes more than a month. During embryonic development the offspring of viviparous species are subject to the vicissitudes that beset the mother. As we have shown, premature death of the mother may release the embryos from her brood sac. However, if the female were killed before the embryos had developed sufficiently to maintain themselves without the protection of the brood sac, the eggs would die with her.

The admitted success of the common oviparous cockroaches, in establishing themselves in practically every man-made niche, may in part stem from the ability of the embryo to develop independently of the female. Coupled with this are an increased egg-laying rate and the ease with which egg cases may accidentally be transported far beyond the territory occupied by the mother. These factors may offset any apparent advantage gained by viviparous cockroaches through internal incubation of their eggs.

Shelford (1906) grouped several genera and species of cockroaches according to whether the oöthecal membrane is complete or incomplete. Hagan (1951) has suggested that an almost complete series of

cockroaches is available to illustrate a tendency toward the elimination of the blattid oötheca: "The list could start with species dropping the oötheca early, followed by species retaining a protruded oötheca until shortly before hatching occurs. Then there are species with internally retained oötheca [sic] with varying degrees of fragility to *Diploptera* whose oötheca is most delicate and imperfect, and finally ending with species which are said to secrete none at all" (Imms, 1925).

We have arranged the types of oviposition behavior found in cockroaches in a similar series to show a progressive tendency toward retention of the eggs within the body of the female until hatching. We, like Hagan, do not imply that this is an evolutionary series, but it serves to summarize what is known about blattid oviposition.

Ancestral types:
   (1) Cockroaches with long ovipositors that presumably deposited single (?) eggs not enclosed in an oötheca.
   (2) Cockroaches that deposited eggs enclosed in an oötheca.

Present-day cockroaches:
   (1) Oötheca extruded, not rotated, carried by female for only a short time, then deposited and abandoned. (*Periplaneta americana, Blatta orientalis, Eurycotis floridana, Supella supellectilium.*)
   (2) Oötheca extruded, rotated, carried by female for a longer period than in first category, but eventually deposited a long time before hatching. (*Ectobius panzeri.*)
   (3) Oötheca extruded, rotated, carried by female until, or shortly before, hatching. (*Blattella germanica, Blattella vaga, Blattella humbertiana.*)
   (4) Oötheca extruded, rotated, and retracted into the brood sac where the embryos develop until, or shortly before, hatching. (*Nauphoeta cinerea, Pycnoscelus surinamensis, Leucophaea maderae, Blaberus craniifer, Gromphadorhina laevigata.*)
   (5) Oötheca possibly not extruded (see p. 33); eggs possibly directed from oviduct into brood sac where they remain until hatching (*Diploptera dytiscoides.*)

Coincident with the retention of the eggs within the body of the female is a reduction in the hardness, thickness, and extent of the walls of the oötheca. In *Blattella germanica* the walls of the oötheca are relatively thin, and premature dropping of the egg case may be detrimental to hatching, undoubtedly because of desiccation. Parker and Campbell (1940) found that, although there may be a reduction in hatching, some eggs in shriveled oöthecae that had been removed from the female did hatch. One such egg case hatched 24 days after removal from the female. These workers found 36 percent complete and 29 percent partial hatching of detached oöthecae, kept under

laboratory conditions, compared to 70 percent complete and 3 percent partial hatching in the controls.

On the other hand, the eggs of ovoviviparous cockroaches apparently never hatch if the oötheca is expelled from the brood sac before the embryos are well developed. The oöthecae of these species are less well developed than in *Blattella germanica*. Not only is the wall of the oötheca thinner, but in several genera the oötheca is incomplete, being absent along the anterior ends of the eggs. We have found that at a very low humidity the eggs (in the oötheca) of *Pycnoscelus surinamensis* and *Nauphoeta cinerea* lost water much more rapidly than the eggs of *B. germanica*, which in turn lost water more rapidly than the eggs of *Periplaneta americana*.

We have noticed that in the laboratory *Cariblatta lutea minima* invariably deposited its oöthecae on the cotton stoppers of water vials. The only eggs that hatched were from oöthecae left on the moist cotton; eggs in oöthecae removed from the cotton and placed in dry vials did not hatch.

EGG PARASITES

This, then, is reproduction in cockroaches; with the oviparous forms sexual behavior of the female culminates with the deposition of the oöthecae. But her entire effort to perpetuate the species may have been in vain, for in spite of a hard oötheca which presumably protects the eggs, the eggs may be destroyed by various parasites. The Diptera parasitic on cockroach eggs are *Coenosia basalis* Stein and *Megaselia* sp. Edmunds (1952) reared these flies from two different oöthecae of *Parcoblatta* species.

In searching the literature we have found about 25 species, in about 15 genera, of hymenopterous parasites of cockroach eggs. For example, *Tetrastichus hagenowii* (Ratz.) is a parasitic wasp which has been reared from the oöthecae of several species of cockroaches. This small wasp pierces the oötheca with her ovipositor (pl. 9, fig. 67) and deposits her eggs in the eggs of the cockroach. The wasp deposits over half her eggs during the first 2 days after emergence (Roth and Willis, 1954b). Development (pl. 9, fig. 68) is completed in from 23 to 57 days at about 30° C. or higher. Developmental time is a function of the size of the parasite brood. The smaller the brood the longer the wasps take to complete development. If sufficiently numerous, the wasp larvae destroy all the cockroach eggs (pl. 9, fig. 71). With an average of 48 wasps per oötheca all the cockroach eggs are eaten. With an average of 18 wasps per oötheca not all the cockroach eggs are

eaten, but the uneaten eggs fail to hatch. When there is an average of only eight wasps per oötheca, about eight cockroaches complete development and hatch. Eventually the larvae pupate (pl. 9, fig. 69), metamorphose into adults, and emerge from a hole chewed through the side of the egg case (pl. 9, fig. 70). The wasps mate immediately and the females soon seek out other oöthecae and parasitize the eggs.

The evaniids or "ensign flies" are another group of parasites that destroy cockroach eggs; however, in contrast to other cockroach-egg parasites, only one evaniid develops within each oötheca, the single parasite larva destroying all the eggs. These wasps (pl. 10, figs. 72, 73) are frequently seen at windows, indicators of otherwise well-hidden cockroach infestations (Edmunds, 1953).

SUMMARY

The reproductive behavior of most of the more than 3,500 species of cockroaches is still unknown. Less than half a dozen species have been studied intensively, and it is from these, the species most closely associated with man, that most of our knowledge of the behavior of the group comes. Enough additional information now exists, on some of the less common forms, to enable us to summarize the reproduction of cockroaches of quite dissimilar habits.

Courtship.—Male cockroaches prior to copulation engage in several kinds of activity or display. In *Periplaneta americana* this is a response to an odor from the female; in *Blattella germanica* it is a response to a chemical substance on the body of the female which the male detects by antennal contact. Among species in which the males are alate, the male raises his wings, still folded and crossed, exposing the dorsal surface of his abdomen. This activity is probably general throughout the group; it has been seen in several genera: *Blatta, Blattella, Periplaneta, Supella, Blaberus, Leucophaea,* and *Nauphoeta.* Males of certain species perform characteristic body movements during courtship. In *Leucophaea maderae* the male moves his body rapidly up and down against the substrate producing a tapping sound. The male of *Blaberus craniifer* butts the female with his head and his abdomen trembles. The male of *Eurycotis floridana* vibrates his body from side to side and extends it posteriorly.

In response to the male's display the females of many species apply their mouthparts to the male's dorsum; starting near the anal end of his abdomen the female gradually works forward, apparently feeding on a secretion on the surface of the abdomen, until she is astride the male. This activity has been observed in these genera: *Blatta, Blat-*

tella, Blaberus, Ectobius, Supella, Eurycotis, and *Nauphoeta.* The males of many genera have specialized tergal glands which secrete the substance attractive to the female.

Copulation.—When the female is astride the male, he pushes his abdomen farther backward until he can make genital contact with her. The male grasps the female with the aid of the hooked left phallomere and moves out from under her. The cockroaches complete copulation in the opposed position with their heads in opposite directions. This final act of copulation has been seen in *Blatta, Blattella, Parcoblatta, Periplaneta, Eurycotis, Leucophaea, Nauphoeta, Polyzosteria, Supella,* and *Blaberus.*

Fertilization.—Sperm transfer from male to female is accomplished by means of a spermatophore which is elaborated by the male accessory glands. The spermatophore is only formed during copulation, and after it is transferred to the female the sperm migrate from the spermatophore into the spermathecae of the female. Within a day or longer the dry, shrunken, empty spermatophore drops from the female's genital cavity. Spermatophore formation has been seen in *Blatta, Blattella, Periplaneta, Nauphoeta, Leucophaea, Eurycotis,* and *Blaberus.*

As each egg passes out of the oviduct into the genital chamber of the female, sperm are forced out of the spermatheca against the micropylar end of the egg. The eggs are fertilized as they pass along the vestibulum.

Parthenogenesis.—Parthenogenesis can occur among several species of cockroaches. It occurs regularly in *Pycnoscelus surinamensis* in North America and Europe. We have found some parthenogenesis in *Supella, Blattella, Periplaneta,* and *Blatta.* Unfertilized eggs of only *Blatta orientalis* and *Periplaneta americana* hatched normally.

The oötheca.—The eggs of all cockroaches, so far as we know, are invested with a covering, the oötheca. This may be hard and protective as in *Periplaneta, Blatta, Eurycotis, Blattella, Parcoblatta, Cariblatta, Ectobius, Supella,* and others, or the oötheca may be reduced in thickness and/or enclose only part of the eggs as in *Blaberus, Leucophaea, Nauphoeta, Pycnoscelus, Diploptera,* and others. Reduction of the oötheca is associated with viviparity; hard protective oöthecae are characteristic of oviparous forms.

The oötheca of *Blatta orientalis,* and presumably of other species, is formed from a protein, a phenol, and an oxidase secreted by the colleterial glands. This material stretches around the eggs as they are erected in a double row in the forming oötheca. In oviparous species the dorsal edge of the oötheca is modified into a series of respiratory

chambers, usually one per egg, which admit air to the developing embryo.

Oviposition and hatching.—The oöthecae of some oviparous forms are not rotated but are carried for a few days or less until the female drops them (e.g., *Blatta, Periplaneta, Eurycotis, Cariblatta, Supella*). Some of these cockroaches cement the oötheca to the substrate and cover it with debris. Other oviparous cockroaches rotate the completed oötheca and retain the proximal end between the plates of the genital chamber for some time before deposition (e.g., *Ectobius panzeri*), or retain the egg case until or shortly before the eggs hatch (e.g., *Blattella*).

Nymphs hatch from the eggs of oviparous cockroaches by a concerted swallowing of air, thereby increasing their bulk which spreads apart the dorsal seam of the oötheca. At hatching each nymph is invested with a membrane which it sheds while emerging from, or when free of, the oötheca.

