













# SMITHSONIAN

## MISCELLANEOUS COLLECTIONS

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VOL. 89

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"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES,  
AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—SMITHSON

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## ADVERTISEMENT

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The present series, entitled "Smithsonian Miscellaneous Collections," is intended to embrace all the octavo publications of the Institution, except the Annual Report. Its scope is not limited, and the volumes thus far issued relate to nearly every branch of science. Among these various subjects zoology, bibliography, geology, mineralogy, anthropology, and astrophysics have predominated.

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C. G. ABBOT,  
*Secretary of the Smithsonian Institution.*



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SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 89, NUMBER 1

AMPHIBIANS AND REPTILES COLLECTED  
BY THE SMITHSONIAN BIOLOGICAL  
SURVEY OF THE PANAMA  
CANAL ZONE

BY

KARL PATTERSON SCHMIDT

Assistant Curator of Reptiles and Amphibians, Field Museum of Natural History



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AMPHIBIANS AND REPTILES COLLECTED BY THE  
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*Assistant Curator of Reptiles and Amphibians, Field Museum of Natural History*

The opportunity to study the plant and animal life of a tropical area presented during the construction of the Panama Canal was seized by the Smithsonian Biological Survey of the Panama Canal Zone. The collections of cold-blooded vertebrates for this survey were made under a cooperative agreement between the Smithsonian Institution, the United States Bureau of Fisheries, and the Field Museum of Natural History. Dr. S. E. Meek of the Field Museum and Dr. S. F. Hildebrand of the Bureau of Fisheries were actively engaged in collecting in Panama from January to May, 1911, and from January to March, 1912; their collecting was primarily ichthyological but considerable numbers of amphibians and reptiles were incidentally preserved. This collection was more than equalled by the material collected by E. A. Goldman in the course of his field-work in Panama for the Smithsonian Survey. Goldman's report on the "Mammals of Panama"<sup>1</sup> contains an excellent account of his field-work and a map on which his collecting stations may be located. Spelling of locality names in the present paper follows Goldman's map wherever possible. Minor additions to the Survey collection of amphibians and reptiles were made by H. Pittier and E. D. Christopherson. The total collection (exclusive of the turtles) amounts to 758 specimens, representing 82 species.

So much attention is now focussed on the biology of the Panama Canal Zone by the existence of the Barro Colorado Island Laboratory, maintained by the Institute for Research in Tropical America, that it seems desirable to record the herpetological collections of the Smithsonian Survey, and the following list has been prepared at the suggestion of Dr. Leonhard Stejneger. I am indebted to Miss Doris Cochran of the United States National Museum for assembling this material for shipment to the Field Museum, and to Dr. E. R. Dunn of Haverford College, who has an extensive report on the amphibians

<sup>1</sup> Smithsonian Misc. Coll., vol. 69, no. 5, 1920.

and reptiles of Panama, Costa Rica, and Nicaragua in preparation, for much information and assistance in identification, obtained during a memorable association with him on Barro Colorado Island in 1928. A short paper by Dr. G. K. Noble of the American Museum of Natural History lists the frogs of the Panama collection, describing one of them as a new species, *Eleutherodactylus goldmani*.<sup>2</sup>

Doctor Dunn has examined a number of specimens, including especially the frogs of the genera *Phyllobates* and *Atelopus*, which are listed by him,<sup>3</sup> and has differed with Noble in various identifications.<sup>4</sup> Amaral has listed some of the snakes of this collection in connection with various studies. A new pit-viper, *Bothrops leptura*, was described in 1923.<sup>5</sup> This is now placed in the synonymy of *Bothrops monticellii* (Peracca).

The present paper lists the entire collection with the exception of the turtles, which are to be reported upon in a separate paper by Doctor Stejneger. Bibliographic references have been omitted in view of the expected appearance of a complete review of the fauna in question by Doctor Dunn.

## Class AMPHIBIA

### Order APODA

#### CAECILIA OCHROCEPHALA (Cope)

Two specimens, U.S.N.M. No. 54058, from Porto Bello, May 26, 1911, and 50249, from Cana, April 10, 1912, both collected by E. A. Goldman.

### Order SALIENTIA

#### BUFO GRANULOSUS Spix

The single specimen of this species measures as follows: Length of body 55 mm; length of head 15 mm; width of head 20 mm; arm

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<sup>2</sup> Noble, G. K., Some neotropical batrachians preserved in the United States National Museum with a note on the secondary sexual characters of these and other amphibians. Proc. Biol. Soc. Washington, vol. 37, pp. 65-72, 1924.

<sup>3</sup> Dunn, Emmett R., New frogs from Panama and Costa Rica. Occ. Papers Boston Soc. Nat. Hist., vol. 5, pp. 385-401, 1931.

<sup>4</sup> Dunn, Emmett R., The amphibians of Barro Colorado Island. Occ. Papers Boston Soc. Nat. Hist., vol. 5, pp. 403-421, 1931.

<sup>5</sup> Amaral, Afranio do., New genera and species of snakes. Proc. New England Zool. Club, vol. 8, pp. 85-105, 1923.

27 mm; leg 56 mm. The back is marbled with brown and brownish yellow.

U.S.N.M. No. 53739, collected at Rio Calobre, March 18, 1911, by S. E. Meek and S. F. Hildebrand.

#### BUFO HAEMATITICUS Cope

The normal color pattern of this species exhibits two pairs of black spots on the back; but these may be entirely absent. There is usually a light preocular spot on the lip. Some specimens have a light vertebral line; one, No. 53769, has small spots sharply outlined with very narrow yellow rims. No. 50221 is much the largest specimen in the collection, measuring 78 mm from snout to vent, the length of arm 54 mm, length of leg 106 mm. There are 73 specimens in the collection, collected as follows:

| U.S.N.M. No.               | Locality                        | Date            | Collector         |
|----------------------------|---------------------------------|-----------------|-------------------|
| 50179-96                   | Cana, 1,800-2,000 ft.           | Mar. 1-24, 1912 | E. A. Goldman     |
| 50210                      | " 2,000 ft.                     | Mar. 30, 1912   | " " "             |
| 50216                      | " 3,000 ft.                     | June 6, 1912    | " " "             |
| 50221                      | " 2,000 ft.                     | Mar. 28, 1912   | " " "             |
| 50228                      | Rio Chilibrillo                 | Jan. 30, 1912   | " " "             |
| 53740, 53757-59            | Chepo                           | Mar. 21, 1911   | Meek & Hildebrand |
| 53769-70 }<br>53772-81 }   | Gatun River, above<br>Mitchells | .....           | " " "             |
| 53782-97                   | Upper Chagres River             | Feb. 24, 1911   | " " "             |
| 53822                      | Rio Juan                        | Apr. 22, 1911   | " " "             |
| 53959-63                   | Rio Jappe                       | Mar. 22, 1912   | " " "             |
| 53986-88                   | Rio Mamoni                      | Mar. 20, 1911   | " " "             |
| 54040                      | Porto Bello                     | May 27, 1911    | E. A. Goldman     |
| 54236, 54239, }<br>54248 } | Oruza                           | Feb. 27, 1912   | Meek & Hildebrand |
| 54241-46                   | Rio Capeti                      | Mar. 5, 1912    | " " "             |

#### BUFO TYPHONIUS (Linné)

Out of 43 specimens, 14 have the vertebral light stripe; the vivid black dorsal pattern frequent in this species is present in 6 specimens; 4 have two pairs of black dorsal spots, like *Bufo haematiticus*.

Out of the 43 specimens, 10, U.S.N.M. Nos. 50176, 50211-15, 50217-20, were collected at Cana during March, May, and June, 1912, by E. A. Goldman, who collected further specimens of this species as follows: 53721 and 54010, Rio Indio, near Gatun, March 3 and February 16, 1911; 54006 and 54054, Panama; 54035-39, 54041-48 and 54050-53, Porto Bello, May 26, 1911; and 54055, Cerro Brujo, June 7, 1911. Specimens collected by Meek and Hildebrand are

Nos. 53716, Arrijan, February 19, 1911; 53736, Rio Calobre, March 18, 1911; 53745, Paraiso, March 3, 1911; 53751-52, Empire, February 8, 1911; 53844-45, Mirallores, January 18, 1911; 53865-66, Rio Cardenas, Corozal, February 16, 1911; and 53957-58, Rio Jappe, March 2, 1912.

#### **BUFO MARINUS (Linné)**

One hundred and forty-one specimens, collected at the following localities in Panama: U.S.N.M. Nos. 50154-67, Las Cruces, January 29, 1912; 50201, east slope of Pirri Range, May 2, 1912; 50202-5, 50223, 50224, Cana, February to June, 1912; 54065, Buenaventura Island, May 30, 1911; 54066, Porto Bello, May 24, 1911; and 54173, Gatun, January 14, 1911, collected by E. A. Goldman; Nos. 53728 and 53760-68, Chepo, March 21, 1911; 53744, Mindi Cut, January 28, 1911; 53771, Gatun River, above Mitchells; 53823, Pectine River, February 22, 1911; 53860-64 and 53906-17, Agua Clara, March 8, 1911; 53898-99, Frijoles, February 13, 1911; 53920-24, 53929-52, 54233, 54259-60, Gorgona, March 29-31, 1912; 53953-56, 54229, 54232, Cana, March 1, 1912; 53966-72, Upper Chagres River, February 24, 1911; 53977, Pedro Miguel, January 13, 1911; 53978, Chagres River at Gatun, February 10, 1911; 53985, Rio Mamoni, March 20, 1911; 54201, Porto Bello, April 24-28, 1911; 54237-38, 54240, 54247, 54256-58, Oruza, February 27, 1912; 54248-55, Rio Capeti, March 5, 1912; 54261, Rio Cascajal, Porto Bello, March 17, 1912; 54273, Rio Cupe, Darien, February 26, 1912; 54274-75, Rio Tuyra, February 28, 1912; 54277-78, Rio Jappe, Darien, March 6, 1912; and 54279-92, Rio Chame, February 14, 1912, collected by Meek and Hildebrand; No. 54149 from the Canal Zone Survey without further data.

#### **BUFO CONIFERUS Cope**

A single specimen, U.S.N.M. No. 53719, collected on the Upper Trinidad River, March 7, 1911, by Meek and Hildebrand, has been referred to this species by Dunn.

#### **ENGYSTOMOPS PUSTULOSUS (Cope)**

One specimen, U.S.N.M. No. 53992, collected by Meek and Hildebrand on the Rio Mamoni, March 20, 1911, and one, No. 54294, from the Canal Zone, without further data, collected by E. D. Christopherson.

#### **LEPTODACTYLUS PENTADACTYLUS (Linné)**

A single specimen, U.S.N.M. No. 54068, from Porto Bello, collected May 26, 1911, by E. A. Goldman.

**LEPTODACTYLUS QUADRIVITTATUS** Cope

A single specimen, U.S.N.M. No. 54177, from Gatun, collected May 19, 1911, by E. A. Goldman.

This specimen, a male, differs from descriptions in having a projecting snout with sharp horizontal edge. Dimorphism in this character appears in a number of species of *Leptodactylus*. It is interpreted by Noble,<sup>6</sup> as a breeding season character of the male sex, used in excavating the hollow in which the eggs are to be laid. A pair of internal vocal sacs are present, their openings rather posteriorly placed; they are indicated externally by a fold and darker coloration.

**LEPTODACTYLUS BOLIVIANUS** Boulenger

Eight specimens, collected at the localities shown in the following table:

| U.S.N.M. No. | Locality         | Date          | Collector         |
|--------------|------------------|---------------|-------------------|
| 50222        | Cana, 1,800 ft.  | Mar. 22, 1912 | E. A. Goldman     |
| 53720        | Tabernailla      | Mar. 12, 1911 | " " "             |
| 53841        | Miraflores       | Jan. 18, 1911 | Meek & Hildebrand |
| 53885        | Rio Chorrera     | Apr. 4, 1911  | " " "             |
| 53928        | Rio Marte Arnade | Mar. 26, 1912 | " " "             |
| 53982-83     | Rio Mamoni       | Mar. 20, 1911 | " " "             |
| 54176        | Gatun            | Jan. 13, 1911 | E. A. Goldman     |

**ELEUTHERODACTYLUS GOLLMERI** (Peters)

Two specimens, U.S.N.M. Nos. 54033-34, from Cerro Brujo, collected June 7, 1911, by E. A. Goldman. No. 54033 is the type of *Eleutherodactylus goldmani* Noble, which is placed in the synonymy of *E. gollmeri* by Dunn.

**ELEUTHERODACTYLUS FITZINGERI** (Schmidt)

Twenty-one specimens of this species are in the collections of the Smithsonian Biological Survey of the Canal Zone. These may be listed as follows:

| U.S.N.M. No. | Locality        | Date            | Collector         |
|--------------|-----------------|-----------------|-------------------|
| 50178        | Cana            | Mar. 1-24, 1912 | E. A. Goldman     |
| 50229        | Rio Chilibrillo | Jan. 30, 1912   | " " "             |
| 53717        | Arrijan         | Feb. 19, 1911   | Meek & Hildebrand |
| 53726-27     | Toro Point      | Jan. 9, 1911    | " " "             |
| 53729        | Pedro Miguel    | Feb. 11, 1911   | " " "             |
| 53732        | Culebra         | Apr. 1911       | " " "             |
| 53798-807    | Upper Chagres   | Feb. 24, 1911   | " " "             |
| 53843        | Miraflores      | Jan. 18, 1911   | " " "             |
| 53990        | Rio Mamoni      | Mar. 20, 1911   | " " "             |
| 54148        | Gatun           | Jan. 21, 1911   | E. A. Goldman     |
| 54178        | "               | Apr. 6, 1911    | " " "             |

<sup>6</sup> Noble, G. K., The biology of the Amphibia, p. 120, 1931.

**ELEUTHERODACTYLUS LONGIROSTRIS (Boulenger)**

Three specimens, U.S.N.M. Nos. 54180-82, collected at Cerro Azul, March 25, 1911, by E. A. Goldman.

**ELEUTHERODACTYLUS LATIDISCUS (Boulenger)**

Two specimens, U.S.N.M. Nos. 54022-23, from Cerro Brujo, collected June 7, 1911, by E. A. Goldman. Two additional specimens, U.S.N.M. Nos. 50207-8, were collected near the head waters of the Rio Limon in the Pirri Range, Darien, April 15 and 22, 1912, by E. A. Goldman.

No. 50207 has a generally pale coloration, with brownish marbling which defines a pair of conspicuous light bands extending from the eyelids to the mid-back.

**ELEUTHERODACTYLUS DIASTEMA (Cope)**

A single specimen of this very distinct form, U.S.N.M. No. 53718, from the Rio Calobre, was collected March 18, 1911, by Meek and Hildebrand.

**HYLA GABBII Cope**

Two specimens, U.S.N.M. No. 53722, from the Rio Calobre, collected by Meek and Hildebrand; and No. 53886, with no further data than Panama.

**HYLA ROSENBERGI Boulenger**

A single specimen, U.S.N.M. No. 50209, from Cana, at 2,000 feet altitude, collected June 6, 1912, by E. A. Goldman, agrees very closely with Boulenger's description and figure. The vomerine teeth in the present specimen are in more elongate and more angularly bent series than is shown in the original figure. A second specimen, No. 53979, from the Rio Bayano, was collected March 22, 1911, by Meek and Hildebrand.

**PHYLLOBATES LATINASUS (Cope)**

Two specimens, Nos. 54174-75, from Cerro Azul, collected March 26, 1911, by E. A. Goldman; and No. 54231 from Cana, collected March 1, 1912, by Meek and Hildebrand.

**PHYLLOBATES FLOTATOR Dunn**

One specimen, U.S.N.M. No. 50177, from Cana, collected March 1-24, 1912, by E. A. Goldman, is a paratype of this species.

**PHYLLOBATES KINGSBURYI** Boulenger

Four specimens, U.S.N.M. Nos. 50197-200, with no data, and two, 53737-38, from the Rio Calobre, collected March 18, 1911, by Meek and Hildebrand, represent this species. Dunn lists Nos. 50197-200 as from Cana, Darien, which is probably their true provenance; but they are unfortunately without locality data.

**DENDROBATES AURATUS** (Girard)

Twenty-four specimens in the Smithsonian Survey collections were collected as follows:

| U.S.N.M. No. | Locality      | Date           | Collector            |
|--------------|---------------|----------------|----------------------|
| 54025-32     | Cerro Brujo   | June 6-7, 1911 | E. A. Goldman        |
| 54235        | Oruza, Darien | Feb. 27, 1912  | Meek & Hildebrand    |
| 54296-310    | Canal Zone    | 1911-1912      | E. D. Christopherson |

**DENDROBATES PUMILIO** (Schmidt)

One specimen, U.S.N.M. No. 54168, from Gatun, collected April 14, 1911, by E. A. Goldman.

**ATELOPUS VARIUS GLYPHUS** Dunn

Forty-four specimens, collected as follows:

| U.S.N.M. No. | Locality                               | Date            | Collector         |
|--------------|--|-----------------|-------------------|
| 50168-75     | Cana                                   | Mar. 1-24, 1912 | E. A. Goldman     |
| 50226        | "                                      | Mar. 30, 1912   | " " "             |
| 50230-48     | Pirri Range, near head<br>of Rio Limon | Apr. 15, 1912   | " " "             |
| 53964-65     | Rio Jappe                              | Mar. 2, 1912    | Meek & Hildebrand |
| 54183-84     | Cerro Azul                             | Mar. 25, 1911   | E. A. Goldman     |
| 54186-96     | " "                                    | " " "           | " " "             |
| 54230        | Cana                                   | Mar. 1, 1912    | Meek & Hildebrand |

**RANA PALMIPES** Spix

Four frogs and five tadpoles are referred to this species:

| U.S.N.M. No. | Locality              | Date          | Collector         |
|--------------|-----------------------|---------------|-------------------|
| 50225        | Cana                  | May 24, 1912  | E. A. Goldman     |
| 53887        | Panama                | 1911-1912     | Meek & Hildebrand |
| 54067        | Porto Bello           | May 24, 1911  | E. A. Goldman     |
| 54276        | Upper Reservoir Creek | Jan. 25, 1912 | Meek & Hildebrand |
| 54293        | Rio Sabiganti         | Mar. 1, 1912  | " " "             |

## Class REPTILIA

## Suborder SAURIA

**GONATODES FUSCUS** (Hallowell)

Twenty-five specimens represent this common species. Of these, U.S.N.M. Nos. 54208-16 and 54218 were collected by E. D. Christopherson in the Canal Zone, and Nos. 54311-21, collected by Meek and Hildebrand, bear the same indefinite data. Nos. 50145-48 were collected at Cana, Darien, by E. A. Goldman, in May and June, 1912.

**SPHAERODACTYLUS LINEOLATUS** (Lichtenstein)

Six specimens collected as follows:

| U.S.N.M. No. | Locality    | Date          | Collector            |
|--------------|-------------|---------------|----------------------|
| 53734        | Rio Bayaria | Mar. 23, 1911 | Meek & Hildebrand    |
| 53991        | Rio Mamoni  | Mar. 20, 1911 | " " "                |
| 54219-22     | Canal Zone  | 1911-1912     | E. D. Christopherson |

**THECADACTYLUS RAPICAUDUS** (Houttuyn)

Two specimens in the collection, No. 54202 collected at Porto Bello, April 24-28, 1911, by Meek and Hildebrand, and No. 54267 with no locality except the Canal Zone, collected by E. D. Christopherson.

**NOROPS AURATUS** (Daudin)

Six specimens represent this widespread form. These were collected as follows:

| U.S.N.M. No. | Locality   | Date             | Collector            |
|--------------|------------|------------------|----------------------|
| 50126-27     | Empire     | Feb. 15-16, 1912 | E. A. Goldman        |
| 53817        | Alhamel    | 1911             | Meek & Hildebrand    |
| 53989        | Rio Mamoni | Mar. 20, 1911    | " " "                |
| 54226        | Canal Zone | 1911-1912        | E. D. Christopherson |
| 54269        | Gorgona    | Mar. 28, 1912    | Meek & Hildebrand    |

**ANOLIS HUMILIS** Peters

A single specimen, U.S.N.M. No. 54056, collected June 7, 1911, by E. A. Goldman at Cerro Brujo.

**ANOLIS LEMURINUS** (Cope)

A single specimen, U.S.N.M. No. 50150, collected May 2, 1912, at 4,000 feet altitude on the east slope of the Pirri Range, by E. A. Goldman, is referred to this species. The ventrals are keeled; the dorsals strongly keeled but not greatly enlarged, in at least 16 or 18 rows; laterals small, keeled; a dorso-lateral light stripe on each side; semicircles separated by a single scale. Dunn writes me that this is what he has called *vittigerus*.

**ANOLIS POECILOPUS (Cope)**

U.S.N.M. No. 50149, collected at Cana, at 2,000 feet, March 27, 1912, by E. A. Goldman, is tentatively referred to this species. This specimen agrees in detail with Cope's original description with the exception that the occipital is large and well distinguished. The rugosity of the head scales extends to the occipital, and this might account for an error in the original description. The species is characterized by its very small keeled scales; 13 loreal rows from labials to canthals; no elongate superciliary; and the caudal scales are notably small.

**ANOLIS STIGMOSUS Bocourt**

Twelve specimens represent this species:

| U.S.N.M. No. | Locality   | Date          | Collector            |
|--------------|------------|---------------|----------------------|
| 53724        | Toro Point | Jan. 9, 1911  | Meek & Hildebrand    |
| 53750        | Empire     | Feb. 8, 1911  | " " "                |
| 53821        | Chorrera   | Apr. 10, 1911 | " " "                |
| 53889-90     | Panama     | 1911-1912     | " " "                |
| 54179        | Cerro Azul | Mar. 25, 1911 | E. A. Goldman        |
| 54217        | Panama     | 1911-1912     | E. D. Christopherson |
| 54223-25     | "          | " "           | " " "                |
| 54263        | Cristobal  | Feb. 15, 1911 | Meek & Hildebrand    |
| 54324        | Canal Zone | 1911-1912     | E. D. Christopherson |

**ANOLIS PETERSII Bocourt**

Two specimens, U.S.N.M. No. 53888, collected by Meek and Hildebrand, without definite locality, and No. 54144, collected at Gatun, May 2, 1911, by E. A. Goldman, run directly to this species in Dunn's recent arrangement of the anoles of Central America.<sup>7</sup>

**ANOLIS LIMIFRONS (Cope)**

Eleven specimens represent this species:

| U.S.N.M. No. | Locality                | Date          | Collector         |
|--------------|-------------------------|---------------|-------------------|
| 48597        | Viento Frio             | 1911          | H. Pittier        |
| 50129        | Old Panama              | Feb. 7, 1912  | E. A. Goldman     |
| 50151-52     | Pirri Range, east slope | Apr. 22, 1912 | " " "             |
| 53725        | Toro Point              | Jan. 9, 1911  | Meek & Hildebrand |
| 53731        | Panama                  | 1911-1912     | " " "             |
| 54007        | Rio Indio               | Feb. 13, 1911 | E. A. Goldman     |
| 54011-12     | Gatun                   | Feb. 3, 1911  | " " "             |
| 54172        | Lion Hill               | Jan. 13, 1911 | " " "             |
| 54325        | Canal Zone              | .....         | .....             |

<sup>7</sup> Notes on Central American Anolis. Proc. New England Zool. Club, vol. 12, p. 19, 1930.

**ANOLIS PENTAPRION (Cope)**

A single specimen, U.S.N.M. No. 45574, collected at Bohio, April, 1911, by H. Pittier, is referred to this species.

**IGUANA IGUANA IGUANA (Linné)**

Five specimens with the following data:

| U.S.N.M. No. | Locality | Date          | Collector        |
|--------------|----------|---------------|------------------|
| 53709        | Gatun    | Jan. 24, 1911 | S. F. Hildebrand |
| 54116        | "        | Jan. 15, 1911 | E. A. Goldman    |
| 54117        | "        | Apr. 26, 1911 | " " "            |
| 54118        | Bohio    | Apr. 29, 1911 | " " "            |
| 54143        | "        | " " "         | " " "            |

**BASILISCUS BASILISCUS (Linné)**

Out of a total of 113 specimens, 70 were collected by Meek and Hildebrand at the following localities: Gatun, Nos. 53710-13, January 24, 1911; 53747-48, January 9, 1911; 53828, March 30, 1911; 53836-40, February 10, 1911; Alhajuela(?), No. 53714; Arrijan, No. 53715, February 19, 1911; Toro Point, No. 53723, January 9, 1911; Mindi, No. 53735, January 17, 1911; 53824-25, (no date); 53833-34, January 28, 1911; Empire, Nos. 53753-56, February 8, 1911; Corozal, Rio Cardenas, Nos. 53809-10, February 17, 1911; 53869-71, 53903-5, February 16, 1911; Alhamel, Nos. 53818-19, 1911; Tabernilla, Nos. 53846-58, April 9, 1911; Upper Trinidad, Nos. 53872-76, 53901-2, March 7, 1911; Culebra, No. 53877, February 11, 1911; Rio Chorrera, No. 53884, April 4, 1911; Porto Bello, No. 53918, March 17, 1912; Rio Marte Arnade, Nos. 53935-36, May 26, 1912; Dimon Creek, Alhajuela, Nos. 53973-76, February 26, 1911; Rio Bayano, No. 53981, March 22, 1911; Gorgona, No. 54270, March 28-April 2, 1912; Panama (no locality or date), Nos. 53811, 53859, 53891. Forty-three were collected by E. A. Goldman as follows: Cana, Darien, Nos. 50065-75, 50079-81, 50083-84, February-May, 1912; Seteganti River, Cana, No. 50076, March 20, 1912; Empire, No. 50077, February 17, 1912; Marraganti, No. 50078, June 20, 1912; Boca de Cupe, No. 50082, June 14, 1912; Old Panama, No. 50128, February 7, 1912; Lion Hill, Nos. 54016-17, February 6, 1911; Gatun, No. 54018, January 12, 1911; 54121-22, April 24-26, 1911; Corozal, Nos. 54061-62, June 15-19, 1911; Buenaventura Id., Nos. 54063-64, May 29-30, 1911; Cerro Azul, Nos. 54120, 54124-25, 54127, March 22, 1911; Tabernilla, No. 54123, April 20, 1911; Miraflores, No. 54126, May 13, 1911; Panama (no locality or date), Nos. 54001-4.

**CORYTHOPHANES CRISTATUS** Gray

A single specimen, U.S.N.M. No. 50153, was shot from a bird's nest in the forest at Gatun, July 30, 1911, by E. A. Goldman.

**CTENOSAURA SIMILIS** (Gray)

A single specimen, U.S.N.M. No. 54204, was collected at Corozal, April 20, 1911, by Meek and Hildebrand.

**ENYALIOIDES HETEROLEPIS** (Bocourt)

Two specimens, U.S.N.M. No. 54005, from Panama, collected by E. A. Goldman, with no further data, and No. 54019, from Gatun, January 20, 1911, also collected by E. A. Goldman. The latter specimen was shot along a cliff in the forest. This species has been recorded from Gatun by Fowler.\* The femoral pores are two on each side.

**AMEIVA FESTIVA** (Lichtenstein)

Fourteen specimens of this species may be listed as follows:

| U.S.N.M. No. | Locality    | Date          | Collector     |
|--------------|-------------|---------------|---------------|
| 50134        | Cana        | Mar. 27, 1912 | E. A. Goldman |
| 50136        | "           | Apr. 4, 1912  | " " "         |
| 50138        | "           | Apr. 2, 1912  | " " "         |
| 50139        | "           | May 30, 1912  | " " "         |
| 50142        | "           | May 21, 1912  | " " "         |
| 50143        | "           | May 19, 1912  | " " "         |
| 54072-75     | Porto Bello | May 25, 1911  | " " "         |
| 54134        | Gatun       | Apr. 26, 1911 | " " "         |
| 54135        | "           | May 4, 1911   | " " "         |
| 54137        | Chepo       | Mar. 28, 1911 | " " "         |
| 54169        | Gatun       | Apr. 26, 1911 | " " "         |

**AMEIVA UNDULATA** (Wiegmann)

Sixteen specimens represent this species. Eight were collected by Meek and Hildebrand as follows: Chepo, No. 53741, March 21, 1911; Alhamel, Nos. 53813-16, 1911; Miraflores, No. 53842, January 18, 1911; Rio Cardenas, Corozal, No. 53868, February 16, 1911; Culebra, No. 53880, February 11, 1911. Eight were obtained by E. A. Goldman as follows: Cana, No. 50135, June 10, 1912; 50137, June 6, 1912; 50140, May 21, 1912; 50141, May 16, 1912; Cerro Azul, Nos. 54136, 54147, March 22, 1911; Gatun, No. 54142, January 2, 1911; Panama (no locality or date), No. 53999.

\* Proc. Acad. Nat. Sci. Philadelphia, 1916, p. 406.

**AMEIVA PRAESIGNIS** (Baird and Girard)

Out of the series of 45 specimens in the Survey collection, 25 were collected by Meek and Hildebrand as follows: Toro Point, No. 53742, April 14, 1911; Gatun, No. 53746, January 9, 1911; 53826-27, March 30, 1911; Mindi Cut, No. 53835, January 28, 1911; Rio Cardenas, Corozal, No. 53867, February 16, 1911; Culebra, Nos. 53878-79, 53881, February 11, 1911; Rio Marte Arnade, No. 53927, March 26, 1912; Rio Bayabo, No. 53980, March 22, 1911; Rio Mamoni, Nos. 53993-95, March 20, 1911; Taboga Id., Nos. 54197-98, 54206, May 12-15, 1911; Gorgona, Nos. 54271-72, March 28, April 2, 1912; Canal Zone (no further data), Nos. 53733, 53892-95, 54323. Specimens collected by E. A. Goldman may be listed as follows: Gatun, Nos. 54000, March 6, 1911; 54020, January 19, 1911; 54021, April 5, 1911; 54069, January 15, 1911; 54131, April 21, 1911; 54133, 54140, January 3, 1911; 54142, January 2, 1911; Corozal, Nos. 54070-71, June 15, 1911; Miraflores, Nos. 54128, 54139, 54141, May 13, 1911; Bas Obispo, No. 54129, May 5, 1911; Tabernilla, Nos. 54130, 54132, 54138, April 13-20, 1911; Panama (no further data), Nos. 53996-98.

**ECHINOSAURA PANAMENSIS** Barbour

A single specimen, U.S.N.M. No. 50144, from the Pirri Range, near the headwaters of the Rio Limon, was collected by E. A. Goldman, April 22, 1912. The species was described from La Loma, Bocas del Toro Prov., near the other end of Panama.

**MABUYA AGILIS** (Raddi)

Two specimens, U.S.N.M. No. 50133, collected at Cana, June 12, 1912, by E. A. Goldman, and 54322 from the "Canal Zone," collected by Meek and Hildebrand.

## Suborder SERPENTES

**UNGALIOPHIS PANAMENSIS** sp. nov.

*Diagnosis.*—Distinguished from *Ungaliophis continentalis* Müller by having 21 dorsal scale rows instead of 25, 3 postoculars instead of 2, and 2 elongate loreals, the nostril being in the single small nasal, instead of a single loreal and divided nasal of the Guatemalan species.

*Type.*—U.S.N.M. No. 54059, from Cerro Brujo, Panama, altitude 2,000 feet, collected on June 6, 1911, by E. A. Goldman.

*Description of the type.*—Head small, little wider than the neck, depressed, the snout projecting beyond the lower jaw; eye small with a very small vertical pupil; body strongly compressed; tail incomplete.

Rostral just visible from above, about twice as wide as high; a single large prefrontal, roughly 7-sided, separated from the rostral by the small internasals; frontal subtriangular, shorter than the prefrontal; parietals not distinguished from the adjacent scales; nostril in a single small scale; two elongate loreals; a single preocular; three postoculars; upper labials 8 to 9, the fourth and fifth and sixth on the respective sides entering the eye; lower labials 10, the first pair very large and in contact; one pair of chin shields slightly enlarged; dorsal scales in 21 rows, dropping to 15 anterior to the anus; centrals 236; tail incomplete.

*Coloration (in alcohol).*—Ground color pale, punctate with brown dots and maculation; a large brown spot on the head, behind which are about 53 pairs of triangular spots with their apices at the vertebral line, frequently confluent into hour-glass shaped spots, more often offset, *i. e.* alternate; an incomplete lateral row of small brown spots; 44 lateroventral brown spots, mostly extending across the belly; a brown line from the angle of the mouth to the eye.

*Dimensions.*—Total length about 500 mm.

*Remarks.*—The nasal and loreal arrangement in this snake are radically different from that in *Ungaliophis continentalis*, which has only a single loreal, and a divided nasal. The anterior loreal of the present specimen apparently corresponds with the posterior nasal of *continentalis*. The constancy of this arrangement of the nasals requires verification from additional specimens. In addition to the characters mentioned in the diagnosis, *panamensis* differs from the Guatemalan species in the separation of the prefrontal and rostral by the internasals. The inclusion of Panama in the range of *continentalis* by Amaral<sup>9</sup> appears to be based on the present specimen which was entered as *continentalis* in the United States National Museum catalogue.

#### CONSTRUCTOR CONSTRUCTOR IMPERATOR (Daudin)

Three specimens, from the following localities:

| U.S.N.M.<br>No. | Locality   | Date          | Collector     | Sex | Ven-<br>trals | Cau-<br>dals |
|-----------------|------------|---------------|---------------|-----|---------------|--------------|
| 50094           | Cana       | May 25, 1912  | E. A. Goldman | ♀   | 243           | 59           |
| 54060           | Gatun      | June 23, 1911 | " " "         | ♀   | 236           | 62           |
| 54145           | Tabernilla | Apr. 29, 1911 | " " "         | ♀   | 239           | 60           |

<sup>9</sup> Lista remissiva dos ophidios da regio neotropica. Mem. Inst. Butantan, vol. 4, p. 145, 1929.

The dorsal dark cross-bars in No. 50094 number 20½ on the body and 5 on the tail. The transformation of a narrow cross-bar, constricted on the mid-dorsal line anteriorly, to an oval longitudinally elongated spot on the posterior part of the body is clearly shown on this specimen.

#### **EPICRATES CENCHRIS MAURUS (Gray)**

A single female specimen, U.S.N.M. No. 50125, collected at Gatun, July 31, 1911, by E. A. Goldman, has 238 ventrals and 54 subcaudals. The remains of a Boqueron cotton rat (*Sigmodon hispidus chiriquensis* Allen) are contained in the stomach.

#### **BOA RUSCHENBERGII (Cope)**

A single male specimen, U.S.N.M. No. 53896, was collected by Meek and Hildebrand, without data other than "Panama." The ventrals number 267, the subcaudals 86.

#### **TRETANORHINUS MOCQUARDI Bocourt**

Two specimens, U.S.N.M. Nos. 54200, 54203, collected at Corozal, April 20, 1911, by Meek and Hildebrand. The first of these, a female with tail incomplete, has 168 ventrals; the second is a male with 166 ventrals and 78 subcaudals.

The venter is nearly uniform dark brownish; lateral yellow stripe with scales narrowly outlined with brown. The lateral scales just above the anal cleft have well developed supra-anal ridges in the male specimen.

#### **TRETANORHINUS NIGROLUTEUS Cope**

One specimen, U.S.N.M. No. 54151, collected at Gatun, May 13, 1911, by E. A. Goldman, is referred to this species. It is in excellent agreement with Cope's description except that the internasals are narrowly in contact with the rostral, and that there is a mid-ventral series of widely spaced brownish spots, as described by Bocourt for his *lateralis*. The specimen is a female, with 147 ventrals and 61 subcaudals.

#### **NINIA ATRATA SEBAE (Duméril and Bibron)**

A single specimen, U.S.N.M. No. 50114, collected at Cana, April 10, 1912, by E. A. Goldman, is a male, with strongly tuberculate chin-shields. The ventrals number 140, the subcaudals 60.

**DRYMOBIUS BODDAERTII (Sentzen)**

Four specimens of this species were collected as follows:

| U.S.N.M.<br>No. | Locality   | Date          | Collector     | Sex | Ventrals | Caudals |
|-----------------|------------|---------------|---------------|-----|----------|---------|
| 54013           | Gatun      | Jan. 14, 1911 | E. A. Goldman | ♀   | 188      | 95      |
| 54014           | "          | " " "         | " " "         | ♀   | 184      | ..      |
| 54156           | "          | May 6, 1911   | " " "         | ♀   | 189      | 97      |
| 54158           | Tabernilla | May, 1911     | " " "         | ♀   | 183      | 95      |

**DRYMOBIUS DENDROPHIS (Schlegel)**

Two specimens collected at Gatun by E. A. Goldman, U.S.N.M. No. 54080, January 14, 1911, and 54150, April 6, 1911. The first, a female, has 161 ventrals and 144 subcaudals; the other, a male, has 158 ventrals and 140 subcaudals.

**DRYMOBIUS MARGARITIFERUS (Schlegel)**

A single female specimen, U.S.N.M. No. 53830, collected at Rio Cardenas, February 16, 1911, by Meek and Hildebrand, has 151 ventrals and 116 subcaudals.

**PHRYNONAX POECILONOTUS SHROPSHIREI Barbour and Amaral**

Two male specimens collected by E. A. Goldman, U.S.N.M. No. 50100, at Gatun, July 9, 1911, with 199 ventrals and 125 subcaudals, and 54084 at Corozal, June 19, 1911, with 209 ventrals and 138 subcaudals.

**SPILOTES PULLATUS PULLATUS (Linné)**

Two male specimens collected at Cana, by E. A. Goldman, U.S.N.M. No. 50095, June 7, 1912, has 224 ventrals and 125 subcaudals, and No. 50096, May 24, 1912, has 217 ventrals and 126 subcaudals.

**DRYMARCHON CORAIS MELANURUS (Duméril and Bibron)**

A single female specimen, U.S.N.M. No. 54166, was collected at Gatun, January 10, 1911, by E. A. Goldman. It has 206 ventrals and 71 subcaudals.

**CHIRONIUS CARINATUS (Linné)**

Seven specimens collected as follows:

| U.S.N.M.<br>No. | Locality       | Date          | Collector         | Sex | Ventrals | Caudals |
|-----------------|----------------|---------------|-------------------|-----|----------|---------|
| 50097           | Cana           | Apr. 5, 1912  | E. A. Goldman     | ♀   | 163      | 126     |
| 53743           | Mindi          | Jan. 13, 1911 | Meek & Hildebrand | ♀   | 157      | 122     |
| 53900           | Upper Trinidad | Mar. 7, 1911  | " " "             | ♂   | 157      | 127     |
| 54159           | Bohio          | Apr. 29, 1911 | E. A. Goldman     | ♀   | 151      | 127     |
| 54165           | Tabernilla     | May, 1911     | " " "             | ♂   | 158      | 124     |
| 54167           | Gatun          | May 8, 1911   | " " "             | ♂   | 155      | ...     |
| 54199           | Panama         | 1911-1912     | Meek & Hildebrand | ♀   | 162      | 126     |

**LEPTOPHIS MEXICANUS (Duméril and Bibron)**

Two specimens of this species, U.S.N.M. Nos. 54082-83, collected at Porto Bello, May 24-25, 1911, by E. A. Goldman. The first, a male, has 156 ventrals, the tail incomplete; the second is a female with 158 ventrals and 165 subcaudals.

**LEPTOPHIS OCCIDENTALIS (Günther)**

Five specimens may be listed as follows:

| U.S.N.M.<br>No. | Locality   | Date          | Collector         | Sex | Ventrals | Caudals |
|-----------------|------------|---------------|-------------------|-----|----------|---------|
| 53820           | Chorrera   | Apr. 10, 1911 | Meek & Hildebrand | ♂   | 169      | 150     |
| 54015           | Gatun      | Jan. 15, 1911 | E. A. Goldman     | ♂   | 164      | 144     |
| 54163           | Tabernilla | May, 1911     | " " "             | ♀   | 166      | ...     |
| 50106           | Gatun      | .....         | .....             | ♀   | 182      | 175     |
| 50124           | Old Panama | Jan. 21, 1912 | E. A. Goldman     | ♂   | 167      | 156     |

**DROMICUS TAENIURUS (Tschudi)**

Four specimens of this species may be listed as follows:

| U.S.N.M.<br>No. | Locality | Date          | Collector            | Sex | Ventrals | Caudals |
|-----------------|----------|---------------|----------------------|-----|----------|---------|
| 50118           | Cana     | May 30, 1912  | E. A. Goldman        | ♀   | 137      | 61      |
| 50119           | "        | Apr. 10, 1912 | " " "                | ♀   | 140      | 63      |
| 50120           | "        | June 12, 1912 | " " "                | ♀   | 139      | ..      |
| 54228           | Empire   | 1911-1912     | E. D. Christopherson | ♀   | 144      | 56      |

**RHADINEA FULVICEPS (Cope)**

One specimen, a male, U.S.N.M. No. 50121, was collected at Cana, June 12, 1912, by E. A. Goldman. The tail is incomplete; the ventrals number 142.