Viviparous cockroaches, which incubate their eggs in a brood sac within the mother's body, extrude the oötheca as it is formed around the eggs. However, in contrast to the oviparous forms, the viviparous cockroaches retract the completely formed egg case into a brood sac, where it remains until, or shortly before, hatching (e.g., *Pycnoscelus, Nauphoeta, Leucophaea, Gromphadorhina, Blaberus*). Hatching of the eggs of viviparous cockroaches apparently may occur either within the vestibulum, while the oötheca is being extruded, or shortly after the oötheca is dropped by the female.

The types of oviposition among cockroaches may be arranged in a series showing a tendency toward retention of the oötheca within the body of the female until hatching: Shortly after extrusion the oötheca may be dropped, sometimes buried or covered, and then abandoned; the egg case may be carried, extending from the female's body, for various periods up to and including hatching; the oötheca may be retracted into a brood sac until or shortly before hatching.

Egg parasites.—Although the oötheca of oviparous cockroaches protects the eggs from desiccation, it does not prevent destruction of the eggs by parasites, particularly Hymenoptera. The wasp egg parasites insert their ovipositors through the wall of the oötheca and deposit their eggs in or on the eggs of the cockroach. Frequently the wasp larvae destroy all the cockroach eggs. The eggs of viviparous cockroaches, being protected within the brood sac, are apparently not subject to attack by these parasites.

ACKNOWLEDGMENTS

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PLATES

PLATE I

Fig. 1. The male of *Blattella germanica* in a courting position (induced by touching his antennae with the isolated antennae of a female). × 1.8.

Fig. 2. The female of *Blattella germanica* feeding on the male's tergal-gland secretion. × 1.8.

Figs. 3-5. Courting behavior of *Eurycotis floridana*. 3, The male (top) vibrating his body while standing near the female and exposing the intersegmental membrane between his sixth and seventh tergites. 4, The female has commenced feeding on the dorsal surface of the male. 5, The female in working her mouthparts over male's dorsum has nearly placed herself in a position from which male can initiate copulation. × 1.1.

(Figures 1 and 2 from Roth and Willis, 1952.)
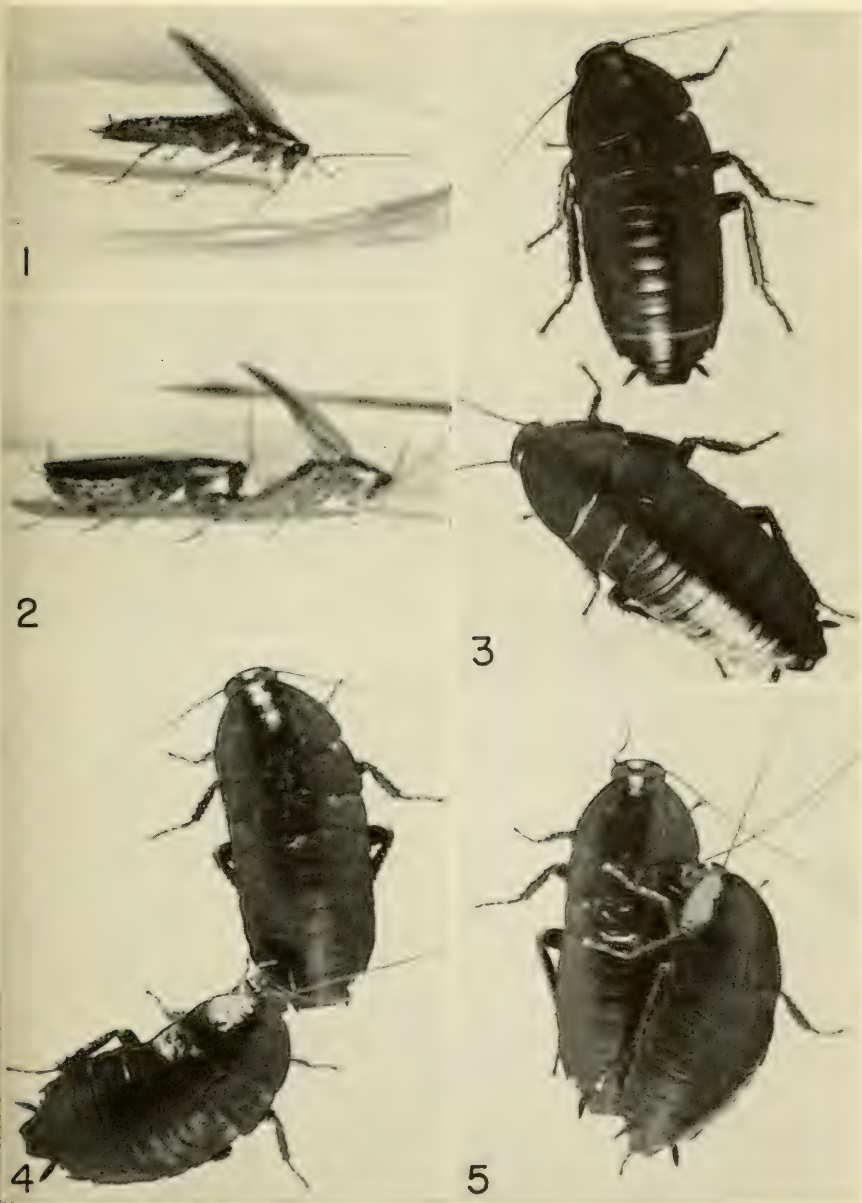
(See opposite page for legend.)
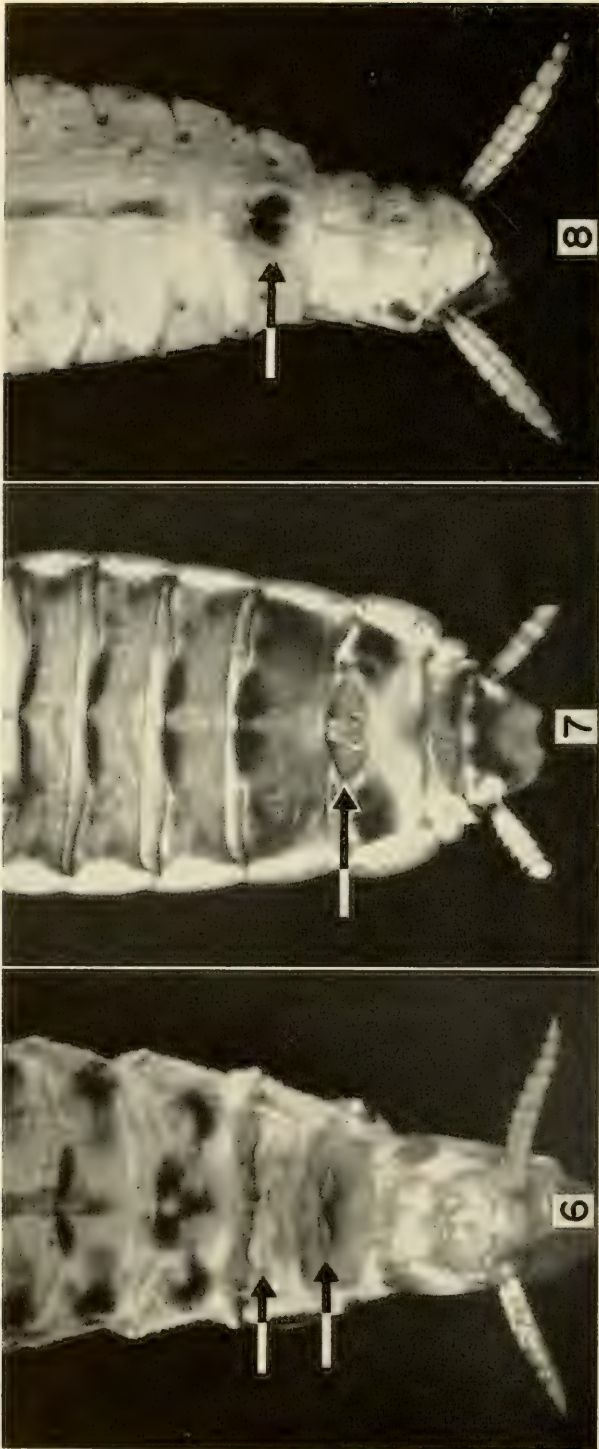
Figs. 6-8. Dorsal views of portions of the abdomens of three species of male cockroaches showing the characteristic tergal glands (arrows). 6, *Blattella germanica*. 7, *Blattella vaga*. 8, *Supella supellectilium*; notice the brush-like groups of setae. About × 12.
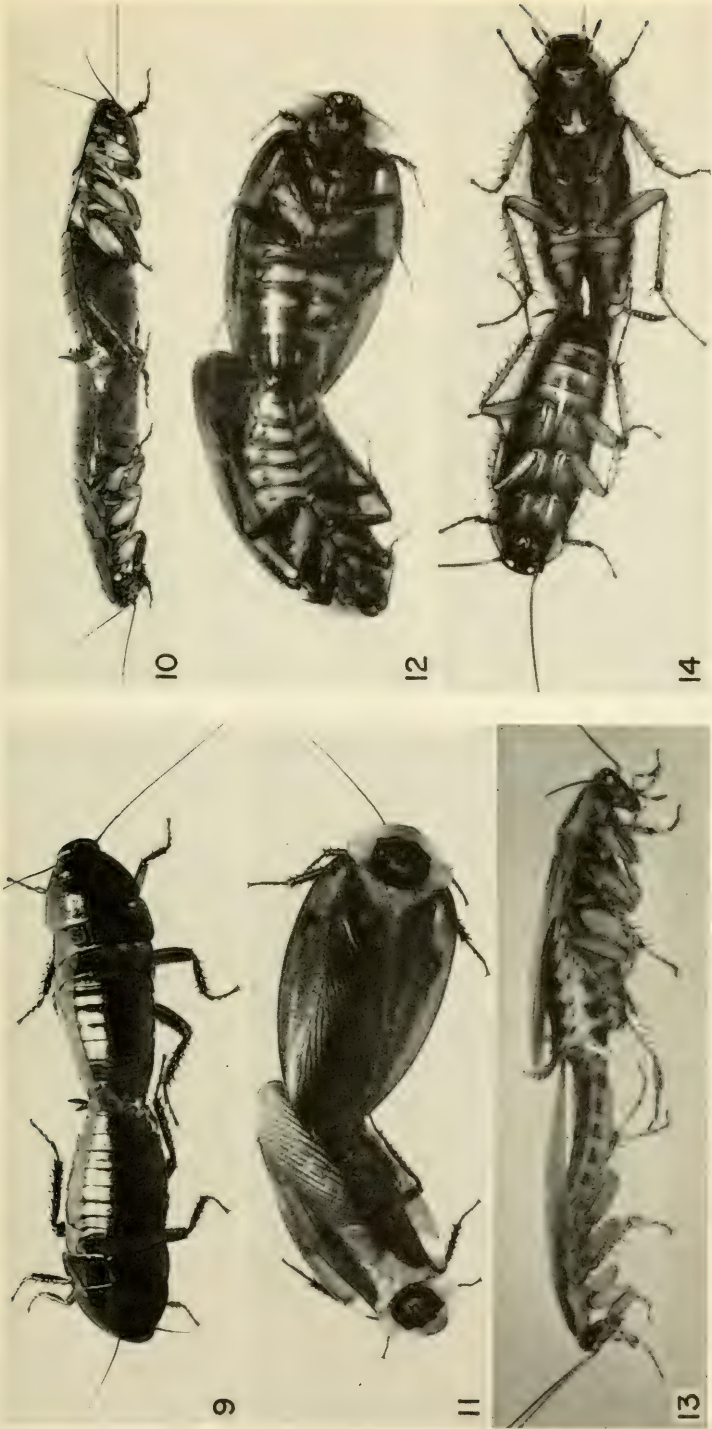
Figs. 9-14. Cockroaches in copula. The male is on the right in figures 9 and 10 but on the left in figures 11-14. 9-10, *Eurycotis floridana*: 9, Dorsal view; 10, lateral view. ×0.9. 11-12, *Blaberus craniifer*: 11, Dorsal view; 12, ventral view. ×0.7. 13-14, *Blattella vaga*: 13, Lateral view; 14, ventral view. ×3.3.