**XENODON COLUBRINUS (Günther)**

Four specimens representing this species may be listed as follows:

| U.S.N.M.<br>No. | Locality | Date          | Collector     | Sex | Ventrals | Caudals |
|-----------------|----------|---------------|---------------|-----|----------|---------|
| 50105           | Gatun    | July 11, 1911 | E. A. Goldman | ♀   | 150      | 48      |
| 50109           | Cana     | June 7, 1912  | " " "         | ♀   | 147      | 46      |
| 54146           | Panama   | 1911-1912     | " " "         | ♀   | 151      | 44      |
| 54154           | Gatun    | May 12, 1911  | " " "         | ♀   | 146      | 45      |

**LEPTOCALAMUS TORQUATUS Günther**

One specimen, U.S.N.M. No. 50107, was collected in Panama by the Smithsonian Biological Survey of the Panama Canal Zone, but it bears no further data. It is a female with 185 ventrals and 92 subcaudals.

**SIBON SIBON (Linné)**

Two specimens of this species were collected by E. A. Goldman for the Canal Zone Survey; U.S.N.M. No. 50117, Cana, June 12, 1912, a female, has 190 ventrals and 86 subcaudals; No. 54079, Corozal, June 15, 1911, also a female, has 178 ventrals and 82 subcaudals.

**SIBYNOMORPHUS VIGUIERI (Bocourt)**

A single specimen, U.S.N.M. No. 50112, a female, comes from Cana, collected May 24, 1912, by E. A. Goldman. It has 190 ventrals and 115 subcaudals.

**SIPHLOPHIS CERVINUS GEMINATUS Duméril and Bibron**

One specimen, U.S.N.M. No. 50113, collected at Boca de Cupe, June 15, 1912, by E. A. Goldman. A male specimen, it has 204 ventrals and 109 subcaudals.

**LEPTODEIRA ANNULATA (Linné)**

Nine specimens of this species were collected as follows:

| U.S.N.M.<br>No. | Locality     | Date          | Collector            | Sex | Ventrals | Caudals |
|-----------------|--------------|---------------|----------------------|-----|----------|---------|
| 50115           | Cana         | May 24, 1911  | E. A. Goldman        | ..  | ...      | ..      |
| 53829           | Rio Cardenas | Feb. 16, 1911 | Meek & Hildebrand    | ♀   | 172      | 75      |
| 54077           | Gatun        | June 21, 1911 | E. A. Goldman        | ♂   | 170      | 76      |
| 54078           | "            | May 23, 1911  | " " "                | ♂   | 168      | 74      |
| 54155           | "            | May 11, 1911  | " " "                | ♀   | ...      | 78      |
| 54160           | "            | May 13, 1911  | " " "                | ♂   | 173      | 86      |
| 54161           | "            | " " "         | " " "                | ♂   | 173      | 82      |
| 54227           | Rio Aruza    | Feb. 27, 1912 | E. D. Christopherson | ♂   | 169      | 79      |
| 54266           | Empire       | 1911-1912     | " " "                | ♀   | 172      | 75      |

**CLELIA CLOELIA (Daudin)**

Two specimens collected by E. A. Goldman; U.S.N.M. No. 50098, a female, Pirri Range, April 22, 1912, with 209 ventrals and 73 caudals; and No. 50099, Gatun, July 5, 1911, with 245 ventrals and 85 subcaudals.

**CLELIA PETOLA (Linné)**

A single specimen, U.S.N.M. No. 50111, collected at Cana, May 24, 1912, by E. A. Goldman, is a female with 210 ventrals and 113 subcaudals.

**PSEUDOBOA NEUWIEDII** (Duméril and Bibron)

A single female specimen, U.S.N.M. No. 54207, collected at Corozal, April 21, 1911, by Meek and Hildebrand, has 203 ventrals and 76 caudals.

**OXYBELIS ACUMINATUS** (Wied)

Five specimens collected as follows:

| U.S.N.M. No. | Locality   | Date         | Collector         | Sex | Ventrals | Caudals |
|--------------|------------|--------------|-------------------|-----|----------|---------|
| 50108        | .....      | .....        | .....             | ♀   | 189      | 158     |
| 50122        | Empire     | Feb. 1, 1912 | E. A. Goldman     | ♀   | 189      | 140     |
| 53749        | Frijoles   | Feb. 8, 1911 | H. Pittier        | ♂   | 186      | ...     |
| 53812        | Alhamel    | 1911         | Meek & Hildebrand | ♂   | 185      | 180     |
| 54157        | Tabernilla | May, 1911    | E. A. Goldman     | ♀   | 183      | 184     |

**ERYTHROLAMPRUS AESCULAPII** (Linné)

A single male specimen, with no precise locality, U.S.N.M. No. 54008, was collected by E. D. Christopherson. It has 193 ventrals and 56 subcaudals.

**STENORHINA DEGENHARDTII** (Berthold)

Two specimens with the following data:

| U.S.N.M. No. | Locality | Date          | Collector     | Sex | Ventrals | Caudals |
|--------------|----------|---------------|---------------|-----|----------|---------|
| 50116        | Cana     | May 30, 1912  | E. A. Goldman | ♂   | 155      | 47      |
| 54081        | Gatun    | June 23, 1911 | " " "         | ♀   | 166      | 33      |

**PELAMIS PLATURUS** (Linné)

A single specimen, U.S.N.M. No. 53919, collected at Chame Point, February 4, 1912, by Meek and Hildebrand, a female, has 341 ventrals.

**MICRURUS NIGROCINCTUS NIGROCINCTUS** (Girard)

Seven specimens of the common Panama coral snake are included in the collection, from the following localities:

| U.S.N.M. No. | Locality   | Date          | Collector            | Sex | Ventrals | Caudals |
|--------------|------------|---------------|----------------------|-----|----------|---------|
| 50103        | Gatun      | July 15, 1911 | E. A. Goldman        | ♀   | 215      | 36      |
| 50104        | "          | July 11, 1911 | " " "                | ♂   | 194      | 47      |
| 54076        | "          | June 23, 1911 | " " "                | ♂   | 196      | 47      |
| 54152        | Tabernilla | May, 1911     | " " "                | ♂   | 204      | 48      |
| 54153        | Gatun      | May 8, 1911   | " " "                | ♀   | 215      | 30      |
| 54162        | Tabernilla | May, 1911     | " " "                | ♀   | 218      | 35      |
| 54268        | Canal Zone | 1911-1912     | E. D. Christopherson | ♀   | 214      | 34      |

**BOTHROPS SCHLEGELII (Berthold)**

Three specimens with the following data:

| U.S.N.M.<br>No. | Locality | Date          | Collector            | Sex | Ven-<br>trals | Cau-<br>dals |
|-----------------|----------|---------------|----------------------|-----|---------------|--------------|
| 50101           | Gatun    | July 30, 1911 | "L.L.J."             | ♀   | 153           | 58           |
| 50102           | "        | July 4, 1911  | "                    | ♀   | 161           | 61           |
| 54264           | "        | 1911-1912     | E. D. Christopherson | ♂   | 165           | 61           |

**BOTHROPS NASUTA (Bocourt)**

A single specimen, in bad state of preservation, U.S.N.M. No. 54057, collected at Cerro Brujo, June 6, 1911, by E. A. Goldman, represents this species in the collection.

**BOTHROPS MONTICELLII (Peracca)**

A single specimen, U.S.N.M. No. 50110, is the type of *Bothrops leptura* Amaral. It comes from Cana, collected June 7, 1912, by E. A. Goldman.

## Order LORICATA

**CROCODYLUS ACUTUS Cuvier**

A single specimen, U.S.N.M. No. 50088, was collected at Boca de Cupe, June 14, 1912, by E. A. Goldman.

**CAIMAN FUSCUS (Cope)**

The distinction of the Central American caiman, as *Caiman fuscus* (Cope), from the Amazonian *Caiman sclerops* has been proposed by myself in a recent paper.<sup>30</sup>

The skull of the Central American form is decidedly more massive, with a relatively broader snout, and the palatines are inflated anteriorly. The pterygoid border of the palatine fenestra is longer than in *sclerops*, and thus presents the extreme of divergence in this character from the Paraguayan *Caiman yacare*.

In the Panama series listed below, the nuchal scutes are regularly 4-4-2-2 in number, but an additional pair of small scutes is frequently intercalated between the nuchals and the dorsal shield. No. 54093 has the nuchal formula 2-4-2-2. The dorsal shield is composed of

<sup>30</sup> Publ. Field Mus. Nat. Hist., Zool., vol. 12, p. 227, 1928.

8 longitudinal and 16 or 17 transverse rows of scutes. The double crested verticils of caudal scutes number 14 in 7 specimens, 15 in 3, and 16 in 1.

The data for the caimans in the present collection are as follows:

| U.S.N.M. No. | Locality   | Date             | Collector         |
|--------------|------------|------------------|-------------------|
| 50089        | .....      | .....            | .....             |
| 50090-93     | Cana       | Mar. 18-20, 1912 | E. A. Goldman     |
| 54089        | Mindi      | Mar. 2, 1911     | Meek & Hildebrand |
| 54090        | El Capitan | Mar. 20, 1911    | " " "             |
| 54092-93     | Mindi      | Mar. 2, 1911     | " " "             |
| 54095        | "          | " " "            | " " "             |
| 54096        | Chorrera   | Apr. 9, 1911     | " " "             |





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# THE LATITUDE SHIFT OF THE STORM TRACK IN THE 11-YEAR SOLAR PERIOD

STORM FREQUENCY MAPS OF THE UNITED STATES,  
1883-1930

BY  
G. J. KULLMER  
Syracuse University



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BY C. J. KULLMER

*Syracuse University*

The United States is unique among nations in possessing a splendid series of maps of tracks of barometric depressions. These have been published each month from 1874 to the present in the *Monthly Weather Review*. Nothing similar is available for any other part of the world.

For the 10-year international period from 1878-87 H. H. Dunwoody published in 1893 storm frequency maps for the whole of the Northern Hemisphere. Dunwoody divided the map of the Northern Hemisphere into squares measuring  $5^{\circ}$  on a side and recorded the number of centers of barometric depressions that crossed each square. In order to determine whether a general shift of the storm track had taken place in an interval of 21 years, I remade the maps of storm frequency in the United States for 1899-1908 according to Dunwoody's plan of  $5^{\circ}$  squares.<sup>1</sup> A comparison of the two periods showed a slight but definite southerly and westerly shift.

Considering the numerous observed correlations between sun spots and meteorological elements, it seemed worth while to ascertain whether or not Spoerer's latitude shift of sun spots is accompanied by a corresponding latitude shift of the vortexes in the earth's atmosphere. This latitude shift is one of the most striking features of the sun-spot cycle; each new cycle begins at about  $25^{\circ}$  solar latitude and ends at  $10^{\circ}$ , with maximum positions of about  $30^{\circ}$  and  $5^{\circ}$ .

For such a study it is evident that  $5^{\circ}$  of latitude, approximately 345 miles, is too large a unit. I have, therefore, chosen a unit area half the size of Dunwoody's, namely  $5^{\circ}$  in longitude and  $2\frac{1}{2}^{\circ}$  in latitude. The series of year maps from 1874-1912 were made in 1913, furnishing comparison material for three solar periods; since then two more

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<sup>1</sup>The shift of the storm track. Chap. 16 in Huntington, *The climatic factor*, Carnegie Inst. Publ. 192, 1914.

solar periods have become available. The year maps from 1874 to 1882 do not extend west of the 100th meridian; the series of storm frequency maps here published begins, therefore, with 1883, the first year that the entire area of the United States was covered. Furthermore, according to the Weather Bureau, the earlier maps are not statistically comparable with the later ones. A more extended network of stations began with the year 1891. Although the year maps are here published for the first time, the material for 1883-1912, assembled by months in 10-year periods, was presented at the Second Pan American Scientific Congress in 1915.<sup>2</sup> It is not the purpose of this paper to discuss the storm frequency of the United States; the maps, made with care according to a uniform technique, are published in order to make the material available to other investigators. How complex the factors involved must be, will be evident from a comparison of the two years 1900 and 1911, both at solar minimum; a similar pair, also separated by 11 years, 2 years after solar maximum, is 1919 and 1930.

#### THE LATITUDE SHIFT

With these two striking pairs in mind, it is evident that any uniform latitude shift within the 11-year solar period must be masked by other meteorological factors. The method of yearly departures from a mean map suggests itself; I have in manuscript a complete series of such departure maps, which confirm the latitude shift, but illustrate primarily the complexity of the factors involved. The most powerful method of attack seemed to be to add together three years at solar maximum and three years at solar minimum, and compare one set of figures with the other. I have done this for five solar periods:

Maximum 1882-84 versus Minimum 1877-79  
 Maximum 1892-94 versus Minimum 1888-90  
 Maximum 1905-07 versus Minimum 1900-02  
 Maximum 1916-18 versus Minimum 1911-13  
 Maximum 1927-29 versus Minimum 1922-24

and present the results in Figures 2-6.<sup>3</sup> This method allows for possible difference in recording the tracks of barometric depressions, since the comparisons are with periods separated by only five or six years.

<sup>2</sup> Monthly storm frequency in the United States. Proc. Second Pan Amer. Sci. Congr., Sec. 2, vol. 2, pp. 338-391, 1917.

<sup>3</sup> Preliminary publication of parts of this study appeared in: Huntington, The solar hypothesis of climatic changes. Bull. Geol. Soc. Amer., vol. 25, pp. 477-590, 1914. Huntington, Earth and sun, New Haven, Yale Univ. Press, 1923.

It also allows shifts in longitude to appear; in fact, the longitude shifts are almost as significant as the latitude shifts.

The most striking feature of the resulting maps is that all five maps present the same pattern: 1, a curved area of excess during solar maximum, with a southerly projection (I have drawn a dotted line through this area and its southerly extension); 2, south of this, and on both sides of the southerly projection, areas of deficiency during solar maximum; 3, more variable areas of excess adjacent to the areas of deficiency.

The areas of deficiency are separated from the main area of excess by about  $6^{\circ}$ - $8^{\circ}$  of latitude. But the location of the main area of excess is subject to a displacement in both longitude and latitude. In Figure 1 I have assembled the dotted lines drawn through this area of excess and its southerly projection. In the eastern extremity they follow almost a common path. After watching the eastward advance of the southerly projection in periods II, III, and IV, it came as a distinct surprise to find that in period V the whole system had gone back to a position even farther west and south than in period II, and that the large excess in Western Canada had given place to a relatively large deficiency. There seems to be an indication of a cycle of three solar periods: period I has almost the same position as period IV; the periods II, III, and IV seem to show an orderly progression. If these represent a cycle, then period V is the first of the next cycle, and, to make my meaning clear, the coming solar period should occupy the position VI, given by the dotted line.

It should be noted that the maxima are in each case compared with a *preceding* minimum; the approaching solar minimum will give an opportunity to remake these maps for five solar periods to bring out the comparison of maximum with *following* minimum, which is, of course, the true period.

#### SUMMARY

A latitude shift of the storm track in the United States, corresponding to Spoerer's latitude shift of sun spots, is demonstrated for five solar periods by a comparison of three year maps of storm frequency at solar maximum with three year maps at solar minimum. A uniform pattern of distribution is shown with marked variation in latitude and longitude in the five solar periods.

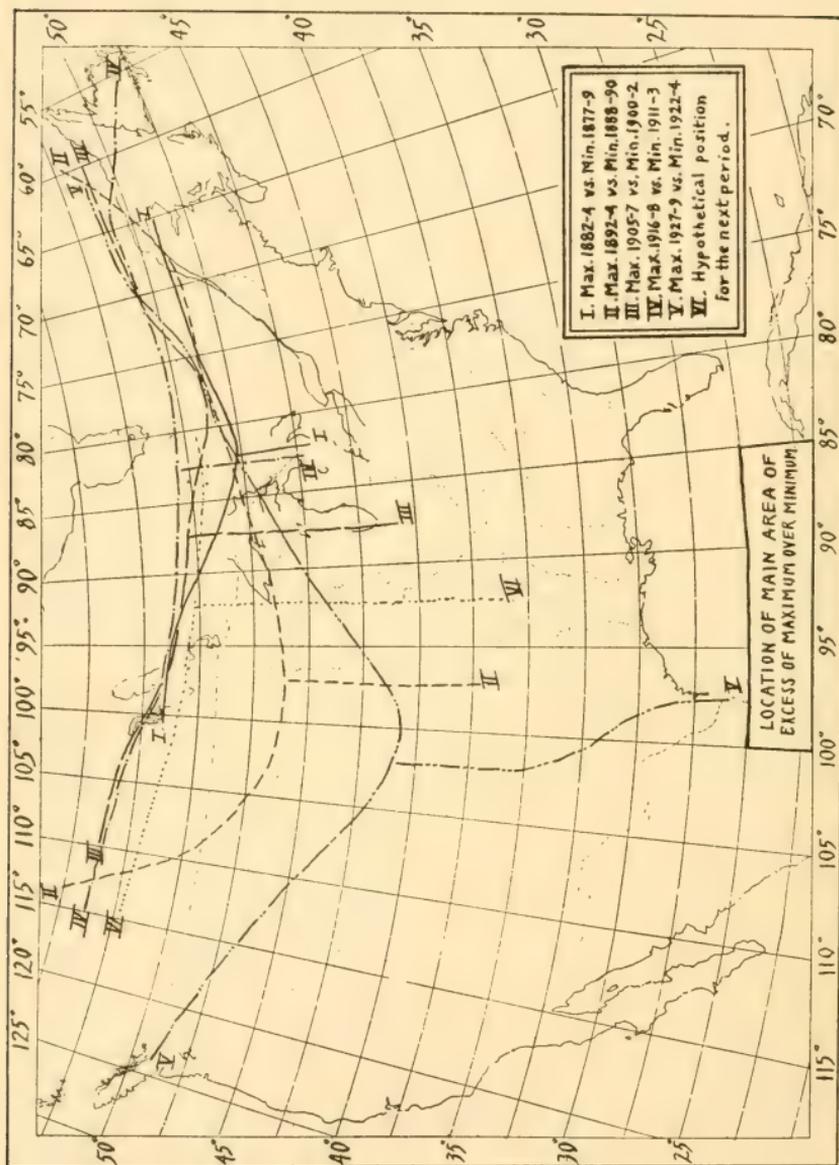


FIG. 1.

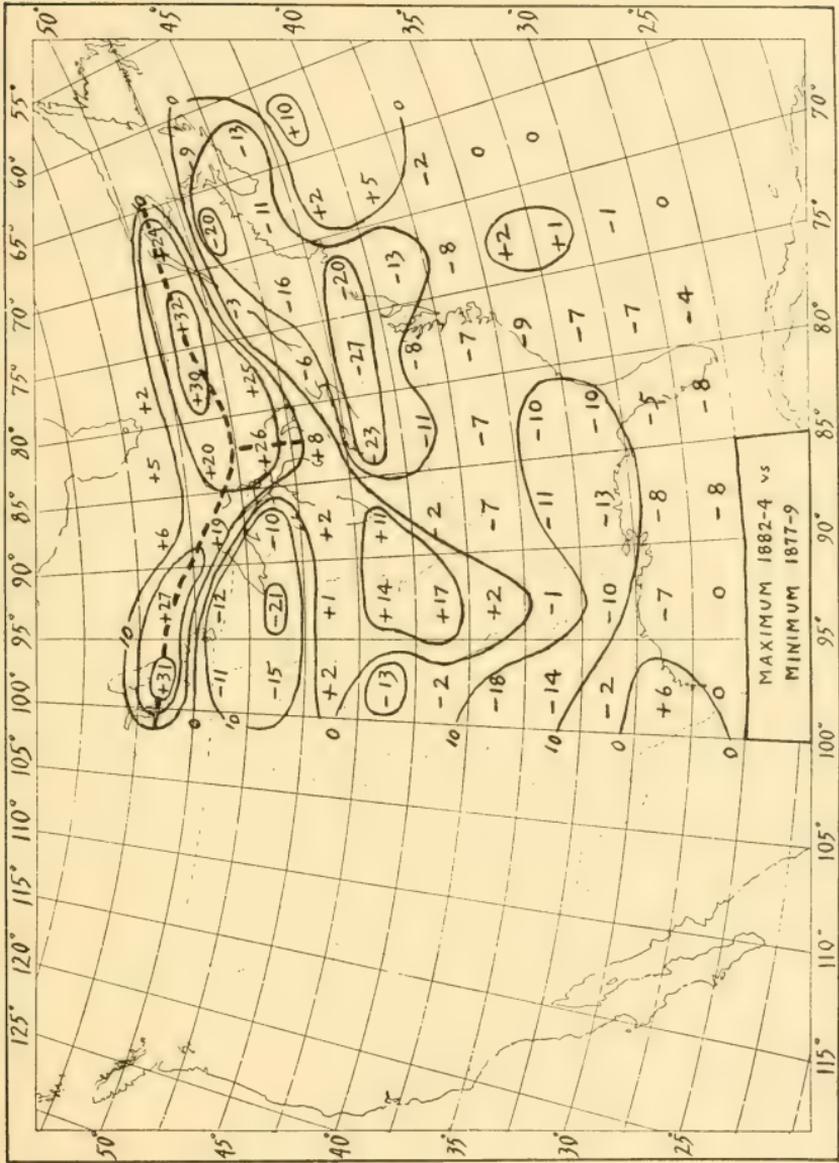


FIG. 2.

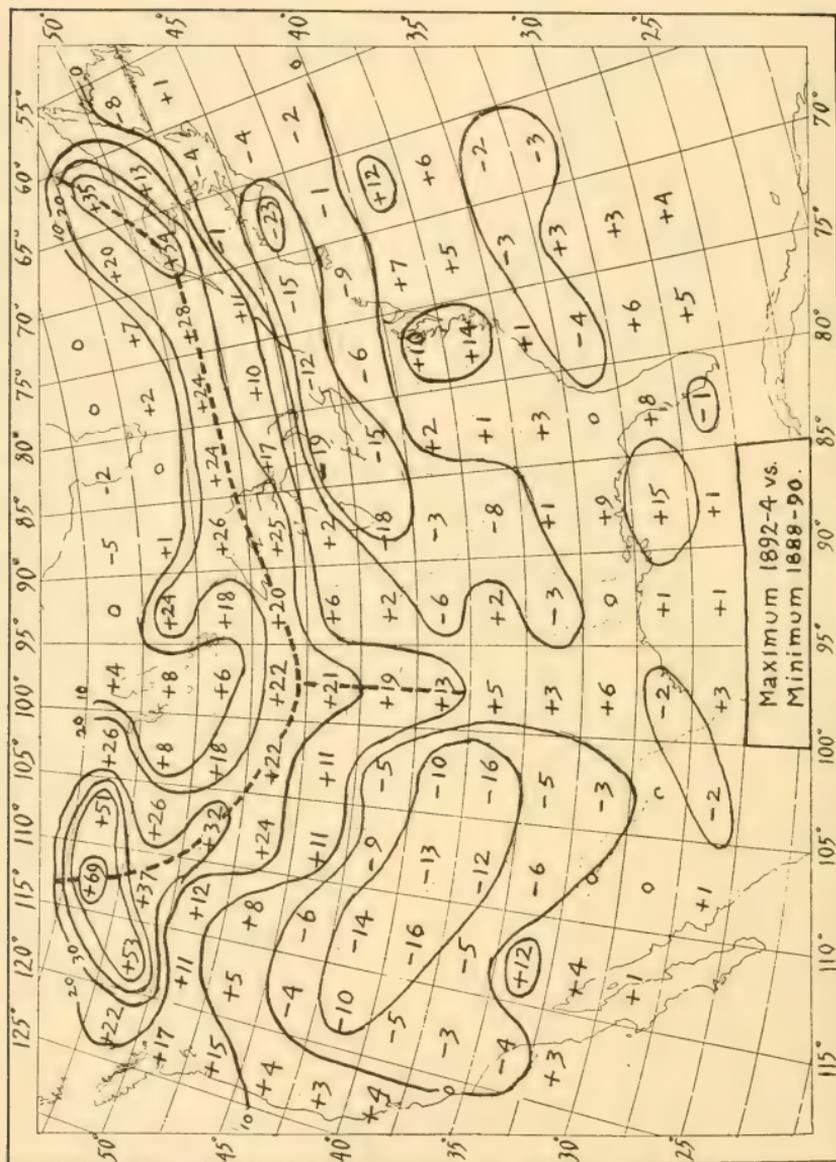


FIG. 3.

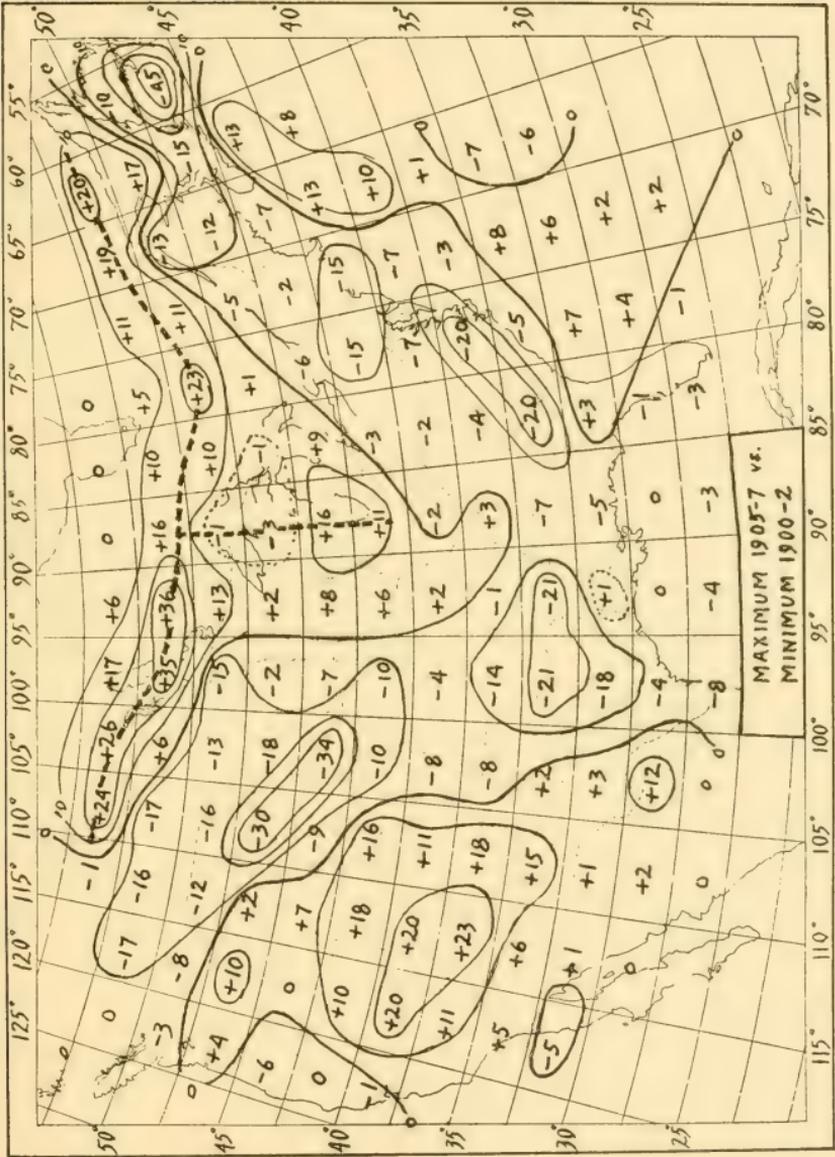


FIG. 4.

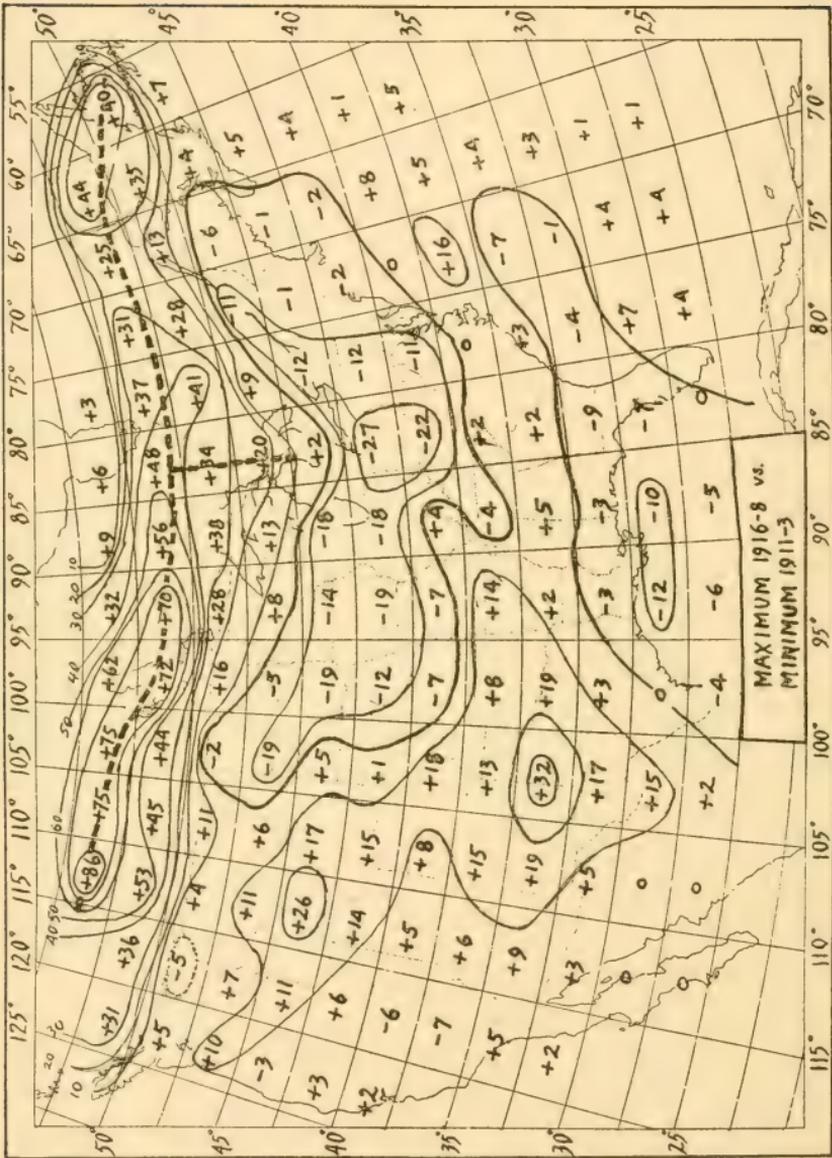


FIG. 5.

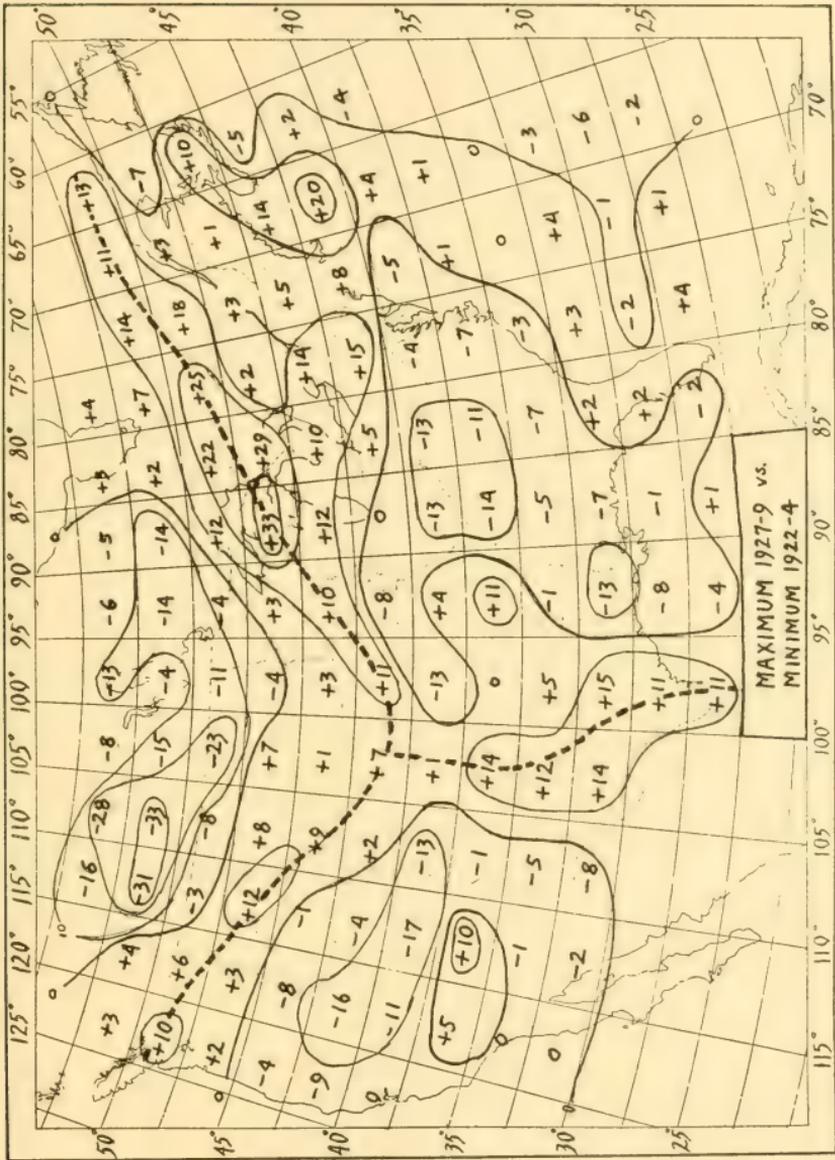
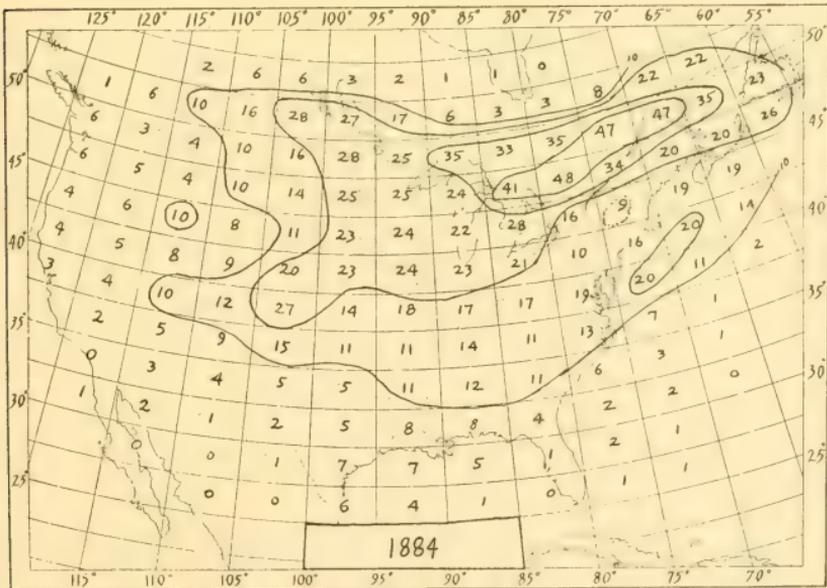
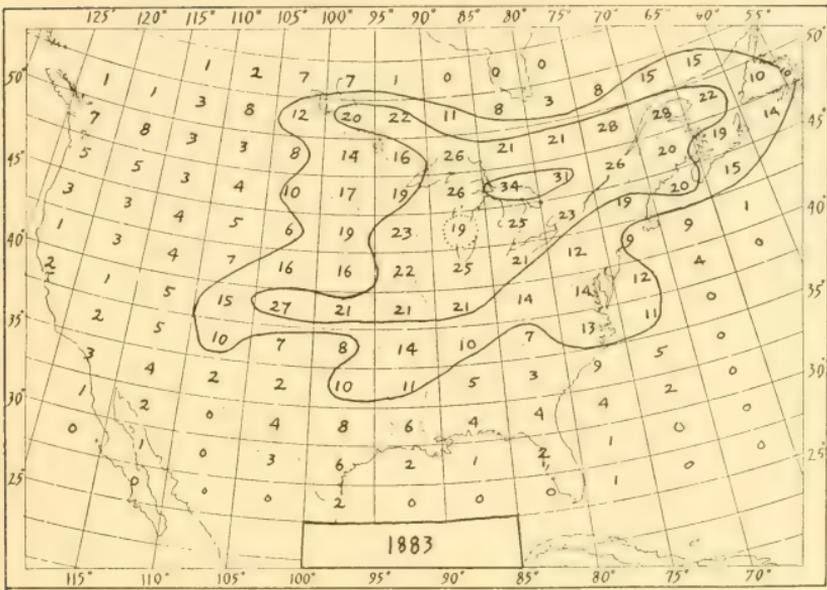


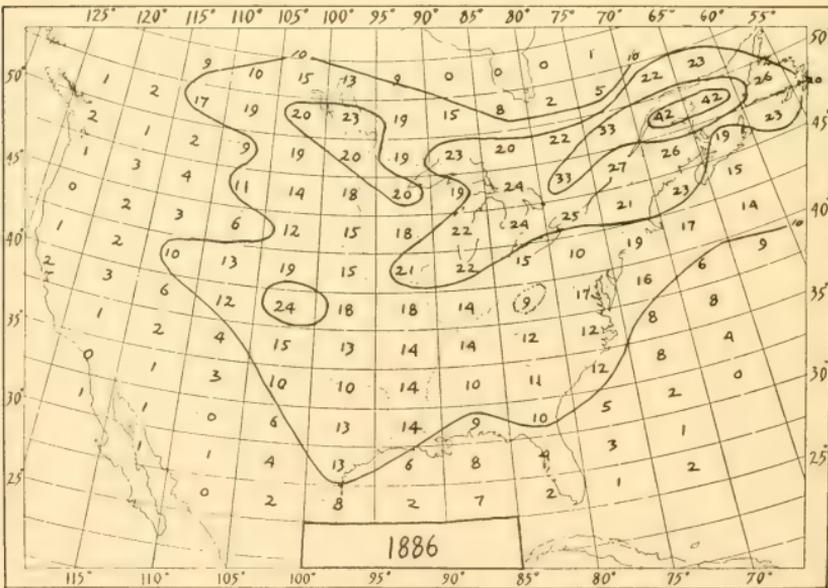
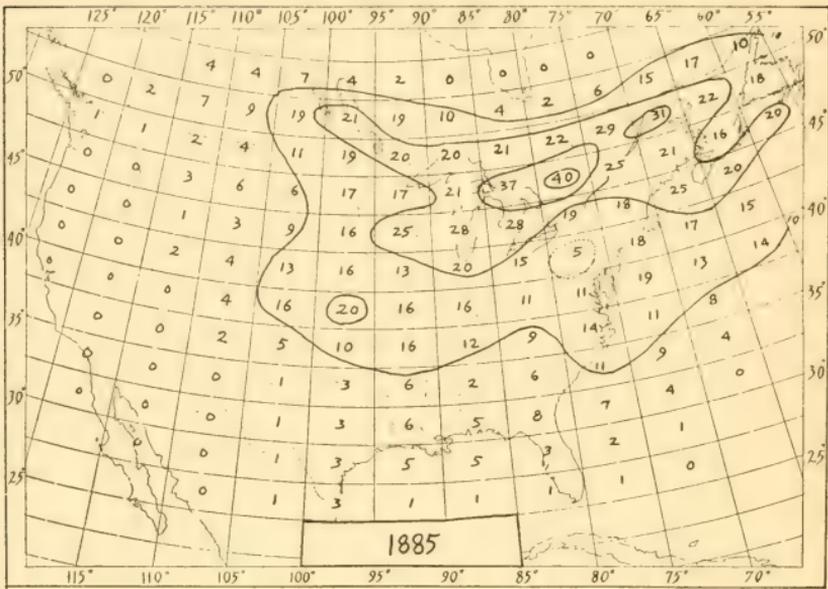
FIG. 6.