(See opposite page for legend.)

Figs. 25-34. A female of *Eurycotis floridana* in the process of forming an oötheca. Elapsed time during oötheca formation is given in hours (hrs.) and minutes (min.). 25, 0 hrs. (oötheca just beginning to form; the remaining values are taken from this as the starting point.) 26, 1 hr. 30 min. 27, 2 hrs. 20 min. 28, 3 hrs. 5 min. 29, 3 hrs. 40 min. 30, 4 hrs. 10 min. 31, 5 hrs. 10 min. 32, 20 hrs. 22 min. 33-34, 21 hrs. 5 min. (25-32, Dorsal views; 33, lateral view; 34, ventral view). Natural size.

25   26   27

28   29   30

33

31   32   34
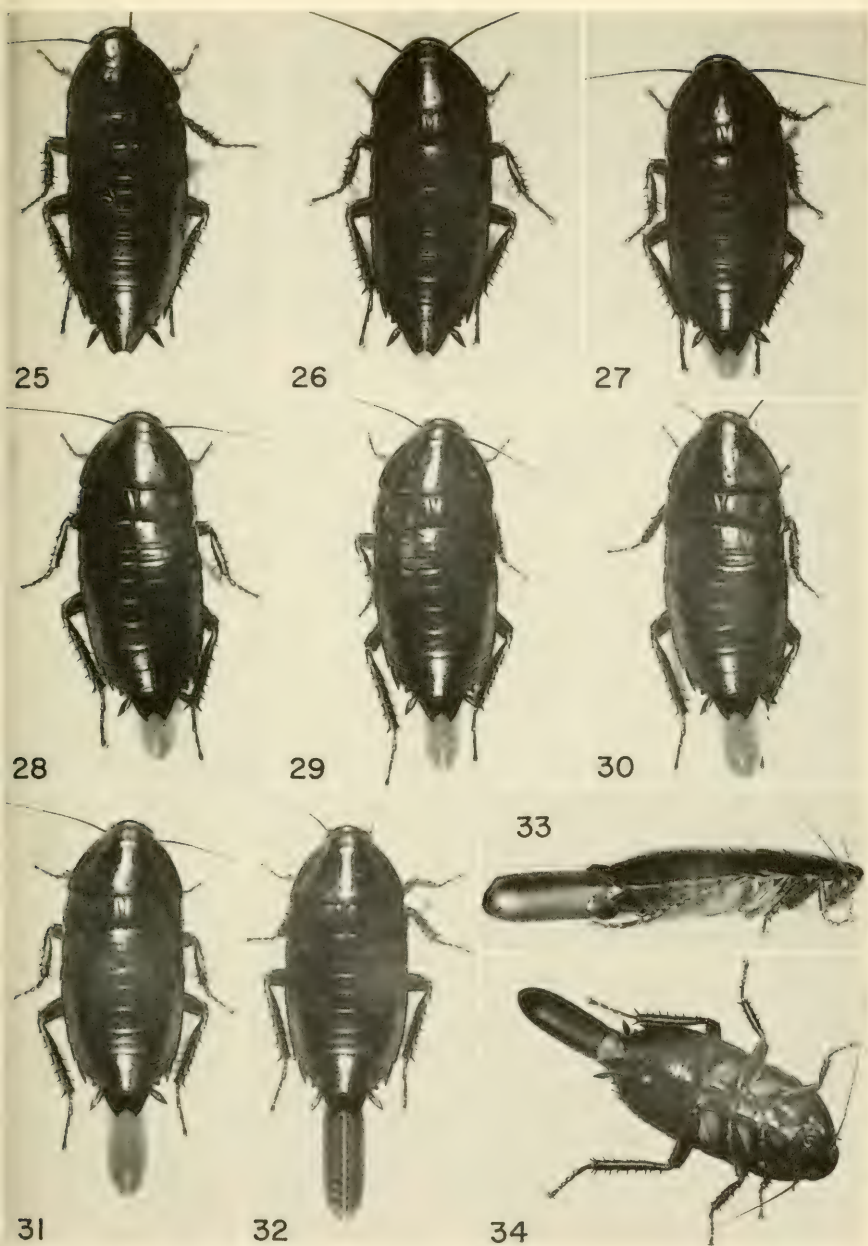
(See opposite page for legend.)

Figs. 35-38. *Supella supellectilium.* 35, Normal oötheca (top view) containing well-developed embryos; the black eyes of the embryos show through the walls of the egg case. × 6.1. 36, Oötheca containing unfertilized eggs; one (arrow) has developed but, failing to hatch, died and turned dark. × 6.1. 37, Oötheca shown in figure 36 with one wall removed to reveal the well-developed embryo. × 6.1. 38, Embryo shown in previous two figures removed from the oötheca. × 9.

Figs. 39-40. *Blattella germanica.* 39, Oötheca containing unfertilized eggs one of which has developed (arrow). × 6.1. 40, Developed embryo removed from the oötheca. × 9.

Figs. 41-45. A parthenogenetically developed embryo of *Supella supellectilium* which, when dissected out of the oötheca (41), succeeded in shedding (42-45) its embryonic membrane (44, arrow). This individual later developed into an adult female. × 9.

Figs. 46-48. Hatching of a parthenogenetically developed egg of *Periplaneta americana.* The embryonic membrane (47, arrow) was left behind attached to the oötheca. Two embryos were caught between the lips of the keel and failed to hatch. × 7.7.
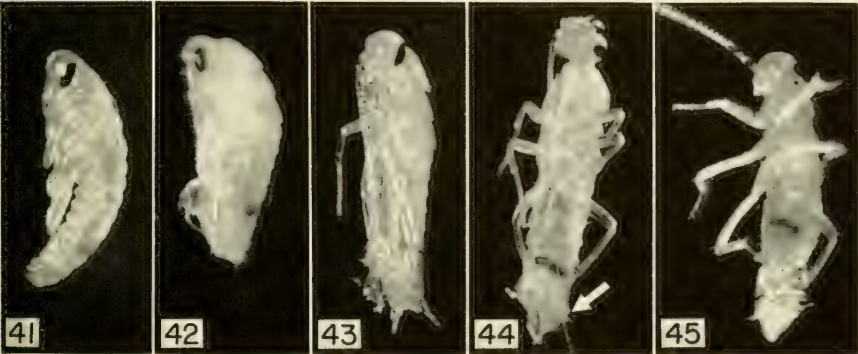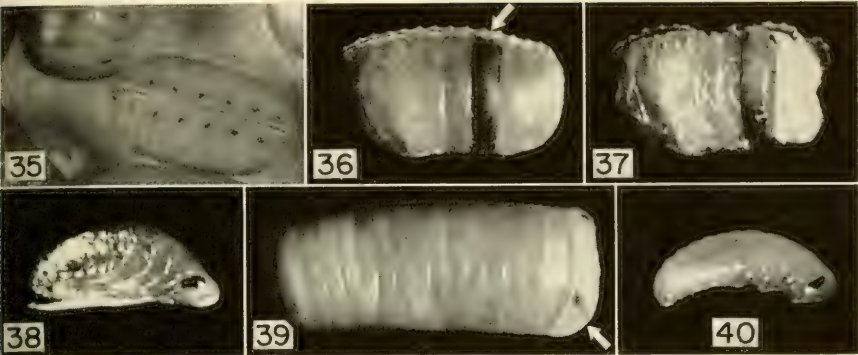
(See opposite page for legend.)

PLATE 7

Figs. 49-58. *Periplaneta americana.* 49, Oötheca containing 16 eggs; there are
16 respiratory chambers and ducts in the keel. 50, Dorsal aspect of oötheca.
51, Anterior end of oötheca (portion held in the oöthecal chamber after the
egg case is formed). 52, Posterior end of oötheca showing pattern impressed
by apical lobes of female's genitalia. 53, Portion of the keel showing some
of the ducts and evaginated respiratory chambers ($\times$ 11.3). 54, Oötheca
which contained seven eggs; there are 10 "teeth" or evaginations in the keel
and 11 ducts; the tooth (arrow) of one of the ducts is missing. 55, Oötheca
which contained 13 eggs; there are only 13 teeth but 14 ducts, one of the
teeth (arrow) being missing. 56-57, Oöthecae in which the keels have been
partly (56) and completely (57) eaten by cockroaches. 58, Eggs which were
deposited without the formation of an oötheca. All figures except 53 are
$\times$ 4.5.

Figs. 59-60. *Blatta orientalis.* 59, Normal oötheca. 60, Abnormal egg case
which did not harden or develop normal pigmentation; respiratory chambers
and ducts were not molded in the keel.

Figs. 61-62. *Blattella germanica.* 61, Newly formed oötheca that partially col-
lapsed 2 days after it had been removed from the female. 62, Two attached
oöthecae; eggs from the egg case on the left have hatched. Notice that the
first oötheca rotated to the right; the keel of the second is upward. $\times$ 4.5.
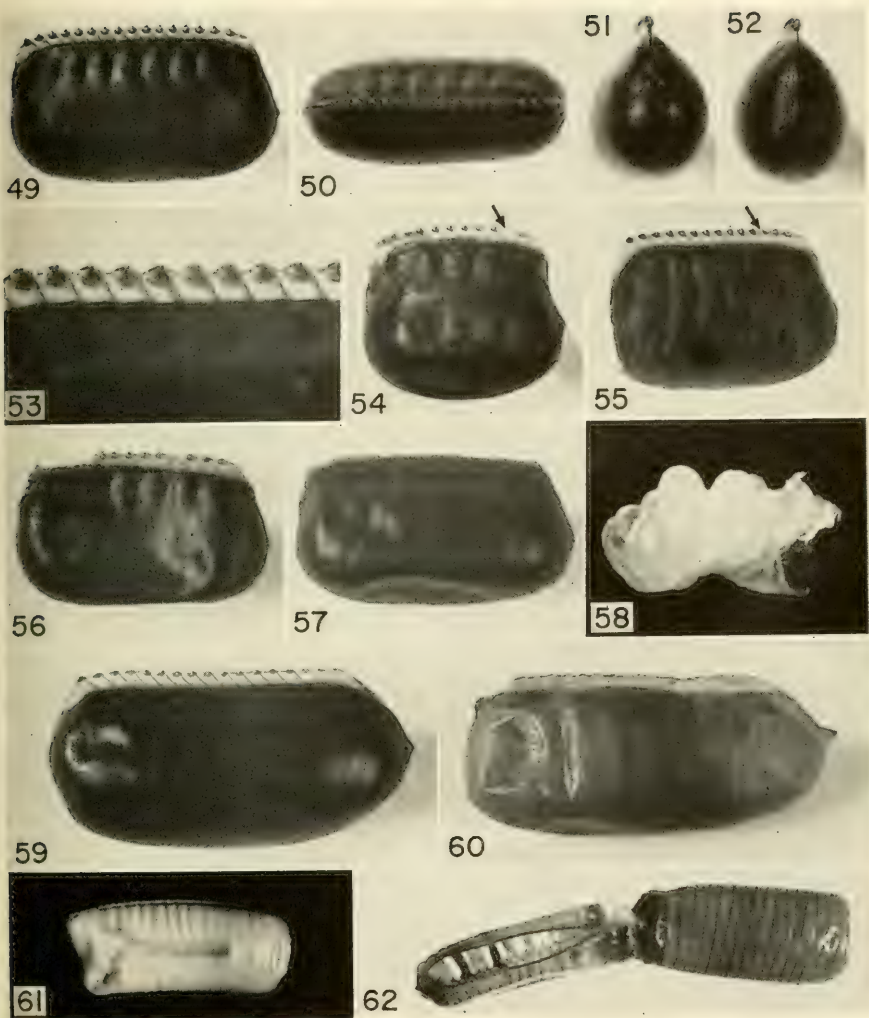
(See opposite page for legend.)

PLATE 8

Figs. 63-65. *Blattella vaga*. Dorsal (63) and ventral (64) views of a female carrying an oötheca. The keel is turned toward the female's right. $\times$ 5.8. 65, Newly hatched nymphs clustering around and climbing over the female. This female was still carrying the oötheca (keel to the right) at hatching, but dropped it soon after this photograph was taken. The nymphs crawled all over the mother and seemingly fed on the greasy material covering the surface of her body; the female raised her wings and some of the nymphs crawled under them on the dorsal surface of her abdomen. $\times$ 5.8.

63   64
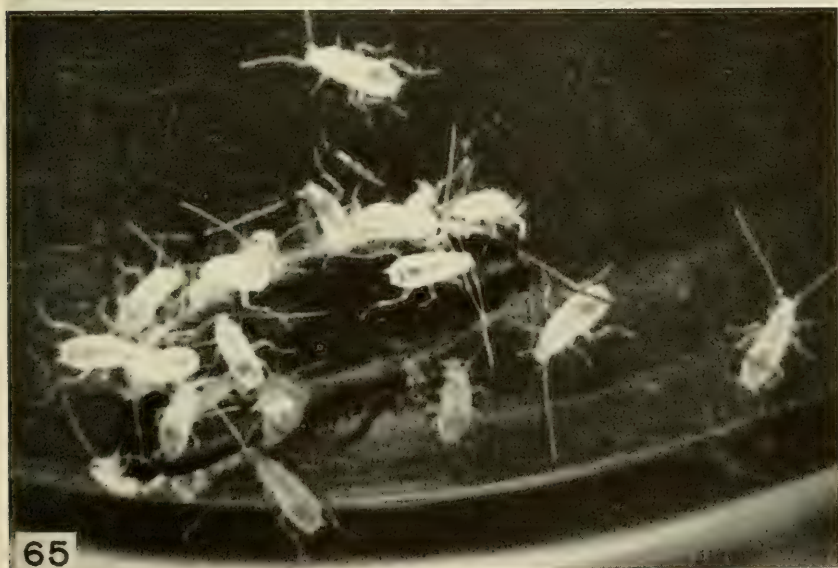
65

(See opposite page for legend.)
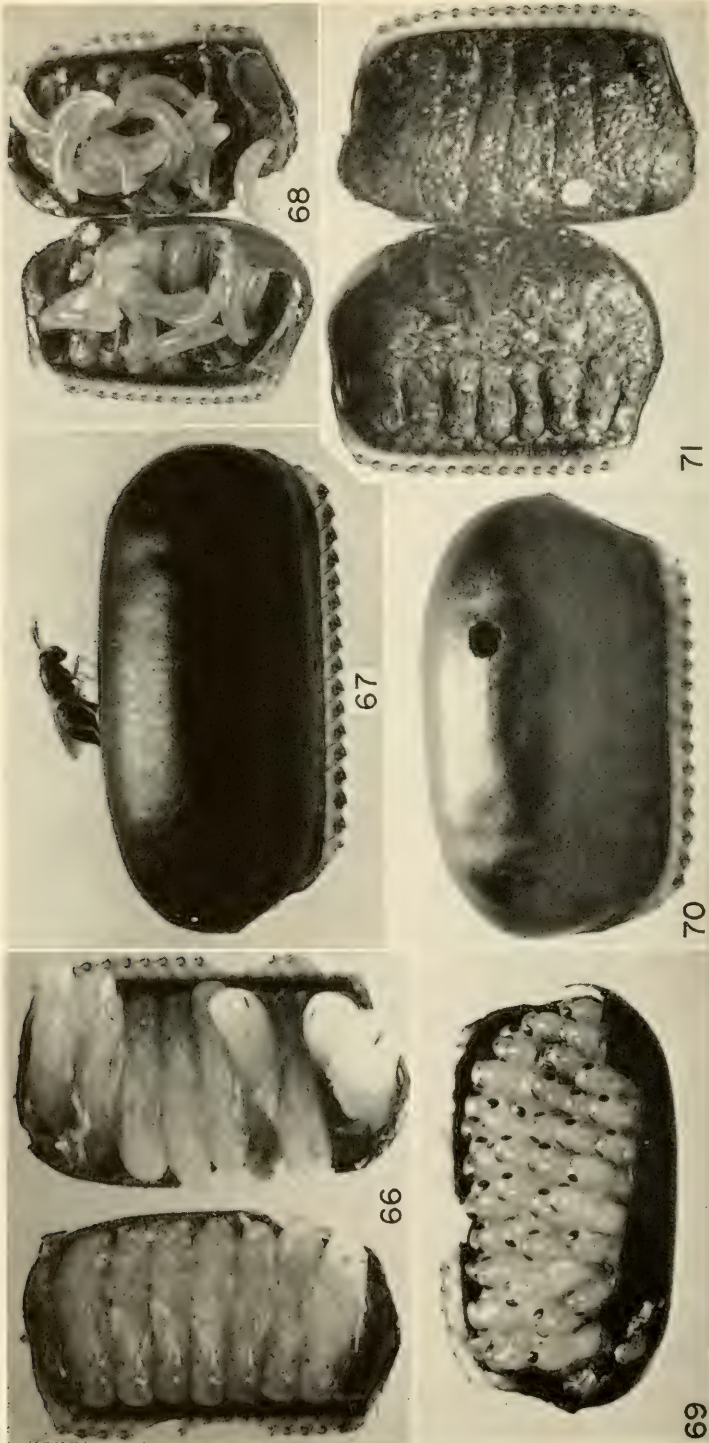
Fig. 66. Oötheca of *Periplaneta americana* cut open to show two rows of well-developed embryos. The respiratory ducts open into the oötheca above the head of each embryo. × 5.8. Figs. 67-71. Oöthecae of the American cockroach parasitized by the wasp *Tetrastichus hagenowii*. 67, Female wasp ovipositing. × 6.9. 68-69, Oötheca opened to show wasp larvae (68, × 6.9), and pupae (69, × 4.5). 70, Oötheca showing hole made by the adult wasps in emerging. × 6.9. 71, Oötheca (in fig. 70) opened to show complete destruction of the cockroach eggs by the wasps. × 5.8.
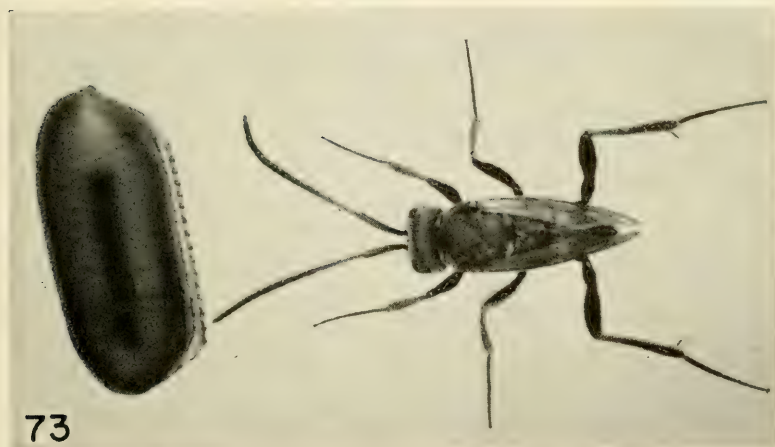
Figs. 72-73. The evaniid *Proscvania punctata* (Brullé) which parasitizes the eggs of the American and oriental cockroaches. 72, Male with an oötheca of *Periplaneta americana*. ✕ 4. 73, Female with an oötheca of *Blatta orientalis*. ✕ 3.3. Notice the size of these wasps in relation to the oöthecae and compare with figure 67.

Figs. 74-79. *Pycnoscelus surinamensis* forming and retracting an egg case, August 18, 1953. Notice position of her head with the frons ventrad. 74, 9:30 a.m. The female is forming and simultaneously extruding the egg case; the seam of the egg case is dorsad. 75, 9:45 a.m. Maximum extent to which the female extruded her egg case; about 24 eggs protrude beyond the end of the abdomen. The axes of the eggs are still vertical. 76, 9:55 a. m. Within a period of 10 minutes the female rotated the egg case, seam to her left, and retracted most of it into her brood sac. 77, 10:00 a.m. 78, 10:01 a.m. 79, 10:01+ a.m. The egg case was completely retracted by 10:01.5 a.m., at which time the female raised her head and scurried off. The female was decapitated September 21, 1953, at which time she expelled this egg case. Five nymphs, of 21 that developed, hatched, and there were 11 undeveloped eggs.

Figs. 80-85. Premature expulsion of an egg case by a decapitated female of *Pycnoscelus surinamensis* with concurrent hatching of the eggs. Series of photographs taken within a 5-minute period. 80, In the few seconds that elapsed between decapitating the insect and placing it beneath the camera, the egg case was ejected about half its length. 81, Nymphs began to emerge through the suture along the dorsal edge of the egg case before it had been completely expelled. 82-85, Sequence of hatching of 15 nymphs from the dropped egg case. A few other eggs had developed but the nymphs failed to hatch. The embryonic membrane shed by one of the nymphs is indicated by arrows.