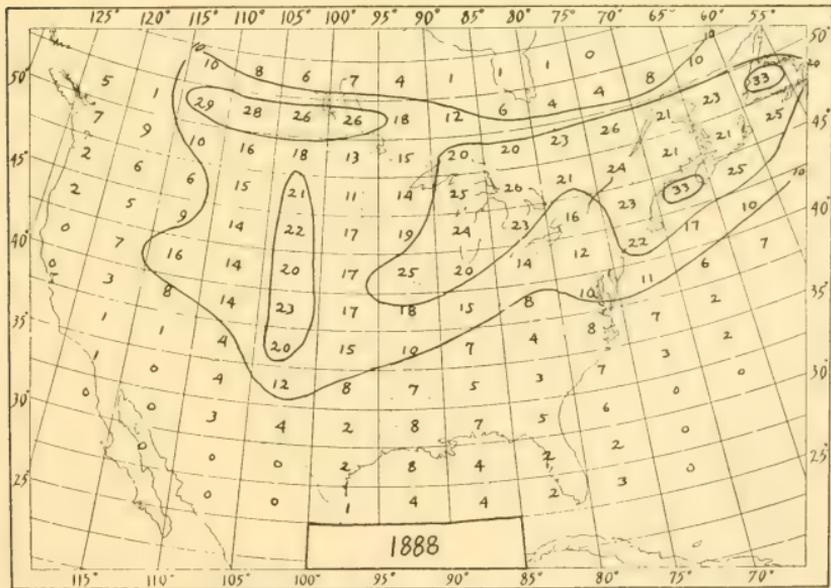
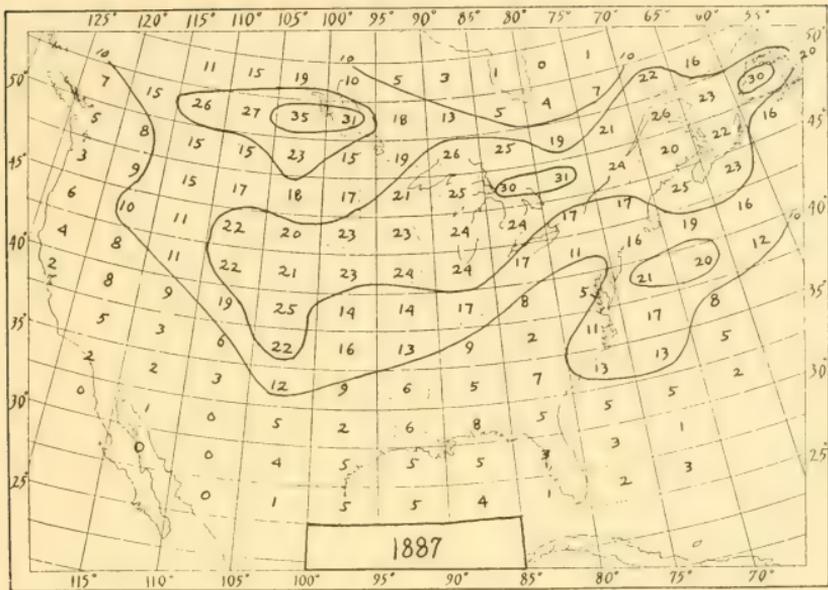
1883 and 1884



1885 and 1886

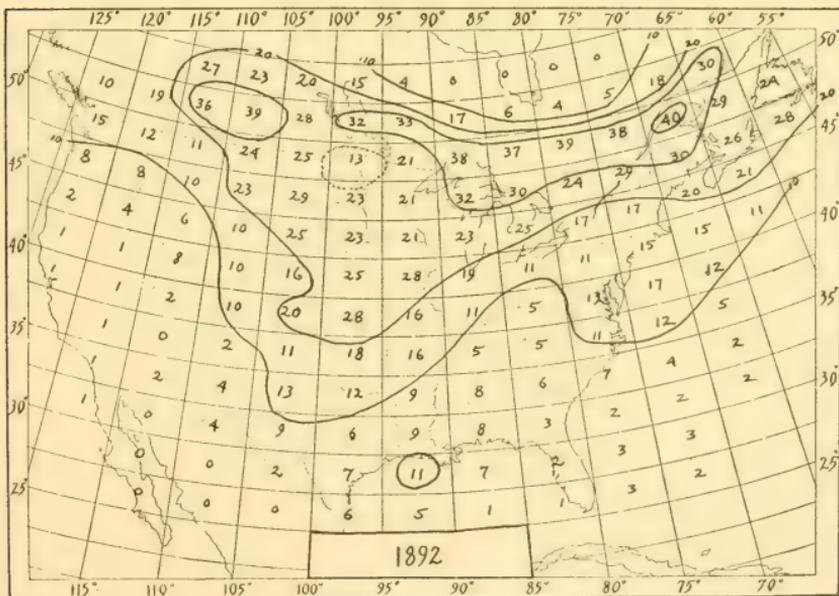
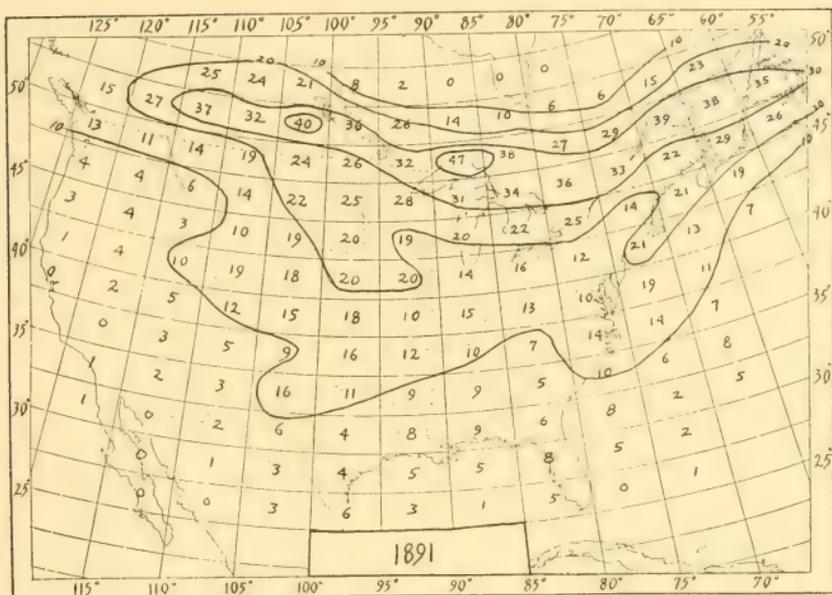


1887 and 1888

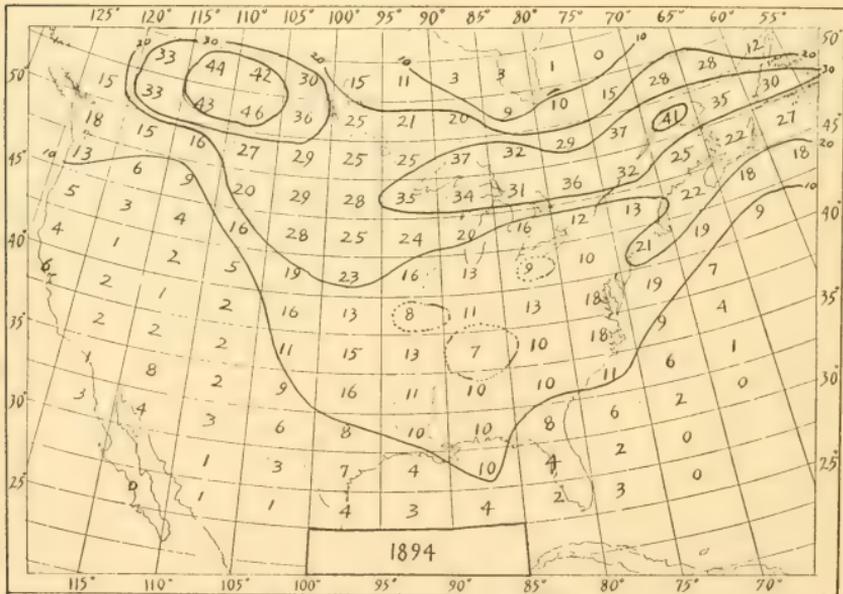
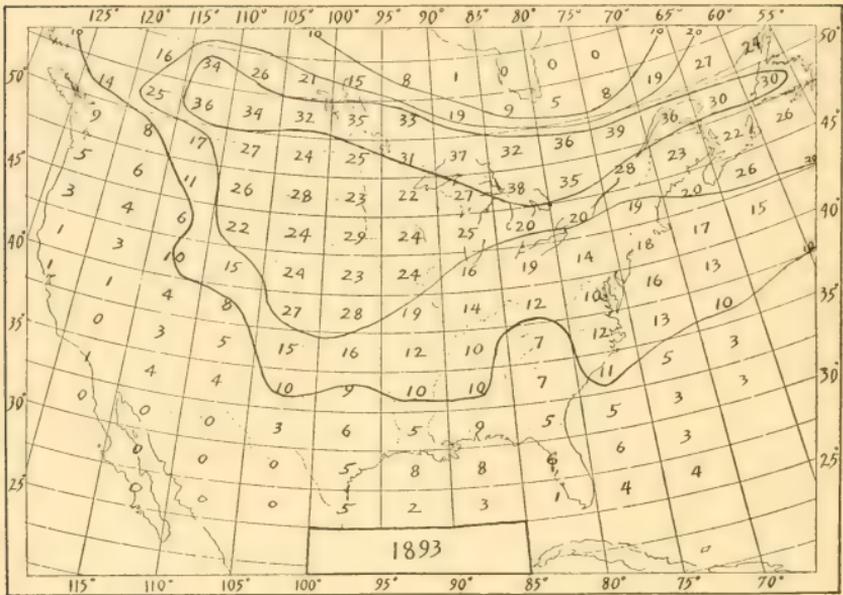




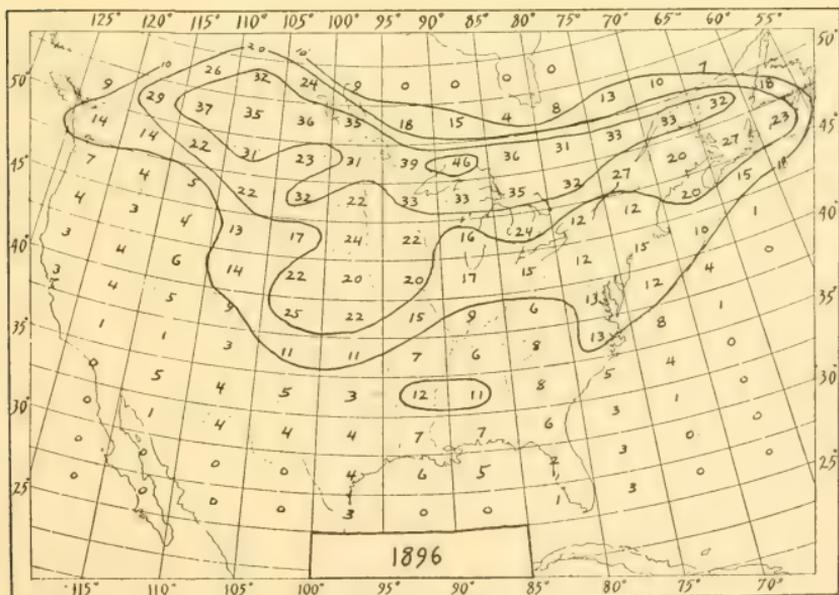
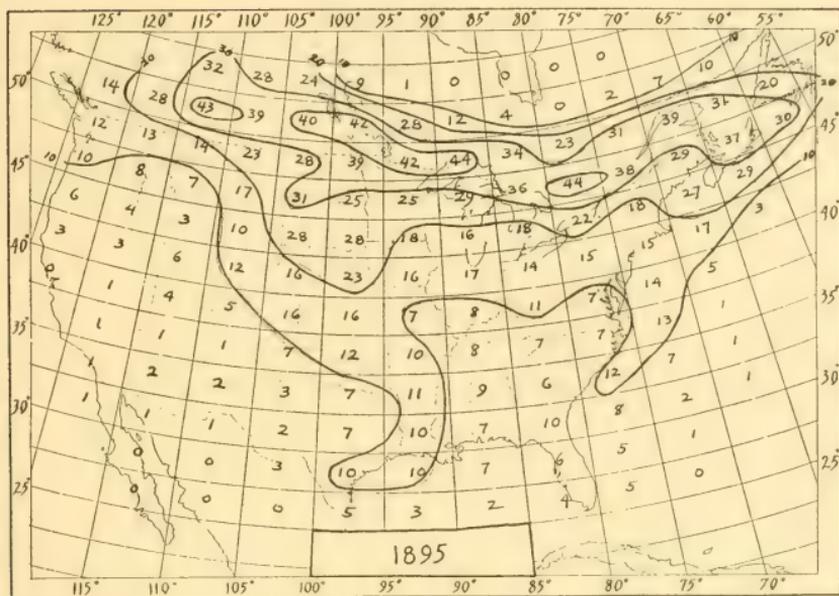
1891 and 1892



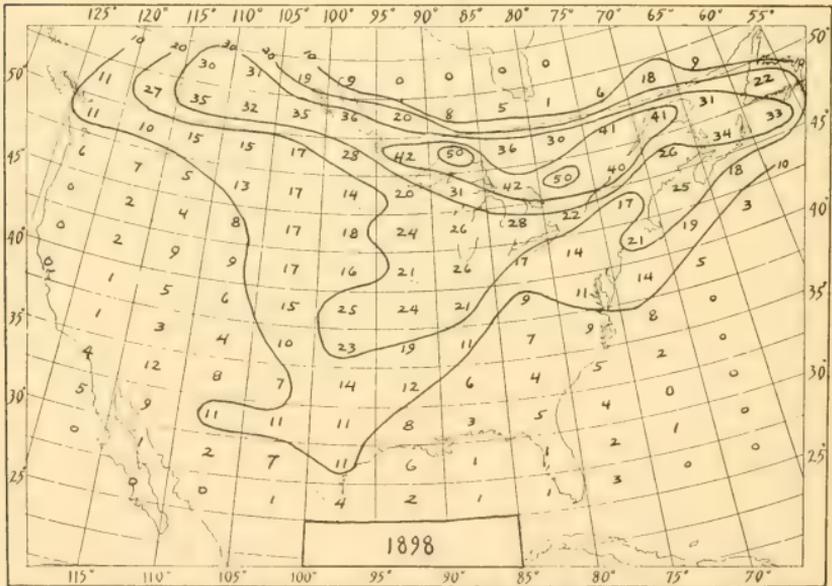
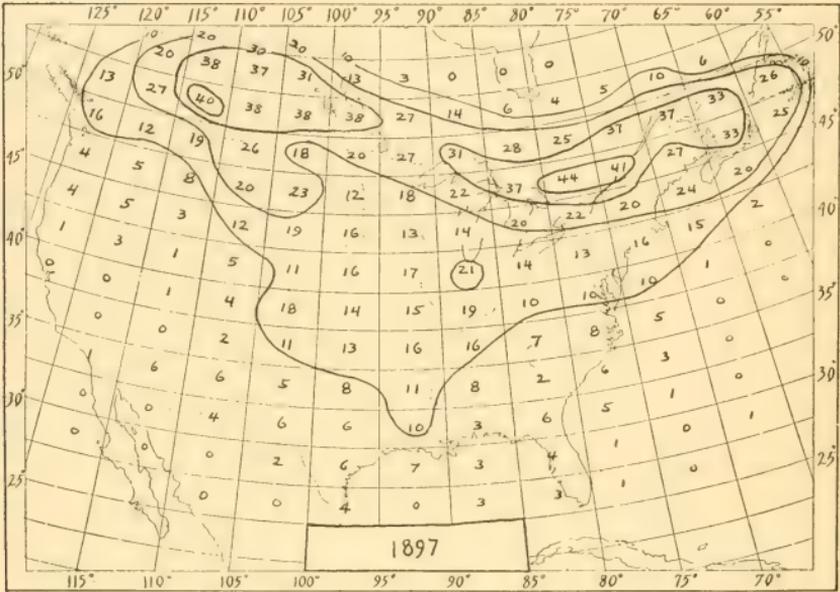
1893 and 1894



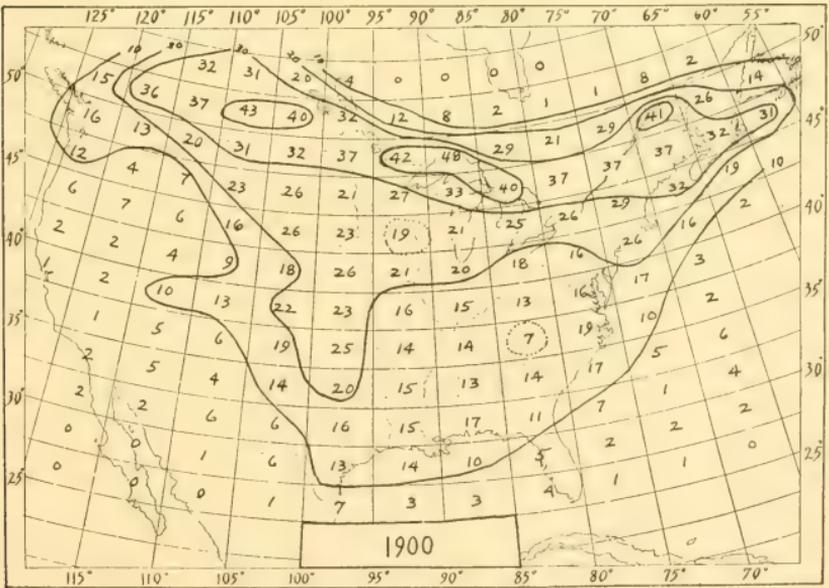
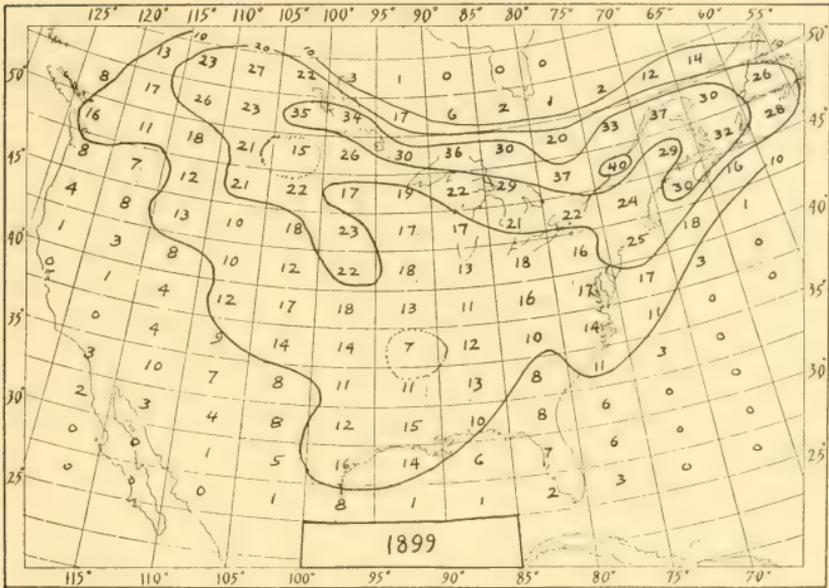
1895 and 1896



1897 and 1898

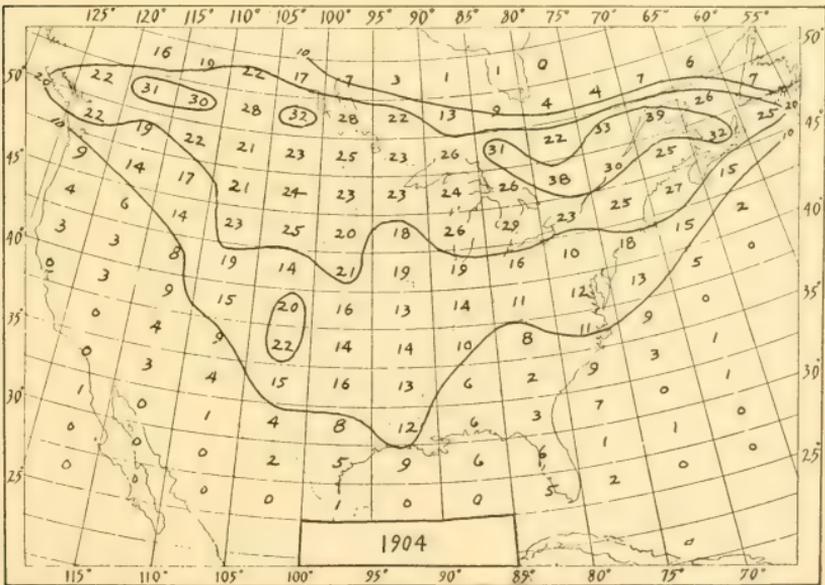
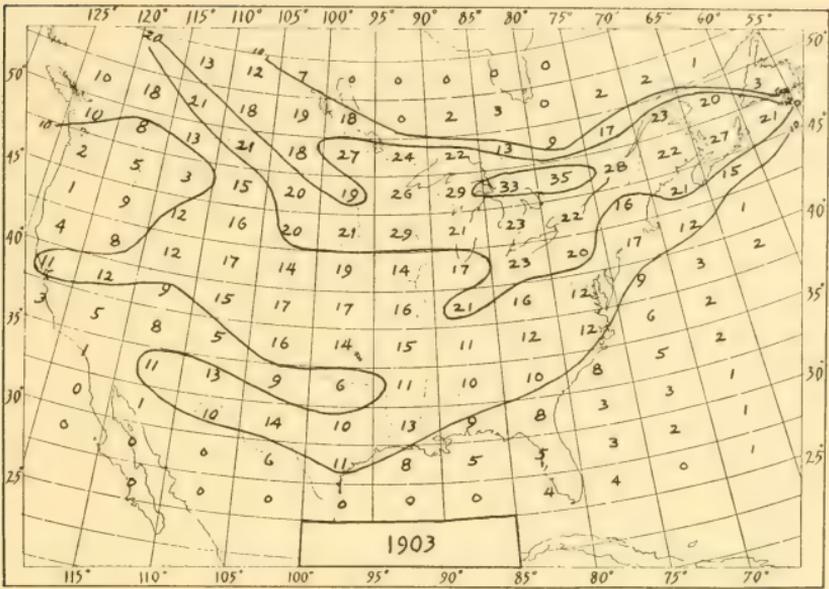


1899 and 1900

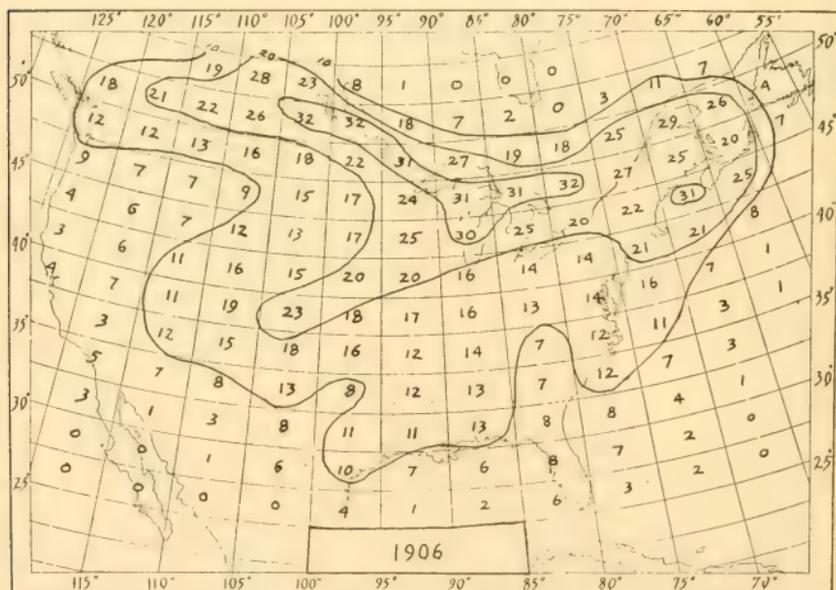
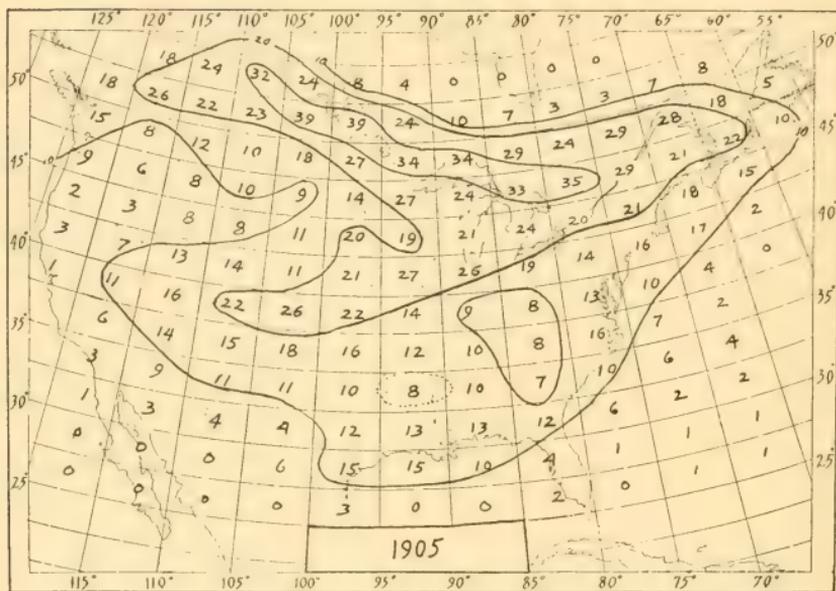




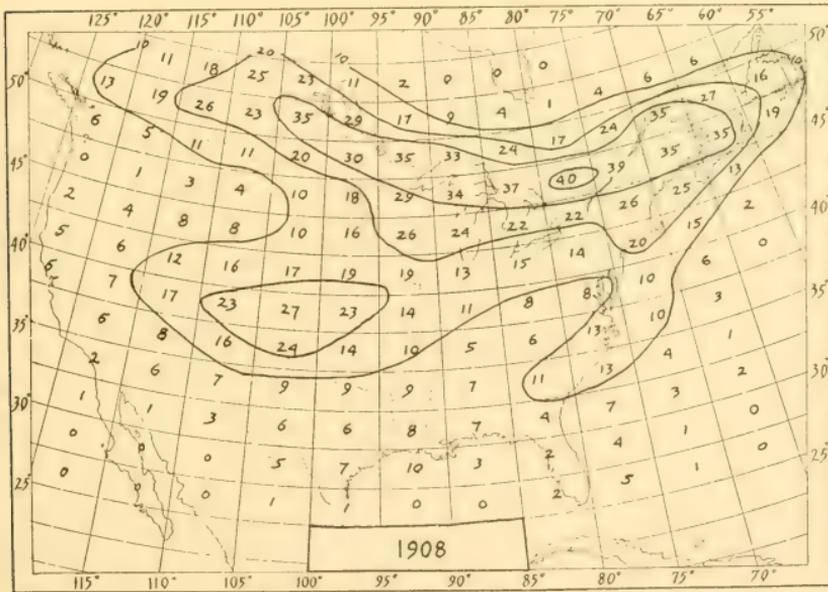
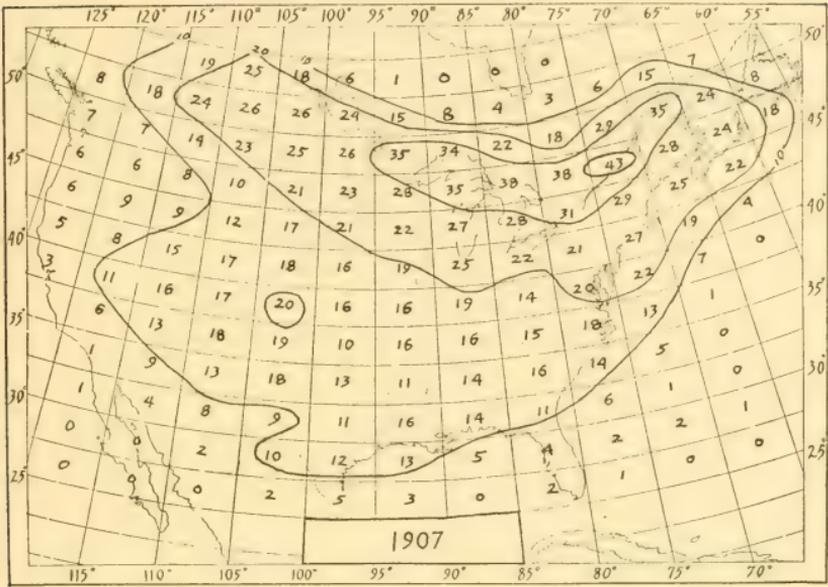
1903 and 1904



## 1905 and 1906

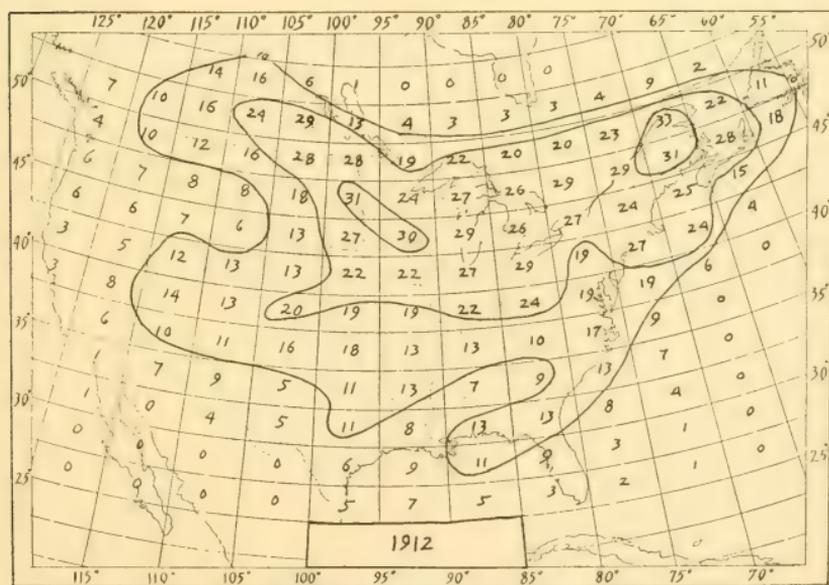
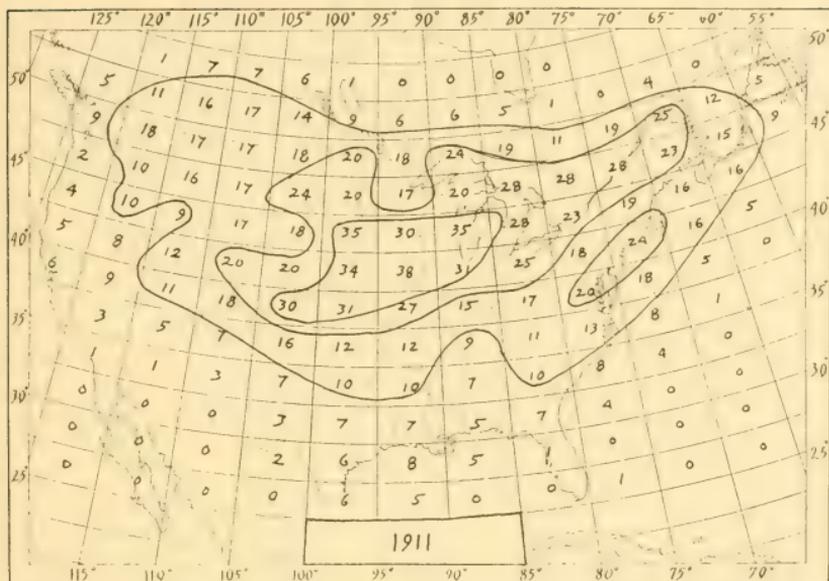


1907 and 1908

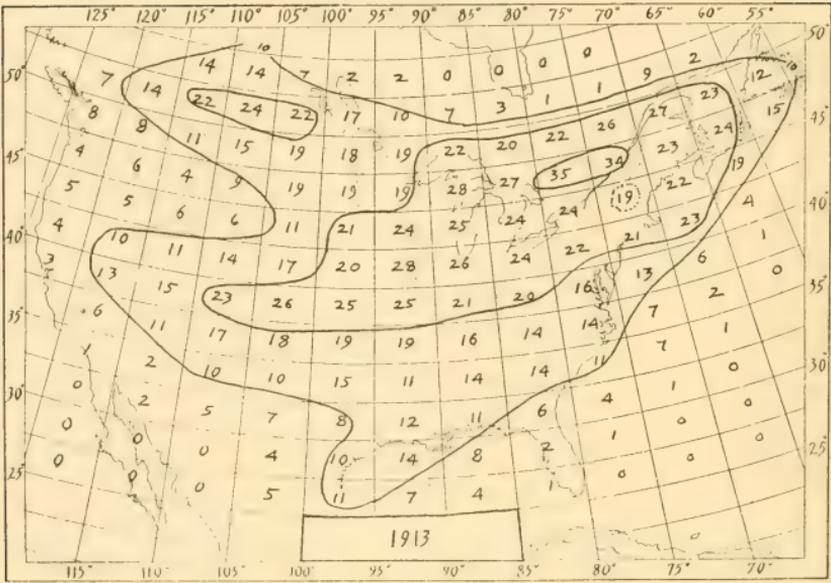




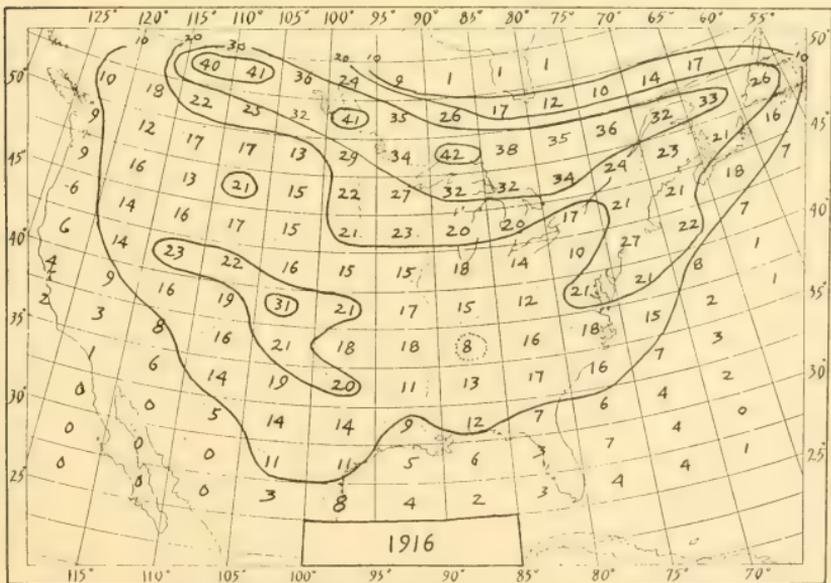
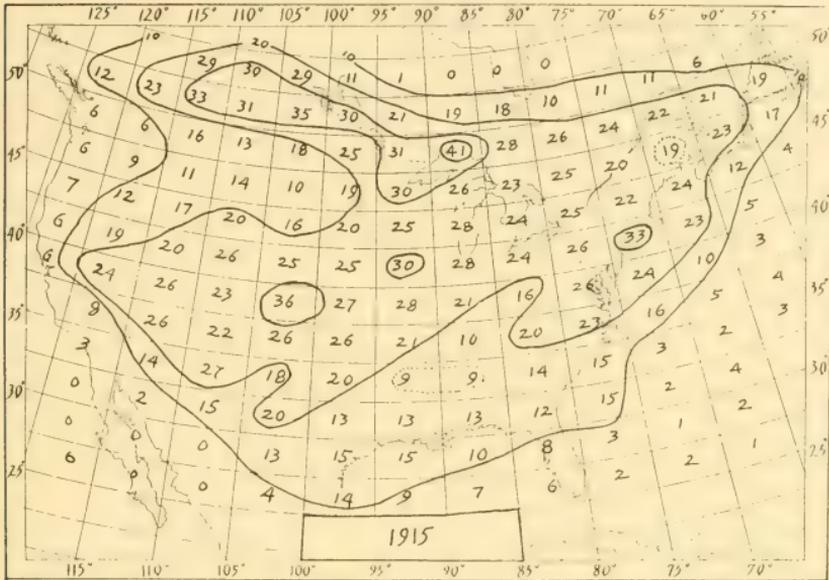
1911 and 1912



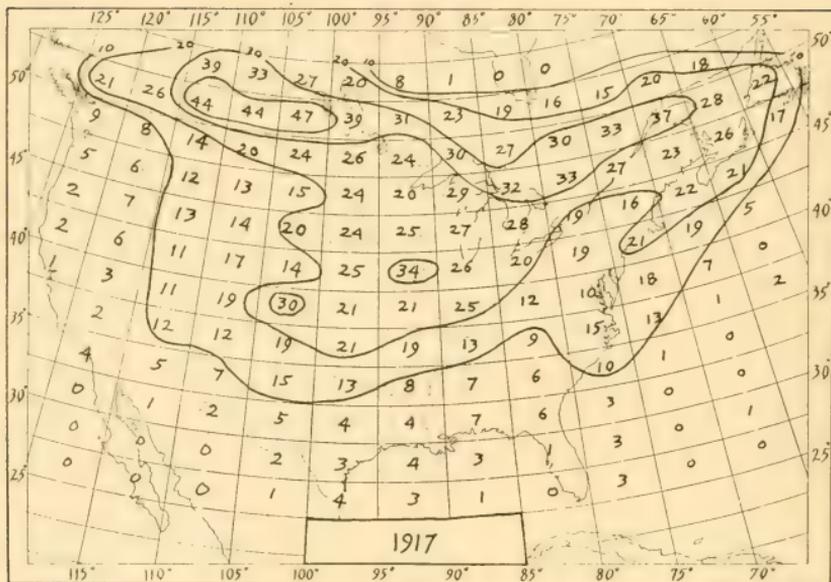
1913 and 1914



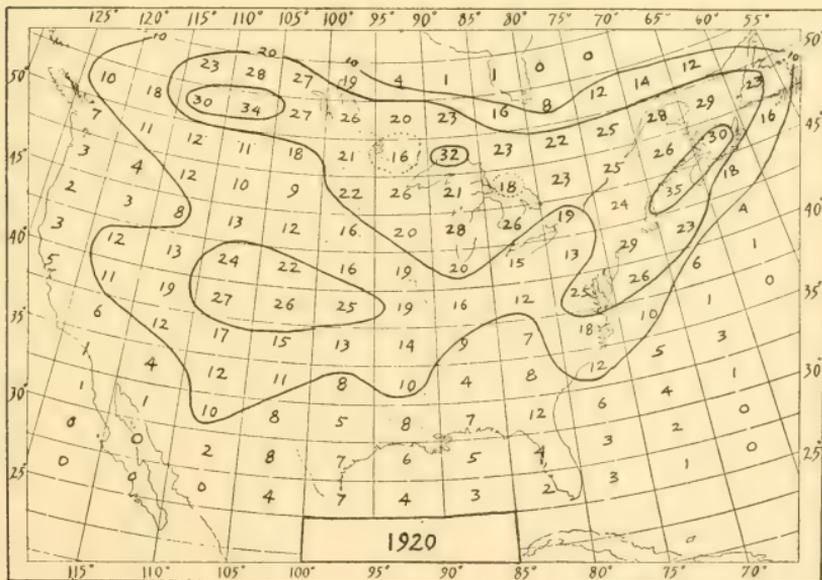
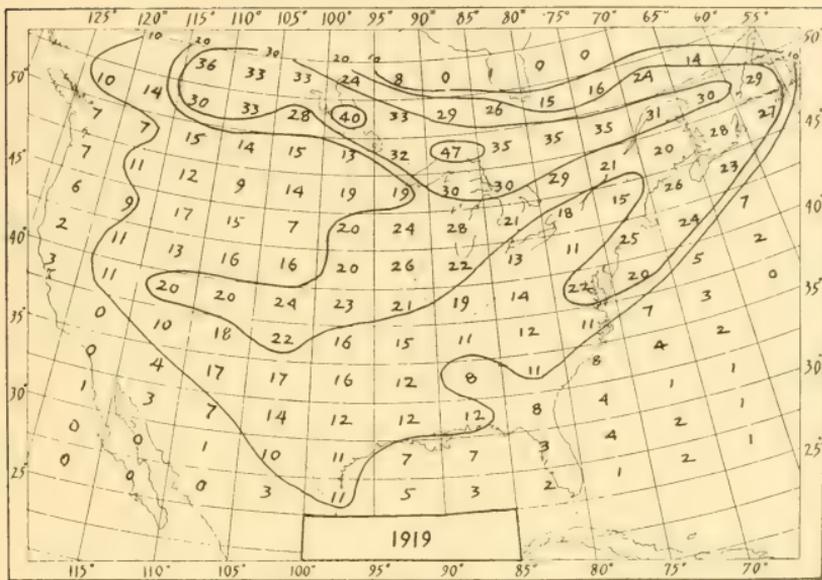
1915 and 1916



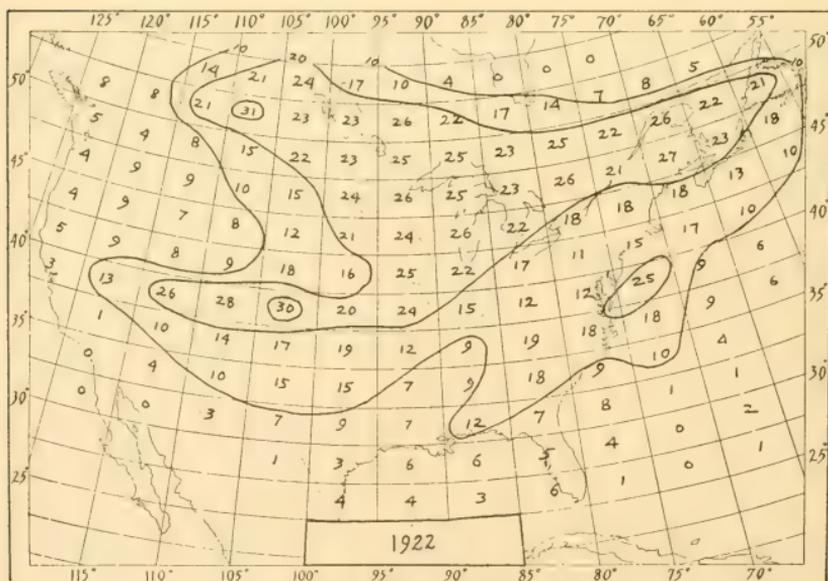
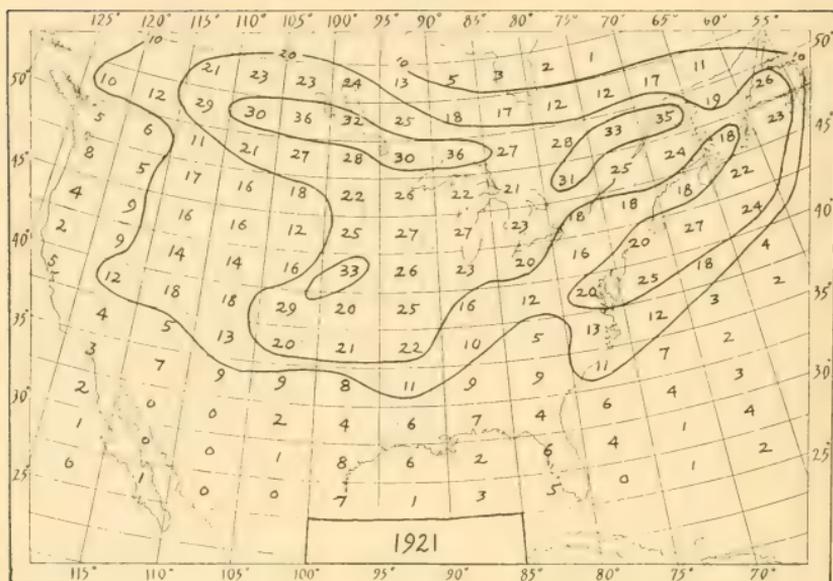
## 1917 and 1918



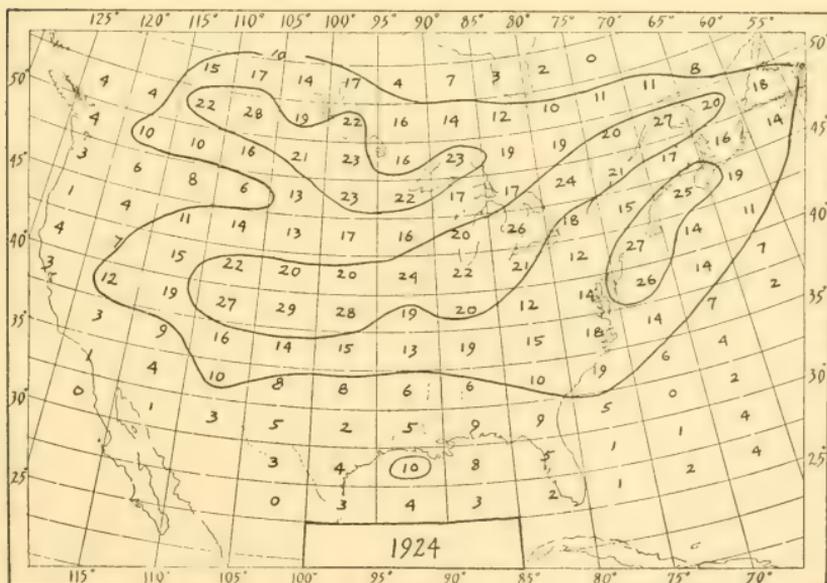
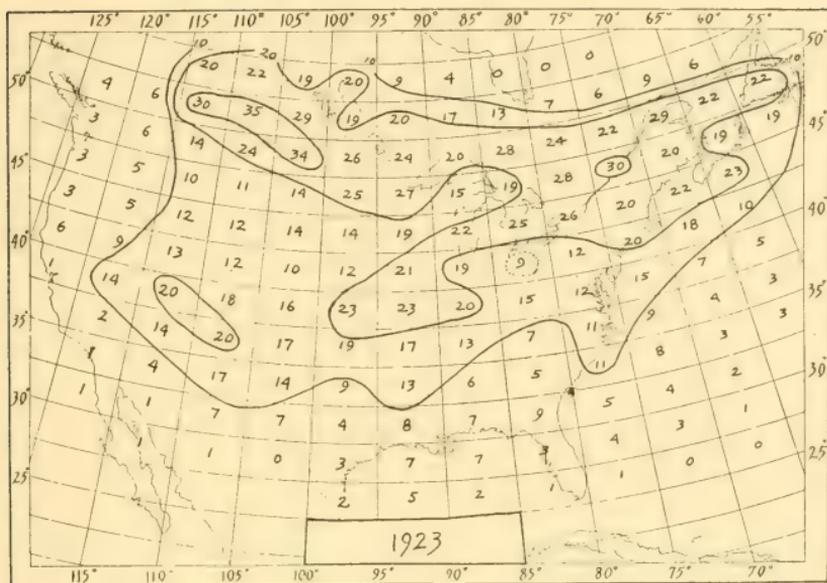
1919 and 1920



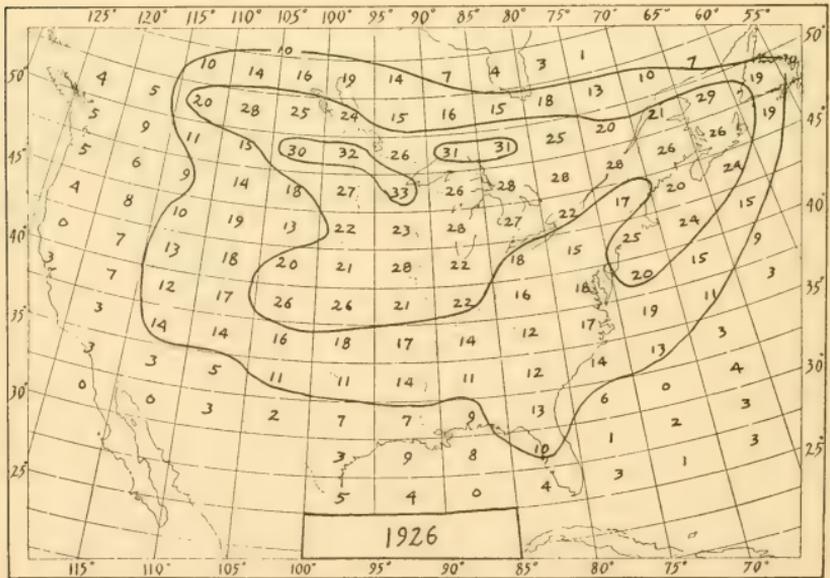
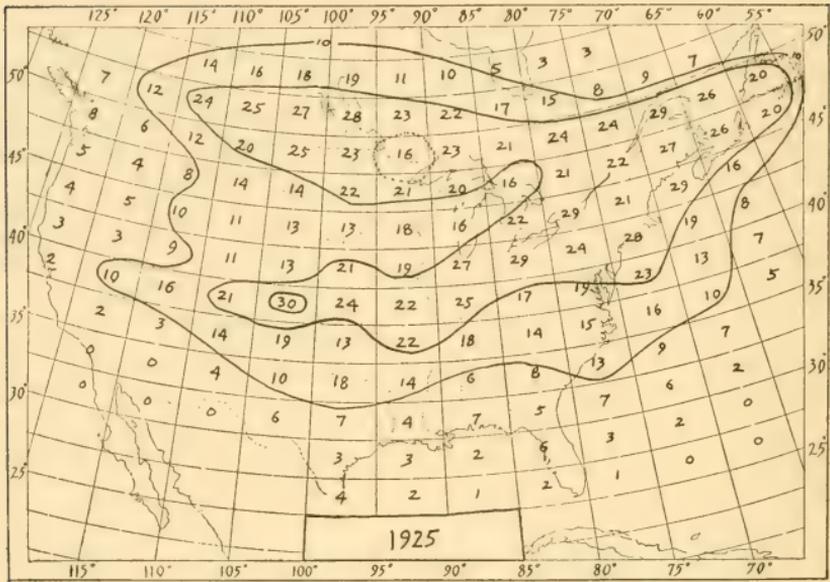
1921 and 1922



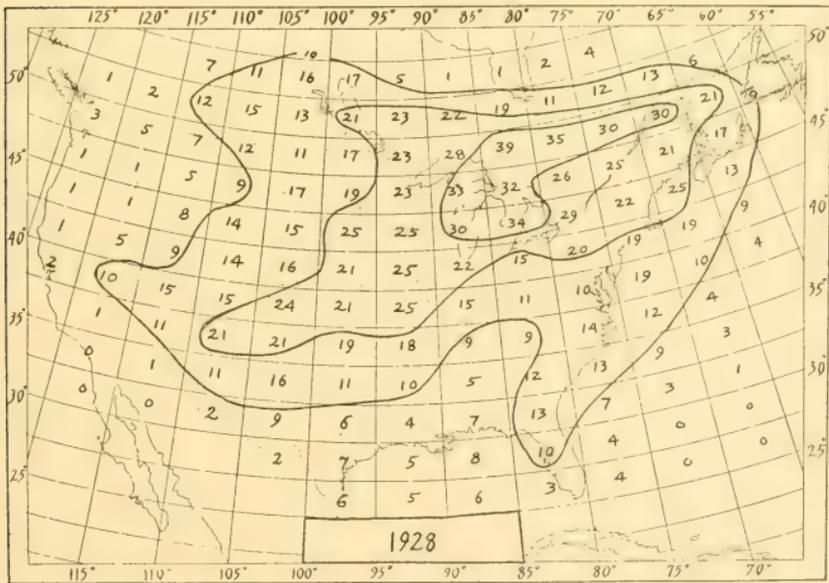
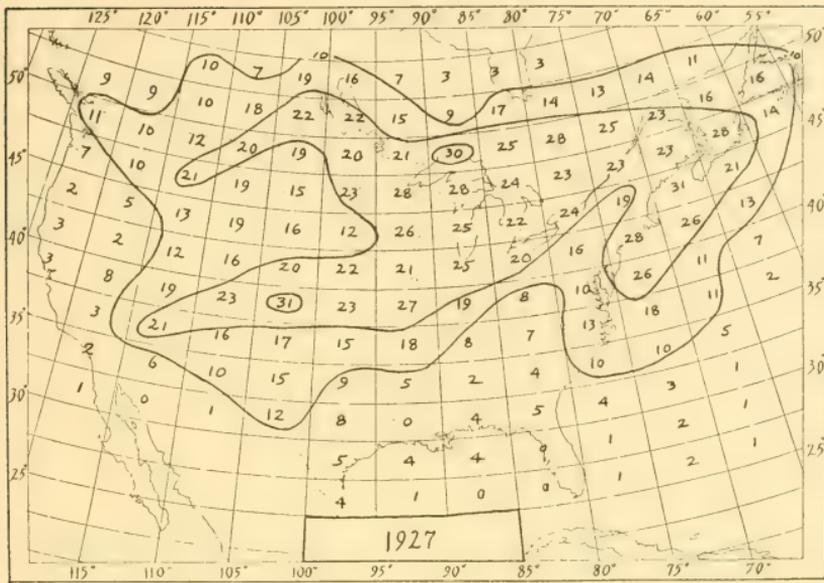
1923 and 1924



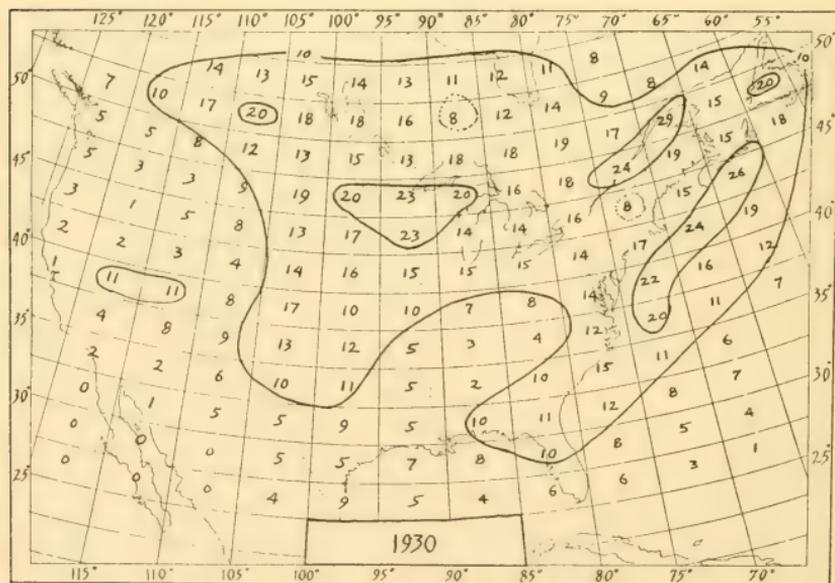
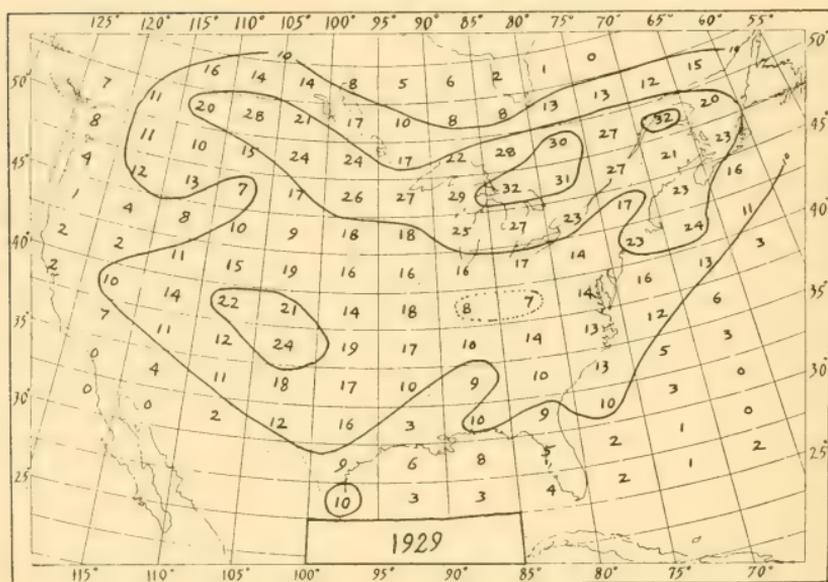
## 1925 and 1926



1927 and 1928



1929 and 1930



SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 89, NUMBER 3

## Roebling Fund

# THE KAMPOMETER, A NEW INSTRUMENT OF EXTREME SENSITIVENESS FOR MEASURING RADIATION

BY

C. G. ABBOT

Secretary, Smithsonian Institution



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## Roebling Fund

### THE KAMPOMETER, A NEW INSTRUMENT OF EXTREME SENSITIVENESS FOR MEASURING RADIATION

BY C. G. ABBOT

*Secretary, Smithsonian Institution*

About 25 years ago, as I was using a reflecting galvanometer by White of Glasgow, I noticed that when sunlight fell on its mirror a small deflection occurred without the flow of electric current. I found that this happened because the mirror was fastened to one of the groups of magnets of the suspension instead of lying between the coils as is now more usual. The system was in fact slightly twisted by the warmth of the sun ray. It occurred to me that if an astatic suspended system was purposely designed to be deformed by radiation, perhaps it might give large deflections with feeble rays. I constructed such an instrument about March, 1908, and tested it a few months later in the presence of Doctor Hale and Doctor Adams on Mount Wilson. It did indeed show high sensitiveness to radiation impulses but had too large a moment of inertia and a very long period of swing. I never used it for serious work.

In June, 1932, being again on Mount Wilson, and in need of a quick-acting radiation-measuring instrument of the highest sensibility, beyond what I could hope to get with the bolometer or even the radiometer, my thought recurred to this old instrument. It occurred to me that the two groups of magnets of the astatic system could be supported upon a stem made of two close curls of thin metallic ribbon, the two curls being of opposite senses to avoid distortion of the parallelism of the upper and lower magnet groups due to changes of surrounding temperature. I believed that when radiation should fall on one only of the two curls, the parallelism would be distorted and a tendency to rotate the system through  $90^\circ$  would ensue. Doctor Anderson, who encouraged me in this idea, suggested the obvious advantage of making the two curls of bimetallic strips. I constructed such an instrument, and found it to exceed my expectations as regards sensitiveness and satisfactory behavior.

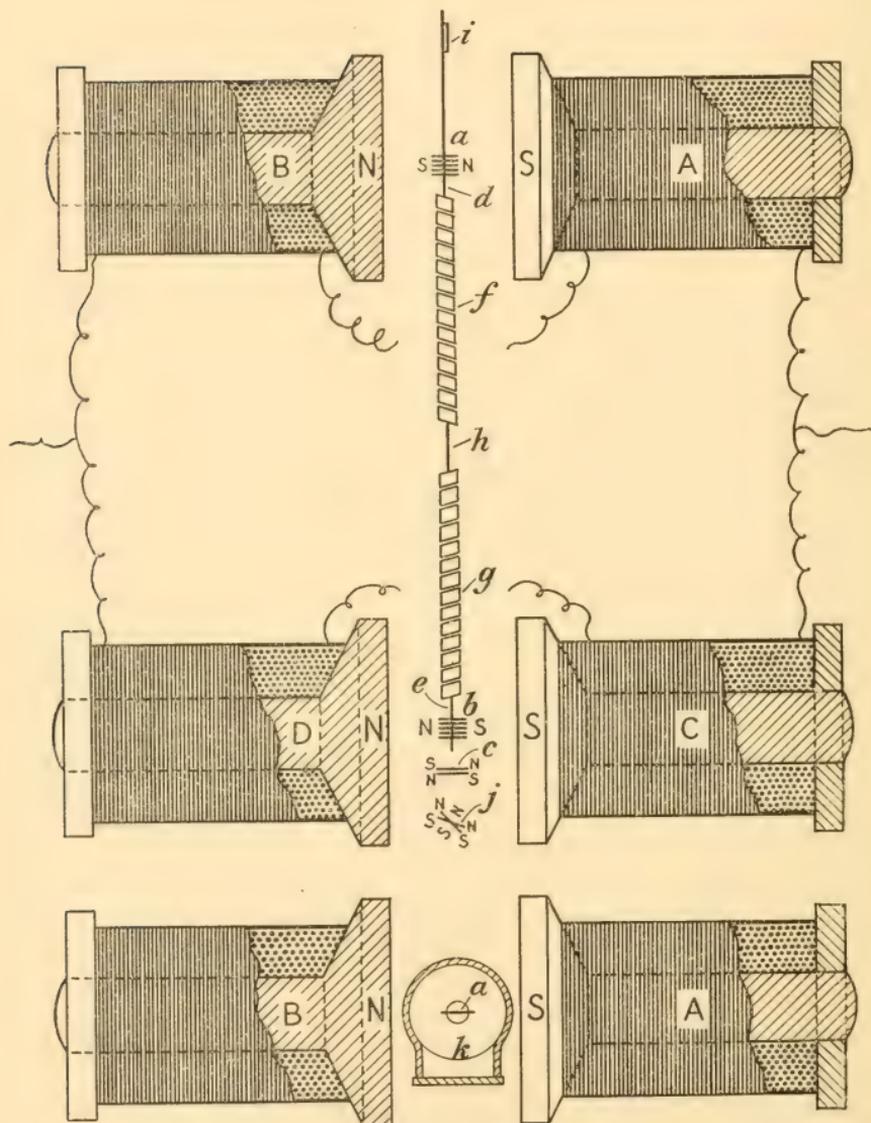


FIG. 1.—The kampfometer.

The figure shows the principal features of the kampometer<sup>1</sup> in diagrammatic fashion. The two equal groups of suspended magnets, *a*, *b*, of opposite polarity, are fastened so to be as nearly as possible in parallel vertical planes, as indicated just below the suspension at *c*, where one is supposed to be viewing them nearly from above, but neglecting the curled stem which connects them. Each group is cemented to a short, thin, vertical rod of glass, *d*, *e*, and these two rods in turn are cemented to the ends of the bimetallic curled strips, *f*, *g*, of opposite curvature. The two curled bimetallic strips are connected by a third short, thin rod of glass, *h*, so that the whole forms a suspension similar to that of an astatic reflecting galvanometer. A small mirror, *i*, is affixed to the glass rod, *a*, in the usual way to indicate deflections of the system.

The suspended system hangs within a vacuum tube having a side window, as indicated in the plan view at *k*. On either side of the evacuated tube are electromagnets *A*, *B*, *C*, *D*, adapted as will be explained below to produce any desired degree of astatic sensibility.

Under the influence of a beam of radiation falling on the curl, *f*, the magnet groups, before parallel, are rotated with respect to one another. This changes the effective polarity of the system as indicated at *j*. Consequently the system tends to turn through  $90^\circ$  so that the new polarity may coincide with the direction of the magnetic field. Being opposed by the torsion of the quartz fiber and by inequalities of magnetization of the two fields the system actually takes up some such position as shown at *j*.

I find it more convenient to use electromagnets rather than permanent magnets to control the astatic condition of the system. It is necessary to change the relative strengths of the upper and lower fields, and also to rotate these two fields with reference to each other, in order to raise the astatic condition of the system to any desired degree. It is very easy with electromagnets to make relative alterations of the two fields in large or small steps by resistance-box changes. Both fields, of course, are operated in parallel from a common storage battery, and changes in the distribution of the current are produced by operating resistances in shunt circuits. In order to produce the relative rotation of fields which is required, quick and slow adjustments of the azimuth of the pair of magnets, *C*, *D*, are provided by means of tangent screws and a clamped tangent arm in the usual way. This rotation requires very fine adjustment to secure high sensibility.

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<sup>1</sup> From the Greek words *καμπή*, a bend, and *μετρέω*, to measure.

In my first-constructed kampometer, I rolled a bimetallic strip, composed of brass and invar in about equal thicknesses, until the total thickness was reduced to 0.008 millimeter. I cut the strip as well as I could with scissors to a width of about 0.8 millimeter. I wound from it a pair of close spirals of opposite curvature, each of about 0.7 millimeter diameter. In each spiral there were 14 complete turns, with brass on the outside. Before cementing them to the glass rods, as described above, each spiral or curl was painted with lamp-black in alcohol and shellac suspension. The total weight of the suspension, including mirror, glass rods, and bimetallic curls, was approximately 4 milligrams.

The suspension was mounted, as stated above, in a glass tube. A ground-glass cone joint at the top enabled one to rotate the system with respect to the magnetic field. Opposite the upper bimetallic curl was a window of potassium iodide, a substance highly transparent to rays of great wave length. The glass work was very kindly blown for me by Doctor Smith of Mount Wilson Observatory, and the potassium iodide for the window was kindly given me by Doctor Strong of the California Institute of Technology. I found great difficulty at first in sealing the window onto the glass, because potassium iodide fractures so easily under the strain of slight inequalities of temperature. Tight sealing was at length secured by using "Arrowhead Cement," a quick-drying water-impervious cement manufactured by the Webb Products Company in San Bernardino, Calif.

With my colleague, L. B. Aldrich, I mounted the kampometer in the Smithsonian laboratory on Mount Wilson in direct connection through stop cocks and drying tubes with a mercury-vapor pump. We used it at a pressure of 0.003 millimeter of mercury.

Owing to the crude construction of the suspended system it was impossible to get it perfectly straight. Thus its moment of inertia was much greater than necessary. Moreover, because one of its metals, invar, was magnetic, the slightly crooked system gave in effect still another pair of suspended magnets besides the two principal groups in the control fields. Accordingly there was more than one position of equilibrium. At highly sensitive adjustments when illuminated by too strong a beam of radiation, the system would easily reverse itself and remain so.

Nevertheless, despite these drawbacks due to the crudeness of the construction, the kampometer proved highly sensitive. On August 11, 1932, with a time of single swing only  $\frac{5}{8}$  of one second, a candle at 1 meter produced a deflection of 116 millimeters on a scale at 1.2

meters. As the damping was very slight, the sensitiveness was almost exactly proportional to the square of the time of single swing up to 2.0 seconds, which was the maximum we employed last autumn. Probably this proportionality would have held closely to much higher times of swing.

We are now proposing to construct a kampometer of molybdenum plated with cadmium. This combination gives about  $1\frac{1}{2}$  times as great temperature-bending tendency as brass-invar, and is nearly nonmagnetic. We shall try different thicknesses of cadmium on molybdenum of 0.005 millimeter thickness until we find the best proportions. We shall use refined methods to give a perfectly straight and balanced stem, and shall use the best modern magnet steel for the magnet groups. This steel we believe will be not only of higher magnetic susceptibility, but also will be more resistive to demagnetization than that which we used last autumn. Thus we expect to be able to use stronger controlling fields without reversing the magnetization of the weaker of the two suspended magnet groups. In all these ways we expect to increase the sensitiveness for a given time of swing, and we expect to be able to control the system at 5 seconds single swing. If so, we believe we may reach 1,000 times the sensitiveness which we actually observed on August 11, 1932, with the first crude kampometer.

It will be noted that the kampometer has an advantage over both the bolometer and thermopile, in that there is no appreciable escape of heat from its sensitive part by metallic conduction. It has also an advantage over the radiometer in that there is no appreciable escape of heat by convection. Cooling only by radiation, it tends to assume a higher temperature under illumination by a beam of radiant energy than any of its three competitors. It lacks, of course, the capacity to be inclined to any angle with the vertical, which is an advantage of the bolometer and thermopile. With more robustly constructed kampometers the quartz fiber might perhaps be replaced by a jewelled bearing, and freedom for inclination to the vertical thus secured. Various forms of the instrument will perhaps suggest themselves to investigators. Anyone is at liberty to construct them as he pleases, and I hope the kampometer may have a useful future.



SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 89, NUMBER 4

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SCOUTING FOR A SITE FOR A  
SOLAR-RADIATION  
STATION

(WITH FOUR PLATES)

BY

A. F. MOORE

Astrophysical Observatory, Smithsonian Institution



(PUBLICATION 3212)

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*Astrophysical Observatory, Smithsonian Institution*

(WITH 4 PLATES)

During the early part of 1930 it became apparent that if measurements of the solar constant of radiation were to be made by the Smithsonian Institution with sufficient accuracy on a large percentage of the days of the year to make possible dependable analyses of the various cycles included in the changes in the sun's radiation, it would be very desirable, if not necessary, to find a location for a solar-radiation station in the Eastern Hemisphere, which would be nearly, if not quite the equal of the Montezuma station in northern Chile. This was becoming all the more desirable because of the increasing interest being manifested in the investigation of the possibility of weather forecasting, particularly long-range forecasting, by means of changes in solar radiation.

In 1930 the Smithsonian Institution was operating three solar stations in widely separated parts of the globe, viz: on Mount Montezuma in the Atacama Desert of northern Chile; on Table Mountain in the Sierra Madre range, bordering upon the Mojave Desert in southern California; and on Mount Brukkaros in the south-central part of Southwest Africa. The Chilean station was established near Calama in 1918 and two years later was moved to Mount Montezuma, where it has since been in continuous operation. Its elevation is about 9,000 feet above sea-level, and the large percentage of clear, uniform skies found there has not been equalled elsewhere to date. The Table Mountain station was moved to its present site in 1925, from Mount Harqua Hala in western Arizona where it had been located since 1920. Table Mountain is 7,500 feet above sea-level, and although the percentage of observable days approximately equals that of the Chilean station, the quality of the skies, particularly as regards uniformity, falls considerably short of that of the latter. Observations were begun at Mount Brukkaros in 1926, and this station was built and operated for about four years under a grant from the National

Geographic Society. Later a friend of the Institution furnished the funds for its operation. Unfortunately, the Mount Brukkaros site did not prove as good as had been anticipated, owing to the cloudiness, haziness, and high winds prevailing there at certain seasons. The elevation was considerably less than the other two stations, being only about 5,200 feet above sea-level.

Through the generosity of the same friend of the Institution, it was planned to send an expedition to Southwest Africa early in 1931 to investigate several widely separated mountain peaks in that country, all of them considerably higher than Mount Brukkaros, the idea being, if possible, to get above the haze that was causing so much trouble there. The writer was chosen to head this expedition and it was arranged that Mrs. Moore should accompany him.

From past experience it had been learned that visual observations are not sufficient for selecting a site of a solar-radiation station, and also that a few days' visit to a place, even by an experienced observer, would not suffice to judge its qualifications. Hence it was planned to equip the expedition with various portable instruments to measure the meteorological conditions prevailing on the peaks under investigation, and it was also arranged for the expedition to visit the sites at different seasons.

The prime meteorological requisites of a good observing location are: 1, that it have skies which, for a large percentage of the days throughout the year, are free of clouds, haze, dust, smoke, etc., and with little wind; 2, that the sky conditions remain nearly constant, especially from sunrise until an hour or two before noon; 3, that the site be at an elevation of at least 7,000 feet above sea-level in order to rise above the low-lying haze, dust, and smoke.

A brief description will now be given of the various instruments carried and their purpose. In order to get an accurate measure of the uniformity of the transparency of the atmosphere over a peak, the expedition was equipped with an Ångström pyrliometer for the purpose of measuring the radiation of the sun at the earth's surface. This instrument consists of two blackened strips of manganin foil, each provided with an electric thermocouple in contact with the lower surface of the strip. It is also arranged that an electric heating current can be passed through each strip at will. The thermocouples are connected so that the electromotive forces generated when the strips are heated oppose one another. The remaining terminals are connected to a fairly sensitive moving-coil galvanometer. The strips are alternately exposed to the radiation. A measured current is passed through the other strip such that its temperature is raised to exactly that of the

strip exposed to the radiation. When the current is adjusted so that this condition prevails, no current will pass from the thermocouples to the galvanometer. From the measured current which passed through the strip and the constant of the instrument, the intensity of the radiation can readily be computed.

In order to lessen the weight of the equipment to be carried up the high and rugged peaks, no theodolite was included, but instead, the altitude of the sun was obtained by measuring the length of a shadow cast upon a level surface over a triangle 10 centimeters in height. With low sun the angle was increased by  $45^\circ$  in order to get a shorter and sharper shadow. From the length of the shadow the elevation of the sun (neglecting refraction) was obtained, and from this the air-mass was read from a Bemporad "air mass versus altitude" plot.

When sky conditions permitted, 10 observations were made at approximately equal spacing of air mass, between air mass 5.60 (about  $10^\circ$  solar altitude) and nearly meridian sun. The logarithm of the solar calories per square centimeter per minute was plotted versus the air mass through which the solar beam had passed. Such a plot should be nearly a straight line (slightly convex toward the origin), with a sky of uniform transparency. If such a line were not obtained in the plot, it would indicate nonuniformity of transparency in the atmosphere above the peak during the observations.

Disregarding small changes in the heat radiated by the sun, the main terrestrial causes of nonuniformity in atmospheric transparency are changes in invisible water vapor, haze, dust, smoke, and ozone. Visible clouds should, of course, be included, but solar observations are never undertaken through clouds. The changes of radiation due to changes in ozone in the path of the beam are small and were not taken into account in the work of this expedition. But the first four agencies mentioned are very important causes of nonuniformity of transparency of the atmosphere, and instruments were carried to measure fairly accurately their effect.

Invisible water vapor is perhaps of first importance, and for determining the uniformity of water vapor prevailing in the path of the solar beam a new (and as yet unnamed) instrument was included in the equipment. The instrument is essentially a spectroscope, so arranged that the difference in radiation of the selective absorption water-vapor band called  $\rho$ , and the radiation of the region immediately adjacent to this band, is indicated by a small, sensitive thermocouple. In addition, by suitably interposing a shutter the difference between the  $\rho$  band and zero radiation (given by the shadow of the shutter), is obtained. Figure 1 represents the solar-radiation curve as measured

at the earth's surface, in the vicinity of the  $\rho$  water-vapor band.  $a$  indicates the depth of the  $\rho$  band, and  $b$  shows the intensity of the radiation of the band itself as compared with no solar radiation. In other words,  $b$  represents the minimum value of radiation in the water-vapor absorption band,  $\rho$ , and  $b + a$  is the so-called "smooth-curve" value as given in Smithsonian publications, or the intensity of the radiation of the infra-red region adjacent to the  $\rho$  band, as compared with no solar radiation. The ratio "minimum/smooth-curve" is a measure of the precipitable water vapor prevailing in the path of the solar beam through the earth's atmosphere. By plotting "log 'minimum/smooth-curve' versus air mass" a curve similar to the corresponding "log pyrhelometry calories versus air mass" is obtained.

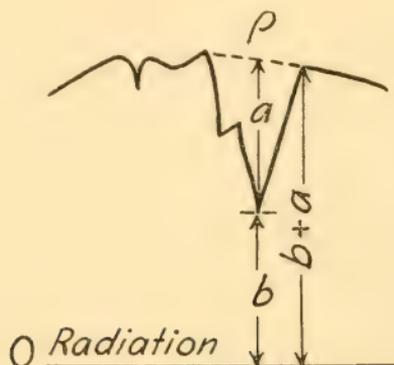


FIG. 1.

Hence by such a plot the uniformity of the water vapor prevailing in the path of the solar beam can be determined, and by comparing the plot with the corresponding pyrhelometry plot, it can be concluded whether any nonuniformity in the pyrhelometry was caused by changing amounts of water vapor or by other agencies such as haze, dust, and smoke.

In order to ascertain the amount and uniformity of the haze, dust, and smoke prevailing in the atmosphere, the Ångström pyrhelimeter was again employed, but this time with the direct sunlight shaded off, so that the radiation from a concentric ring of sky around the sun of approximately  $17^\circ$  outer radius was measured. During the observations on Fogo Peak and those in Southwest Africa including part of the first visit to Ganzberg Mountain, a much larger area of sky was seen by the instrument. Throughout the remainder of the observations in Southwest Africa and in all of the Sinai observations, an

arrangement as shown in Figure 2 was employed. *a* was a circular disk of slightly larger diameter than the opening in the hood, *b*. The latter was blackened within as was the under surface of disk, *a*. *c* represents the Ångström pyrheliometer with the two blackened strips on which the radiation fell. This arrangement gave a fairly accurate measurement of the sky radiation adjacent to the sun, and while water vapor also entered into the readings, it was possible to determine in a general way whether the haze near the sun was due mostly to water vapor or to scattering caused by dust and smoke particles. In other words, on most days any deviation from the curve of uniform pyrheliometry could be explained by nonuniformity in water vapor, haze, dust, or smoke, or by combinations of these agencies.

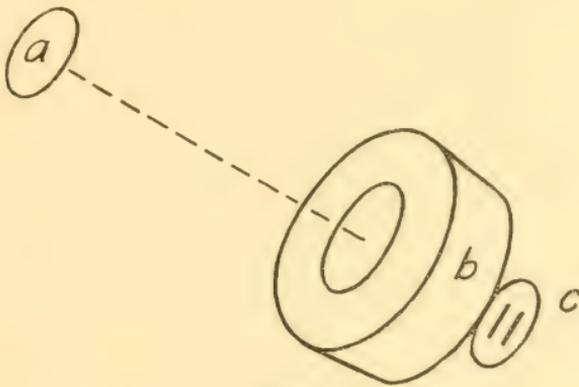


FIG. 2.

In addition to these measurements, general meteorological records were kept of the relative humidity, dry shade temperatures, wind direction and approximate intensity, and of cloudiness, fogginess, etc.

It was planned that the expedition should leave the United States, in January, 1931. A few weeks before the time of departure, H. H. Clayton of Canton, Mass., who has done much in correlating weather changes with changes in solar radiation, suggested that the expedition should include in the itinerary a high peak on the island of Fogo in the Cape Verde Islands, about 500 miles off the west coast of Africa. About 25 years before, Mr. Clayton had been a member of a French meteorological expedition that had visited Fogo, and he had found such clear skies and other promising conditions on the island that he thought it worth our investigation.

A stop of a few days was made at Washington prior to sailing, in order to acquaint ourselves with the apparatus and other details of

the expedition. Unfortunately, cloudy weather prevailed during most of our stay in Washington, so that it was impossible to test the instruments properly, particularly the water-vapor instrument, before our departure.

The expedition sailed from New York on the American freighter *West Kebar* on January 31, 1931, bound directly for the port of

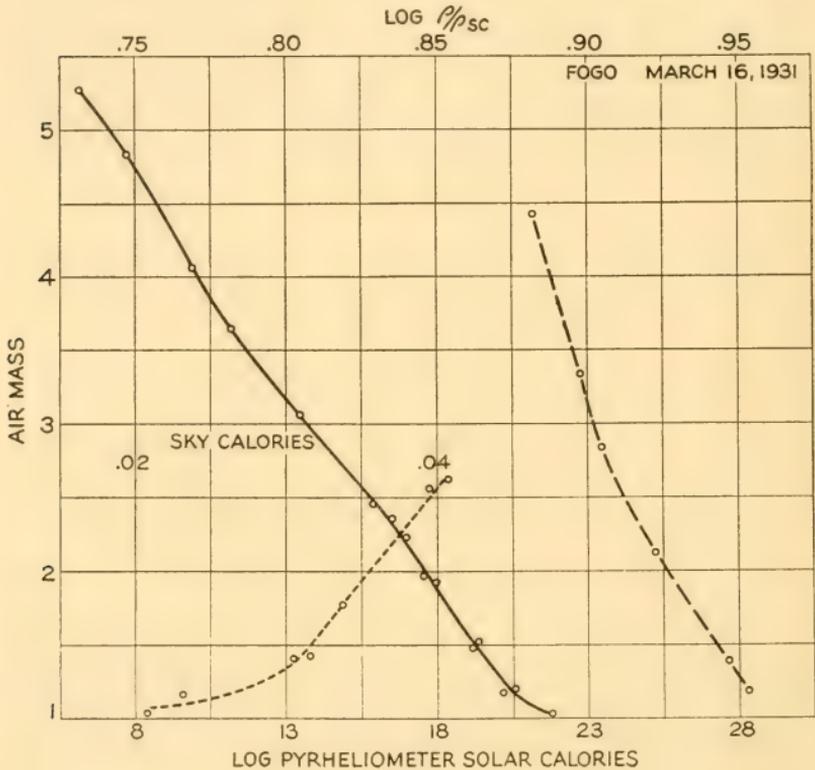


FIG. 3.

(NOTE.—This day was much better than the average as regards haze at Fogo. Used this day because it was the only one on which both the Ångström pyrheliometer and the  $p/p_{sc}$  instrument were operating satisfactorily.)

St. Vincent in the Cape Verde Islands. Upon arriving at St. Vincent we learned that the small inter-island steamer was not due to sail for at least two weeks, so we took passage on the little two-masted sailing schooner *Ernestina*, bound for the island of Fogo. With fair winds it would have been a 24-hour trip. However, a calm necessitated our remaining aboard the craft an additional night, since landing through the surf at San Filipe, the chief town and port of the island,

was not possible in the darkness. Owing to the great skill of the native boys, the landing of ourselves and our boxes was made without mishap.

The ascent of the peak or "vulcan," as the Portuguese call it, was to start from the town of Cova Figuiera, about 20 miles from San Filipe. There being no roads of any consequence outside of the town of San Filipe, we proceeded mule-back to Cova Figuiera, accompanied by our guide and interpreter whom we had brought with us from St. Vincent. The boxes were carried from San Filipe to Cova Figuiera on the shoulders of native men, and up the ascent from the latter place to the peak by men and women. The Cape Verde Islanders are truly marvels at carrying heavy burdens up mountains. The women carried boxes weighing around 70 pounds on their heads up the 4,500-foot climb with apparently no exertion whatever.

A camp site was chosen on a smaller peak just north of the main cone and at 6,000 feet above sea-level. The "vulcan" rises to about 9,000 feet elevation, but its extreme ruggedness and the smoke issuing from the summit precluded its selection for observing purposes. The observing peak was located at approximately latitude  $14^{\circ} 57'$  N. and longitude  $24^{\circ} 21'$  W.

The peak on which observations were made would not have been practical for a permanent station, owing to its proximity to the smoking volcano, but trips were made to both the northern and southern outer rims of the main crater to investigate possible observatory sites at those points. On the north rim a place was found at 6,700 feet elevation, but there was a much better site on the south rim near Ponto Alto do Sul, an 8,000-foot peak. Water would have been available from the San Filipe-Cova Figuiera pipe line, about 3 miles distant.

We spent a few days over a month on Fogo Peak, but found extreme haziness most of the time. Clouds were a negligible factor, but the haze which extended far above the summit of the volcano was much too bad for a station site. The cloudlessness, lack of high winds, dry air, and large range of temperature between day and night were favorable features, but the intense haze and the fact that thunderstorms are prevalent there during the summer months more than offset the good qualities.

Owing to a misunderstanding on the part of the native in charge of our packing from the peak to Cova Figuiera, we had to remain in San Filipe for two weeks awaiting the inter-island steamer to return to St. Vincent and nearly a week longer in the latter place awaiting the steamer for Madeira. A. F. Pacey, our good English friend in St. Vincent, entertained us and rendered us much aid, both before and after

our trip to Fogo. Owing to a revolution in progress in Madeira, the port of Funchal was blockaded, so we found it necessary to proceed to England in order to catch our steamer for Cape Town. Landing at Tilbury one afternoon, we had our boxes transferred, made our reservations, and sailed from Southampton the following afternoon. We arrived in Cape Town 17 days later, and after a few days spent there, journeyed by train to Keetmanshoop, which was to be our headquarters in Southwest Africa. We then went to Mount Brukkaros, where the Smithsonian solar-radiation station was located, and with Mr. Sordahl, in charge of the station, made many comparisons of our instruments with the instruments which were regularly in use at that station. An auto truck was ordered from Cape Town, and on its arrival in Keetmanshoop we returned to that place and made preparations for observing on Lord Hill, in the Great Karras Mountains, 60 miles southeast of Keetmanshoop. This peak has an elevation of about 7,200 feet, and is located at approximately latitude  $27^{\circ}$  S. and longitude  $19^{\circ}$  E., being on the Kraikluft farm, owned by Mrs. E. R. West and her son Austin, both of whom were of great assistance to us during our two visits to Lord Hill. This peak was occupied by us from June 17 to 30, and from September 16 to 30, inclusive.