All figures × 1.9.
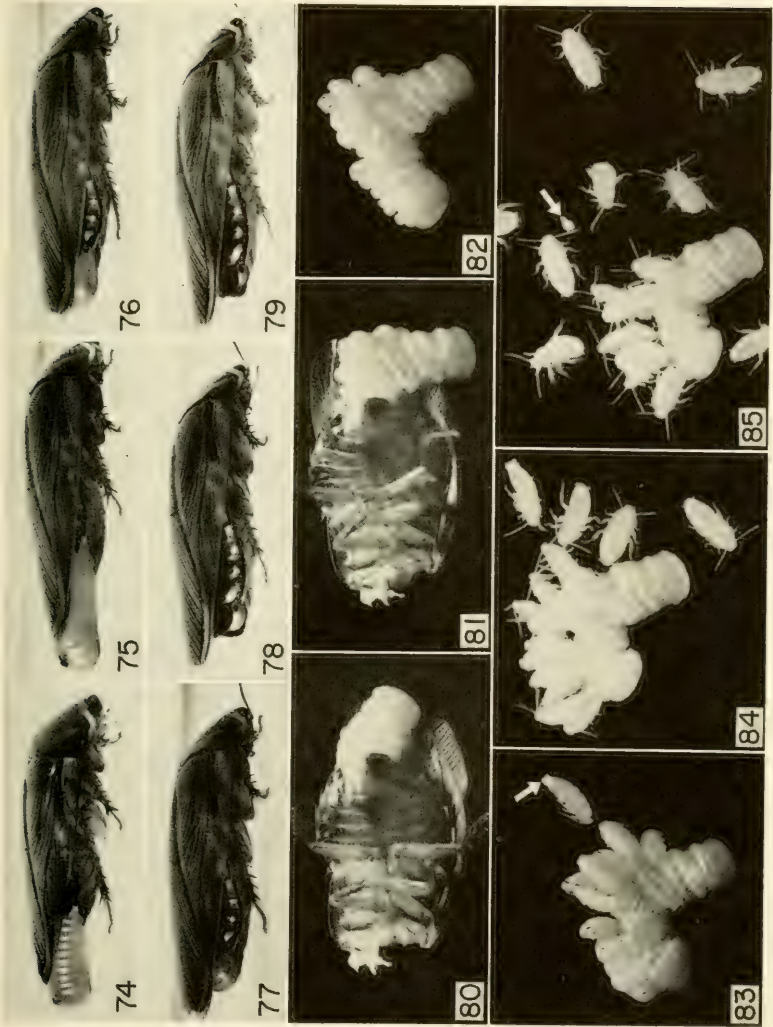
(See opposite page for legend.)

PLATE 12

Figs. 86-90. *Nauphoeta cinerea* forming and retracting an egg case, August 18 and 19, 1953. 86, 1 :30 p.m., August 18. The female is forming and extruding the egg case. The cephalic ends of the eggs are dorsad at this time. 87, 2 :30 p.m. Maximum extent to which the female extruded her egg case; about 30 eggs are visible beyond end of her abdomen. The egg case curves strongly ventrad, and its distal end twists to the side from contact with the substrate. The axes of the eggs in the proximal end of the oötheca have been tilted slightly to the female's left. 88, 2 :45 p.m. The female has retracted part of the egg case. The axes of the eggs now lie in a horizontal plane. 89, 4 :40 p.m. Extent of retraction while the insect was under direct observation. 90, 7 :25 a.m., August 19. The female had completely retracted the egg case into the brood sac during the night. The female carried this oötheca until September 11, 1953, when she expelled it. Only 10 embryos had developed; about 15 eggs did not develop. × 1.4.

Fig. 91. Female of *Nauphoeta cinerea* killed 30 minutes after she had begun to retract the oötheca into her brood sac. × 1.9.

Fig. 92. Dissection of female in figure 91 showing anterior end of oötheca lying in the brood sac which has been cut open. × 1.9.

Fig. 93. Female of *Nauphoeta cinerea* dissected 27 days after she had formed an oötheca. The oötheca fills nearly the entire body cavity. Notice the well-developed embryos with dark eyes and mandibles which show through the transparent wall of the oötheca. × 1.9.

Fig. 94. The oötheca in figure 93 removed from the female's brood sac. Notice the two groups of undeveloped eggs at the left. × 3.6.
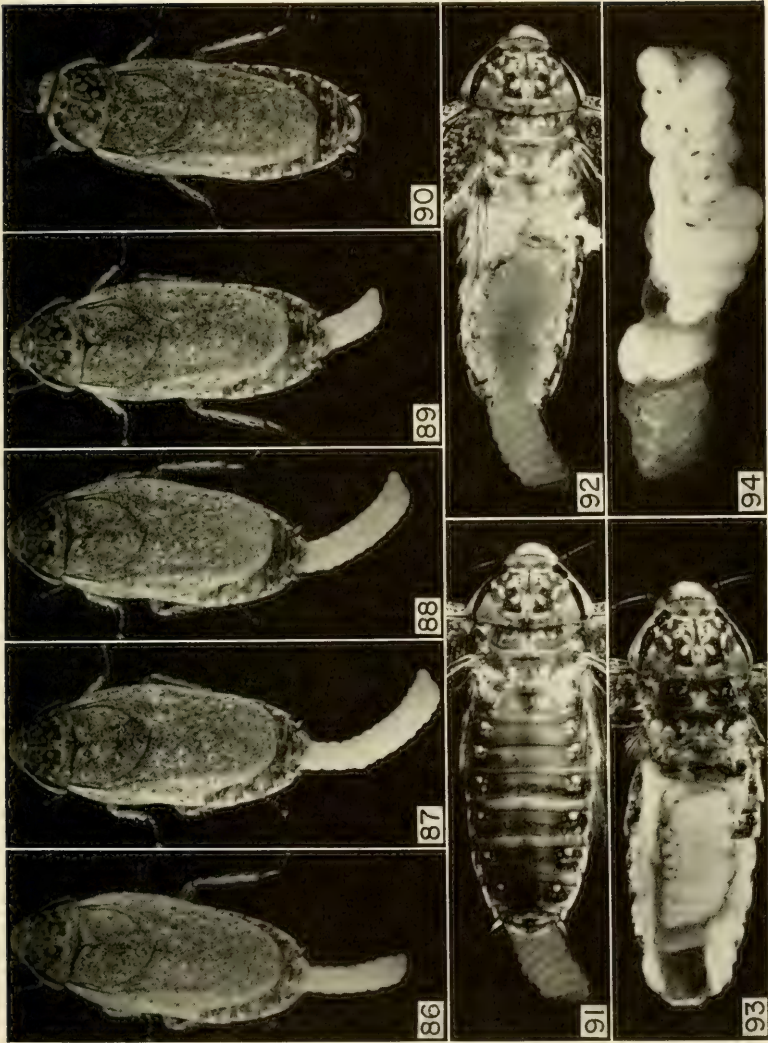
(See opposite page for legend.)

Roebling Fund

WASHINGTON, D. C., PRECIPITATION
OF 1953 AND 1954

By

C. G. ABBOT
Research Associate, Smithsonian Institution

(Publication 4170)

WASHINGTON, D. C., PRECIPITATION OF 1953 AND 1954

By C. G. ABBOT

Research Associate, Smithsonian Institution

This is the tenth year of these publications regarding precipitation on individual days at Washington, D. C. The distribution of precipitation at Washington in 1952 and 1953 was very different from that of averages which appeared representative of 18 years preceding 1952.

In the year 1953 only the months January, April, September, October, and December followed the distribution of precipitation, as regards "preferred" days, that prevailed in the majority of months for all the 18 years preceding 1952. For the year 1953, the average precipitation falling on "preferred" days was but 75 percent of the average precipitation on all other days. During the 18 years preceding 1952, that ratio averaged 146 percent, as against 142 percent expected. It is true, however, that if the months of March and May were omitted altogether from 1953 the ratio would be above unity, at about 110 percent. In March it rained 3.42 inches from the 24th to the 26th, and in May 5.49 inches from the 4th to the 6th. These floods upset those months.

Last year I published a chart purporting to show the distribution of Washington precipitation through the average 27-day cycle of 1952. In some way, which I cannot now trace, I got the phases of that graph completely wrong. I have now redrawn it (fig. 1, curve *b*) and also one to represent the distribution that occurred in 1953 (curve *c*). Along with them, I include a graph (curve *a*, heavy line) of the average distribution which prevailed from 1924 to 1941, when the basis for these forecasts was recorded. All three graphs are on the same scale of ordinates, representing the average inches of precipitation per day of the individual days of the 27-day cycle.

It is surprising to see that in both 1952 and 1953 (graphs *b* and *c*) *a high peak of precipitation occurs on the eleventh day of the cycle.* No such feature occurs in the graph *a* representing the years 1924 to 1941. That this high peak occurs on the identical day of the cycle for

1952 and 1953 is the strongest proof yet appearing of the veridity of the cycle, as an actual cosmic phenomenon. At the same time it shows that a remarkable change of conditions of some sort occurred after 1951, as compared with the years 1924 to 1951 inclusive. And yet a trifling decrease of the decimal .0074 would bring the highest peak of curve *a* on the *eleventh* day in 1952 and 1953, as actually found in curves *b* and *c*.