After the first visit to Lord Hill, the long journey was made to the Erongo Mountains, about 20 miles north of Usakos, and at latitude  $21^{\circ} 44'$  S. and longitude  $15^{\circ} 34'$  E. The only passable road, although much out of a direct line, was via Windhoek, the capital of Southwest Africa. There we obtained passes, permits, and much valuable information from the Government officials, particularly Mr. Smit, the Secretary for Southwest Africa. The Ebrecht farm at the foot of the Erongos was reached July 13, and Erongo Mountain was occupied from the 15th to the 28th of that month, inclusive. This mountain is of granite formation and is extremely steep and rugged, and much difficulty was encountered by the Klip Kafir porters in making the ascent. So rough was the region that no donkeys could be used in packing, since the boxes had to be carried underneath and among enormous boulders in many places in making the ascent. Mr. Ebrecht kindly arranged the details of our packing for us.

While on Erongo Mountain a record was kept also of the apparent sky conditions over the Brandberg Range, about 60 miles to the west. There appeared to be more cloudiness, particularly of the cirrus variety, in the region north of Windhoek than farther south. Although there were some excellent skies seen from Erongo Mountain, the record was not at all encouraging, and Brandberg, which is the highest mountain in Southwest Africa, and in a region of less than 2 inches

annual rainfall, seemed to be enshrouded in cirrus even more than the Erongos. On many days the intense haziness intervening entirely hid Brandberg from view.

We had originally planned to visit this high mountain after completing our observations on Erongo Mountain, but the record of cloudiness made this seem useless, so after communicating with Washington by cable, we turned south to investigate Ganzberg Mountain,

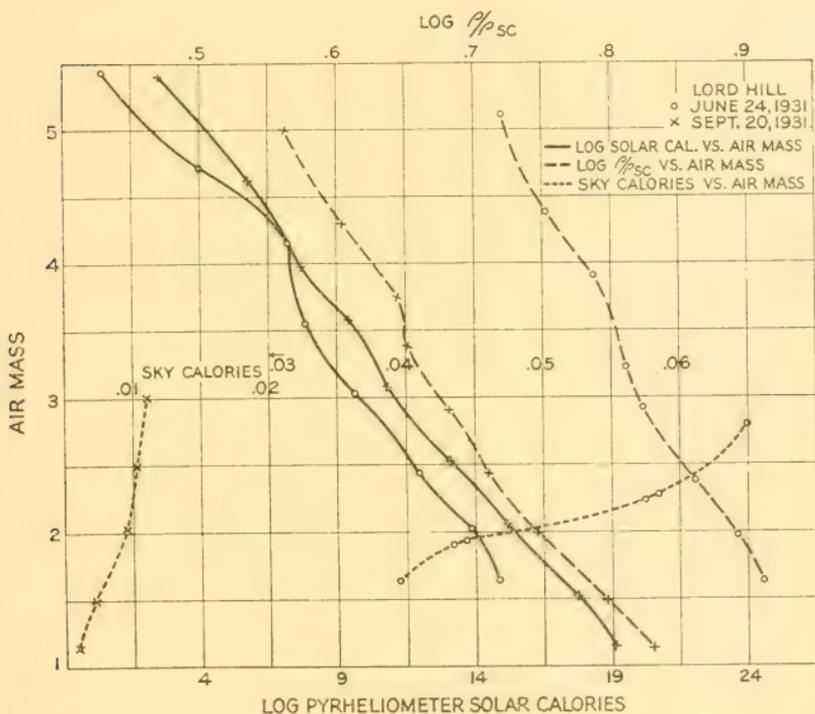


FIG. 4.

(NOTE.—June 24, sky calories measured before changing sky vestibule; September 20, after changing.)

west of Rehoboth. This mountain lies at latitude  $23^{\circ} 19'$  S. and longitude  $16^{\circ} 15'$  E., on the Gruendoorn farm owned by Otto Bassingthwaight, and is about 7,600 feet in elevation. It is situated on the border between the nearly rainless Namib and an area in the Rehoboth section, which in some years has a rainfall as high as 16 inches. The mountain has the advantage of comparative accessibility, since its base, which can be reached by automobile, lies at nearly 6,000 feet elevation. Ganzberg consists of two separate flat-topped mountains of equal

altitude, being, in fact, the sole remnants of an extensive high plateau, the remainder of which has been cut down by erosion. We carried on our observations on the easterly and smaller of the two peaks, the westerly one being nearly 2 miles square. That very heavy rains occur at times was shown by the fact that a cloudburst had, a few months before, caused Mr. Bassingthwaight's reservoir to overflow, carrying

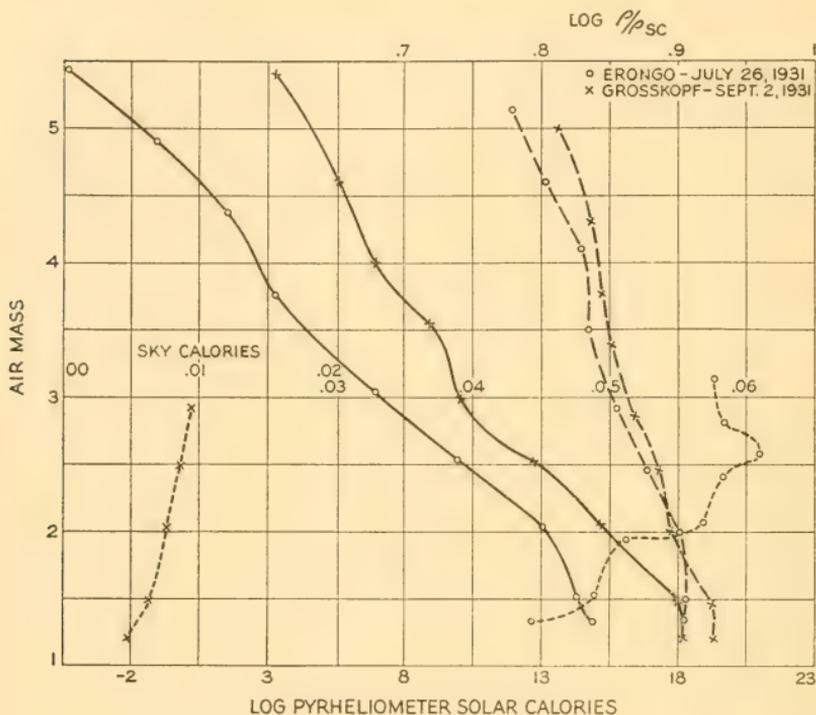


FIG. 5.

(NOTE.—Erongo sky calories measured before changing vestibule; Grosskopf after changing it.)

away the dam. He was repairing the break when we were there, and he very generously allowed us to use his native boys to carry our equipment up the mountain. He used three scrapers drawn by 12 oxen each, while repairing his dam, and the boys packed up our outfit on a day while the oxen were resting. Mr. and Mrs. Bassingthwaight were most hospitable to us, and he even accompanied the natives up the mountain each time to superintend the packing. He spoke Hottentot with all its peculiar clicks, just as well as the natives.

We made two visits to Ganzberg, viz: from August 8 to 21, and from November 3 to 14, inclusive. Although much less cirrus cloudiness was encountered than farther north, the prevalence of intense haze together with much cumulus cloudiness during the second visit militated against its suitability as an observing station site. More details will be given in later tabulations and plots.

After the first visit to Ganzberg we proceeded south to Grosskopf Mountain, located at latitude  $25^{\circ} 45' S.$  and longitude  $16^{\circ} 30' E.$ , or about 90 miles a little north of west of Mount Brukkaros. It was the

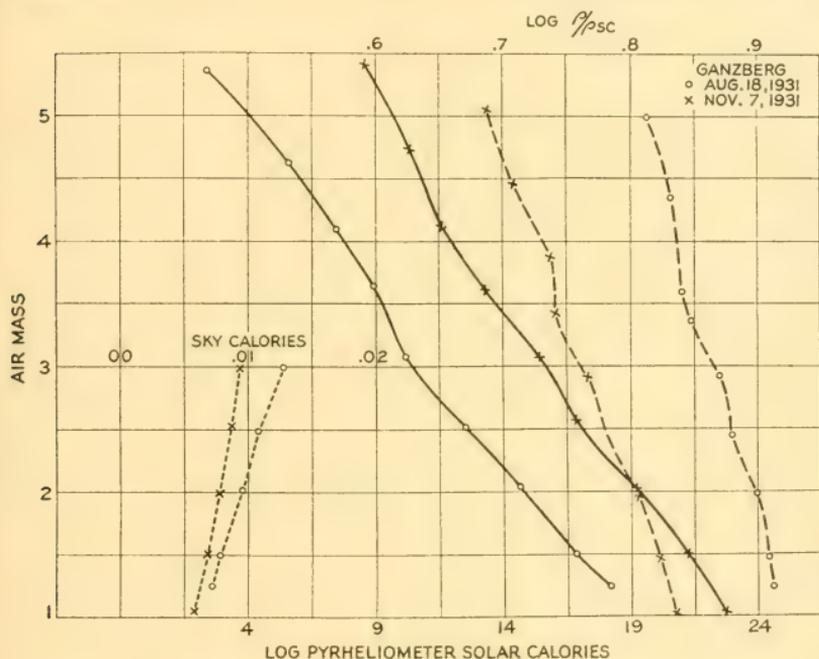


FIG. 6.

lowest peak on which we observed in Southwest Africa, being 6,400 feet above sea-level. Like Ganzberg, the mountain was flat-topped and divided into two parts. It lies in a region of slight precipitation, the annual rainfall being between 2 and 3 inches. There was scant shelter for our camp, and because we found it necessary to leave our tent at the foot of the mountain, owing to a lack of porters, we felt the cold keenly on this peak, especially since the coldest September weather in many years in Southwest Africa occurred during our stay there. We occupied the mountain from September 1 to 7, inclusive. On several occasions heavy fog blew across Grosskopf from the ocean,

and this, together with considerable cirrus cloudiness that we encountered, caused grave doubt in our minds as to its suitability for a solar station. The peak was in a very dry region as regards rainfall, but nevertheless, a good spring was found within easy access of the summit, and the climb was comparatively easy from the canyon where our car was left.

The kind hospitality that had been shown us at other places in Southwest Africa was repeated during our stay in the Grosskopf region. Especially were we indebted to John Campbell, who entertained us at his farm, and to John Buchler, the superintendent of a copper mine near Grosskopf, who greatly aided us in obtaining native boys to carry our equipment up and down the mountain.

Following our visit to Grosskopf we proceeded to Keetmanshoop, and then to Lord Hill for our second series of observations on that peak. These completed, we started north again, stopping at Mount Brukkaros for a few days to calibrate our instruments. We then began the long trip north to investigate further the possibilities of the Brandberg Mountains. We stopped at Windhoek to get the necessary government permits and then proceeded to Omaruru, where our supplies were to be purchased. The whole coastal region of Southwest Africa is a restricted area on account of the diamonds found there, and the Brandberg Mountains lie just within this area: hence the necessity of obtaining permits at Windhoek and of reporting to the commandant of the police at Omaruru.

The nearest habitation to Brandberg is the tin mine at Uis, 20 miles distant, and owned and operated by the Solar Development Company, a subsidiary of a large Canadian mining concern. The Uis mine is under the direction of Mr. McDonald, whose headquarters are in Omaruru. He had given us valuable information concerning Brandberg and the roads leading thereto, and when we arrived he directed his men to aid us in every way possible and even put a vacant mine building 5 miles toward Brandberg from Uis at our disposal during our stay there. Uis lies 80 miles nearly due west of Omaruru, and owing to the energy of the Canadian concern we found the intervening road to be one of the best over which we had driven in Southwest Africa, even though it traversed a very desolate section of the country.

After reaching Uis we got in touch with Mr. Donnett, a German employed by the mine, who had made several trips to the Brandberg Mountains. He stated that there were two possibilities for attacking the ascent, viz: via the Zizab Canyon on the northeast side of the range, or via the Hungarob water-hole on the south. He advised the former route, for the reasons that there was more water and a more

gradual ascent, although it was considerably farther. We realized, in conversing with Mr. Donnett, that we had a very hard climb ahead of us, especially for the native boys who would carry our supplies and equipment. The lack of water in this extremely dry region, coupled with the fact that there was a climb of about 6,600 feet, with practically no trail, made the prospect rather forbidding. The base of the mountain, accessible by automobile, is less than 2,000 feet above sea-level, as compared with nearly 6,000 feet at Ganzberg, and the summit is over 8,500 feet, or 900 feet higher than Ganzberg. Brandberg lies at latitude  $21^{\circ} 7' S.$  and longitude  $14^{\circ} 33' E.$

But having come thus far, we decided to make the attempt, to learn first-hand of the actual conditions. Mr. Donnett could not arrange to accompany us up the mountain, although he did guide us to the Zizab Canyon, a considerable part of the route having no road. We arranged to have as a guide an old Klip Kafir who had accompanied Mr. Donnett on two trips to Brandberg. The Zizab water-hole is visited by much game, including lions, so we slept in our car while the boys had a camp-fire all night to keep the wild animals at a safe distance. Early the next morning, leaving the car in the canyon, we got under way afoot. The farther we proceeded the rougher the canyon became. Near the upper end of the water-hole we found huge boulders as large as good-sized houses, and under some of them our guide showed us some of the ancient Bushman paintings on the rocks. These paintings represented men and various animals, and the pigments were remarkable in maintaining their colors.

After leaving the water-hole we soon came upon an old Kafir and a youngster of about 6 years. Their garb, or lack of garb, was quite in keeping with the rugged surroundings. The old man said that he lived in the Brandberg Mountains and that we could expect no more water before the next day about noon. I had the boys return to the water-hole and fill all the water cans. After lunch we resumed the climb and we found the whole bottom of the canyon filled with enormous boulders, so that it became very difficult for the boys to make progress with their packs. Discontent could plainly be discerned in their demeanor, so about mid-afternoon, while they were resting, I climbed to a high point from which I could see up the canyon, and found that for several miles ahead there could not be much hope of improvement. The aneroid showed a rise of only about 1,000 feet for the day. With over 5,000 feet yet to climb and the morale of the boys none too good, no choice seemed to be left but to abandon the attempt. The boys did not think that they could return to the car

that night, but by a promise of double rations of tea and sugar, the impossible became possible and the car was reached just after dark.

The general cirrus cloudiness and the observations that we had made from the Erongo Mountain three months before did not offer much encouragement for continuing the attempt. However, after discharging most of the boys we took two boys and drove around to the Hungarob entrance to Brandberg. But we found the climbing conditions there similar to the Zizab Canyon, so abandoned Brandberg altogether. By the bad record of cloudiness in July in the Erongo Mountains and in October in the Brandberg region it became apparent that most likely the northern part of Southwest Africa did not warrant further consideration.

Hence, on our return to Omaruru, realizing that we probably would not be so far north again, we decided to make a trip of a few days to the Etosha Pan, the wild game reserve of the country. We proceeded via Grootfontein, visiting the 50-ton meteorite on the Hoba West farm near that town; then to Tsumeb, a copper mining town; then to Namutoni, a police post located in an old German fort on the edge of the Etosha Pan. We remained overnight in the fort, as it was not safe to sleep out-of-doors on account of the lions. We saw considerable game including zebra, wildebeeste (gnu), kudü, springbok, etc., but not as many varieties as we had hoped.

The journey northward from Omaruru convinced us as to the unsuitability of the northern part of the country for solar work, for the cloudiness and poor skies increased as we approached the tropics. And the long journey from the Etosha Pan to Ganzberg showed the reverse, viz: that better skies were to be found toward the south. However, summer conditions were approaching, and our second stay at Ganzberg did not prove as favorable as the visit in August. After Ganzberg we proceeded south to Maltahöhe, intending to go, if possible, to Grosskopf for a second visit. The uncertainty was caused by heavy rains having fallen in scattered places, and the huge salt-pan between Maltahöhe and Grosskopf would have been impassable when wet.

However, at Maltahöhe we received instructions from Washington to go to Mount Brukkaros, help dismantle the apparatus there, and proceed to Mount St. Katherine on the Sinai Peninsula, unless, in our judgment, Ganzberg or Brandberg had proven enough better than Mount Brukkaros to warrant further observations. With Brandberg definitely out of consideration and with Ganzberg, the best of the peaks that we had visited in Southwest Africa, not much better than Mount Brukkaros, it seemed best to move our operations to the Sinai Penin-

sula. About a month was required to pack the Brukkaros apparatus for shipment to Washington, and the day after Christmas we left Keetmanshoop en route to the east coast of Africa via Johannesburg. We made a short side trip to Victoria Falls on the Zambezi River, and sailed from Durban on January 20, arriving at Port Said on February 19.

Nearly two weeks were required to make arrangements for proceeding to Mount St. Katherine. We learned from Maj. D. J. Wallace Bey, in charge of the Frontiers Department of the Egyptian Government, that it would be perfectly safe for Mrs. Moore to accompany the expedition, and he gave us the necessary permit to proceed across the Sinai desert. Mrs. Moore had kindly assisted with the observing during the whole sojourn in Southwest Africa, and it was good news indeed when we learned that she would not have to remain in Cairo during the expedition's stay in Sinai.

By a strict government rule, not less than two cars may undertake the desert journey across the Sinai Peninsula. We had only the car that we had used in Southwest Africa, so it became necessary for us to rent an additional car. Three natives had to be engaged: a dragoman or guide to act as interpreter and arrange the details of our trip; a chauffeur for the rented car; and owing to the sort of caste system prevailing in the country, a third man for water carrier and guard.

Three trips were made to Mount St. Katherine, and in each instance Cairo served as the base of supplies, although the actual start across the desert was made from Suez. The road led north from Suez to Kubri, where we were ferried across the Canal, then south along the east bank of the canal to a point opposite Suez, thence it turned inland, in a few miles passing the Springs of Moses, a beautiful oasis where, tradition states, the Israelites first camped after leaving Egypt. The road then traversed a most barren and desolate region a short distance inland, but again returned to the coast at the little port of Abu Zenima, belonging to an English manganese mining company. On the first two trips we entered the mountains at Wadi Sidri, about 20 miles south of Abu Zenima, but on the third trip we continued on to the mouth of Wadi Feiran, and remained in this wadi (or canyon) until we had passed the Feiran oasis and convent. The route via Wadi Sidri is shorter but much more sandy. There is no well-established road, for the most part, in any of these canyons, a person just picking his way as best he can. The Feiran oasis, about 7 miles long, is the largest and most beautiful in the Sinai Peninsula. The stately palms, set off against the very rugged mountains, present a striking picture. Feiran is the site of the ancient Paran of early Bible history. The monk

at the little convent always served us with coffee and presented us with vegetables and fruit from his garden.

Soon after passing the oasis the road left Wadi Feiran and entered Wadi Sheikh, which brought us nearly to the St. Katherine Monastery. This is the oldest monastery now in existence and has been in continuous operation for over 15 centuries. It is under the Greek Orthodox Church, with headquarters in Cairo, in which city the Archbishop resides. At present there are about 20 monks living at the monastery, and without exception, they proved most hospitable and friendly toward us. The Archbishop spent several weeks at the monastery, and he with five of the monks visited us on Mount St. Katherine during our second sojourn there. The Archbishop and monks made it clear that they would gladly welcome the establishment of a solar-radiation station on or near Mount St. Katherine, and would do all in their power to aid in its construction and operation. Since it is entirely due to the presence of the monastery that this wild region is safe from Bedouin brigands, and since the monastery virtually controls all the native labor in the vicinity, we were indeed glad to find those in charge so kindly disposed toward our venture.

The main monastery is located near the base of Mount Sinai, but there are also other smaller convents and shrines under the control of the monks, among which may be mentioned the shrine on the summit of Mount St. Katherine, "El Arbain," or the Convent of the Forty Martyrs, and "Rabba," or the convent rest-house near the Plain of the Law. Through the kindness and generosity of the monks we were permitted to occupy guest rooms in the shrine on Mount St. Katherine during our entire 15 weeks' stay on that mountain. Archimandrite Joakim, the Head Monk at the large monastery, did all in his power to add to our comfort and instructed all the monks under him to do likewise. Father Moissi, in charge of the El Arbain convent also had the shrine on Mount St. Katherine under his care. He even went so far as to send up fruit and vegetables from his garden, and they were a happy change from our menus from tin cans. On our second and third departures from Mount St. Katherine, Archimandrite Joakim and one of his assistants met us personally at the Rabba rest-house, had a wonderful luncheon prepared for us, and rooms ready so that we might rest after the tiring journey down the mountain.

The trail that the monks have constructed up Mount St. Katherine is truly a marvel, of even gradient, well constructed, and the equal of our best mountain trails. On it camels can proceed to a point only 150 feet lower than the summit, and excellent stone steps complete the trail to the top. A strong spring was found about 800 feet below the

summit and in a small canyon to the northeast of the shrine. Unfortunately, some Bedouin goat-herders polluted this spring near the close of our second visit, so that during the third visit it was necessary to have our water packed up on camels from the large monastery. In order to insure its coming from the monastery and not from some water-hole as bad or worse than the polluted spring, we arranged that the water boy should carry a paper from me each trip, which would have to be stamped with the monastery seal in the Head Monk's office and returned to me when he brought the water.

Mount St. Katherine or rather Gebel Zebir, adjacent to it, is the highest mountain in the Sinai Peninsula and in all of Egypt, being about 8,600 feet above sea-level. The mountains of crystalline formation, in which this peak is located, are among the most rugged to be found in the world, and make of this desert a wilderness in every sense of the word. The mountain lies at latitude  $28^{\circ} 31' N.$  and longitude  $33^{\circ} 58' E.$  It is nearly in the center of the triangular mountainous region forming the southern end of the Sinai Peninsula. To the north of this triangle sandy table-lands slope toward the Mediterranean.

The view from Mount St. Katherine is grand indeed. It towers above the varicolored mountains and chasms to be found on all sides. Particularly do Mount Sinai (Gebel Musa), Gebel El Shomer, and Gebel Serbal stand out in the north, south, and west, respectively. Beyond the Sinai mountains toward the west lies the Gulf of Suez, where, although it is over 30 miles distant, one can count the ships on a clear day. To the south the Red Sea appears, and to the east are seen stretches of the Gulf of Akaba, separating the Sinai Peninsula from Arabia. On most days the mountains of the Egyptian and Arabian mainlands could distinctly be seen.

On our first visit we occupied the mountain top from March 9 until April 18, inclusive. During this period we experienced some most excellent skies, some moderately good, and others very hazy. The clearness of the excellent skies was remarkable, equalling, if not excelling, the very best that northern Chile and Table Mountain, Calif., have afforded. The absolute absence of haze near the sun persisted until sunset, a most unusual thing. On two or three such days there was a very thick, sharply defined layer of haze extending perhaps a half degree above the horizon in the west at sunset. When the last vestige of the solar disk buried itself in this sharp layer of haze a distinct green ray was seen; and strangely enough, we saw another flash of green as the sun disappeared behind the distant Egyptian mainland. On the other hand, during the first visit, there were nearly half of the days with very hazy skies, but with only three days lost by

clouds in the six weeks' period. Cloudiness was nearly negligible. The most remarkable feature of the weather, particularly for March and early April, was the lack of wind. Nearly half of the days were entirely calm, and another fourth had only a light breeze. On less than three per cent of the days was there a brisk wind.

On our second visit to Mount St. Katherine, our records covered the period from April 30 to May 30. During this interval the number of excellent and satisfactory days increased quite materially,

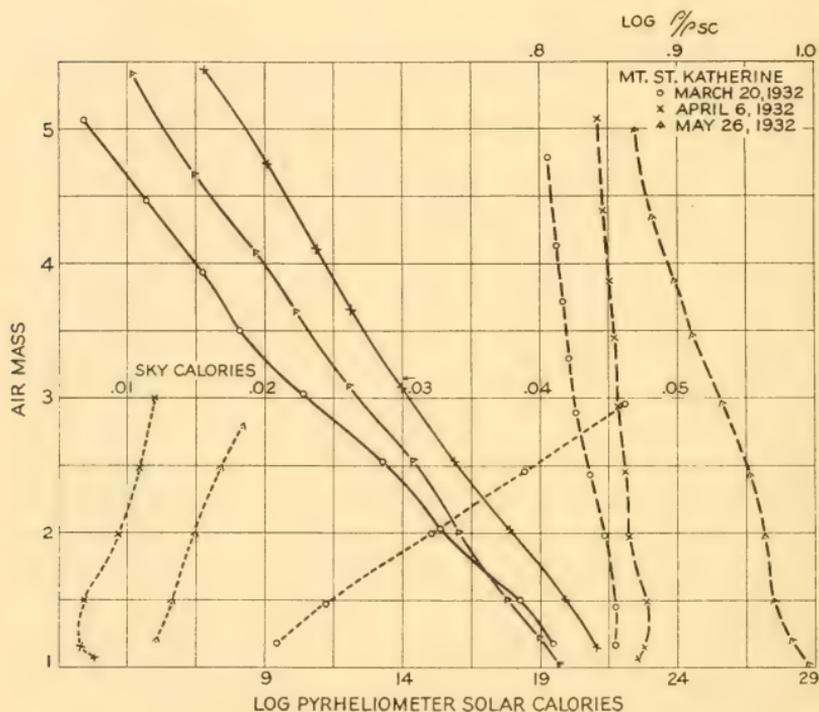


FIG. 7.

owing to less haze. Ten per cent of the days were lost by clouds, and the windiness increased somewhat, although nearly two-thirds of the days were calm or with light wind.

Our third visit extended from June 12 to July 19, and from a standpoint of weather should be divided into two separate groups, the June days and the July days, for there was a marked change for the better between June 30 and July 1. This change seemed to be permanent, for it lasted during the nearly three weeks of July in which we were on the mountain. During this period the excellent

and satisfactory days totaled nearly 95 per cent, while there were 84 per cent of days of calm or light wind. During June, however, the wind was rated as moderate or brisk on over half of the days. No days were lost by clouds in either June or July.

From the above it is seen that during the four months of March, April, May, and June, the chief drawback in the weather conditions on Mount St. Katherine was the haziness. Only six days out of a total of 106 were lost by clouds, which is a very admirable record,

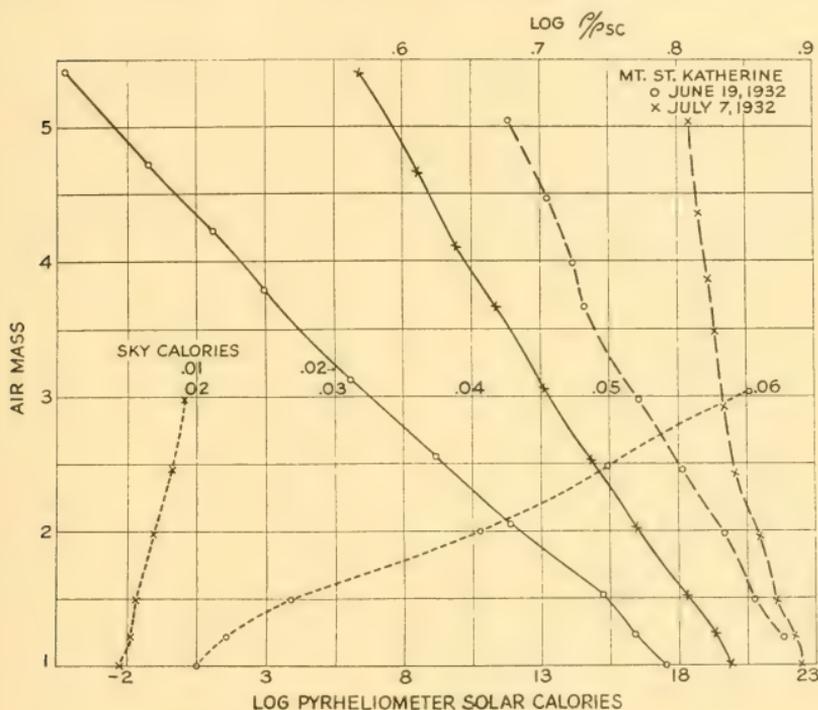


FIG. 8.

particularly for spring months. And the prevailing calmness is a strong point in favor of the place, especially as compared with Southwest Africa, where the wind was found to be a very serious handicap to accurate observations. We made inquiry regarding summer thunderstorms and from all sources learned that they are exceedingly rare. Lightning does occasionally accompany winter storms, but the absence of marks made by lightning on the rocks of the high peaks in Sinai is in great contrast to such peaks in Southwest Africa, where the rocks are literally covered with the markings.

Returning to the subject of cloudiness, our record covered 106 days in the period from March 10 to July 19, and during this interval only six days were lost by clouds while we were on the mountain. Possibly 10 days would be an outside estimate for cloudy days during the entire 131 days between the above dates. Dr. W. F. Hume, the Government geologist of Egypt, was very much interested in our work, and being familiar with the Sinai region, gave us much valuable information and data concerning it. In 1898-99 he made an extended geological survey of southeastern Sinai, and a meteorological record was kept by the late H. G. Skill. Doctor Hume kindly presented us with a copy of this publication. The weather record covered whatever location the geological party happened to be occupying, hence it probably shows more cloudiness than would have been encountered on the summit of Mount St. Katherine, and quite likely some observing could have been done on days that Mr. Skill listed as cloudy. In any event their record shows the following for morning hours from October 15 until March 10, when our record begins:

| Month          | Days<br>observed | Clouds<br>in a. m. |
|----------------|------------------|--------------------|
| October .....  | 15               | 1                  |
| November ..... | 30               | 6                  |
| December ..... | 31               | 6                  |
| January .....  | 31               | 5                  |
| February ..... | 28               | 6                  |
| March .....    | 10               | 1                  |
|                | —                | —                  |
| Total .....    | 145              | 25                 |

It appears that 25 days lost by reason of clouds from October 15 to March 10 would be a very fair estimate. There are no records available from July 19 to October 15, but from our record of July and Doctor Hume's record of the last half of October, it would appear that six days would be an outside estimate of days lost by clouds during this interval. Hence if 1932 and 1898-99 were average years, it would seem that approximately 40 days per year would thus be lost on Mount St. Katherine. From several conversations that we had with Mr. Smith, the superintendent of the British manganese mine at Abu Zenima, where he has been stationed for four years, it would appear that 1932 was more cloudy and hazy than normal. Unfortunately, the monks at the monastery have kept no weather records during the long period of the monastery's existence.

The above figures would indicate that about 89 per cent of the days throughout the year could be used for observations as far as actual clouds are concerned. Doctor Hume's record of windiness would not

be of much worth to us, since most of his observations were made in canyons, along the Gulf of Akaba, a very windy region, and in other places not at all comparable with Mount St. Katherine. But a quotation from his book may be of interest. It states: "With regard

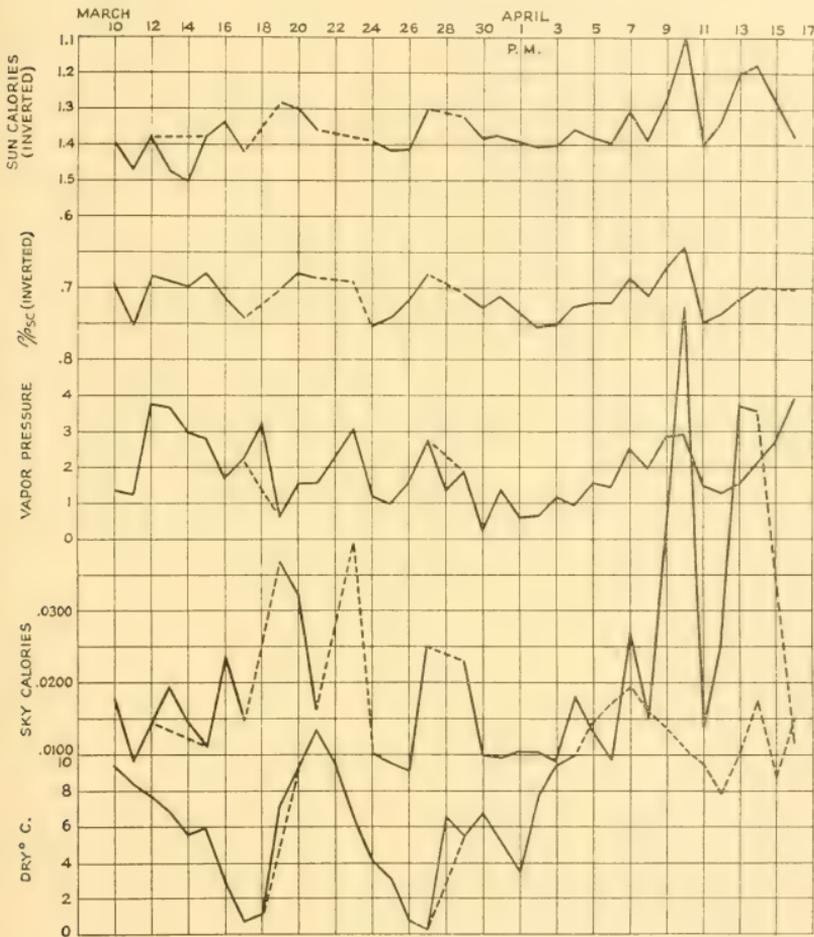


FIG. 9.—Mount St. Katherine daily means versus days.

to wind effects, as different districts were passed over, it is difficult to give definite conclusions, but in general the stillness of the air is a marked feature in the mountain regions, especially at night or in the morning. In the afternoon, especially in spring, a light breeze prevails, but probably rarely exceeds a velocity of 15 miles per hour."

We now come to the matter of the haziness encountered during our observations on Mount St. Katherine, and by far the most serious meteorological handicap found there. It is not remarkable that haziness should have occurred during the months from March to June, but one would not expect to find it so intense at nearly 9,000 feet elevation. Before visiting the mountain it was supposed that the prevailing northwest and north winds sweeping down from the Mediterranean would carry all haze due to sand storms and other disturbances having their origin in the great Sahara Desert, to the south and southwest of Mount St. Katherine. But from observations during the spring months the above assumption was found to be incorrect. The cirrus clouds nearly always moved from west toward east or from southwest toward northeast. Such clouds probably lay from 10 to 20 kilometers above sea-level and hence showed that the prevailing winds at such high elevations were moving from over the Sahara Desert toward the Sinai Peninsula. Our observations showed that about 80 per cent of the haze storms moved in from the west or southwest, and also that the haziness was usually fairly closely correlated to the water-vapor content of the atmosphere, as indicated by the  $\rho/\rho_{sc}$  instrument. At times, however, it was apparently due more to dust particles and molecular scattering. It seems quite likely that fine dust particles are carried to great altitudes during sand storms in the vast area of the Sahara Desert, and being carried eastward or northeastward by the prevailing winds at such high altitudes, finally, by force of gravity, tend to settle, and in doing so, come in contact with the moisture-laden north and northwest winds from the Mediterranean. These particles act as nuclei for condensation, and the result is a haze particle of considerable water-vapor content. This condensation occurs at times at a much higher elevation than any mountains in Sinai or Egypt, and hence no hope is had at such times to get above the haze.

The one redeeming feature concerning the haziness is that our observations showed much more uniformity of conditions during observing hours, particularly in the morning, than prevail at either the peaks of Southwest Africa or at Table Mountain in California. The accompanying graphs, which are taken from observations on average days in all cases, clearly show the superiority of Sinai over Southwest Africa. Hence, with such uniformity prevailing, even on very hazy days, there is much hope that the solar transmission coefficients over Mount St. Katherine can be quite accurately determined, in which case the haze would not be fatal to good observations of the solar constant.

In conclusion, in addition to the acknowledgments already cited, may I express the thanks of the expedition to the following: to the

native officials of the Egyptian Government; to Dr. John Ball, in charge of the Desert Survey of Egypt, for valuable advice and furnishing us with an excellent map of the Sinai Peninsula; to Dr. Robert McClenahan, Dean of the American University, on whom we often called for advice and help, and who recommended a reliable dragoman to us; to the ever-helpful missionaries of the American Mission; to Mr. Davidson in charge of the Near East Foundation work in Cairo; and to Mr. Salameh, of Cook's Agency, for their generous part in making our stay in Egypt a pleasant one.

*Summary.*—Observations for determining the suitability of various high mountains in the Eastern Hemisphere for sites for solar-radiation stations were carried on in the island of Fogo, in the Cape Verde group; in Southwest Africa; and on Mount St. Katherine in the Sinai Peninsula. About two months were spent in the Cape Verde Islands, seven months in Southwest Africa, and five months in the Sinai Peninsula and Egypt. Owing to freedom from clouds and wind, Mount St. Katherine proved to be considerably better than the Cape Verde Islands and Southwest Africa. The haziness which sometimes enshrouds Mount St. Katherine during the spring months probably causes it to fall short of northern Chile as regards suitability, but doubtless it will prove considerably superior to Mount Brukkaros and Table Mountain for solar-constant work.





1. North side of volcano, Fogo, with rough lava flow in foreground.



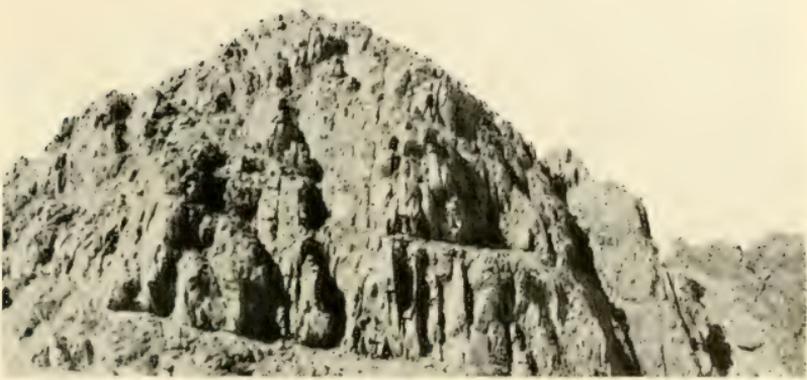
2. Packing equipment up the Erongo Mountains, Southwest Africa.



1. Boulders in Zizab Canyon, Brandberg.



2. Rugged mountains near Mount Sinai and Mount St. Katherine.



1. Shrine on the summit of Mount St. Katherine.



2. Closer view of shrine on the summit of Mount St. Katherine.



1. Observing on summit of Mount St. Katherine.



2. The St. Katherine Monastery.





SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 89, NUMBER 5

# Roebling Fund

## FORECASTS OF SOLAR VARIATION

BY

G. G. ABBOT

Secretary, Smithsonian Institution



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## Roebling Fund

### FORECASTS OF SOLAR VARIATION

By C. G. ABBOT,

*Secretary, Smithsonian Institution*

In my paper entitled "Weather Dominated by Solar Changes,"<sup>1</sup> I showed that the variation of monthly mean values of the radiation of the sun, apparently irregular, is really comprised of a small number of regular periodicities. From the analysis of a preliminary series of solar-constant values, extending from July 1918 to December 1930, I discovered and evaluated five periodicities of 8, 11, 25, 45, and 68 months, respectively. The curve constructed as their summation fitted the curve of observation so closely that in November 1930 I ventured to predict the march of the variation of the sun to the end of December 1932. This prediction is given as curve I, Figure 3, of the publication cited.

Monthly mean values of the solar constant of radiation of a preliminary character are now available to test this long-range forecast up to December 1932. They have been computed from the daily telegraphic reports received by the Smithsonian Institution from distant solar observing stations. From January 1931 to the end of May 1932, they represented Montezuma, Chile, alone. Owing to the volcanic eruption in southern Chile, Montezuma values since that time are not as yet available, though they will be later on. The remaining months up to and including February 1933, used in this paper, are taken from observations reported from Table Mountain, Calif.

In Figure 1, I give in the full curve the prediction made in November 1930 and in the dotted curve the march of the values of observation. At the time the forecast was made the solar-constant values for several years had been nearly all the time below the normal value, 1.940 calories per square centimeter per minute. The prediction indicated an expectation of values continuously above normal, and rising, indeed, to the highest levels observed since 1921. The event closely verified the forecast in both of these respects. The average deviation between expectation and observation is 0.0058 calorie, or 0.3 of 1 per cent. The forecast averaged a little too high.

<sup>1</sup> Smithsonian Misc. Coll., vol. 85, no. 1, 1931.

Meteorologists generally do not unreservedly accept the reality of solar variation. Much less do they admit the conclusiveness of the studies of periodicity just referred to. Definitive monthly mean values of solar variation having been published up to the end of 1930 in Table 45 of the *Annals of the Astrophysical Observatory*, Volume V, and preliminary values being now available including February 1933, I have made a new analysis based solely on the latest results beginning with January 1924. During this recent period, excepting since June 1932, when Montezuma work is not yet available, the daily observations are of the highest weight yet reached in our solar-constant research.

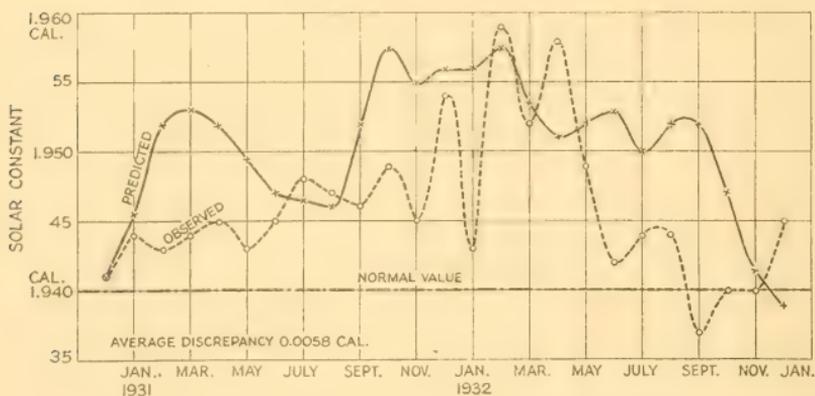


FIG. 1.—Forecast made November 1930 and verification.