TABLE I.—*Washington precipitation 1954*

	Jan.	Feb.	Mar.	Apr.	May	June
I......	7	3	2, 29	25	22	18
II......	8	4	3, 30	26	23	19
III......	9	5	4, 31	27	24	20
IV......	10	6	5	1, 28	25	21
V......	11	7	6	2, 29	26	22
XII......	18	14	13	9	6	2, 29
XIII......	19	15	14	10	7	3, 30
XV......	21	17	16	12	9	5
XVII......	23	19	18	14	11	7
XVIII......	24	20	19	15	12	8
XXII......	1, 28	24	23	19	16	12
XXVI......	5	1, 28	27	23	20	16
XXVII......	6	2	1, 28	24	21	17

	July	Aug.	Sept.	Oct.	Nov.	Dec.
I......	15	11	7	4, 31	27	24
II......	16	12	8	5	1, 28	25
III......	17	13	9	6	2, 29	26
IV......	18	14	10	7	3, 30	27
V......	19	15	11	8	4	1, 28
XII......	26	22	18	15	11	8
XIII......	27	23	19	16	12	9
XV......	2, 29	25	21	18	14	11
XVII......	4, 31	27	23	20	16	13
XVIII......	5	1, 28	24	21	17	14
XXII......	9	5	1, 28	25	21	18
XXVI......	13	9	5	2, 29	25	22
XXVII......	14	10	6	3, 30	26	23

It is difficult to decide whether to cling to the old "preferred cycle days," based on the data of 1924 to 1941, or to use a new set based on consideration of the distribution of 1952 and 1953. Two reasons incline me to use the old basis this year. First: In 1953, as stated above, the precipitation came near giving good results on the old basis. So it may be that conditions have returned to the old normal. Indeed the high peak on the eleventh day of the cycle is but 0.6 as
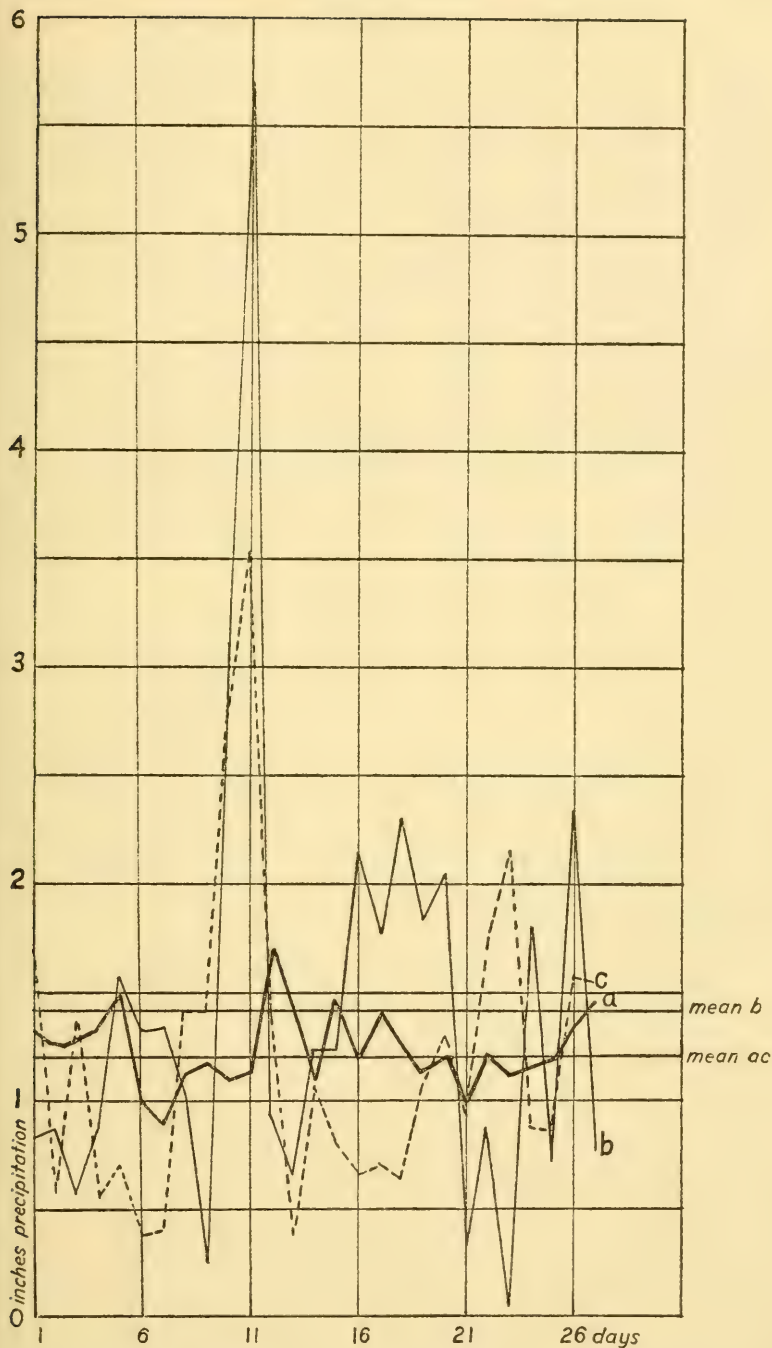
FIG. 1.—Observed distribution of precipitation in Washington on cycles of 27.0074 days. *a*, January 1, 1924, to December 31, 1941. *b*, January 1 to December 31, 1952. *c*, January 1 to December 31, 1953.

3

high in 1953 as in 1952, which may indicate a gradual return toward normal. Second: Advices from E. Fraselle of Etterbeck, Brussels, Belgium, who has used the 27.0074-day cycle in Equatorial Africa and in Belgium, state that since 1949 there has been no failure or change of phase in the cycle.

So I give in the accompanying table the 175 dates when higher average precipitation in Washington may perhaps be expected in 1954 than the average precipitation of all other dates of 1954. The first column, in Roman figures, gives the "preferred days" of the 27-day cycle. The remaining columns give the actual dates in the 12 months of 1954 when these preferred cycle days recur, and when higher than average daily precipitation in Washington may be expected.

The basic tabulation, on which the table rests, began with January 1, 1924, and ended with December 1941. The "cycle" deduced from those records is of 27.0074 days, which corresponds nearly with the average period of the rotation of the sun.[1]

TEMPERATURE AT WASHINGTON

In previous papers on Washington weather, I have shown that it has a regular period of 6.6485 days, and also of $\frac{6.6485}{2}$ days. In previous years I have made predictions, based on these periods, when days would be warmer than the days immediately before and after. But the periods are so short that, with local and temporary atmospheric influences displacing phases of the periods frequently by one day, and sometimes by two days, such forecasts are of doubtful interest. I therefore discontinue them.

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[1] See A 27-day period in Washington precipitation, Smithsonian Misc. Coll., vol. 104, No. 3, 1944. (Publ. 3765.)

Mary Vaux Walcott Fund for Publications in Botany

A NEW GENUS AND SPECIES OF PLANKTON DIATOM FROM THE FLORIDA STRAITS

(With Four Plates)

BY

PAUL S. CONGER

Associate Curator, Division of Cryptogams
Department of Botany, U. S. National Museum

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(With Four Plates)

The diatom here described was first found in plankton gatherings in the summers of 1938 and 1939, while I was working at the Carnegie Institution of Washington Marine Laboratory, Dry Tortugas, Fla., but its study was not completed at that time. It was taken in a No. 20 silk bolting-cloth tow net in waters adjacent to the laboratory, in sea water of 60° to 70° F. temperature and approximately 35‰ salinity. The water was so clear that the very presence of plankton would be doubted, and only after a haul of 20 minutes or more could an appreciable quantity be secured.

To the best of my knowledge this form represents both a distinctive new species and a new genus, which may be monotypic.

THALASSIOPHYSA RHIPIDIS Conger, gen. et sp. nov.

Frustula magna, delicatissima, in aspectu zonali hemisphaerica, dimidio mali aurantii longitudinaliter secti similis sed sectores multo tenuiores et numerosiores; valvae tenues, reniformes, in plana vel fere in plana insidentes, marginibus ventralibus vicinis, globulos uniseriatos prope marginem dorselem ubique ferentes, eos fere deficientes in margine ventrali; volumen frustulae in regione zonali fere inclusum; ora angusta vel tenuis.

Mature, fully grown frustules rounded-basket or cradle-shaped, re-

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sembling in general the structure of half an orange cut end to end, a double elbow section of stovepipe, an armadillo or chiton shell, a tropical sun helmet, or an accordion flexed so that the ends held by one's hands lie in the same plane, or but slightly hinged planes; the less fully grown individuals, resembling sectors, less than half, but always more than a quarter, of an orange cut end to end, the intercalary bands of the diatom simulating the sections of the fruit, these intercalary bands being, however, much narrower (thinner) in proportion and more numerous. Girdle-band or connective zone constituting almost the total volume of the diatom, comprised of many intercalary bands, these bands thin, wedge-shaped in pervalvar axis, auriculate-shaped in apical-transapical plane. Shells thin, exceptionally delicate, auriculate-shaped in valvar plane, with almost no rim (mantle), bearing a single row of very small, round beads around the edge, close to the border, except for a clear central space about one-third to one-half the length of the ventral edge, the dorsal edge with a deeply notched line (simulating the notched "channel-raphe" of *Epithemia* in appearance, but not a groove). Apical axis of the shell about one-half again as long as the transapical axis. Shell surface virtually hyaline and structureless, though probably ultrafinely punctate-striate with radiate design. Over-all structure of the frustule dorsiventral, the convex side being the dorsal aspect, the flatter (or valve) side the ventral; in the shells (valves) the notched edge dorsal, the smooth, pore- or bead-free edge, ventral. Pervalvar axis very extended, an arc of a circle as viewed from the narrow-girdle-band side of the frustule, the arc attaining a half circle in fully grown individuals, only very rarely slightly more; extension of the pervalvar axis achieved by interpolation of more intercalary bands, and at the same time revolution of the valves about the line of their adjacent ventral edges until they come to lie in a plane or close approximation thereof, in a position presenting a right-left-hand symmetry, daughter cells and younger stages comprising somewhat smaller angular sectors of a half circle or half sphere, but usually greater than a third of a circle. Frustule with a narrow, half-round-bottomed groove, between the approximated ventral edges of the shells and at right angles to the pervalvar axis, formed by adjunction of narrow edges of the intercalary bands, this groove shallowing and broadening into a slightly wider zone of narrow, closely set intercalary bands (newly forming ones) as it rounds up the sides and over the dorsal area.

Chromatophore single, thin, flat, pale pea green in color, broadly rounded rectangular to broad-elliptical, about two-thirds the total

length of the frustule in the pervalvar-apical plane, suspended by plasma threads from various points of the inner frustular surface, in the central area of the cell, in a plane parallel to, or coincident with, a plane segment to a central sector of the arched pervalvar-apical plane, and cutting the transapical axis perpendicular to it and somewhat below its center.

Nucleus approximately round to elliptical, flat, hyaline, lying adjacent to and dorsally, in the center of the chromatophore, about one-third to one-half the diameter of the chromatophore in size; not visible except in cell division.

Symmetry.—Cell in pervalvar axis, dorsiventrally asymmetrical, laterally symmetrical. Apical axis isopolar, transapical axis heteropolar. Shells symmetrical with respect to the transapical axis, asymmetrical in respect to the apical axis. Plane of cell division between the ventral edges of the shells and cutting the pervalvar axis perpendicular to its center in the plane of the other two axes.

Resting spores not known.

Cell measurements.—Pervalvar length of frustule 200-300 microns; apical axis of shell (long diameter) 130-190 microns; transapical axis of shell (short diameter) 80-100 microns. The greatest variation in shape seen in proportional lengths of apical to transapical axes.

Remarks.—The hemispherical configuration of this diatom represents an extreme extension of the narrower, wedge-shaped (cuneate) symmetry found in many groups of diatoms (e.g., *Licmophora, Gomphonema, Cymbella, Hemidiscus*).

The central, narrow region of extremely thin, closely set intercalary bands across the dorsal surface of the frustule in apical-transapical plane is evidently the growing zone in which new intercalary bands are formed, although by what morphological beginnings such growth is initiated cannot be seen.

The broad-girdle-band view of this diatom is the one that is described as basket-shaped, the narrow-girdle-band view (end view, looking in direction of the apical axis) is fan-shaped.