In the meantime, the periodometer, an instrument for discovering and evaluating periodicities,<sup>2</sup> has been invented. By means of it a new analysis of the definitive solar-constant values of 1920 to 1930 inclusive was made by Mrs. A. M. Bond, as described in pages 5 and 6 and Figure 3 of a paper entitled "Periodicity in Solar Variation."<sup>3</sup> In addition to the five periodicities found in my earlier work, she discovered two more of 7 and 21 months period, respectively.

Assuming, then, that seven periodicities of 7, 8, 11, 21, 25, 45, and 68 months period, respectively, are requisite and sufficient to comprise the variation of the sun, I sought to evaluate them as accurately as possible from the data of January 1924 to February 1933, inclusive. To minimize error I preferred to use the method of computing explained

<sup>2</sup> Smithsonian Misc. Coll., vol. 87, no. 4, 1932.

<sup>3</sup> Smithsonian Misc. Coll., vol. 87, no. 9, 1932. By mistake the side scale numbers on curves B to H are on twice the proper scale.

in my paper "Weather Dominated by Solar Changes," rather than the mechanical process of the periodometer.

There were 110 months of observations available. This left unused values of 5 months and 6 months, respectively, in evaluating periodicities of 7 and 8 months period, and of 5, 10, and 20 months, respectively, in evaluating those of 21, 25, and 45 months period. Only in the case of the 11-month periodicity were all available data used. It was impossible without a longer interval to evaluate satisfactorily the 68-month periodicity. I found that all the other periodicities agreed closely in form and phase with those published in "Periodicities in Solar Variation," except that the amplitudes now found average but 0.7 as great as those found in that paper by Mrs. Bond from the longer series of earlier values. Hence to supply the place of the 68-month

TABLE I.—*Solar constants. Monthly mean values*

| Month       | Year  |       |       |       |       |       |       |       |       |       |
|-------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|             | 1924  | 1925  | 1926  | 1927  | 1928  | 1929  | 1930  | 1931  | 1932  | 1933  |
| January ..  | 1.938 | 1.944 | 1.940 | 1.941 | 1.938 | 1.933 | 1.941 | 1.944 | 1.943 | 1.948 |
| February .  | 1.936 | 1.943 | 1.936 | 1.942 | 1.942 | 1.933 | 1.940 | 1.943 | 1.959 | 1.947 |
| March ...   | 1.941 | 1.939 | 1.937 | 1.943 | 1.945 | 1.932 | 1.939 | 1.944 | 1.952 | ....  |
| April ....  | 1.942 | 1.947 | 1.936 | 1.944 | 1.942 | 1.934 | 1.941 | 1.945 | 1.958 | ....  |
| May .....   | 1.945 | 1.950 | 1.940 | 1.944 | 1.946 | 1.936 | 1.944 | 1.943 | 1.949 | ....  |
| June .....  | 1.952 | 1.945 | 1.943 | 1.947 | 1.948 | 1.933 | 1.943 | 1.945 | 1.942 | ....  |
| July .....  | 1.946 | 1.951 | 1.942 | 1.945 | 1.943 | 1.933 | 1.943 | 1.948 | 1.944 | ....  |
| August ...  | 1.940 | 1.944 | 1.943 | 1.943 | 1.940 | 1.932 | 1.941 | 1.947 | 1.944 | ....  |
| September . | 1.946 | 1.951 | 1.941 | 1.944 | 1.939 | 1.929 | 1.935 | 1.946 | 1.937 | ....  |
| October ..  | 1.950 | 1.946 | 1.935 | 1.944 | 1.931 | 1.931 | 1.935 | 1.949 | 1.940 | ....  |
| November .  | 1.947 | 1.945 | 1.932 | 1.944 | 1.929 | 1.938 | 1.938 | 1.945 | 1.940 | ....  |
| December .  | 1.943 | 1.945 | 1.938 | 1.941 | 1.928 | 1.942 | 1.941 | 1.954 | 1.945 | ....  |

periodicity I used her curve for it, first reducing its amplitude to 0.7. I found, too, that the periodicity assumed to be 7 months should preferably be taken as  $6\frac{2}{3}$  months. Without re-evaluating it on that basis I retarded the 7-month curve by one month at the end of each 21 months, in building up the curve of summation.

As remarked above, none of the periodicities excepting that of 11-months interval were evaluated by using any data later than September 1932, and the intense periodicities of 25, 45, and 68 months were determined solely by data that ended prior to April 1932. Hence it is fair to regard at least all parts of the curve given in Figure 2 later than October 1932 as forecasts, and the plotted points of observation from October 1932 to February 1933 as parts of the verification of the prediction.

Table I gives the data used. Figure 2 shows the result. The average deviation between observation and computation from January 1924 to

January 1933 is 0.0027 calorie, or 0.15 per cent. The probable error of a monthly mean value of observation as given in Table 1 is about 0.10 per cent.

I now venture to give in detail a new forecast for two years of the march of solar variation. It will be seen that it contemplates experi-

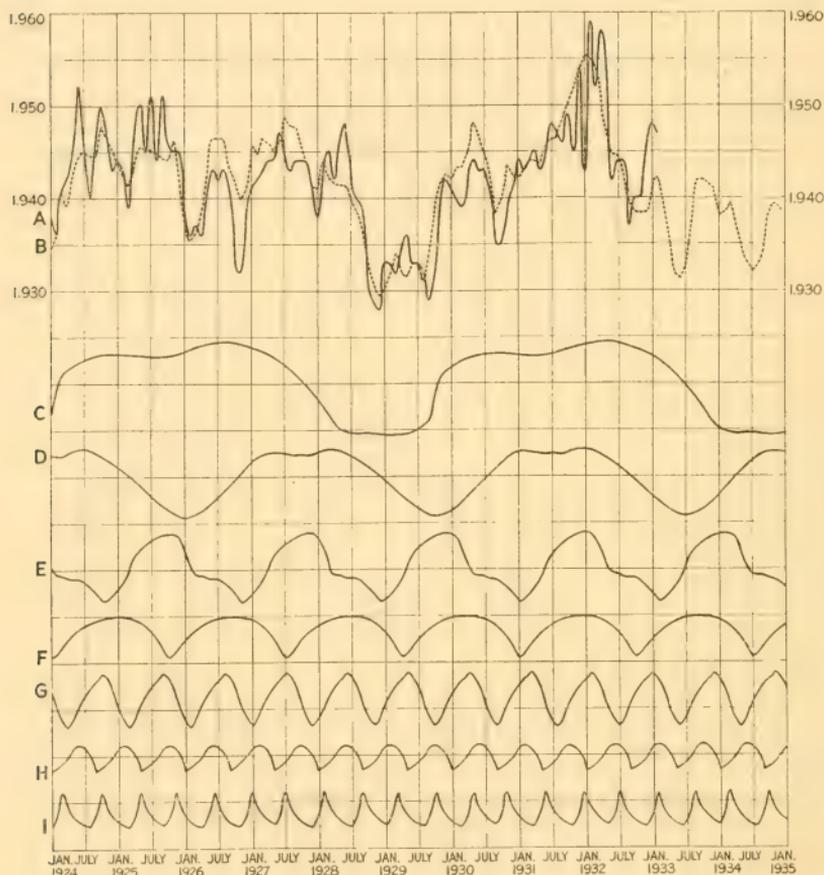


FIG. 2.—Analysis of solar variation, 1924 to 1932, and forecast 1933 to 1934 inclusive. A, observation; B, summation of seven periodic curves C, D, E, F, G, H, I of 68, 45, 25, 21, 11, 8, and  $6\frac{2}{3}$  months, respectively.

encing solar radiation generally below normal. The expected monthly mean values are stated in Table 2.

It is emphasized that the above is a long-range forecast of the variation of the sun, and emphatically not of the departures from normal temperature in the weather. The weather is much more complex, owing to the circumstances of mountains, deserts, vegetation, oceans,

ocean currents, snow, clouds, humidity, wind, which affect localities differently. Yet I am firmly persuaded that the main part of the departures from normal monthly mean temperatures at many localities are produced by the 7 periodic variations of the sun above referred to. There are, it is true, several additional periodic terms in the weather changes, which seem to be at least indirectly of terrestrial causation. The difficulty in long-range weather forecasting from periodicities lies in the fact that though the periodicities of definite interval obviously

TABLE 2.—*Solar-constant values expressing a long-range forecast of solar variation*

| Year          | Jan.  | Feb.  | Mar.  | Apr.  | May   | June  | July  | Aug.  | Sept. | Oct.  | Nov.  | Dec.  |
|---------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1933. . . . . | 1.941 | 1.942 | 1.939 | 1.936 | 1.932 | 1.931 | 1.932 | 1.936 | 1.941 | 1.942 | 1.941 | 1.940 |
| 1934. . . . . | 1.938 | 1.938 | 1.939 | 1.936 | 1.934 | 1.932 | 1.932 | 1.932 | 1.934 | 1.938 | 1.939 | 1.938 |

continually remain, their amplitudes and forms change, and they shift in phase forward and backward from time to time owing to local terrestrial influences. In an effort to overcome these obstacles Mrs. Bond and I are discussing the monthly mean values of temperature departures at several inland stations of the United States from 1875 to 1925. We hope to determine such controls of the variations of amplitude, phase, and form of the periodicities as shall enable us to make forecasts of temperature departures from 1926 to 1933 which may immediately be tested against observation. We shall present these results in a later paper.



SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 89, NUMBER 6

THE CLASSIFICATION OF THE FREE-  
LIVING NEMATODES AND THEIR  
RELATION TO THE PARASITIC  
NEMATODES

(WITH EIGHT PLATES)

BY

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Leningrad, U.S.S.R., Seessel Research Fellow,  
Yale University 1928-29



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ERRATA

On pages 29 and 30, the portion under the heading "Subfamilies and genera of the family Anguillulidae" should read as follows:

Subfamily Anguillulinae.

Genera: *Rhabditis* Dujardin, 1845 (sg. *Rhabditella* Cobb, 1929); *Rhabditoides* Goodey, 1929; *Asymmetricus* Kreis, 1930 (syn. *Pseudorhabditis* Kreis, 1929, preocc.); *Diploscapter* Cobb, 1913; *Hyalaimus* Cobb, 1920; *Hemicycliophora* de Man, 1921; *Cheilobus* Cobb, 1924; *Anguillula* O. F. Mueller, 1783 (syn. *Turbatrix* Peters, 1927\*); *Macrolaimus* Maupas, 1900; *Myolaimus* Cobb, 1920; *Himatidiophila* Rahm, 1924.

Subfamily Steinerneminae.

Genera: *Neoaplectana* Steiner, 1929; *Steinernema* Travassos, 1927c (syn. *Steinera* Travassos, 1927a, preocc.).

Subfamily Cephalobinae.

Genera: Read as printed in original at top of p. 30.

Subfamily Cephalobiinae.

Genus: *Cephalobium* Cobb, 1920. Delete subsequent reference to Peters, as this refers to *Turbatrix*, as noted above, and not to *Cephalobium*.

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\* The objections of Peters to the use of the old name, well established and universally used since Bastian, are at least questionable. Even if they should prove to be valid, an exception to the rules of priority should be made for this case.



THE CLASSIFICATION OF THE FREE-LIVING  
NEMATODES AND THEIR RELATION  
TO THE PARASITIC NEMATODES

By I. N. FILIPJEV,

*Leningrad, U.S.S.R.; Seessel Research Fellow, Yale University 1928-29*

(WITH EIGHT PLATES)

There are several opinions as to the position of the Nematoda in the animal kingdom. Cobb (1920) suggests that they constitute an independent phylum. There is much in favor of that point of view, as the Nematoda do not have very near relatives among other animal forms. However, in dealing with forms of such low organization as the nematodes, we must consider not only the purely morphological peculiarities, but the general structure and embryology as well. A consideration of these things shows that there are some related forms, perhaps not so very closely related, but with the same chitinous cuticle and bilateral determinative type of cleavage. The group received its definition, as well as its name, from Grobben, who called it Aschelminthes and included in it the Rotatoria, Gastrotricha, Echinoderida, Nematoda, Gordiacea, and Acanthocephala. Besides the above-mentioned embryological resemblance, all of these have the following common features: A functional primary body cavity, absence of a circulatory blood system, an anal opening if there is an intestine, a more or less cylindrical form of body with a circular cross-section, and a firm external cuticula. The recognition of this group is very convenient and as yet is not contrary to our knowledge of these forms, although not all of its members show unquestioned relationships (cf. Brandes).

The last three groups are often treated together as a phylum or class, the Nematelminthes. This does not seem to be an entirely satisfactory point of view, especially as regards the Acanthocephala, which are compared by Cholodkovsky to the Platodes, although recently Meyer has found that the type of cleavage is the same as in the Rotatoria. The Gordiacea, although showing a greater resemblance, are, of course, not directly connected with the Nematoda (Vejdovsky). Heider's discussion also seems to permit of recognizing a systematic relationship among these groups.

Probably the most convenient systematic arrangement would be one which treated the Aschelminthes as a phylum or subphylum, if one is inclined to retain the useful group Vermes as a phylum. The Nematoda would then be a class. But if one considers the Nematoda as a phylum, it seems impossible as yet to distinguish classes within the group. In the animal kingdom a class is a unit of very high morphologic differentiation. Such differences do not seem to exist among the various groups of Nematoda, their organization being very uniform when compared with the classes of a well-established phylum, such as the Mollusca or Vertebrata. If it is a phylum, it is a phylum with only one class.

The class Nematoda could be defined as having, in addition to the chief characters shared with the other Aschelminthes, the following characters:

Small worms, consisting of comparatively few cells; body elongated, bilateral in structure, although without a physiological differentiation between dorsal and ventral sides; with a hard external cuticula; with a single layer of longitudinal muscle cells, divided by two large lateral epidermal thickenings, the lateral cords; a muscular esophagus, usually with a triangular lumen; separate sexes; double genital organs, the female genital opening being situated in the ventral line, as a rule, at varying points from anterior to posterior; in the male the terminal genital tract and the posterior intestine unite and have a common aperture; with a very feeble regenerating power and an absence of cilia.

There are several exceptions to this definition, but they are manifestly secondary. The purpose here is neither to discuss these exceptions nor to advance theories as to how they arose. The feature which should be expressly pointed out is the importance of the cuticula in the nematode history. It could be considered as differentiating the Nematoda as a separate group, because their simple musculature, and, in this connection, the peculiar mode of motion, the absence of power of regeneration, and the peculiar biology of many of them, are possible only by virtue of the presence of this cuticular armor.

The classification of the Nematoda is in a rather bad state. Much has been gained in the last 15 years in arranging the parasitic forms, and several systems have been proposed for the free-living ones. But inasmuch as the systems for the two groups are widely different, an attempt to combine the two in one whole was made only by Baylis and Daubney, but it must be regarded as wholly inadequate where it deals with the free-living forms.

The first question arising in any attempt at nemic taxonomy is the general relation of the free-living and parasitic forms. Until recently there have been expressed in the literature opinions to the effect that the Nematoda are chiefly parasitic, a small part of them being free-living, mostly living in decaying substances. That point of view is completely wrong and is, of course, merely a result of the historical sequence in the study of this group, because in its early development much more attention was paid to the larger and economically more important parasites than to the inconspicuous and apparently economically unimportant free-living forms.

The comparison of the number of described species in both groups is somewhat suggestive. The very approximate number of species described up to the end of 1930 is as follows:

| Order            | Free-living |                      | Parasitic in— |             | Total |
|------------------|-------------|----------------------|---------------|-------------|-------|
|                  | Marine      | Fresh-water and soil | Invertebrates | Vertebrates |       |
| Enoplata .....   | 450         | 380                  | 110           | —           | 940   |
| Chromadorata .   | 350         | 110                  | —             | —           | 460   |
| Desmoscolecata . | 60          | —                    | —             | —           | 60    |
| Monhysterata ..  | 310         | 60                   | —             | —           | 370   |
| Anguillulata ... | 5           | 440                  | 30            | 610         | 1,085 |
| Oxyurata .....   | —           | —                    | 90            | 320         | 410   |
| Ascaridata ..... | —           | —                    | —             | 240         | 240   |
| Spirurata .....  | —           | —                    | 1             | 605         | 606   |
| Filariata .....  | —           | —                    | —             | 245         | 245   |
| Diectophymata .  | —           | —                    | —             | 25          | 25    |
| Trichurata ..... | —           | —                    | —             | 160         | 160   |
|                  | 1,175       | 990                  | 231           | 2,205       | 4,601 |

Free-living, 2,165; parasitic, 2,436.

These figures must be regarded as subject to considerable correction, as it is probable that a much larger number of parasites than of free-living forms are known to science. Systematic studies of the former were begun more than a century ago by Rudolphi in 1819, and since then hundreds of workers have been engaged in a study of them. The study of free-living forms began with Bastian in 1865, almost 50 years later; and it is only in the last 15 years that there has been a notable increase in number of workers, making a total today of about 15 workers engaged in the study of them, which is, of course, a decided gain when compared with two or three working along this line at any one time before about 1912.

In the collections of the parasitic species today there are no more than 20 to 30 percent of new species. In the collections of free-living forms from the fresh waters of Europe, this percentage is even lower, but among the terricolous forms, Cobb (1917) described as new 45 percent of his species of *Mononchus*, and Thorne (1925) described as new 75 percent of his species of *Acrobeles*. This last figure is especially interesting as these are the results of careful collecting in a very restricted area. Among the marine nematodes in each large collection the new species are more numerous than the described ones. Thus from the Black Sea the writer found 80 percent of the species new; from the Glacial Sea, in only one of the best known orders, 70 percent. Steiner (1927) in the *Epsilonematinae* found nearly 100 new species to add to the three which were all those previously known.

Furthermore, the parasitic species are known more or less over the entire world. The free-living nonmarine forms have been most fully studied in Europe, much less in North America and Australia, and very little in the tropical countries. The marine forms also have been systematically studied only in Europe, practically speaking.

From the foregoing it seems probable that the free-living marine species exceed in number, perhaps equal several times the number of, both parasitic and fresh-water species, the two latter being nearly equal in number of species. A comparison of the number of genera would not give an adequate conception because of the lack of uniformity in the classifications of different workers. The parasitic forms seem to be split up more than the free-living ones (cf. Baylis, 1924).

A second line of evidence as to the relations of free-living and parasitic nematodes is in regard to their physiology. The marine forms, probably with secondary exceptions among the few marine Anguillulidae, are in free relations with the external world, the water enters into their body through the cuticula, and probably the ion concentration is the same outside the body as inside. If one puts a marine nematode in a solution of some intravital stain, for instance, methylene blue, the first things to be colored are the granulations of the skin and the peripheral nerve endings included therein. Then the stain is concentrated in phagocytic cells, some muscles, deeper-lying nerve cells, etc. In fresh-water forms the color penetrates through the cuticula more slowly, and penetrates chiefly through the thin cuticula of the papillae, and through the mouth, anal, and vaginal openings. In the intestinal parasites or in the

saprozoic forms, the stain penetrates only through these openings, being chiefly ingested through the mouth, the cuticula being quite impermeable to the stain. We know that the internal fluids of the latter forms are of peculiar chemical and osmotic composition, quite different from their external medium which is sometimes variable. The relations existing in marine nematodes, as well as in other marine animals, are generally regarded as primary ones, and we have no reason to consider them as secondary in the nematodes in general.

There are several morphological structures leading us to the same conclusions, as, for example, the cervical gland or renette. In free marine forms this appears mostly as a simple skin gland, participating in the general mosaic of the body epithelium just as do the ordinary epithelial cells. It is more complexly developed in parasites or saprozoic forms, having in its primary form two outgrowths lying before and two behind the cervical pore. In young *Ascaris* larvae it is a rounded cell only, the outgrowths appearing in its later development. But throughout the parasitic nematodes it is always the same unicellular skin gland as it is in the free-living forms, as was shown 30 years ago by Jägerskiöld and Golovin. It probably has a function similar to that of the protonephridia, to which it was compared by Cobb (1890-1891), Steiner (1920), and some others, in that the latter organs also are skin glands of one sort. The nematode excretory apparatus is more primitive than the nephridia. The structure of a comparatively complexly developed organ consisting of only one cell (or sometimes of two, which makes no difference in principle) could be considered only as a secondary matter. Its excessive and complex development in saprozoic and parasitic forms is probably correlated with the necessity for an independent osmotic relation to the external medium.

Another point of comparison is the cell constancy of the parasites, affecting in some instances all their organs except the genitalia (cf. Martini, 1916). In musculature it is known as meromyarity and, since A. Schneider, has been regarded by many scientists as a very important systematic character. I do not consider this character as a primary one; really it means that there are less cells, but that each cell is more complex. The primitive condition is, of course, an indeterminate number of cells not highly differentiated. Therefore we could not regard these forms as primitive ones, but merely as neotenic larvae of forms with determinate development. The large parasitic forms could be considered as hypertrophic larvae (cf. Filipjev, 1918, 1927). The full-cell nematodes are found mostly among marine forms.

All this speaks in my opinion for the primitiveness of free-living nematodes and especially the marine ones.

But we hardly could point to these differences for a primary division into two orders or subclasses as was proposed by Perrier and apparently on ground of convenience by Stiles and Hassall (1926). Bastian's classical words that the organization of free-living forms "as a whole, differs in no obvious or important manner from that of their parasitic kindred" hold true today. Moreover, the differences between systematic groups within the broad groups of parasites and free-living nematodes, and an apparent absence of intermediate forms between them, demands a direct division of Nematoda into several orders without any subclasses. If one wishes to use such a division, then the dividing line must be drawn between the Anguillulata and the other free-living forms, rather than between the Anguillulata and the parasitic ones.<sup>1</sup>

A proposed classification is presented herewith:

Class NEMATODA

Order ENOPLATA

- Family Enoplidae
- Trilobidae
- Dorylaimidae
- Mermitidae

Order CHROMADORATA

- Family Camacolaimidae
- Plectidae
- Chromadoridae

Order DESMOSCOLECATA

Order MONHYSTERATA

- Family Monhysteridae
- Linhomoeidae

Order ANGUILLULATA

- Family Anguillulidae
- Tylenchidae
- Strongyliidae

Order OXYURATA

Order ASCARIDATA

Order SPIRURATA

Order FILARIATA

Order DIOCTOPHYMATA

Order TRICHURATA

KEY TO ORDERS OF NEMATODA

1. (8) Tail with tail glands and spinneret (when without, then with amphids pocketlike). Amphids of various forms, mostly well developed. Mostly free-living, nonsaprozoic.
2. (3) Amphids pocketlike. Cuticle smooth. Bulb absent. Ovaria reflexed. Free-living, marine or fresh-water and soil-inhabiting, or parasites of insects ..... **Enoplata**
3. (2) Amphids spiral or of derived form; circular, bubble-like, horseshoe-shaped, or transverse and slitlike.

<sup>1</sup> All parasitic forms studied by Martini (1906, 1909) have a primary division of the epidermis into six cell rows, but the few Enoplata studied by Retzius and by Filipjev (1912, 1923) have eight. The scarcity of forms studied does not as yet permit one to draw any decisive conclusions.

- Cuticle annulated or smooth. Bulb present or absent.
4. (7) Cuticle annulated or smooth, without secreted rings or setaceous appendages; or if setaceous, then with ordinary spiral amphids.
  5. (6) Ovaries reflexed. Cuticle annulated. Free-living marine, fresh-water or soil forms .....**Chromadorata**
  6. (5) Ovaries straight. Cuticle annulated or smooth. Free-living, mostly marine forms .....**Monhysterata**
  7. (4) Cuticle with 12 to 84 coarse secreted annules or setaceous appendages. Amphids bubblelike. Free-living marine forms .....**Desmoscolecta**
  8. (1) Tail without tail glands and spinneret. Amphids poorly developed, slit or papillalike, never pocketlike. Saprozoic or parasitic.
  9. (12) Esophagus with a cardiac or middle bulb, sometimes degenerated or completely lost. Free-living, saprozoic or parasitic.
  10. (11) Body without a large body cavity. Renette not very prominent. Free-living saprozoic or parasites of invertebrates .....**Anguillulata**
  11. (10) Body with large body cavity. Renette very prominent, with four large longitudinal ducts. Parasites of the intestines of vertebrates and invertebrates .....**Oxyurata**
  12. (9) Esophagus muscular or tubular, always well developed, without a bulb. Parasites of vertebrates.
  13. (16) Male with a well-developed bell-shaped bursa.
  14. (15) Bursa with longitudinal ribs .....**Anguillulata** (Strongylidae)
  15. (14) Bursa without ribs .....**Diectophymata**
  16. (13) Male without a bursa, or male absent in the parasitic stage.
  17. (24) Esophagus normal or with reduced musculature.
  18. (19) Head with three well-developed lips. Parasites of intestines .....**Ascaridata**
  19. (18) Head with two or four prominent lips or three obscure ones.
  20. (23) Parasites of intestines or respiratory system.
  21. (22) Head with three poorly developed lips or without lips. Parasitic generation syngonic; digenetic, free-living bisexual generation rhabditoid .....**Anguillulata** (Rhabdiasinae)
  22. (21) Head with two or four lips .....**Spirurata**
  23. (20) Parasites of tissues or circulatory system of vertebrates. Head with two lips or without lips. Esophagus often without musculature .....**Filariata**
  24. (17) Esophagus tubular, consisting of one row of cells. Body very narrow, filiform in its anterior part .....**Trichurata**

### Order ENOPLATA

The Enoplata were defined by Filipjev (1918, 1927) primarily as a family, and this was directly divided into several subfamilies.

All these have a smooth cuticle, except for only a very few forms which have a very fine striation. The esophagus is uniform, without a bulb (fig. 1). The head presents a typical structure, bearing the typical six labial papillae, ten cephalic setae, in some forms transformed into papillae, and two amphids (figs. 4, 5), the latter present in the form of a pocket, with an anterior aperture (figs. 2, 3, 4); the cuticle on the head presents a very typical reduplication with a circular cavity around it, bordered behind by the so-called cephalic line (figs. 2, 4); the esophagus adjoins the inner layer of the cephalic cuticle along a very wide surface (figs. 2, 3). The ovaries are always reflexed (fig. 1). The musculature is polmyarian. Some of these nematodes are the largest of all free-living nematodes. There are exceptions to nearly all these characters inside the order, but most of these are present in any given form discussed here.

## KEY TO FAMILIES OF ENOPLATA

1. (2) Cuticle with duplication on the head. Males mostly with one or two preanal tubes. Most genera marine ..... **Enoplidae**
2. (1) Cuticle without duplication on the head.
3. (6) Esophagus with muscles. Free-living forms.
4. (5) Esophagus strong, of nearly uniform thickness throughout its whole length. Free-living, fresh-water and marine forms ..... **Trilobidae**
5. (4) Esophagus dorylaimoid, i.e., bottle-shaped, weak, almost without musculature anteriorly, then suddenly enlarged and strongly muscular posteriorly. Free-living, mostly fresh-water and soil forms, some marine forms ..... **Dorylaimidae**
6. (3) Esophagus without muscles, forming a long narrow chitinous tube with some adhering, large, epidermal cells. Adults mostly free-living, soil and fresh-water forms; larvae parasitic in insects and other invertebrates ..... **Mermittidae**

## SUBFAMILIES AND GENERA OF THE FAMILY ENOPLIDAE

## Subfamily Leptosomatinae.

Genera: *Anticomma* Bastian, 1865 (syn. *Stenolaimus* Marion, 1870); *Leptosomella* Filipjev, 1927; *Barbonema* Filipjev, 1927; *Platycoma* Cobb, 1893; *Platycomopsis* Ditlevsen, 1926 (syn. *Dactylonema* Filipjev, 1927); *Synonchus* Cobb, 1893 (sg. *Fiacra* Southern, 1914; sg. *Jägerskiöldia* Filipjev, 1916); *Cylicolaimus* de Man, 1889; *Nudolaimus* Allgén, 1929; *Leptosomatium* Bastian, 1865; *Leptosomatides* Filipjev, 1918; *Deontostoma* Filipjev, 1916; *Thoracostoma* Marion, 1870 (sg. *Pseudocella* Filipjev, 1927); *Triodontolaimus* de Man, 1893.

## Subfamily Enoplinae.

Genera: *Enoplus* Dujardin, 1845 (syn. *Enoplostoma* Marion, 1870); *Enoploides* Saveljev, 1912; *Filipjevia* Kreis, 1928; *Enoplolaimus* de Man, 1893 (sg. *Mesacanthion* Filipjev, 1927; sg. *Oxyonchus* Filipjev, 1927); *Saveljevvia* Filipjev, 1927; *Parenoplus* Filipjev, 1927.

## Subfamily Oxystominae.

Genera: *Thalassoalaimus* de Man, 1893; *Nuadella* Allgén, 1927; *Trefusia* de Man, 1893; *Acoma* Steiner, 1916; *Paroxystomina* Micoletzky, 1924; ? *Asymmetrica* Kreis, 1929; *Nemanema* Cobb, 1920; *Nemanemella* Filipjev, 1927; *Oxystomina* Filipjev, 1918 (syn. *Oxystoma* Bütschli, 1874, preocc.; syn. *Schistodera* Cobb, 1920); *Halalaimus* de Man, 1888; *Tycnodora* Cobb, 1920; *Nuada* Southern, 1914; ? *Xemella* Cobb, 1920.

## Subfamily Phanodermatinae.

Genera: *Crenopharynx*, nom. nov. (syn. *Stenolaimus* Southern, 1914, nec Marion, 1870, type *Anoplostoma gracile* Linstow, 1900); *Nasinema* Filipjev, 1927; *Micoletzkyia* Ditlevsen, 1926; *Phanodermopsis* Ditlevsen, 1926 (syn. *Galeonema* Filipjev, 1927); *Phanoderma* Bastian, 1865 (syn. *Heterocephalus* Marion, 1870; syn. *Cophonchus* Cobb, 1920); *Phanodermella* Kreis, 1928; *Klugea* Filipjev, 1927 (syn. *Gullmarnia* Allgén, 1929).

## Subfamily Thoracostomopsinae.

Genus: *Thoracostomopsis* Ditlevsen, 1919.

## Subfamily Oncholaiminae.

Genera: *Anoncholaimus* Cobb, 1920; *Pelagonema* Cobb, 1893; *Vasculonema* Kreis, 1928; *Pandolaimus* Allgén, 1929; *Pontonema* Leidy, 1855 (syn. *Paroncholaimus* Filipjev, 1916); *Viscosia* de Man, 1890 (syn. *Steineria* Ditlevsen, 1926, preocc.); *Oncholaimus* Dujardin, 1845; *Convexolaimus* Kreis, 1928; *Krampia* Ditlevsen, 1922; *Prooncholaimus* Micoletzky, 1924; *Adoncholaimus* Filipjev, 1918; *Metoncholaimus* Filipjev, 1918; *Filoncholaimus* Filipjev, 1927; *Mononcholaimus* Kreis, 1924; *Oncholaimellus* de Man, 1893; *Anoplostoma* Bütschli, 1874; *Trilepta* Cobb, 1920.

## Subfamily Rhabdodemaniinae.

Genus: *Rhabdodemia* Baylis and Daubney, 1926 (syn. *Demania* Southern, 1914, preocc.).

## Subfamily Eurystominae.

Genera: *Ditlevsenella* Filipjev, 1927; *Eurystomina* Filipjev, 1918 (syn. *Eurystoma* Marion, 1870, preocc.; syn. *Marionella* Cobb, 1921); *Bolbella* Cobb, 1920; *Thoonchus* Cobb, 1920; *Ledovitia* Filipjev, 1927.

## Subfamily Enchelidiinae.

Genera: *Enchelidium* Ehrenberg, 1836 (syn. *Lasiomitus* Marion, 1870; syn. *Calyptronema* Marion, 1870); *Chaetonema* Filipjev, 1927; *Asymmetrella* Cobb, 1920; *Ilium* Cobb, 1920; *Catalaimus* Cobb, 1920; *Dilaimus* Filipjev, 1926; *Polygastrophora* de Man, 1922; *Symplocostoma* Bastian, 1865 (syn. *Amphistenus* Marion, 1870; sg. *Isonemella* Cobb, 1920); *Fenestrolaimus* Filipjev, 1927; *Rhinoplostoma* Allgén, 1929; *Pseudodilaimus* Kreis, 1928.

## KEY TO SUBFAMILIES OF ENOPLIDAE

1. (10) Buccal capsule surrounded by the esophageal musculature; absent in certain genera.
2. (3) The cephalic armor (i.e., the chitinized part of the external cephalic cuticle) present. Three well-developed lips present. The buccal organs complicated, consisting of three unequally developed jaws (reduced in *Saveljevia*) with a cuticular ring around them, homologous to the cephalic capsule of other forms; onchi in some genera ..... **Enoplinae**
3. (2) The cephalic armor absent (in *Phanoderma* there is present, besides the true cephalic capsule, which is always absent in *Enoplinae*, a longitudinally striated cervical armor). Lips mostly absent.
4. (5) Esophageal contour straight; the cephalic circle always single, composed of 10 setae or papillae ..... **Leptosomatinae**
5. (4) Esophageal contour crenated.
6. (9) Spear absent; buccal capsule absent or very small.
7. (8) Esophagus broadly incised posteriorly. Body mostly elongate, in some species very thin. Spicules short, preanal tube absent ..... **Oxystominae**
8. (7) Esophagus rounded posteriorly. Body mostly moderately elongate. Spicules long, preanal tube present in most forms ..... **Phanodermatinae**
9. (6) Spear present, long and thin, followed by a modified part of the esophageal tube loosely articulated with it ..... **Thoracostomopsinae**
10. (1) The buccal capsule free (as least for a part), generally with strong chitinized walls (except when reduced as in *Enchelidium*).
11. (14) The buccal capsule closed by six mobile lips, its walls strongly chitinized, mostly bearing three immobile onchi.
12. (13) The walls of the capsule without clefts, therefore completely immobile. Spicules very dissimilar; one preanal tube or none ..... **Oncholaiminae**
13. (12) The walls of the buccal capsule with clefts, therefore somewhat mobile. Spicules thin, curved; two preanal tubes ..... **Eurystominae** (*Ditlevsenella*)
14. (11) Three lips or none, buccal capsule broadly open.
15. (16) Buccal capsule conoid with chitinous folds in the walls, teeth short ..... **Rhabdodemaniinae**
16. (15) Buccal capsule cup-shaped with spear-shaped tooth or teeth, or reduced to form a narrow chitinous tube.
17. (18) Spicules curved, preanal tubes two; one tooth ..... **Eurystominae**
18. (17) Spicules elongated, no preanal tubes; one tooth, three teeth, or none ..... **Enchelidiinae**

The Leptosomatinae are the simplest forms, showing all the primitive characters of the family preserved; the mouth organs are mostly very simple (fig. 2). The differentiation goes here in two directions. One development is the hardening of the head by the so called cephalic capsule, simple in *Synonchus* and very complex in *Thoracostoma* (fig. 3). The other development is the acquisition of movable mouth structures; a simple small movable tooth is found in *Leptosomatum* and *Synonchus*; *Fiacra* and *Platycoma* have three teeth situated more anteriorly, quite near the lips; and *Triodontolaimus* has three large jaws in the same position. *Triodontolaimus* presents a connecting link with the following subfamily.

In the Enoplinae are united several closely related genera. *Enoplus* has three jaws more specialized than in *Triodontolaimus* (figs. 4, 5). The esophagus has here an expanded attachment to the cuticle as in the preceding subfamily. The chitinous ring surrounding the jaws probably corresponds to the cephalic capsule; the outer chitinization of the head, the "cephalic armor", corresponds to the inner layer of the reduplicated head cuticle in the Leptosomatinae. Besides the ordinary head armature of ten cephalic setae and the amphids, there are two "cephalic organs", lateral in position (the "lateral lips" of de Man), another organ of sense, probably present in all Leptosomatinae also. The spicules are often very complex, and a typical glandular and sensitive organ, the "preanal tube", is to be seen anteriorly (it is probably also present in all Leptosomatinae, although less developed). *Enoploides* (fig. 6) presents an enormous development of lips probably correlated with its rapacious habits; the jaws are present but profoundly split posteriorly. In *Enoplo-laimus* (fig. 7) the jaws are weak, each in the form of two parallel, chitinous rods connected anteriorly and provided with two hooks spreading sideways; between the rods of the jaws there are true onchi which spread inside the mouth capsule (cf. Saveljev, 1912). The amphid is very small and difficult to see, but the cephalic organ is well developed, sometimes spreading outside the contour of the head and probably substituting in its functions for the reduced amphids. An interesting transformation occurs in the labial papillae in most of the genera; they project anteriorly and greatly resemble setae, but they lack the distinct articulation with the cuticle which is characteristic of true setae.

The Oxyostominae are characterized by the excessive elongation of the body. The most primitive forms are very similar to the Leptosomatinae, but in others the elongation involves the head

organs. In *Oxystomina* (fig. 8) the amphid is very remote from the anterior end and becomes very much elongated, with a large anterior aperture, the reverse of the common condition. The cephalic circle of the setae is divided into two circles, with six setae in the anterior and four in the posterior circle, an evidence of its complex nature. *Halalaimus* (fig. 9) presents a further step in the elongation of the amphids, so that the primitive pocket form could hardly be recognized without the intermediate *Oxystomina*.

The Phanodermatinae in its most simple members, for example, *Crenopharynx*, closely resembles the Leptosomatinae as regards the structure of the head. The differences are in the always elongated spicules and the esophagus of a distinct cellular structure. The type genus *Phanoderma* (fig. 10) is ocellate and has a cephalic capsule like *Thoracostoma* but of a different type, four-lobed instead of six-lobed, and followed by a cephalic armor probably homologous to that of the Enoplinae. Several other genera closely resemble *Phanoderma*.

The Thoracostomopsinae are very distinctive. The cellular esophagus and the four-lobed cephalic capsule resemble those of *Phanoderma*, but there is a peculiar spear followed by a modified part of the esophageal tube, to which the spear is joined by an articulation.

The Oncholaiminae have a spacious mouth capsule, provided in typical representatives with three immobile onchi (fig. 11). Generally they do not have the preanal organ typical for all the three preceding subfamilies, although *Pontonema* has a reduced one, so its absence in other genera could be considered as secondary. The existence of the spacious mouth capsule does not permit the esophageal musculature to adhere to the cuticle directly as in the previous forms. But there is the same duplication of the cuticle on the head as in *Leptosomatum*, and the cuticle of the mouth capsule is folded in that place. Actually the mouth capsule is nothing other than the enlargement of the interior of the esophageal tube lacking the surrounding musculature; the epidermal cells that form the esophagus in that region adhere over a wide area to the cuticle just as do the muscle cells in other forms. *Krampia* should be considered as a reduced *Oncholaimus*, a parallel to the conditions in *Catalaimus* discussed below.

In the Rhabdodemaniinae, *Rhabdodemia* (fig. 12) is a very distinctive genus, the only genus at present in an isolated subfamily erected for it. The large buccal capsule resembles that in the

Oncholaiminae, but the taxonomic relations of these nematodes are not quite certain.

The Eurystominae (fig. 13) are related to the Oncholaiminae but distinct enough to be separated. They do not have lips around the mouth except in *Ditlevsenella*. In typical genera the single onchium is protrusible. Very characteristic is the spicular apparatus (fig. 14) with the thin and strongly curved spicules and two distinctive pre-anal organs. In the genus *Bolbella* the esophagus is divided posteriorly into eight bulbi, an exceptional structure, not only among the bulbless Enoplata, but also among all other Nematoda; its mouth capsule and the spicular apparatus are quite typical.

The Enchelidiinae are similar to the Eurystominae as regards the mouth capsule with its protrusible onchium (fig. 15). The long spicules suggest a possible relation to the Phanodermatinae. Oddly enough there exists a polybulbous genus, *Polygastrophora*, with all the peculiarities of the subfamily, parallel to *Bolbella* of the Eurystominae. Very interesting is the disappearance of the mouth capsule in the males of certain genera. De Man (1922c) described a form belonging to *Catalaimus*, in which the male lacks the mouth capsule although the female has a typical one. Such males were known long ago under the name of *Enchelidium* (fig. 16). In describing the Black Sea species, I called attention to the strange fact that only the males of this genus were described by the numerous authors studying them, but only De Man's discovery provided an explanation of the problem. In the head, which is always very narrow, there are two cuticular lenses very similar to those of *Symplocostoma*; the esophageal tube anterior to them is very narrow, as if really reduced. The pigment spot is in the vicinity of the lens. The cuticular lens, as one concludes from comparison with some species of *Symplocostoma*, represents nothing other than the bottom plate of the mouth capsule. Two interesting points are to be noted here: first, that of the change of functions; second, an example of an organ so highly rated by systematists, disappearing in the same species, in the same individual even, during its molts.

#### SUBFAMILIES AND GENERA OF THE FAMILY TRILOBIDAE

##### Subfamily Trilobinae.

Genera: *Tripyla* Bastian, 1865 (syn. *Promononchus* Micoletzky, 1923; sg. *Trischistoma* Cobb, 1913); *Diplohystrera* Cillis, 1917; *Trilobus* Bastian, 1865 (syn. *Paratrilobus* Micoletzky, 1922); *Cryptonchus* Cobb, 1913 (syn. *Ditlevsenia* Micoletzky, 1925); *Gymnolaimus* Cobb, 1913; *Udonchus* Cobb, 1913; *Onchulus* Cobb, 1920; *Prismatolaimus* de Man, 1880.