The frustules of this form are so exceptionally delicately silicified that they are not susceptible to any customary laboratory treatment, but instead collapse under all efforts for permanent mounting, including drying, liquid penetration, and transfer; but they may be readily handled for study while fresh in sea water. The frustules are also so delicate as to be readily soluble and consequently must be handled with great care in liquid preservation. This means not changing the osmotic tension too rapidly, or adding any reagent that might have a tendency to dissolve or separate the delicate intercalary bands.

Type locality.—East shore of Loggerhead Key, Dry Tortugas, Fla.

Occurrence (distribution).—This form is ever present (throughout the summer) in rather plentiful numbers in the plankton of this area and is one of the more common components of the phytoplankton population. I have no information of its occurrence through other months of the year, having visited the area only during the summer. Also, I have no material from other places and hence no knowledge of the possible extent of its distribution. One might think it would be found widely in the limy waters of the lower Florida, Gulf, and Caribbean area, a matter which it would be desirable to ascertain. It can be gotten in fair numbers in a short plankton haul at any time during the summer in the above locality, though at all times the water is so clear as to appear practically free of plankton; the very gossamerlike shells of most of the plankton forms are due to the poverty of silica in these waters. It appeared to me, on the basis of collections within a radius of 10 miles, to be more a habitant of the shallower (6 to 15 feet), protected, coral-strand waters (certainly at least more prevalent in these), than of the rough waters and active open-water areas. The east shore of Loggerhead Key running off very gradually for half a mile or more over shallow coral sand and coral-head bottoms, and protected also by the shape and position of the island from the more vigorous sweep of tides, current, and wave action, appeared to represent the ideal habitat for this form. Whether or not it is a habitant of rougher waters and wider areas needs further verification.

Relationships.—This diatom is of uncertain relationships. After considerable study and comparison, it does not fit satisfactorily in any of several genera superficially similar, and it seems best, or necessary, that it be put into a genus by itself. It is well, however, to call attention here to its several close simulations, in case other observers may note affiliations which I have overlooked.

It was first thought, because of its shape and general structure, to be an *Amphora,* but the rounded appearance of the valve and particularly the absence of any observable raphe discouraged this connection.

In girdle view the complete frustule looks very like *Hemidiscus Hardmanianus* (Grev.) Mann (Report on the diatoms of the *Albatross* voyages, etc., Contr. U. S. Nat. Herb., vol. 10, pt. 5, p. 316, 1907), as pictured in Schmidt's Atlas der Diatomaceenkunde, pl. 439, fig. 2, 1940, and in Ann. Mag. Nat. Hist., ser. 3, vol. 16, p. 2, pl. 5, figs. 1-4, 1865 (under the name *Palmeria Hardmaniana* Grev.). The valve is not greatly unlike this species in shape; it has the general shape of members of the genus. However, the valve of *Thalassiophysa*

rhipidis is much more rounded at the ends, and it does not show the radiate structure characteristic of members of the genus *Hemidiscus.* The mantle is likewise different in that it is not wider on the dorsal than on the ventral edge, in contrast to *Hemidiscus,* in which it is wider on the dorsal than the ventral edge, thus giving a wedge shape to the girdle aspect of the valve. Unlike the very slightly wedge-shaped intercalary sections of my form, the additive result of which is the hemispherical frustule described, the valve itself is perfectly flat with almost no mantle, which is, as far as can be seen, of even width all around. *Hemidiscus* derives much of the hemispherical shape of its frustule from the considerable width of the wedge-shaped mantle on the dorsal side of its shell. Members of *Hemidiscus* do not exhibit the close beading around the dorsal edge of the valve as in my form. Although these points have been noted and compared there is really no serious question of my form belonging to this genus.

The valve shape and markings of my species more closely resemble *Auricula,* and it is possible it should be placed there, but if so it is certainly widely different in general appearance from the well-known species of that genus. Most nearly suggestive of the valve shape of my form is *Auricula complexa* Greg. as shown in Peragallo's Diatomées Marines de France, pl. 42, figs. 14, 15.

This new form would doubtless have been observed earlier were it not for its gossamerlike frailty and tendency to collapse or be destroyed in preservation, and the need, therefore, to examine it promptly in freshly collected material. Because of this extreme frailty, and the inability in consequence to mount or preserve it well, there is no type specimen or type material. It must be collected and seen in fresh material.

Morphology and development.—The vegetative reproductive or morphological changes of this diatom are very interesting. They are deliberate, orderly, and precise and are very delicate in visible aspect.

The nucleus, or nuclear area, is not visible in ordinary examination of the mature cell because it is so hyaline and because it is obscured by the broad chromatophore in close proximity to which it lies. Judged from the morphological changes, and from its general position in other diatoms, it is undoubtedly in the center of the cell, supported by the very delicate and almost transparent plasma threads that radiate from this area and attach to all parts of the inner periphery of the frustule.

It is possible that the nucleus or nuclear area might be made visible by staining. Unfortunately I did not attempt this, when I was in

position to obtain living material, as I have since wished I had. The extreme delicacy of the diatom and ease of its collapse suggest that very careful vital staining would be required, and that only staining of very freshly collected living material would be feasible.

The nuclear area, even in its hyaline state, probably largely occupied by the nucleus itself, looking at the cell in the direction of the apical axis, can be seen in a certain stage of the cell development or vegetative reproductive process, namely, at that time when the nucleus and chromatophore have divided and the new daughter chromatophores lie in an angular position, each in its separate part of the dividing cell. At this time the nucleus forms a small, weblike mass across the angle of the chromatophore and is distinguished from the latter by its hyaline character as contrasted with the green of the chromatophore.

Vegetative division, just casually mentioned above, probably takes place, as in many diatoms, mainly at night, most of the cells found during the day being in a more mature state. Vegetative division occurs almost entirely only in cells that are well matured, or of a full hemispherical shape. The first evidence of division is a readily seen slight constriction in the middle of both sides of the broad, pale-green chromatophore. The final resulting halves of the original chromatophore, assume each a right-angular shape with the adjacent faces lying in an apical-transapical plane and extending upward toward the dorsal surface of the cell, the inner side of the angle thus being upward with the nuclear area subtending its vertex. The nucleus and nuclear mass must evidently have divided previously to, or simultaneously with, the division of the chromatophore, to occupy this position as a faint hyaline web across the angle of the newly formed chromatophore. Both subsequently and slowly flatten out as the newly formed daughter cells grow and expand to maturity, attaining again the hemispherical shape. Tension and stretching of the plasma threads play a major role, or appear to be the chief mechanism involved, in bringing these changes about. The daughter cells finally separate as a result of expanding internal pressure which forces them apart. The presence of such internal pressure as a functional agent in the dividing cell process is occasionally evidenced by a snapping apart of the newly formed cells, if one is so fortunate as to be observing them just at the critical moment or brings to bear a micro-needle upon such a cell in a state of being just about to divide, when a slight touch will cause it to spring apart.

Deposition of the new valves back to back in a central apical-transapical plane, cutting perpendicularly the pervalvar axis, is seen to be

occurring as the divided chromatophores assume their angular positions within the new daughter halves. Formation of the new valves becomes more and more evident as a line of increasing density in this central section of the cell, and if the cell be turned at a slight angle, there becomes evident in perspective two new sets of short plasma threads connecting the edges of the new chromatophores to the edges of the newly forming valves, as shown in the accompanying illustration (pl. 4, figs. 3, 4, 7, and 8).

Very close to the newly forming valves in this central region, and almost imperceptible, is a condensed, seemingly striate section of very narrow width, like a considerable number of compressed pleats or folds of a camera bellows or accordion, which are evidently potential or elementary intercalary bands of the prospective new cells. There is, of course, a set of these on either side of the new valves in the central region, one set, that is, in each of the new daughter cells.

This process is carried out with such great precision of cellular mechanics, and this is such a beautiful and advantageous form in which to view this sequence, that it is regrettable that the species is not a somewhat more robust or at least a more available one. It would seem a good one in which to study at least some phases of diatom cell division, to the above cursory discussion of which much remains yet to be added.

Derivation of name.—I have chosen for the generic name of this beautiful diatom a combination of the Greek word "thalassios," meaning "of the sea," since it is so characteristically a marine plankton form, and the Greek word "physa," meaning "bellows," from the great resemblance of its finely folded or pleated appearance to that of an accordion, fireplace bellows, or camera bellows. Especially in certain perspective views from both the apical end and side of the not fully matured cell does one get a typical folded and wedge-shaped effect of a fireplace bellows, as in plate 2, upper left figure.

As a species name for this form I have taken the Greek word "rhipis," meaning "fan," from its fine resemblance to a lady's folded fan, in apical end view as shown in the first (upper) four figures of plate 1. This is a very frequently observed and characteristic view.

Thus the name *Thalassiophysa rhipidis* seems best to indicate the particular features of this diatom.

Importance.—This diatom, in spite of its great delicacy and watery-like consistency, is sufficiently frequent to be an important constituent of the plankton population, and, in an area where the water is very clear and the plankton is in general tenuous and phantomlike,

it is a probably not insignificant factor in the biochemistry and economy of the sea.

It has no really close forms in structure and appearance, and it possesses a simple beauty which in my opinion would cause it to rate high in this respect among the diatoms.