## Subfamily Mononchinae.

Genera: *Mononchulus* Cobb, 1918; *Mononchus* Bastian, 1865 (sg. *Sporonchulus* Cobb, 1917; sg. *Prionchulus* Cobb, 1916; sg. *Mylonchulus* Cobb, 1916; sg. *Anatonchus* Cobb, 1916; sg. *Iotonchus* Cobb, 1916).

## Subfamily Tripyloidinae.

Genera: *Tripyloides* de Man, 1886; *Parachromagaster* Allgén, 1929; *Cothonolaimus* Ditlevsen, 1919 (syn. *Macrolaimus* Ditlevsen, 1919, preocc.); *Bathylaimus* Cobb, 1893; *Bathylaimella* Allgén, 1930; *Halanonchus* Cobb, 1920; ? *Rhabdocoma* Cobb, 1920.

## KEY TO SUBFAMILIES OF TRILOBIDAE

1. (2) Buccal capsule free, large, thick-walled; soil and fresh-water forms ..... **Mononchinae**
2. (1) Buccal capsule absent, or narrow, or if large never thick-walled, and if free then only to a small extent.
3. (4) Amphids typical, pocketlike; spicular apparatus not complex; fresh-water and soil forms ..... **Trilobinae**
4. (3) Amphids mostly atypical, either spiral-shaped or rounded (except *Halanonchus*); spicular apparatus of a complex type, with a large gubernaculum exceeding the spicules in length; marine forms ..... **Tripyloidinae**

The preceding family, with only a very few exceptions, is composed of marine forms; on the other hand, the remaining three families contain mostly fresh-water and soil nematodes, with only comparatively few members occurring in the sea. The Trilobidae, while conserving some of the primitive features of the preceding family, have completely lost the primitive wide attachment of the esophagus to the cuticle of the head. In all its members the esophagus is wide, of nearly the same diameter from the anterior end to the cardia; the cardia is well developed, in some genera with typical glandular cells inside; the caudal glands and the spinneret are present in almost all genera. In the type genus, *Trilobus*, (fig. 17) there is a broad mouth capsule with two denticles at its base. *Tripyla* has a very similar mouth capsule with the same denticles, but it can be closed, thus disappearing almost completely; in such a closed position only the straight contours of its walls anterior to the denticle show the presence of firm, differentiated cuticle. In the preserved specimens of that genus the cuticle is often distinctly striated, but this striation is never apparent in living specimens, the cuticle in these being perfectly smooth as in other members of the Enoplata; the causes of this have never been investigated closely, but probably it is due to some internal striation. In most of the genera there are a larger number of preanal organs instead of one or two as in the Enoplidae. In some, such as *Trilobus*, they are highly differentiated; in

others they are represented as simple papillae, a condition which could be considered as more primitive than that in the Enoplidae; in the Enoplidae there is only one genus, *Enchelidium*, that has such a row of papillae.

The second subfamily, the Mononchinae (fig. 1), has a very wide buccal capsule with thick walls. The cephalic setae are transformed into papillae, perhaps because of the method of swallowing prey, since the mouth capsule functions only as a sucker, without any masticating function, and setae would hinder the close adherence of the prey to the lips. Very typical features here are the preanal row of numerous papillae, sometimes transformed into chitinous tubes, and a very strong bursal musculature. The caudal glands and the spinneret are present, with very rare exceptions.

The Tripyloidinae is a group of marine genera resembling in their head characters the Trilobinae, with a typical complex spicular apparatus in all of them. Some doubts as to whether they belong in the Enoplata arise from the shape of the amphids, which are not of the typical pocket form, but are spiral or rounded (fig. 18). In the genus *Halanonchus*, the males of which have the same typical spicular apparatus, the amphids are almost of the pocket type (fig. 19), which makes very probable the interpretation of the form of the others as being of the modified pocket type.

#### SUBFAMILIES AND GENERA OF THE FAMILY DORYLAIMIDAE

##### Subfamily Alaiminae.

Genera: *Alaimus* de Man, 1880; *Litonema* Cobb, 1920.

##### Subfamily Ironinae.

Genera: *Thalassironus* de Man, 1889; *Dolicholaimus* de Man, 1889; *Ironella* Cobb, 1920; *Trissonchulus* Cobb, 1920; *Syringolaimus* de Man, 1889; *Ironus* Bastian, 1865.

##### Subfamily Tylencholaiminae.

Genera: *Diphtherophora* de Man, 1880 (syn. *Chaolaimus* Cobb, 1893); *Pharetrolaimus* de Man, 1922c; *?Ecthyadophora* de Man, 1922c; *Tylencholaimus* de Man, 1876 (syn. *Brachynema* Cobb, 1893, preocc.); *Tylolaimophorus* de Man, 1880, probably synonymous with *Tylencholaimus* (syn. *Archionchus* Cobb, 1913); *Tylencholaimellus* Cobb, 1915; *Xiphinema* Cobb, 1913; *Triplonchium* Cobb, 1920.

##### Subfamily Dorylaiminae.

Genera: *Trichodorus* Cobb, 1913; *Leptonchus* Cobb, 1920 (probable synonym of *Trichodorus*); *Longidorus* Micoletzky, 1922; *Oionchus* Cobb, 1913; *Campydora* Cobb, 1920; *Sectonema* Thorne, 1930; *Nygolaimus* Cobb, 1913; *Chrysonema* Thorne, 1929; *Dorylaimus* Dujardin, 1845 (sg. *Discolaimus* Cobb, 1913; syn. *Antholaimus* Cobb, 1913; sg. *Dory-*

*laimellus* Cobb, 1913; sg. *Axonchium* Cobb, 1920); *Doryllium* Cobb, 1920; *Actinolaimus* Cobb, 1913.

KEY TO SUBFAMILIES OF DORYLAIMIDAE

1. (2) Buccal capsule completely toothless or absent.....**Alaiminae**
2. (1) Teeth or spear present.
3. (4) Three labial teeth present .....**Ironinae**
4. (3) A buccal spear present, simple or triple, rarely separated into three isolated rods.
5. (6) Spear triple, in *Diphtherophora* separated into three rods ..... **Tylencholaiminae**
6. (5) Spear simple, short or elongated ..... **Dorylaiminae**

The most characteristic feature of members of this family is their esophagus (fig. 20); it is narrow and the musculature is very weak or even quite absent anteriorly, but gradually expanded and normally formed posteriorly. Cobb had good reason to speak of a "dorylaimoid" esophagus. The sensory organs of the head are always in the form of papillae, a feature which is probably correlated with their sucking habits, as in *Mononchus*. The caudal glands and pore are absent in the fresh-water genera but present in the marine ones.

The first subfamily has no differentiated mouth structures. Whether this is a primitive feature or should be considered as a terminal stage in their reduction from previous structures is problematical. The second possibility seems to me more probable because of the general appearance of degeneration of the esophagus in some of them. The Alaiminae, with their typical dorylaimoid esophagus, might have arisen from some of the Dorylaiminae that had lost their spear. It is possible that the investigation of the larval stages will throw more light on this matter.

The characteristic feature of the Ironinae is the presence of three teeth immediately behind the lips. These teeth belong to the esophagus. In the larvae they are formed before each molt in a position posterior to the functional ones, moving forward in the course of the molts. The teeth can be everted outside the mouth, functioning as digging organs (Cobb, 1928).

The Tylencholaiminae and Dorylaiminae are characterized by the presence of protrusible spears. In the first subfamily there is a threefold spear (fig. 21) arising from the three esophageal sectors. In Dorylaiminae there is only one spear, subventral and asymmetrical in position. In *Nygolaimus* it is distinctly separate from the esophageal cuticle and simply acute (fig. 22). In *Dorylaimus* it has

the form of a hollow tube cut obliquely (fig. 23), a "goose feather." The genital region of the male resembles that of *Mononchus* in having numerous papillae, tubular in some species, and a strong bursal musculature (fig. 24).

#### SUBFAMILIES AND GENERA OF THE FAMILY MERMITIDAE

##### Subfamily Tetradonematinae.

Genera: *Aproctonema* Keilin, 1917; *Tetradonema* Cobb, 1919.

##### Subfamily Mermitinae.

Genera: *Neomermis* Linstow, 1904 (syn. *Octomermis* Steiner, 1929); *Mermis* Dujardin, 1842; *Allomermis* Steiner, 1924; *Pseudomermis* de Man, 1904; *Tetramermis* Steiner, 1927; *Agamermis* Cobb, Steiner and Christie, 1923; *Hexamermis* Steiner, 1924; *Bathymermis* Daday, 1913; *Eumermis* Daday, 1913; *Paramermis* Linstow, 1901; *Limnomermis* Daday, 1913; *Hydromermis* Corti, 1903; *Gastromermis* Micoletzky, 1925; *Mesomermis* Daday, 1913; *Eomermis* Steiner, 1929; ?*Bolbinium* Cobb, 1920; ?*Colpurella* Cobb, 1920; ?*Isolaimium* Cobb, 1920.

#### KEY TO SUBFAMILIES OF MERMITIDAE

1. (2) Musculature weak; head papillae feebly developed; amphids obliterated; body soft; adult stage parasitic in midges, *Sciara* spp. . . . . **Tetradonematinae**
2. (1) Musculature, head papillae and amphids well developed; adult stage free-living . . . . . **Mermitinae**

The writer agrees with Steiner (1917) who considers the Mermitidae as descendants of the Dorylaimidae. The most suggestive evidences, as expressly pointed out by him, are the presence of a tylencholaimoid spear in the larvae and the resemblance in the structure of the esophagus. Some other hints in the same direction are to be seen in the structure of the adults. On the head (fig. 26) one can clearly see the pocketlike amphid common to these forms and to the other members of the Enoplata, and absent in any other nematode group. The tail of the male (fig. 25) with its numerous pre-anal papillae is also similar in a general way to that of the Dorylaimidae.

There are two different groups in the family. The Tetradonematinae are parasitic until the end of their life; therefore the cuticle of the body becomes soft, and the musculature and cephalic sense organs reduced. Nevertheless they can be compared with the Mermitidae because of their elongated body, general appearance of the longitudinal chords, and especially because of their esophagus, the "tetrads" of which can be compared with the large esophageal cells of the true mermitids.

The Mermitinae were united in a lone genus, *Mermis*, until 1901, when *Paramermis* was proposed by Von Linstow. An elaborate system of water forms was proposed by Daday (1913). Steiner in the beginning of his studies rejected Daday's system, but afterwards he adopted all Daday's genera and proposed some of his own, thus elaborating the existing system. Dr. G. Steiner has in preparation a complete monograph of the family. Some of Cobb's genera are assigned here with some doubt.

### Order CHROMADORATA

A smooth cuticle was given as one of the characteristic features in the Enoplata; a coarsely striated one, nearly always typically thickened behind the head, is characteristic for the Chromadorata. The amphid, as in the following order, is primarily spiral, the few exceptions being mostly easily explainable. The ovaries are curved as in the Enoplata. A very characteristic tail (cf. figs, 47, 48) with a long terminal tube is present in most genera. Esophageal bulbs are very common but are not present in all forms. The wide attachment of the esophagus to the cuticle is lost except in one form (*Dermatolaimus*). The six anterior cephalic setae are very often transformed into papillae, so that only the four of the posterior circle are retained as setae.

#### KEY TO FAMILIES OF CHROMADORATA

1. (4) Mouth capsule irreversible, mouth organs very simple, vestibulum unfolded.
2. (3) Bulb absent; the mouth surrounded by a thickening of cuticle; amphids placed far anteriorly. **Camacolaimidae**
3. (2) Bulb present; the circumoral cuticular thickening absent; amphids placed somewhat more posteriorly ..... **Plectidae**
4. (1) Mouth capsule eversible, with a folded vestibulum, mostly with a dorsal tooth (with secondary complication of buccal organs—teeth, jaws, spines—in one subfamily) ..... **Chromadoridae**

#### GENERA OF THE FAMILY CAMACOLAIMIDAE

Genera: *Camacolaimus* de Man, 1889 (syn. *Acontiolaimus* Filipjev, 1918; syn. *Digitonchus* Cobb, 1920; syn. *Ypsilon* Cobb, 1920); *Neurella* Cobb, 1920; *Halaphanolaimus* Southern, 1914; *Dermatolaimus* Steiner, 1916; *Stephanolaimus* Ditlevsen, 1919; *Alaimella* Cobb, 1920; *Nemella* Cobb, 1920; *Onchium* Cobb, 1920; *Onchulella* Cobb, 1920; *Ionema* Cobb, 1920; *Cricolaimus* Southern, 1914; *Dagda* Southern, 1914; *Aphanolaimus* de Man, 1880; *Paraphanolaimus* Micoletzky, 1923; *Iotalaimus* Cobb, 1920; *Basti-*

*ania* de Man, 1876; *Dintheria* de Man, 1922; *Deontolaimus* de Man, 1880; *Leptolaimus* de Man, 1876; *Conolaimella* Allgén, 1930; *Antomicron* Cobb, 1920; *Cynura* Cobb, 1920; *Polylainium* Cobb, 1920.

This family should be regarded as the most primitive one in the order. The cuticle is somewhat thickened around the mouth opening, and the esophagus is attached to this thickening by a narrow strip (fig. 27), this simple arrangement being realized in all genera without any complications. The amphids are mostly spiral-shaped and in a forward position. Most of the genera are marine, but some are fresh-water, rarely soil, nematodes.

*Dermatolaimus* is one of the simplest members of the family (fig. 28). It is the single member of the order with a more or less extensive attachment of the esophagus to the cuticle; this is possibly due to the reduction of the musculature in the anterior part of the former. There is no differentiation in the mouth structures. The latter are complicated in *Camacolaimus* and in some other genera by the formation of spears that seem to be protrusible. In the fresh-water genus *Aphanolaimus* there is a complete absence of differentiated mouth structures; the amphids are rounded with a bubblelike median swelling (figs. 29, 30). The closely related *Paraphanolaimus* has typical spiral amphids. In young specimens of *Aphanolaimus* the writer has seen on the larval skin a true spiral amphid and a typical swollen one under it. The preanal tubes are peculiar to that genus and are very similar to that of some species of *Plectus*, thus giving a connecting link to the following family.

#### GENERA OF THE FAMILY PLECTIDAE

Genera: *Plectus* Bastian, 1865; *Pynolaimus* Cobb, 1920; *Haliplectus* Cobb, 1913; *Wilsonema* Cobb, 1913; *Anthonema* Cobb, 1906; *Aulolaimoides* Micoletzky, 1917; *Chronogaster* Cobb, 1913; *Paraplectus* Filipjev, 1929; *Rhabdolaimus* de Man, 1880; *Isolaimium* Cobb, 1920; *Tripylum* Cobb, 1920; *Walcherenia* de Man, 1922c; *Pseudobathylaimus* Filipjev, 1918 (syn. *Bathylaimus* Daday, 1905, preocc.; syn. *Dadaya* Micoletzky, 1922); *Paradoxolaimus* Kreis, 1924; *Pseudochromadora* Daday, 1900; *Aplectus* Cobb, 1914; *Diodontolaimus* Southern, 1914.

This family, like the foregoing one, has irreversible mouth organs, but the circumoral thickening of the cuticle is not so pronounced. The difference between the two is in the complication of the inner esophageal tube; this is simple in the Camacolaimidae, but in the Plectidae it forms ordinarily a well-isolated buccal capsule anteriorly, followed by a valvular constriction, and with a dilatation inside the well-developed bulbus, with or without masticatory plates.

The Plectidae are mostly terrestrial or fresh-water nematodes with only a very few marine genera. All genera have prominent spiral amphids of somewhat aberrant type in a posterior position (fig. 27). In the tail there are caudal glands and spinneret; the tail is mostly of the typical chromadoroid form. Many forms are interesting biologically on account of their ability to revive after complete desiccation. The generic analysis of this group seems to be as yet far from being finished.

SUBFAMILIES AND GENERA OF THE FAMILY CHROMADORIDAE

Subfamily Cyatholaiminae.

Genera: *Necticonema* Marion, 1870; *Cyatholaimus* Bastian, 1865; *Praeacanthonchus* Micoletzky, 1924; *Seuratiella* Ditlevsen, 1921 (syn. *Seuratiella* Ditlevsen, 1919, preocc.); *Paracanthonchus* Micoletzky, 1924; *Acanthonchus* Cobb, 1920; *Paracyatholaimus* Micoletzky, 1924; *Longicyatholaimus* Micoletzky, 1924; *Statenia* Allgén, 1930; *Nannonchus* Cobb, 1913; *Achromadora* Cobb, 1913; *Pomponema* Cobb, 1917; *Nannolaimus* Cobb, 1920; *Ethmolaimus* de Man, 1880; *Odontolaimus* de Man, 1880; *Prodesmodora* Micoletzky, 1923; *Anatonchium* Cobb, 1920.

Subfamily Choanolaiminae.

Genera: *Demonema* Cobb, 1893; *Bulbopharyngiella* Allgén, 1929; *Chonolaimus* Ditlevsen, 1919; *Cobbionema* Filipjev, 1922; *Zygonemella* Cobb, 1920; *Zalonema* Cobb, 1920; *Choanolaimus* de Man, 1880; *Anonchus* Cobb, 1913; *Halichoanolaimus* de Man, 1886; *Smallsundia* Allgén, 1929; *Gammanema* Cobb, 1920; *Trogolaimus* Cobb, 1920; *Selachinema* Cobb, 1915; *Pseudonchus* Cobb, 1920; *Synonchium* Cobb, 1920; *Cheironchus* Cobb, 1917 (syn. *Dignathonema* Filipjev, 1918).

Subfamily Richtersiinae.

Genera: *Richtersia* Steiner, 1916; *Richtersiella* Kreis, 1929.

Subfamily Chromadorinae.<sup>2</sup>

Genera: *Euchromadora* de Man, 1886; *Odontocricus* Steiner, 1918; *Dicriconema* Steiner and Hoeppli, 1926; *Rhabdotoderma* Marion, 1870; *Fusonema* Kreis, 1928; *Actinonema* Cobb, 1920; *Rhips* Cobb, 1920; *Neochromadora* Micoletzky, 1924; *Prochromadora* Filipjev, 1922; *Prochromadorella* Micoletzky, 1924; *Spiliphora* Bastian, 1865; *Deltanema* Kreis, 1929; *Chromadorina* Filipjev, 1918; *Chromadorella* Filipjev, 1918; *Spilophorella* Filipjev, 1918; *Chromadorissa* Filipjev, 1917; *Graphonema* Cobb, 1898; *Punctodora* Filipjev, 1929; *Hypodontolaimus* de Man, 1886 (syn. *Lotadorus* Cobb, 1920); *Ptycholaimellus* Cobb, 1920; *Oistolaimus* Ditlevsen, 1921; *Odontonema* Filipjev, 1929; *Endolaimus* Filipjev, 1922; *Chromadorita* Filipjev, 1922.

Subfamily Desmodorinae.

Genera: *Desmodora* de Man, 1889; *Amphispira* Cobb, 1920; *Xenonema* Cobb, 1920; *Bolbonema* Cobb, 1920; *Micromicron* Cobb, 1920; *Eute-*

<sup>2</sup> Kreis (1929) proposed some generic or subgeneric groups, for which he did not propose types, as follows: *Macrochromadora* (for a part of *Prochromadorella*); *Dichromadora*, *Trichromadora* (for parts of *Chromadora*); *Chromarina* (possibly synonymous with *Punctodora*).

*lolaimus* de Man, 1922; *Antomicron* Cobb, 1920; *Mastodex* Steiner, 1921; *Aculeonchus* Kreis, 1928; *Heterodesmodora* Micoletzky, 1924; *Stilbonema* Cobb, 1920; *Laxonema* Cobb, 1920; *Leptonemella* Cobb, 1920; *Croconema* Cobb, 1920; *Metachromadora* Filipjev, 1918 (syn. *Chromadoropsis* Filipjev, 1918); *Xanthodora* Cobb, 1920; *Onyx* Cobb, 1891; *Acanthopharynx* Marion, 1870; *Cinctonema* Cobb, 1920; *Chromaspirina* Filipjev, 1918 (syn. *Mesodoros* Cobb, 1920); *Polysigma* Cobb, 1920; *Laxus* Cobb, 1893; *Parathalassoalaimus* Allgén, 1929; *Catanema* Cobb, 1920; *Spirina* Filipjev, 1918 (syn. *Spira* Bastian, 1865, preocc.).

#### Subfamily Monoposthiinae.

Genera: *Monoposthia* de Man, 1889; *Xenolaimus* Cobb, 1920; *Dasynema* Cobb, 1920; *Nudora* Cobb, 1920; *Rhinema* Cobb, 1920; ?*Ceramonema* Cobb, 1920 (syn. *Steineria* Filipjev, 1922, preocc.).

#### Subfamily Epsilonematinae.

Genera: *Prochaetosoma* Baylis and Daubney, 1926 (syn. *Rhabdogaster* Metchnikov, 1867, preocc.); *Epsilonema* Steiner, 1926; *Metepsilonema* Steiner, 1926.

#### Subfamily Draconematinae.

Genera: *Notochaetosoma* Irwin-Smith, 1918; *Draconema* Cobb, 1913; *Tristicochaeta* Panceri, 1876; *Claparédiella*, nom. nov. (*Chaetosoma* Claparède, 1863, preocc.).

#### KEY TO THE SUBFAMILIES OF CHROMADORIDAE

1. (8) The cuticular rings with inner spots or dots or short external setae.
2. (7) Amphids located at some distance from the head end, well developed, spiral or roundish. Esophagus usually strong and without bulb.
3. (6) Cuticle without setae, except the ordinary setae; the annules not prominent.
4. (5) Mouth capsule typical, preceded by a folded vestibulum and with a dorsal onchium ..... **Cyatholaiminae**
5. (4) Mouth capsule atypical, very differently built up, with peculiar plates, bristles, jaws, etc., serving for retaining prey. Mostly rapacious marine forms. .... **Choanolaiminae**
6. (3) Cuticle with numerous short setae; body very short ..... **Richtersiinae**
7. (2) Amphids located close to the head end, in some genera obsolete, in form of a transverse slit. Cuticular rings sharply differentiated. Esophagus usually with a well-developed bulb. Mostly small forms ..... **Chromadorinae**
8. (1) The cuticular annules smooth.
9. (12) Without adhesive setae.
10. (11) Without any longitudinal, cuticular crests (except lateral wings in some) ..... **Desmodorinae**

11. (10) With sharp, longitudinal, cuticular crests along the body (differentiated in some as rows of spines).  
Monoposthiinae
12. (9) Special adhesive setae present in two groups, some on the head and some in two or more rows in preanal position.
13. (14) Adhesive setae in form of hooks without a hollow interior ..... Epsilonematiniae
14. (13) Adhesive setae in form of hollow tubes ..... Draconematiniae

The chief distinction between the Chromadoridae and the two other families is in the eversible mouth capsule of this family. In connection with this the vestibulum becomes twelvefold and composed of a soft pliable cuticle. The body cuticle around the mouth also presents a soft portion, the reverse of the cuticular thickening in Plectidae. In all typical forms there is a more or less developed dorsal onchium in the mouth capsule (figs. 31, 32). When the latter is everted, the tooth points forward and functions as an incising or picking organ. Sometimes the tooth is strongly developed and presents a kind of spear, compared by some authors with that of the Dorylaiminae, but its general form and position, dorsal instead of subventral as in the latter, do not permit of considering the two as homologous organs. This typical organization is not clear in the Choanolaiminae where the mouth structures are much more complex. In the Desmodorinae several genera show a reduction of the buccal tooth in size, and in some others it may disappear completely. The folds of the soft cuticle around the unarmed mouth of such forms are the only remains of the typical conditions.

The Cyatholaiminae (figs. 31, 32) have typical spiral amphids, generally with many turns, and a cuticle with very plain rings and transverse rows of points inside. The esophagus is broad, uniform for its full length, and without a bulb except in the somewhat aberrant fresh-water genera *Ethmolaimus*, *Prodesmodora*, and *Achro-madora*, but the characteristic inner cavity of true bulbs is lacking in these genera. There are 10 cephalic setae in all genera.

An offshoot of the Cyatholaiminae are the Choanolaiminae, a group of predacious genera, nearly all marine, with the same cuticle, amphids, and tail as in the true Cyatholaiminae (figs. 33-40). Very characteristic are the large cells of the intestine. The mouth structures are specialized in several directions. In *Halichoanolaimus* there are six true lips and a complex mouth capsule with rows of spines in the form of a comb to retain the nematode's prey inside (figs. 33-35). In *Cheironchus* there are two jaws (figs. 36-38),

very similar to those of *Enoplus*. *Synonchium* (figs. 39-40) has three of them, quite as in *Enoplus*, but it is, of course, nothing other than a very evident case of convergence, no other character being like that genus, whereas many characters resemble *Cyatholaimus* or the other Choanolaiminae.

The peculiar genus *Richtersia* (fig. 41) with its setaceous cuticle shows similarities in its esophagus, its cuticle with the points, and its spiral amphids, with the Cyatholaiminae, but it is advisable to place it in a separate subfamily.

A very large number of species, nearly infinite in their diversity, must be included in the subfamily Chromadorinae. They are mostly small and very variable in the structure of the cuticle, mouth capsule and esophagus. All have only four cephalic setae and nearly all a bulb and preanal papillae giving good diagnostic characters for different species. The amphid in some forms is a typical little spiral lying very far forward (fig. 42), in others the abbreviation of the head flattens the spiral which thus becomes the slitlike amphid typical for these other genera (fig. 43).

The forms with the plain ringed cuticle consist of several subfamilies. The Desmodorinae have ordinary plain annules, without any complications, and spiral amphids. The cuticle of the head is generally strong and smooth, except in a few genera like *Metachromadora* and *Onyx* which have a striation independent of that of the body (fig. 44). *Onyx* has also a strongly developed spearlike tooth and 12 well-isolated lips.

The Monoposthiinae are characterized by a peculiar cuticle with longitudinal rows of spines, in some forms fused into continuous wings (fig. 45). Usually there is a round amphid, although several forms have a spiral one. A very peculiar genus is *Ceramonema*, placed here provisionally because of its cuticular rings (fig. 46). The rings are very prominent and the amphid is horseshoe-shaped instead of being spiral. The reduction of the mouth parts and a very feeble onchium and buccal musculature should also be noted.

The last two subfamilies are treated by many authors as a separate family or even an order, so aberrant are they in a general view. Chaetosomatidae is the name most used for them, but *Chaetosoma* being preoccupied, that family name also falls. The most remarkable feature is the general form of the body with the swollen esophageal part generally called the "head" followed by the thin "neck" (figs. 47, 48), but the same form of the body, although not so well developed, is found in several members of the Desmodorinae. The

coarse, plain striation of the cuticle, coarser behind the head, is a common character of all of the latter. The horseshoe-shaped amphid is quite like that of *Ceramonema*. The tail is typically chromadoroid, the spicules similar to those of *Desmodora*. The esophagus of *Draconema* with its two swellings is quite distinctive, but *Notochaetosoma* has an ordinary unibulbar esophagus. The adhesive setae of these forms, concentrated in two regions, on the head and in the preanal region, are peculiar. Steiner (1926) proposes to treat the Epsilonematidae (fig. 47), with the solid adhesive setae, separately from the Draconematidae, with the tubular ones each connected with a gland which is probably a cement gland. Although agreeing with his principal idea, the writer could hardly ascribe to them a rank more elevated than that of a subfamily, the close connection with the Desmodorinae not justifying their separation.

## Order DESMOSCOLECATA

### FAMILIES AND GENERA OF DESMOSCOLECATA

#### Family Desmoscolecidae.

Genera: *Eudesmoscolex* Steiner, 1916; *Desmoscolex* Claparède, 1863; *Quadricoma* Filipjev, 1922; *Tricoma* Cobb, 1893.

#### Family Greeffiellidae.

Genus: *Greeffiella* Cobb, 1922 (syn. *Trichoderma* Greeff, 1869, preocc.).

### KEY TO FAMILIES OF DESMOSCOLECATA

1. (2) Setae not very numerous, body having a naked appearance. Secreted rings usually present .. **Desmoscolecidae**
2. (1) Setae and nerveless spines very numerous, the body having a hairy appearance. Secreted rings absent ..... **Greeffiellidae**

This order includes a group, comparatively small as yet, of marine forms. The most characteristic feature is their cuticle with its very prominent chitinous rings, from 12 to nearly 84 in number. They have the appearance of body segments and have led to a comparison of these forms with the annelids, but they are purely external or even secreted, having no relation to the internal organs (figs. 49, 50). The large amphids are very prominent. The strong setae of the body constitute a development in connection with the peculiar mode of locomotion, the nematodes traveling on them as on stilts, the dorsal side downward. Interesting also is the habit of bearing the eggs fastened on the outside of the female body. Very little is known about the inner organization of these forms, not even whether they have straight or reflexed ovaries. It is a very isolated group with a somewhat uncertain systematic position.

The genus *Greeffella* is composed of distinctive setaceous, mostly exceedingly minute species. The head is similar to that of the Desmoscolecidae, but they must form a quite separate family.

### Order MONHYSTERATA

Under this name are united all the true free-living forms with the straight (not reflexed) ovaries (fig. 51). The amphids are always very distinct and either spiral, horseshoe-shaped, or circular, the last type probably being a reduced spiral. The other morphological characters are very inconstant. The cuticle is mostly striated, but in some forms smooth. The esophagus is usually without a bulb. The vestibulum is well developed, with a chitinous ring on the bottom which serves as a support to the esophagus (fig. 52). This ring is lacking, probably lost, in most of the Linhomoeidae. Very often there is a strengthening of the vestibulum by means of several chitinous rods inside its walls (figs. 52, 53); these rods are sometimes separated from the walls and can spread forward or sideward when the mouth is open. In spite of the meager morphological characteristics of the group, there are very gradual transitions between its different members, so that it seems to be a very natural one.

#### KEY TO FAMILIES OF MONHYSTERATA

1. (2) Spicules short and strong, distinctly bent to form an arch (rarely double), with a strong gubernaculum guiding their ends and armed with two obliquely backward-pointing processes serving to attach muscles ..... **Linhomoeidae**
2. (1) Spicules short or long, with a gubernaculum without backward-pointing processes, or with feebly developed ones ..... **Monhysteridae**

#### SUBFAMILIES AND GENERA OF THE FAMILY MONHYSTERIDAE

##### Subfamily Monhysterinae.

Genera: *Paramonhyстера* Steiner, 1916; *Amphimonhyстера* Allgén, 1929; *?Porocoma* Cobb, 1920; *Penzancia* de Man, 1889; *Theristus* Bastian, 1865 (syn. *Allomonhyстера* Micoletzky, 1923); *Daptonema* Cobb, 1920; *Tubolaimus* Allgén, 1929; *Monhystrium* Cobb, 1920; *Cobbia* de Man, 1907; *Gonionchus* Cobb, 1920; *?Xyala* Cobb, 1920; *?Rhynchonema* Cobb, 1920; *Dactylaimus* Cobb, 1920; *Microlaimus* de Man, 1880; *?Bolbolaimus* Cobb, 1920; *Monhyстера* Bastian, 1865 (syn. *Tachyhodites* Bastian, 1865); *Diplolaimella* Allgén, 1929; *Monohystrella* Cobb, 1918; *Scaptrella* Cobb, 1917; *Austronema* Cobb, 1914; *Leptogastrella* Cobb, 1920; *Omicronema* Cobb, 1920; *Cylindrolaimus* de Man, 1880.

##### Subfamily Sphaerolaiminae.

Genera: *Crassolaimus* Kreis, 1929; *Sphaerolaimus* Bastian, 1865; *Parasphaerolaimus* Ditlevsen, 1919; *?Cytolaimium* Cobb, 1920.

## Subfamily Comesominae.

Genera: *Comesoma* Bastian, 1865; *Laimella* Cobb, 1920; *Dentatonema* Kreis, 1928.

## KEY TO SUBFAMILIES OF MONHYSTERIDAE

1. (4) Amphids roundish.
2. (3) Mouth capsule variable, but never with thick walls  
or free ..... **Monhysterinae**
3. (2) Mouth capsule with thick chitinized walls, partly  
free and adjoining the cuticle of the head... **Sphaerolaiminae**
4. (1) Amphids spiral in several windings ..... **Comesominae**

The Monhysteridae possess as a rule only one ovary, the anterior one (fig. 51); in relation with this the vulva is situated very far backward. The above mentioned chitinous ring of the vestibulum is well developed; in Sphaerolaiminae it is enlarged and forms a spacious mouth capsule (fig. 53). The amphids are round or spiral (Comesominae, fig. 54); the round form seems to be a secondary one, arising from the spiral by the reduction of its inner coils. The spicules are long or short. The gubernaculum is generally well developed, sometimes with a backward-pointing process, but never so strongly developed as in the following family.

## SUBFAMILIES AND GENERA OF THE FAMILY LINHOMOEIDAE

## Subfamily Linhomoeinae.

Genera: ?*Litotes* Cobb, 1920; *Linhomoeus* Bastian, 1865 (sg. *Eulinhomoeus* de Man, 1907; sg. *Paralinhomoeus* de Man, 1907; syn. *Anticyclus* Cobb, 1920); *Rhadinema* Cobb, 1920; *Monhysteriella* Kreis, 1929; *Crystallonema* Cobb, 1920; *Odontobius* Roussel de Vauzème, 1834; *Linhomoella* Cobb, 1920; *Metalaimus* Kreis, 1928; *Metalinhomoeus* de Man, 1907; *Prosphaerolaimus* Filipjev, 1918 (syn. *Anticyathus* Cobb, 1920); *Synonema* Cobb, 1920; *Desmolaimus* de Man, 1880; *Terschellingia* de Man, 1888; *Aegialolaimus* de Man, 1907; *Eleutherolaimus* Filipjev, 1922; *Oligomonhystera* Micoletzky, 1922; *Zanema* Cobb, 1920; *Chloronemella* Allgén, 1929; *Halinema* Cobb, 1920; *Rhinionema* Allgén, 1927; *Solenolaimus* Cobb, 1893 (syn. *Anthraconema* Zur Strassen, 1904); *Siphonolaimus* de Man, 1893 (syn. *Chromagaster* Cobb, 1893); *Southernia* Allgén, 1929; *Cyartonema* Cobb, 1920; *Disconema* Filipjev, 1918.

## Subfamily Axonolaiminae.

Genera: *Margonema* Cobb, 1920; *Fimbriella* Allgén, 1929; *Axonolaimus* de Man, 1889; *Synodontium* Cobb, 1920; *Ascolaimus* Ditlevsen, 1919 (syn. *Bathylaimus* Ditlevsen, 1919, preocc.); *Apodontium* Cobb, 1920; *Odontophora* Bütschli, 1874 (syn. *Conolaimus* Filipjev, 1918; syn. *Trigonolaimus* Ditlevsen, 1919); *Synonema* Cobb, 1920; *Araeolaimus* de Man, 1888; *Conolaimella* Allgén, 1930; *Araeolaimoides* de Man, 1893; *Coinonema* Cobb, 1920; *Diplopeltis* Cobb, 1905 (syn. *Discophora*

Villot, 1876, preocc.; syn. *Dipeltis* Cobb, 1891, preocc.); *Didelta* Cobb, 1920; *Acmaeolaimus* Filipjev, 1918; *Sphaerocephalum* Filipjev, 1918; *Aponchium* Cobb, 1920; ?*Campylaimus* Cobb, 1920; ?*Pseudolella* Cobb, 1920.

Subfamily Sabatieriinae.

Genera: *Sabatieria* Rouville, 1903 (syn. *Parasabatieria* de Man, 1907); *Kreisia* Allgén, 1929; *Alaimonema* Cobb, 1920; *Pepsonema* Cobb, 1920; *Mesonchium* Cobb, 1920; *Dorylaimopsis* Ditlevsen, 1919 (syn. *Xinema* Cobb, 1920); *Filipjeva* Ditlevsen, 1926.

KEY TO SUBFAMILIES OF LINHOMOEIDAE

1. (2, 3) Amphids roundish, i.e., spiral in one winding. . . **Linhomoeinae**
2. (1, 3) Amphids horseshoe-shaped, oval, or roundish in general shape, sometimes on a specially differentiated cuticular plate; in several genera both ends of the horseshoe come so near together as to touch each other (the amphid can then easily be mistaken for a spiral one) . . . . . **Axonolaiminae**
3. (1, 2) Amphids spiral in several windings . . . . . **Sabatieriinae**

This family is different in many respects from the Monhysteridae. The cuticle is never so coarsely striated as in many members of the Monhysteridae; it is always very soft and pliable, mostly with a very fine striation or plain. The head is rounded and the mouth is formed as in the Monhysteridae, but the chitinous ring conspicuous in monhysterids is less prominent or sometimes quite obliterated (fig. 55). The most characteristic features are the spicules, strongly curved and accompanied by a double backward-pointing gubernaculum (fig. 56). In some genera the spicules are double but with the same gubernaculum (figs. 57, 58). The division of the group into subfamilies is based chiefly on the form of the amphids. In the Linhomoeinae the amphid is roundish, and an oblique incision of its border reveals its true nature as a spiral of a little more than one turn. The manner of their origin seems also to be different from that in the Monhysteridae. In the Axonolaiminae the amphids have the form of a bent horseshoe, an elongated oval, as a rule, or are roundish (fig. 59); it is probable that this form is to be considered as more primitive even than the spiral one. In *Diplopeltis* this horseshoe is supported by a special chitinous plate (fig. 60). In the Sabatieriinae the amphid is a regular spiral in several turns, very similar to that of the Comesominae, but the spicules afford a very good distinguishing character for the two groups.

Herewith we come to the end of the typical free Nematoda.

There are to be noted among them some transitions to the parasitic life. The impulse was certainly given by the peculiar semipara-

sitic feeding habits of many of them, sucking on the body of other larger animals. Thus some *Phanoderma*-like nematodes were found by Ditlevsen (1927) partly buried in the body of Polychaeta. The writer (Filipjev, 1927) found a *Phanodermopsis* with the musculature of the esophagus and nearly all other organs degenerated and apparently not functional except for the genitalia, which also gives a hint of their parasitic nature. *Solenolaimus* and *Siphonolaimus* have a very dark reddish intestine which is explained by Zur Strassen as resulting from their feeding on polychaete worms. The writer found in Neva Bay *Dorylaimus stagnalis* with the intestine colored quite as are the Oligochaeta in the same habitats. The entire group of Mermitidae passes most of its larval life and all the time of feeding inside insects or some other invertebrates. *Odontobius ceti*, a linhomoeid, is found, according to Baylis, in the mouth of whales, although rather in saprozoic than in parasitic conditions. The soft cuticle of all Linhomoeidae suggests that they may be liberated from a host after the fashion of the Mermitidae. It would not be surprising if the young or larvae of some parasites, especially those of marine fishes, would be found very like some free-living marine genera, thus giving a key to the phylogeny of certain parasitic groups.

The same idea was recently expressed by Wülker (1929) but probably he was not entirely happy in the material selected for comparison (cf. pp. 195-196).

#### Order ANGUILLULATA

As has been said, most of the saprozoic and terricolous forms of this order are very different from the foregoing groups in their physiology. The cuticle is very impermeable and does not allow the substances of the external medium to penetrate. This explains the strange fact that many forms of this order can live for hours in such fluids as corrosive sublimate, formaldehyde or osmic solutions capable of killing other animals in a few seconds. The ordinary vinegar eel lives even normally in a medium that would be fatal for most other animals. Possibly it is the same lipid cover that was investigated by Zavadovsky in the eggs of *Ascaris* that preserves these forms.

One of the features of this order is the absence in nearly all of them of the setae on the head and the whole body, these being replaced by papillae; generally the latter are not very prominent aside from the genital papillae of the male. The amphids have a very reduced size and their existence was established with certainty only

within the last few years; externally they are represented by inconspicuous slits or even papillae. The caudal glands are absent; they are replaced in some, if not in all, forms by paired subcaudal glands opening on the sides of the tail; they are probably not homologous with the true caudal glands. In the esophagus there is often a bulb with the masticatory apparatus inside; a preneural swelling is present in several forms (fig. 61); in others it is transformed into a true second bulb, generally called the middle bulb, the posterior or cardiac bulb corresponding to that of the other forms (fig. 65); in still others the musculature is much reduced in the posterior bulb, only the glandular cells being preserved, the only muscular bulb being the anterior one (fig. 67). In *Aphelenchus* and some other genera the cells of the posterior glandular part of the esophagus are not separated from the intestine by any constriction, so that it appears as though the neural ring is situated around the anterior part of the intestine. In the male genitalia there is often a prominent bursa (figs. 62, 63). The whole organization bears traces of reduction and definitiveness; the musculature is mostly meromyarian: a sacrifice to the accelerated development characteristic of and indispensable to these saprozoic forms. There seems to be no group in the families previously discussed to which the organization of this order could be closely compared with good reason.

## KEY TO FAMILIES OF ANGUILLULATA

1. (4) Esophagus with or without a bulb. Free-living or parasites of plants and insects.
2. (3) Esophagus with the cardiac bulb ..... **Anguillulidae**
3. (2) Esophagus with the middle bulb present or reduced ..... **Tylenchidae**
4. (1) Esophagus without bulb, of uniform musculature throughout its length. Parasites of vertebrates.
5. (6) Syngonic; digenetic with a free-living rhabditoid generation ..... **Anguillulidae** (partim)
6. (5) Amphigonic; with direct development, rhabditoid larvae never reaching free-living maturity. .... **Strongylidae**

## SUBFAMILIES AND GENERA OF THE FAMILY ANGUILLULIDAE

## Subfamily Anguillulinae.

Genera: *Rhabditis* Dujardin, 1845 (sg. *Rhabditella* Cobb, 1929); *Rhabditoides* Goodey, 1929; *Asymmetricus* Kreis, 1930 (syn. *Pseudorhabditis* Kreis, 1929, preocc.); *Diploscapter* Cobb, 1913; *Hyalaimus* Cobb, 1920.