PLATES

PLATE I

THALASSIOPHYSA RHIPIDIS

Figs. 1-4, Cell in apical aspect, various views. Fig. 5, Ventral view of mature cell (pervalvar view), showing the two halves with their ventral edges approximate and forming the ventral groove. Fig. 6, Dorsal (pervalvar) aspect of mature cell. Fig. 7, Single valve (in apical-transapical view). Fig. 8, Single valve, with a few intercalary bands showing across the notch. Magnification: All figures approximately 240 diameters.
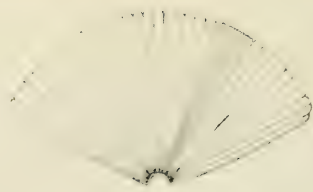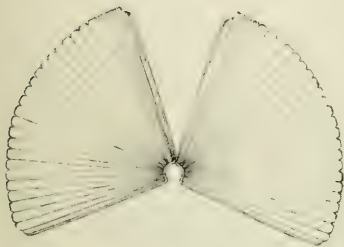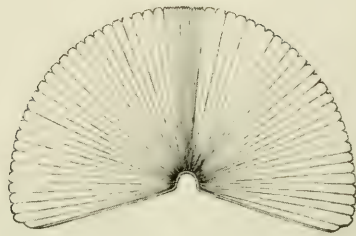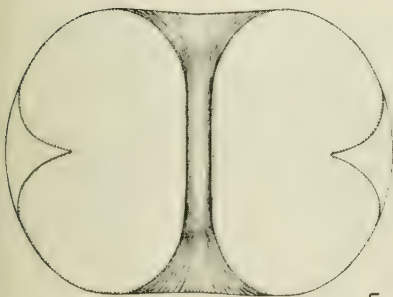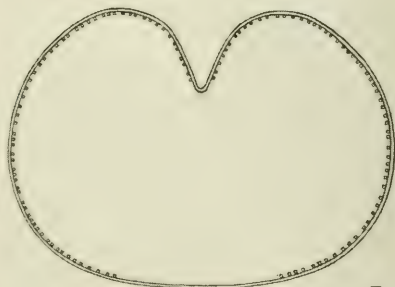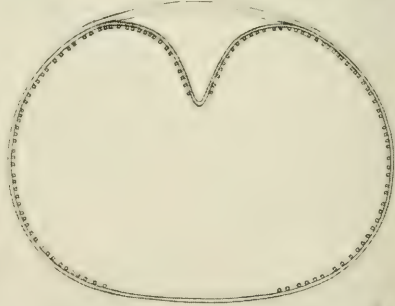
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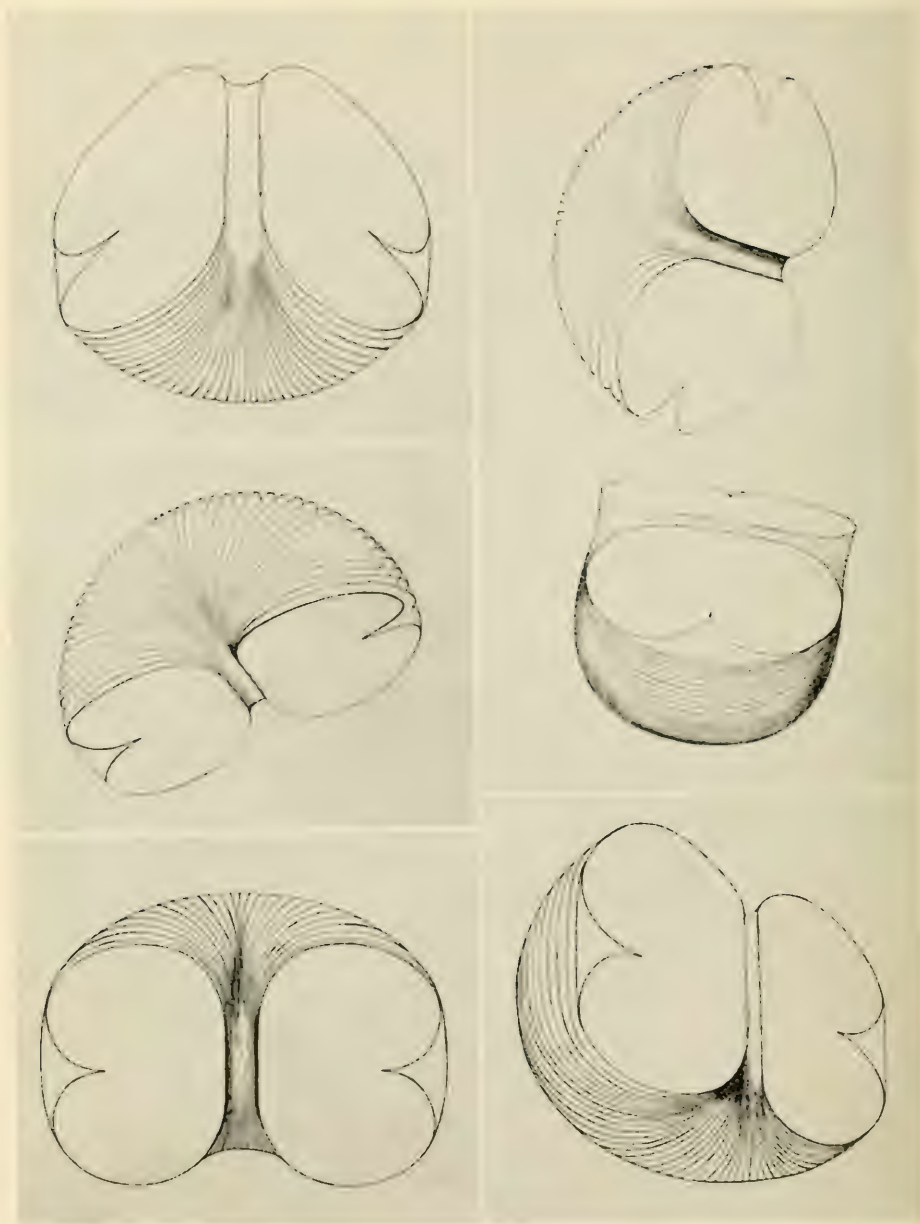
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Various typical views of well-matured cells. Magnification: All figures approximately 240 diameters.
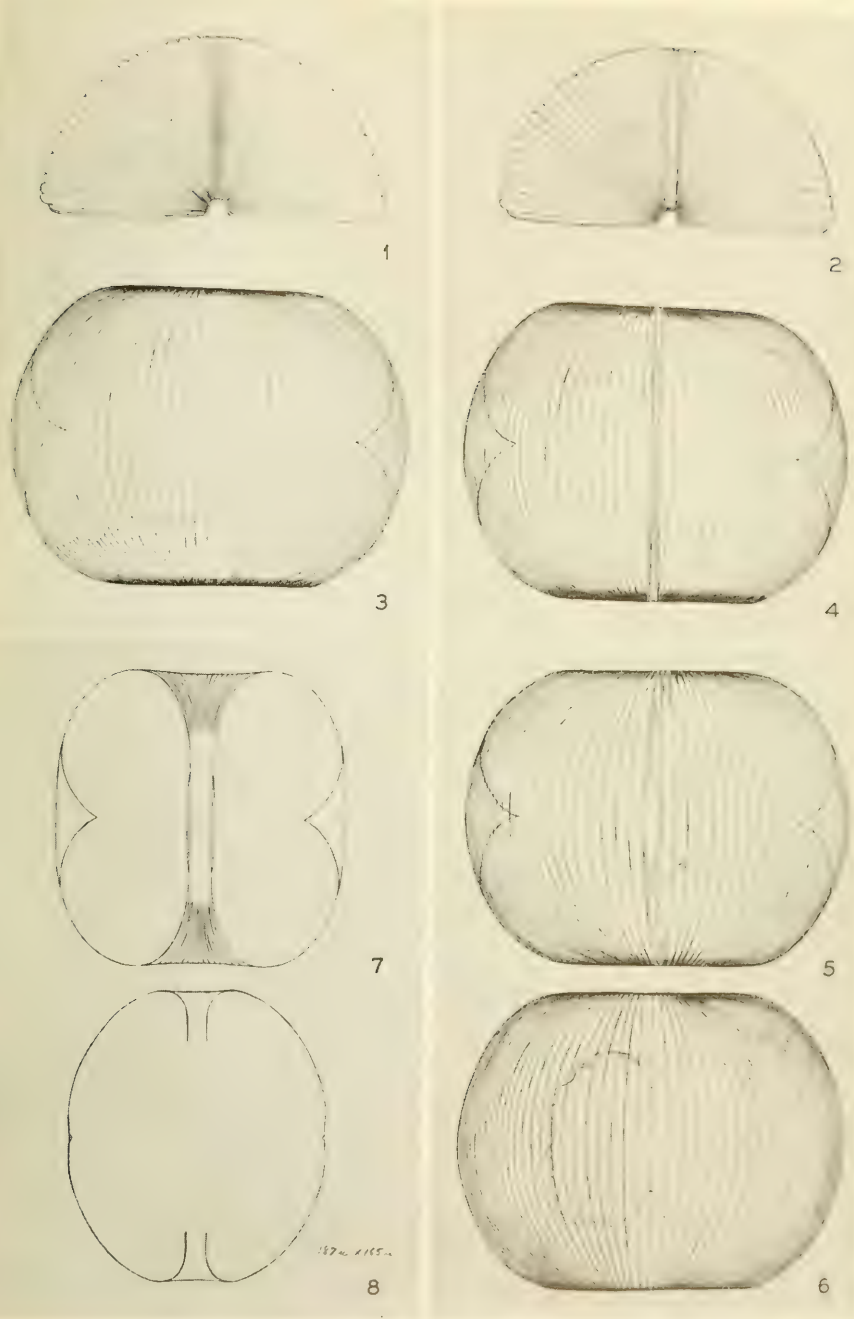
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Figs. 1-6, Various exterior views of the dividing cell, with chromatophore body dimly outlined within. Figs. 7-8, Ventral aspects of a narrower frustule of the same species. Magnification: All figures approximately 240 diameters.
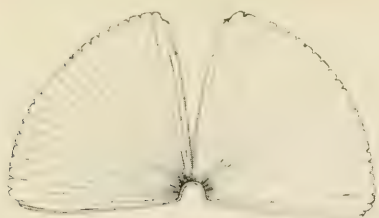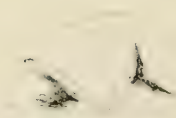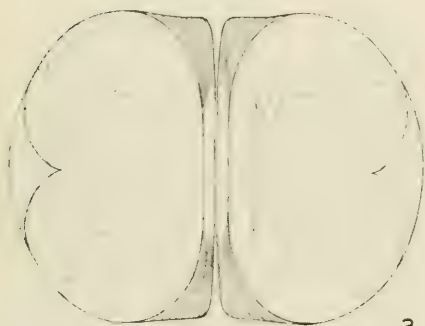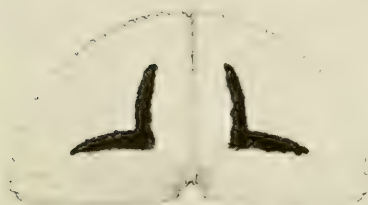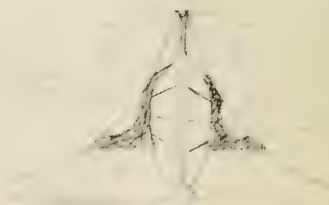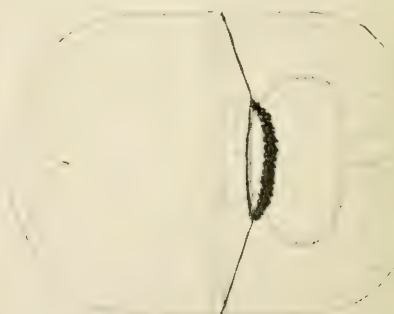
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Fig. 1, A dividing cell in apical aspect. Fig. 2, A cell in process of division with one side collapsed. Fig. 3, Ventral view of a cell in late stage of division; chromatophore outlined with plasmic thread attachments. Fig. 4, Ventral perspective view, showing chromatophore in color, beginning central membrane of newly forming valves, and plasmic thread attachments. Figs. 5 and 6, Apical and pervalvar aspects of mature dividing cells respectively showing chromatophore bodies colored. Figs. 7 and 8, Outline sketches of the same cells as figures 5 and 6 showing, respectively, chromatophore arrangements, nucleus, and plasmic thread attachments. Magnification: All figures approximately 240 diameters.