## Subfamily Steinerneminae.

Genera: *Neoaplectana* Steiner, 1929; *Steinernema* Travassos, 1927c (syn. *Steineria* Travassos, 1927a, preocc.); *Hemicyclophora* de Man, 1921; *Cheilobus* Cobb, 1924; *Anguillula* C. F. Mueller, 1783 (syn. *Turbatrix* Peters, 1927); *Macrolaimus* Maupas, 1900; *Myolaimus* Cobb, 1920; *Himatidiophila* Rahm, 1924.

## Subfamily Cephalobinae.

Genera: *Cephalobus* Bastian, 1865 (syn. *Plectonchus* Fuchs, 1930; sg. *Neocephalobus* Steiner, 1929); *Aloinema* A. Schneider, 1859; *Rhabditophanes* Fuchs, 1930; *Panagrolaimus* Fuchs, 1930; *Poikilolaimus* Fuchs, 1930; *Diastolaimus* Rahm, 1930; *Acrobelloides* Cobb, 1924; *Acrobeles* Linstow, 1877; *Plectonchus* Fuchs, 1930; *Chambersiella* Cobb, 1920; *Panagrolaimus* Fuchs, 1930; *Teratocephalus* de Man, 1876 (syn. ?*Mitrephoros* Linstow, 1877); ? *Choronema* Cobb, 1920.

## Subfamily Cephalobiinae.

Genus: *Cephalobium* Cobb, 1920. The objections of Peters to the use of the old name, well established and universally used since Bastian, are at least questionable. Even if they should prove to be valid, an exception to the rules of priority should be made for this case.

## Subfamily Bunoneminae.

Genera: *Bunonema* Jägerskiöld, 1905; *Craspedonema* Richters, 1908; *Rhodolaimus* Fuchs, 1930.

## Subfamily Rhabdiasinae.

Genera: *Rhabdias* Stiles and Hassall, 1905 (syn. *Rhabdonema* Leuckart, 1879, preocc.); *Strongyloides* Grassi, 1879 (syn. *Pseudorhabditis* Peroncito, 1880; syn. *Stercoralis* Tanaka, 1910).

## KEY TO SUBFAMILIES OF ANGUILLULIDAE

1. (9) Free-living or saprozoic forms; monogenetic. The cardiac bulb developed, with masticatory plates.
2. (5) No special differentiation of the cuticle (aside from lateral wings and the male bursa in some forms).
3. (4) The large part of the wall of the mouth capsule consisting of only one ring of chitinous plates. Anguillulinae
4. (3) The wall of the mouth capsule consisting of several rings of plates with a thinner cuticle between them ..... Cephalobinae
5. (2) Cuticle with peculiar differentiations, such as asymmetrical knobs, wings, or similar things ..... Bunoneminae
6. (9) Parasites of insects.
7. (8) Parasites of the body cavity of insects. Body enlarged with a spacious body cavity ..... Steinerneminae
8. (7) Parasites of the intestine. Body filiform without a large body cavity ..... Cephalobiniinae
9. (6) Digenetic: the free-living generation very like, sometimes indistinguishable from, the Anguillulinae; the parasite generation consisting of syngonic females only, with a uniform muscular esophagus ..... Rhabdiasinae

In this family are united all the forms showing a simple esophagus as in most other nematodes, i.e., without a division into anterior muscular and posterior glandular portion as in the following family. The free-living saprozoic forms have a very characteristic cardiac bulb with masticatory plates inside, which is always the chief, or at least an important, part of the muscular esophageal pump. The pre-

neural esophageal swelling is present in most forms, less conspicuous, and sometimes undeveloped, in Anguillulinae, always very prominent in Cephalobinae. The Anguillulinae are the most simple forms, generally with an elongated, unarmed, well-developed buccal capsule (fig. 61); it is probable that some forms with a narrow buccal capsule acquired this secondarily. It is very probable that most earthworm parasites should be annexed to the Anguillulinae.<sup>3</sup>

Besides the distinction mentioned in the structure of the esophagus, there is another in the structure of the mouth capsule. In the Anguillulinae its walls are for the most part built up of three parallel uninterrupted plates. In the Cephalobinae there are several such plates with a thinner cuticle between them. It is probable that the chief plate of the Anguillulinae is homologous with only one plate of the Cephalobinae; thus the mouth capsules of the two are not homologous to each other.

The peculiar genus *Cephalobium* Cobb, parasites of the intestine of Gryllidae, could be compared, from the tooth of the mouth capsule and the preneural dilatation of the esophagus, with the Diplogasterinae, but the muscular posterior part of the esophagus makes this inclusion impossible. Therefore, the right place should be found among the Anguillulidae. The several peculiarities of structure make impossible the direct inclusion of it in the Cephalobinae, to which it can be compared, and it requires a separate subfamily. I do not find the position among the oxyurids proposed by Artigas (1929) satisfactory. The body cavity parasites, Steinerneminae, are better placed here than in the Oxyurids as proposed by Steiner.

The little group of the Bunoneminae is very closely related to the Anguillulinae. They are all moss-inhabiting species with two rows of remarkable, asymmetrical, cuticular knobs on one side of the body which thus becomes physiologically a ventral side, or other differentiations of the cuticle, often of very strange appearance, and with cephalic outgrowths (fig. 66).

Here should be placed the digenetic Rhabdiasinae, parasites of vertebrates. Baylis and Daubney gave them a place in the same sub-

<sup>3</sup> The nematodes of earthworms are too little known to be included in the list directly. According to Pierantoni, they constitute a separate family, the Drilonemidae Baylis and Daubney, 1926 (syn. Cephalonemidae Pierantoni). The genera reported are: *Drilonema* Pierantoni, 1916; *Mesonema* Pierantoni, 1916; *Opistonema* Pierantoni, 1916; *Pierantonia* Baylis and Daubney, 1926 (syn. *Cephalonema* Pierantoni, 1916, preocc.); *Pharyngonema* Pierantoni, 1923; *Dicelis* Dujardin, 1845 (cf. Wülker, 1926); *Synoeconema* Magalhães, 1905 (syn. *Dionyx* Perrier, 1881, preocc.). There must be added as a doubtful genus *Lumbricicola* Friedländer, 1895 (probably young *Rhabditis* larvae).

family as the free-living genera, because of the close resemblance of their free-living bisexual generation to the free-living forms. Systematically, however, this seems to be untenable, because the syngonic parasitic generation is widely different, although there are traces of the anterior bulb in some species in this stage also (fig. 69). The free-living generation has the typical rhabditoid esophagus as in other free-living forms; the parasitic generation has a simpler esophagus without swellings or bulbs, muscular throughout its length. In some species there are traces of the anterior bulb in this stage also (fig. 69). Some species can entirely omit a free-living generation and thereby lose all hints as to their true systematic position.

#### SUBFAMILIES AND GENERA OF THE FAMILY TYLENCHIDAE

##### Subfamily Diplogasterinae.

Genera: *Aulolaimus* de Man, 1880 (syn. *Myctolaimus* Cobb, 1920; syn. *Cylindrogaster* Goodey, 1927); *Rhabditoides* Rahm, 1930; *Rhabditolaimus* Fuchs, 1915; *Neodiplogaster* Cobb, 1924 (syn. *Tylenchodon* Fuchs, 1930); *Diplogasteroides* de Man, 1912; *Lycolaimus* Rahm, 1930; *Loxolaimus* Rahm, 1930; *Diploscapteroides* Rahm, 1930; *Butlerius* Goodey, 1930; *Demaniella* Steiner, 1914; *Acrostichus* Rahm, 1930; *Diplogaster* M. Schultze, 1859; *Peronilaimus* Rahm, 1930; *Mononchoides* Rahm, 1930; *Odontopharynx* de Man, 1912; *?Ungella* Cobb, 1928; *?Scoleophilus* Baylis and Daubney, 1922.

##### Subfamily Tylopharynginae.

Genus: *Tylopharynx* de Man, 1876.

##### Subfamily Tylenchinae.

Genera: *Aphelenchoides* Fischer, 1894 (syn. *Chitinaphelenchus* Micoletzky, 1922; syn. *Pathoaphelenchus* Cobb, 1927; sg. *Schistonchus* Cobb, 1927; sg. *Parasitaphelenchus* Fuchs, 1930); *Paraphelenchus* Micoletzky, 1922; *Tylenchulus* Cobb, 1913; *Nemonchus* Cobb, 1913; *Heterodera* Mueller, 1883 (syn. *Meloidogyne* Goleđi, 1889; syn. *Heterobolbus* Raillet, 1896; syn. *Caconema* Cobb, 1894); *Aphelenchus* Bastian, 1865 (syn. *Isonchus* Cobb, 1913); *Rotylenchus* n. g. (type *T. robustus* de Man, 1880); *Pratylenchus* n. g. (type *T. pratensis* de Man, 1880); *Chitinotylenchus* Micoletzky, 1922; *Tylenchorhynchus* Cobb, 1913; *Tylenchus* Bastian, 1865; *Psilenchus* de Man, 1922; *Ditylenchus* n. g. (type *A. dipsaci* Kühn, 1859); *Anguillulina* Gervais et van Beneden, 1859; *Neotylenchus* Steiner, 1931; *Iotonchium* Cobb, 1920; *Hexatyulus* Goodey, 1926; *?Macroposthonia* de Man, 1880; *Hemicycliophora* de Man, 1922; *Eutylenchus* Cobb, 1913; *Ecphyadophora* de Man, 1922c; *?Myenchus* Schuberg and Schroeder, 1904.

##### Subfamily Sphaertulariinae.

Genera: *Aphelenchulus* Cobb, 1920; *Tylenchinema* Goodey, 1930; *Allantonema* Leuckart, 1884; *Howardula* Cobb, 1921; *Parasitylenchus* Micoletzky, 1922; *Bradynema* Zur Strassen, 1892; *Atractonema* Leuckart, 1887 (syn. *Asconema* Leuckart, 1886, preocc.); *Sphaerularia* Dufour, 1837.

## Subfamily Hoplolaiminae.

Genera: *Paratylenchus* Micoletzky, 1922; *Atylenchus* Cobb, 1913; *Procriconema* Micoletzky, 1925; *Hoplolaimus* Daday, 1905; *Criconema* Hofmänner and Menzel, 1914; *Iota* Cobb, 1913 (syn. *Ogma* Southern, 1914).

## KEY TO SUBFAMILIES OF TYLENCHIDAE

1. (4) Mouth capsule prominent, wide or narrow, with or without teeth, always spearless.
2. (3) No special knoblike appendages of the mouth capsule. The form of the mouth capsule variable.
  - Diplogasterinae
  3. (2) The narrow mouth capsule has two knoblike hollow appendages ..... Tylopharynginae
  4. (1) Mouth capsule very narrow, spear-bearing, in some genera obsolete together with the spear.
  5. (8) Spear with or without basal knobs, not very large and strong; lost in some genera.
  6. (7) Free-living and plant parasitic. Body of typical nematodelike appearance in free-living forms, swollen in the females of some plant-parasitic species, but without large swollen cells inside.
    - Tylenchinae
    7. (6) Insect parasites. Body of typical appearance in young stages, swollen in mature parasitic females, in some genera losing the nematodelike body form; with swollen cells inside ..... Sphaerulariinae
    8. (5) Spear strong and huge, always cephalated. Cuticle with peculiar annulation ..... Hoplolaiminae

The prominent feature of this family is the structure of the esophagus, muscular in the anterior part with a well-differentiated middle bulb, and glandular in the posterior part. In most of the members of the Tylenchinae, as well as in the Diplogasterinae, the posterior portion of the esophagus is joined together and the boundary between it and the intestine is easily seen. In other Tylenchinae, e.g., *Aphelenchus*, the esophagus is subject to further evolution, the esophageal glands come out of direct connection with the body of the esophagus, the tubular portion becomes narrow, and its connection with the intestine cannot be easily observed; sometimes that part of the esophageal tube becomes short and the beginning of the intestine is quite near to the nerve-ring. In another direction there is a reduction of the anterior muscular part of the esophagus. Throughout there is a reduction in the functions of the esophagus. In most of the species of genera which contain plant-parasitic species, the only remaining muscular part is the middle bulb. A further re-

duction is to be seen in males of many other plant- or animal-parasitic or semiparasitic species in which the adult male does not feed; therefore this reduction is especially confined to males. The peak of the reduction comes in the Sphaerulariinae, parasites of the body cavity of insects. In that group the esophagus and the intestine do not function and the feeding is done through the skin. In some genera the esophagus is still retained, but is always rudimentary and functionless; in others, as in *Allantonema* and *Bradynema*, it is lost completely.

In the simpler genera of the Diplogasterinae there is an unarmed mouth capsule very similar to that of *Rhabditis*; in other genera it is armed with a tooth or teeth (fig. 64) different in different genera. The old genus *Diplogaster*, which, until now, united nearly all the species of the subfamily, must be resolved into several independent genera very distinctly characterized. Some types were given during the last few years by Rahm and Goodey, but the analysis seems to be not yet complete. The earthworm parasite, *Ungella*, apparently should be placed here; the hooklike onchia could be considered as homologous to the teeth of *Diplogaster*, and the preneural esophageal swelling is well developed, but there does not seem to be a sharp division between the two parts of the esophagus as in typical members of the Diplogasterinae.

*Tylopharynx*, the only genus of the next subfamily, was described by de Man as having three separate rods, united in Tylenchinae into a triple spear, a tylenchoid parallel to the tylencholaimoid *Diphtherophora*. The recent description given by Goodey (1929) gives a totally different interpretation of the structure of its mouth parts. There are not three, but only two knobs, hollow inside, chitinous ampullae of the esophageal glands. The position of the genus therefore becomes isolated.

The Tylenchinae are characterized by a triple spear very like that of *Tylencholaimus* but mostly with a strongly marked triple enlarged base (fig. 67).

Here must be located the previously mentioned body cavity parasites of the insects, the Sphaerulariinae. The more primitive forms like *Aphclenchulus*, *Howardula*, and others retain a well-developed spear; *Allantonema* has lost it, together with the esophagus. Although the different genera present some peculiarities in structure and in grade of parasitic reduction, they all have a very peculiar and similar life cycle. The larvae are liberated into the body cavity of the host, they grow inside the host, then leave its body through the anal or genital opening, and after a molt reach maturity outside the

body of the host, in the soil, the burrows of wood-eating beetles, etc. The males reach full maturity, but the females have the ovary undeveloped and without direct connection with the uterus; the vulva is open. Then copulation takes place, the males die, and the fertilized female goes through the skin of a new host into the body, where it grows to the mature parasitic stage.

The Hoplolaiminae should be treated as a separate subfamily (fig. 68). The cuticle has peculiar rings, sometimes subdivided to give a scalelike appearance. There is a peculiar huge spear with proximal knobs. It is a highly specialized terrestrial group.

### Family STRONGYLIDAE

The Strongylidae must be placed as a third family of this order. This large parasitic group was considered as a family long ago; now it is usually recognized as an order. The first-stage larvae are very distinctly similar to some free-living forms of the genus *Rhabditis*. The two dilatations of the esophagus, the posterior one with a masticatory apparatus, and the cylindroid mouth capsule are very similar to *Rhabditis*. The free life of strongylid larvae, and their molts with the ensheathed migratory third stage, correspond strictly to that described by Maupas in *Rhabditis*. Even in the adult stage, the characteristic bursa in typical cases, with its 20 rays, is comparable to that of some species of *Rhabditis* (cf. figs. 62, 63, and 70).

A systematic conclusion from these very real similarities could only be similar to that arrived at in analogous circumstances by the carcinologists in placing the aberrant Rhizocephala in the order Cirripedia, and, similarly, the parasitic copepods with the free-living forms in the Copepoda.

### Order OXYURATA

The Oxyurata with their tripartite esophagus and masticatory cardiac bulb could be compared with the free-living Anguillulata. It is even difficult to find clear diagnostic characters to separate these two orders. Steiner (1923) described a parasite from a sawfly larva and because of its general similarity he referred it to the oxyurid genus *Aplectiana* with all its other species intestinal parasites of Amphibia and Reptilia. (Now it is referred to a separate genus, *Steinernema*.) The writer found a very closely related species, probably congeneric with Steiner's, in a cutworm, fortunately accompanied by their larvae which proved to be typically rhabditoid; the influence of parasitism can also give very similar results in both orders, which is

an indirect evidence of their affinity. The chief difference seems to be their biology: the Oxyurata are parasites from the first stage to the last—no free-living larvae seem to exist among them; there is no clear metamorphosis in this group. A larva just hatched is always readily recognized as a young oxyurid, generally very similar to the adult stage except for its size and genital organs. It could be said that the Oxyurata are modified by parasitism from the beginning to the end of their lives, contrary to which the parasitic Anguillulata always conserve some free-living stage and their larvae are similar to the free-living forms of the order.

Another distinction could be found in the physiology of both orders. As was said, the general character of the free-living Anguillulata is their impermeable thick cuticle; it is fully conserved and even strengthened in the not numerous intestinal parasites belonging to the order, such as *Cephalobium*. The musculature is strong and the movement quick and alert, the body cavity is generally filled up by different cells and conserved only as fine clefts between them. Quite otherwise is the general constitution of the Oxyurata. The cuticle is fine, impermeable enough for organic bodies, but not for water, which easily passes through it. The body cavity is well developed and filled with a fluid content. The body is swollen and its walls are stretched from the inside by the turgor thus arising; it can be easily proved by damaging the body walls, the body cavity fluid, together with the inner organs, being then ejected with force. The semipermeability of the cuticle can easily be demonstrated by placing these nematodes in solutions of different osmotic strengths. The solutions with higher osmotic pressure will produce a general squeezing of the body and finally even the separation of the cuticle and hypodermis, and the further squeezing of the body inside the cuticle, the general picture being then very like that of plasmolyzed plant cells. The solutions with higher osmotic pressure will produce a general swelling and tension of the body and sometimes even its bursting. The musculature of most of the Oxyurata is meromyarian and platymyarian, therefore very weak, and the movements are slow and clumsy.

This order seems to be very natural. The writer does not understand very well why it was separated in several independent families by Baylis and Daubney (1926), but probably it was on purely taxonomic grounds; the elimination of several genera into the Rhabdiasata (i.e., Anguillulata in our classification) by Travassos (1930) seems also to be inadequate. The more common way of uniting them into one order, as was originally proposed by Railliet and

Henry (1915), then followed by Skrjabin (1923), Yorke and Maplestone (1926), and others, seems to be much happier.

The vertebrate parasites in general have been soundly placed in the system of classification, but the same hardly could be said about the parasites of arthropods monographed in recent years in Brazil (Travassos, 1929; Artigas, 1930). In these papers the Brazilian authors tried to build up a system quite independent from the existing system of parasites of vertebrates. But the parasites of invertebrates cannot be considered as different from other Oxyurata as a whole. The one-spiculed genera of oxyurids of arthropods are so similar to the one-spiculed genera of oxyurids of vertebrates that they can not be separated and must be referred to the same systematic group. Travassos (1930) himself in a later paper came to the same general conclusions in trying to build a system embracing both biological groups. Several hints from his work are used in the sketch of the system below.

In the review below there is given the systematic distribution of oxyuroid genera parasitic in invertebrates only. For the parasites of vertebrates Yorke and Maplestone (1926) and Baylis and Daubney (1926) should be consulted.

#### KEY TO FAMILIES OF OXYURATA PARASITIC IN INVERTEBRATES

1. (6) Spicules two (obsolete in some Kathlaniidae).
2. (3) Male without a preanal sucker ..... **Atractidae**
3. (2) Male with preanal sucker or pseudosucker developed as a differentiation of precloacal musculature.
4. (5) Polymyarian. Lips poorly developed ..... **Heterakidae**
5. (4) Meromyarian. Lips strongly developed, well separated ..... **Kathlaniidae**
6. (1) Spicule single ..... **Oxyuridae**

#### SUBFAMILIES AND GENERA OF THE FAMILY ATRACTIDAE

Subfamily Cosmocercinae (including Oxysomatiinae).

Subfamily Atractinae.

Subfamily Carnoyinae, subfam. nov.

Genera: *Rondonema* Artigas, 1926; *Carnoya* Gilson, 1898; *Pararhabditis* Baylis and Daubney, 1926 (= *Pseudorhabditis* Szüts, 1912).

Subfamily Rhigoneminae Artigas.

Genera: *Dudekemia* Artigas, 1930; *Rhigonema* Cobb, 1898; *Ichthyocephalus* Artigas, 1926.

#### KEY TO SUBFAMILIES OF ATRACTIDAE

1. (6) Esophagus with its parts of very different diameters.

2. (5) Esophagus long, with the middle part of uniform or nearly uniform diameter.
3. (4) Female genitalia double ..... **Cosmocercinae**
4. (3) Female genitalia single, extending anteriorly ..... **Atractinae**
5. (2) Esophagus short, with the middle part forming an elongated ovaloid bulbous. Females with spines .. **Carnoyinae**
6. (1) Esophagus with its three parts of nearly uniform diameter, thick and short ..... **Rhigoneminae**

The subfamily *Cosmocercinae* (= *Cosmocercidae* Travassos, 1930) is here understood in the same way as was the corresponding family by Travassos, separating it thus from the one-spiculed forms. The *Atractinae* (= *Atractidae* Travassos) are separated from the *Cosmocercinae* because of the single female genitalia, but the males are so similar in both groups, and the separating character so secondary in most other families of Nematoda, that I have no doubt that both groups should be classified more closely than is done by most authors. Two groups from invertebrates must be added to them, (1) the *Carnoyinae*, highly specialized forms from Myriapoda and Oligochaeta, with a peculiar development of the esophagus and with sexual dimorphism, the females with spines in the anterior part of the body, and (2) the *Rhigoneminae* which have a short thick esophagus with all its three parts of nearly the same diameter.

#### SUBFAMILIES AND GENERA OF THE FAMILY HETERAKIDAE

Subfamily *Subulurinae*.

Subfamily *Heterakinae*.

#### KEY TO SUBFAMILIES OF HETERAKIDAE

1. (2) In males the preloacal sucker or pseudosucker without a chitinous rim ..... **Subulurinae**
2. (1) In males the preloacal sucker well defined with a chitinous rim ..... **Heterakinae**

The outlines of the family and both subfamilies are accepted as by Baylis and Daubney (1926). Both subfamilies are united by some transitions. The suckers of the second subfamily are undoubtedly a development of the pseudosuckers of the first one. Travassos (1930) proposed to separate the *Spinicaudinae*, a proposal which undoubtedly has some grounds. The genera included here are poly-myarian and have feebly developed lips, a character which separates them from the following family.

#### SUBFAMILIES AND GENERA OF THE FAMILY KATHLANIIDAE

Subfamily *Kathlaniinae*.

Genera: *Oniscicola* Schwenck, 1927; *Cruznama* Artigas, 1926.

Subfamily Cissophyllinae.

Subfamily Cruzeinae.

Subfamily Ransomnemiinae Travassos.

Genera: *Ransomnema* Artigas, 1926; *Heth* Cobb, 1898 (syn. *Streptogaster* Cobb, 1898); *Clementeia* Artigas, 1930.

Subfamily Lepidoneminae Travassos.

Genera: *Lepidonema* Cobb, 1898; *Hystrignathus* Leidy, 1850 (syn. *Xyo* Cobb, 1898); *Pulchrocephala* Travassos, 1925.

#### KEY TO SUBFAMILIES OF KATHLANIIDAE

1. (8) Spicules present.
2. (7) Esophagus long, typically developed.
3. (6) Intestinal caecum absent.
4. (5) Lips without teeth and lamellae ..... **Kathlaniinae**
5. (4) Lips armed with powerful teeth and lamellae ... **Cissophyllinae**
6. (3) Intestinal caecum present ..... **Cruzeinae**
7. (2) Esophagus with swollen medial part ..... **Ransomnemiinae**
8. (1) Spicules absent, some chitinous parts (?gubernaculum) present but not evaginable; copulation by apposition of genital openings ..... **Lepidoneminae**

The Kathlaniidae include all genera with a sucker in the male and with meromyarian musculature, our definition thus coming very near to that of Baylis and Daubney (1926), and including the Cruzeidae separated by Travassos. The chief ground for separation of the last is the presence of the intestinal caecum in *Cruzia*, but it is safer to take the taxonomic characters from the more constant mouth parts and male genitalia than from the parts of intestine which are variable in very closely related groups. The Cissophyllinae as separated by Yorke and Maplestone (1926) are based on their specialized mouth parts. Three groups from the invertebrates can be included here. *Oniscicola* and *Cruzinema*, with a typical development of the esophagus, can be included directly in the Kathlaniinae. The Ransomnemiinae should be separated because of the peculiar development of the esophagus which is swollen in its medial part. The Lepidoneminae which have lost the spicules are very peculiar, but also can be classed here because of the preanal sucker which is developed or at least rudimentary.

#### SUBFAMILIES AND GENERA OF THE FAMILY OXYURIDAE

Subfamily Oxyurinae.

Genera: *Thelastoma* Leidy, 1854 (sg. *Thelastomellum* Cobb, 1929; syn. *Bulhõesia* Schwenck, 1926); *Leidyrama* Schwenck, 1929; *Severianoia* Schwenck, 1926; *Cephalobellus* Cobb, 1920 (syn. *Blatticola* Schwenck, 1926); *Binema* Travassos, 1925; *Protrellus* Cobb, 1920; *Pseudonymus* Diesing, 1857 (syn. *Ptychocephalus* Diesing, 1861; syn. *Helicothrix*

Galeb, 1878); *Aorurus* Leidy, 1854 (syn. *Streptostoma* Leidy, 1854; syn. *Blattophila* Cobb, 1920).

Subfamily Syphaciinae.

Genus: *Angra* Travassos, 1929.

KEY TO SUBFAMILIES OF THE OXYURIDAE

1. (2) Males without a gubernaculum ..... **Oxyurinae**
2. (1) Males with a gubernaculum ..... **Syphaciinae**

Here are united most of the known one-spiculed forms of the Oxyurata, with numerous genera and species in both Vertebrata and Invertebrata. The idea of separating them from other Oxyurata belongs to Travassos (1930). The further division as proposed by Walton (1929) and Travassos (1930) would be difficult to follow without a more complete consideration of the subject. The old division proposed by RAILLET and HENRY (1916) and followed by YORKE and MAPLESTONE (1916) should therefore be accepted at this time.

Orders ASCARIDATA, SPIRURATA, FILARIATA,  
DIOCTOPHYMATA and TRICHURATA

Parasitism always transforms an animal. The free-living stages of the Strongylidae saved for us the evidence of their true nature; it is probable that because of the semisaprozoic life of the Oxyurata they conserved traces of typical resemblance to the Anguillulata. But the other parasitic orders do not possess free-living stages and are more specialized in their parasitic life.<sup>4</sup> Thus little could be said about their relationships.

The comparatively small and highly specialized groups of Diocetophymata and Trichurata could be considered as very isolated and natural. The relations between the other orders seem to be not as yet worked out. The Spirurata will probably be subject to most modifications. But the wisest course for the moment would be to keep all the three separate as Yorke and Maplestone have done.

Wülker (1929) has recently suggested a direct relation between the Ascaridata from marine fishes and some free-living groups, thus assuming an evolution of this order independent from other parasitic orders. But it is highly probable that the Ascaridata have had a different mode of evolution, probably a much longer one and one bound with some other parasitic groups.

CONCLUSION

In the writer's opinion the classification of today, especially that of the lower groups, is in reality the same as it was in the time of

<sup>4</sup> An exception are the free-living larvae of *Camallanus*, but these have never been studied in detail.

Linné, i.e., the registration of similarities and dissimilarities, only a little and superficially colored by the theory of evolution. The similarities alone have a value for the building of a natural system. The absence of some distinct feature or the presence of one, should not be a cause of the exclusion of some form from a group when other characters are similar. No character is important by itself, but only in its more or less wide occurrence among similar forms. For this reason I do not hesitate to range a spiral-amphid *Tripyloides* among other pocket-amphid Enoplata, and because of these principles it seems to me wise to class the Strongylidae within the Anguillulata.

Each systematic arrangement of a group, with very rare exceptions, passes, it seems, through three stages. The first is that of chaos, the second is the putting of the closely similar side by side, and the third is a definite classification upon the basis of real resemblances. Stiles and Hassall (1926) are, of course, right in saying that a natural system of the Nematoda is in the stage of making; it seems that we are gradually passing through the second stage, and are rather in it than in the first one.

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## EXPLANATION OF PLATES

## Order ENOPLATA

- PL. I, FIG. 1. *Mononchus trichurus* Cobb, the female showing some typical characters of the order. Note the smooth cuticle, the plain bulbless esophagus, and the female genitalia with the reflected ovaries. *a*, top of ovary; *b*, base of ovary; *c*, oviduct; *d*, *e*, top part of uterus transformed into a receptaculum seminis with sperm inside; *f*, egg in the main part of the uterus; *g*, genital opening; in typical cases there are two ovaries. After Cobb, 1917.
- FIG. 2. *Leptosomatium bacillatum* (Eberth) showing the typical head structure of the Enoplidae. Note the wide surface by which the esophagus attaches to the cuticle anteriorly, the duplication of the cuticle with the "circumoral pocket" between the two layers, and the pocketlike amphid. After Filipjev, 1918.
- FIG. 3. *Thoracostoma coecum* Saveljev, showing an example of a highly developed cephalic capsule. After Filipjev, 1927.
- FIG. 4. *Enoplus communis* Bastian, showing the head viewed from the side and a little ventrally. Note the three typical jaws, surrounded by the ring of the cephalic capsule, the amphids, and the cephalic organ anterior to them, the cephalic line. After de Man, 1886.
- FIG. 5. *Enoplus communis* Bastian, showing the head viewed *en face*. Note the typical disposition of the 10 cephalic setae and 6 labial papillae; note also the symmetrical disposition of the 3 jaws. After de Man, 1886.
- FIG. 6. *Enoploides amphioxi* Filipjev, a head showing the jaws split behind, the lips highly developed, and the setiform labial papillae. After Filipjev, 1918.
- FIG. 7. *Enoplolaimus lucifer* Filipjev, showing the head with the jaws transformed in a framework of the mouth capsule, and an onchium between the two posterior prolongations. Note the cephalic organ pointing externally. After Filipjev, 1927.
- FIG. 8. *Oxystomina elongata* (Bütschli), showing the elongated head, the four sublateral setae shifted backwards to form a second circle, and the amphid very far behind and with an enlarged orifice. After de Man, 1907.
- FIG. 9. *Halalaimus diplocephalus* Filipjev, showing the amphids elongated to form a longitudinal slit. After Filipjev, 1927.
- FIG. 10. *Phanoderma conicaudatum* (Steiner). Note the four-lobed cephalic capsule, the eye with a well-defined lens, and the far-advanced cervical pore. After Filipjev, 1927.
- FIG. 11. *Oncholaimus conicauda* Filipjev, showing a typical mouth capsule with three onchi and the "circumoral pocket". After Filipjev, 1929.
- FIG. 12. *Rhabdodemania major* (Southern). Note that the mouth capsule with three onchi is comparable to that of the On-

cholaiminae, but the lips are more complicated. After Southern, 1913.

- FIG. 13. *Eurystomina assimilis* (de Man), showing the mouth capsule without lips; the large onchium can be protruded outside the capsule. After Filipjev, 1918.
- FIG. 14. *Eurystomina assimilis* (de Man), showing the male tail. Note the strongly curved, thin spicules and the two preanal organs. After Filipjev, 1918.
- PL. 2, FIG. 15. *Symplocostoma ponticum* Filipjev, showing a mouth capsule very similar to that of *Eurystomina*; in addition to the chief onchium or spear, there is a little guiding onchium on its side; a part of the bottom of the mouth capsule has become isolated, forming the cuticular "lens." After Filipjev, 1918.
- FIG. 16. *Enchelidium longicolle* Filipjev, supposed to be the male of a symplocostomoid female; the mouth capsule is reduced except for the "lenses". After Filipjev, 1918.
- FIG. 17. *Trilobus brevisetosus* (W. Schneider), showing the large mouth capsule followed by a back chamber with two little denticles inside; there is no "circumoral pocket". After Filipjev, 1929.
- FIG. 18. *Tripylloides marinus* (Bütschli). Note that the general shape of the mouth capsule recalls that of *Trilobus*, but the mouth can be opened wide as in *Tripyla*; the amphids are spiral. After Filipjev, 1929.
- FIG. 19. *Halanonchus macrurus* Cobb. Note that this is similar to other Tripylloidea as regards its spicular apparatus, but it has a pocketlike amphid. After Cobb, 1920.
- FIG. 20. *Dorylaimus regius* de Man, showing its typical "dorylaimoid" esophagus, narrow anteriorly and gradually widening posteriorly. After Steiner, 1927.
- FIG. 21. *Tylencholaimus mirabilis* (Bütschli), showing the head with the three-lobed spear. After de Man, 1884.
- FIG. 22. *Hygolaimus menzeli* Micoletzky, with the spear distinctly on one side of the mouth capsule. After Micoletzky, 1925.
- FIG. 23. *Dorylaimus stagnalis* Dujardin, with the typical spear guided by the two vestibular rings. After Filipjev, 1929.
- FIG. 24. *Dorylaimus regius* de Man, showing the tail of the male. Note the wide spicules with a longitudinal chitinous ridge in the middle, the preanal median row of papillae, and the strong bursal musculature. After Steiner, 1927.
- FIG. 25. *Mermis nigrescens* Dujardin, showing the tail of the male. Note that the strong bursal musculature and the preanal row of papillae recall the Dorylaimidae. After Hagmeier, 1913.
- FIG. 26. *Mermis tenuis* Hagmeier, showing the head with the huge pocketlike amphids. After Hagmeier, 1912.

## Order CHROMADORATA

- FIG. 27. *Paraplectus pedunculatus* (Hofmänner). Note the striated cuticle, the long and narrow mouth capsule, the strongly marked amphid, and the thickening of the cuticle anteriorly. After Filipjev, 1929.
- FIG. 28. *Dermatolaimus steineri* Filipjev. Note the anterior thickening of the cuticle, more or less wide attachment of the esophagus to it, and the amphid, which is round with a posterior prolongation. After Filipjev, 1922.
- FIG. 29. *Aphanolaimus attentus* de Man. Note the peculiar amphids. After de Man, 1884.
- FIG. 30. *Aphanolaimus attentus* de Man, side view. After de Man, 1884.
- FIG. 31. *Cyatholaimus demani* Filipjev, showing the *en face* view of the head. Note the 12-fold vestibulum and the dorsal onchium in the mouth capsule. After de Man, 1889b.
- FIG. 32. *Cyatholaimus demani* Filipjev, side view. Note the 6 labial papillae, 10 cephalic setae, the folds of the vestibulum, the onchium, the spiral amphid, the points of the cuticle, and the eye, and compare with the preceding figure. After de Man, 1889b.
- PL. 3, FIG. 33. *Halichoanolaimus filicauda* Filipjev, lateral view of the head. Note the two chambers of the mouth capsule, and the amphids and cuticle like those of *Cyatholaimus*. After Filipjev, 1918.
- FIG. 34. *Halichoanolaimus filicauda* Filipjev, view *en face*. Note the true lips with the labial papillae. After Filipjev, 1918.
- FIG. 35. *Halichoanolaimus filicauda* Filipjev, showing at a deeper focus the 12 rods of the anterior part of the mouth capsule, the 3 spines and the comblike apparatus marking the boundary of its two parts. After Filipjev, 1918.
- FIG. 36. *Cheironchus bulbosus* (Filipjev). Note the two high lips, with huge labial papillae, the spiral amphids, and the two powerful jaws. After Filipjev, 1918.
- FIG. 37. *Cheironchus bulbosus* (Filipjev), ventral view. After Filipjev, 1918.
- FIG. 38. *Cheironchus bulbosus* (Filipjev), view *en face*. Note the two jaws, the dorsal rudimentary lip, and the disposition of the papillae and cephalic setae. After Filipjev, 1918.
- FIG. 39. *Synonchium obtusum* Cobb, a nematode with three jaws like *Enoplus*. The cuticle and amphids are like those in the Cyatholaiminae and the other genera of the Choanolaiminae. After Cobb, 1920.
- FIG. 40. *Synonchium obtusum* Cobb, showing the mouth open and the lips protruded. After Cobb, 1920.
- PL. 4, FIG. 41. *Richtersia collaria* Steiner. Note the characteristic short and thick body form, and the longitudinal striation produced by rows of minute cuticular spines; the powerful esophagus, spiral amphids and pointed cuticle leads to a comparison with the Cyatholaiminae. After Steiner, 1916.

- FIG. 42. *Odontonema guido-schneideri* Filipjev, a representative of the Chromadorinae, with a little spiral amphid placed far forward; the large tooth of the mouth capsule is characteristic for a few genera. Note the anterior cephalic circle represented by papillae. After Filipjev, 1929.
- FIG. 43. *Prochromadorella viridis* (Linstow), with the amphid spiral flattened to form a transverse slit; this genus and some other genera of the Chromadorinae have three teeth in the buccal capsule. After Filipjev, 1929.
- FIG. 44. *Metachromadora macroutera* Filipjev; the plain strong rings of the cuticle are characteristic of all the Desmodorinae, but the peculiar striation of the head only for a few of them. After Filipjev, 1918.
- FIG. 45. *Monoposthia mielcki* Steiner; the plain rings of the Monoposthiinae are interrupted by rows of longitudinal crests or spines; a desmodoroid parallel to *Richtersia*; note the roundish amphid. After Steiner, 1916.
- FIG. 46. *Ceramonema annulata* (Filipjev); the four longitudinal crests of the cuticle are like those of the Monoposthiinae; the much-reduced mouth structure and the horseshoe-shaped amphid resemble those of the Draconematinae; the huge rings of the cuticle are very distinctive. After Filipjev, 1922.
- FIG. 47. *Epsilonema* (?) *cygnoides* (Metchnikov). Note the peculiar form of the body with its "neck" and the adhesive non-tubular setae in the middle part of the body. After Steiner, 1916.
- PL. 5, FIG. 48. *Draconema cephalatum* Cobb, a marine nematode of world-wide distribution. There is not only a "neck," but also a "head"; the adhesive setae are tubular (one under a higher magnification is shown right below), and are disposed in two groups, on the head and in several preanal rows (four in that genus). After Cobb, 1913.

#### Order DESMOSCOLECTATA

- FIG. 49. *Desmoscolex minutus* Claparède. The huge secreted cuticular rings are very prominent; the disposition of the ambulatory setae is peculiar to each species. After Filipjev, 1922.
- FIG. 50. *Quadricoma reinhardi* Filipjev, a species with 43 secreted rings. After Filipjev, 1922.

#### Order MONHYSTERATA

- FIG. 51. *Theristus sentiens* (Cobb), a general view of the female to show the female genitalia with the straight ovaries characteristic of the order. *a*, the ovarial part of the gonad; *b*, the oviduct part (*a* and *b* are fused together); *c*, uterus with an egg inside; *d*, vaginal opening; *e*, the rudiment of the posterior gonad. After Cobb, 1914.

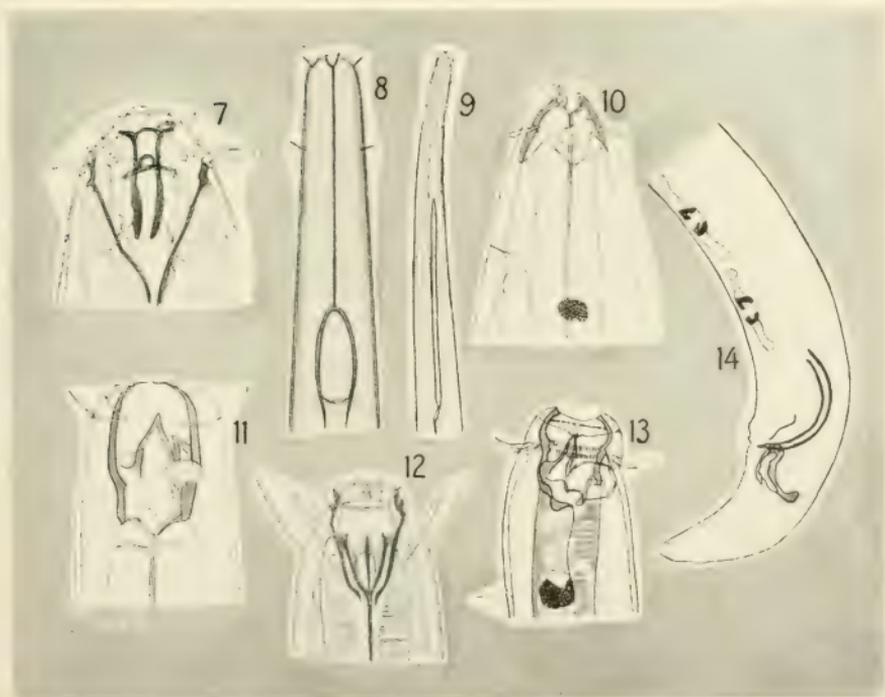
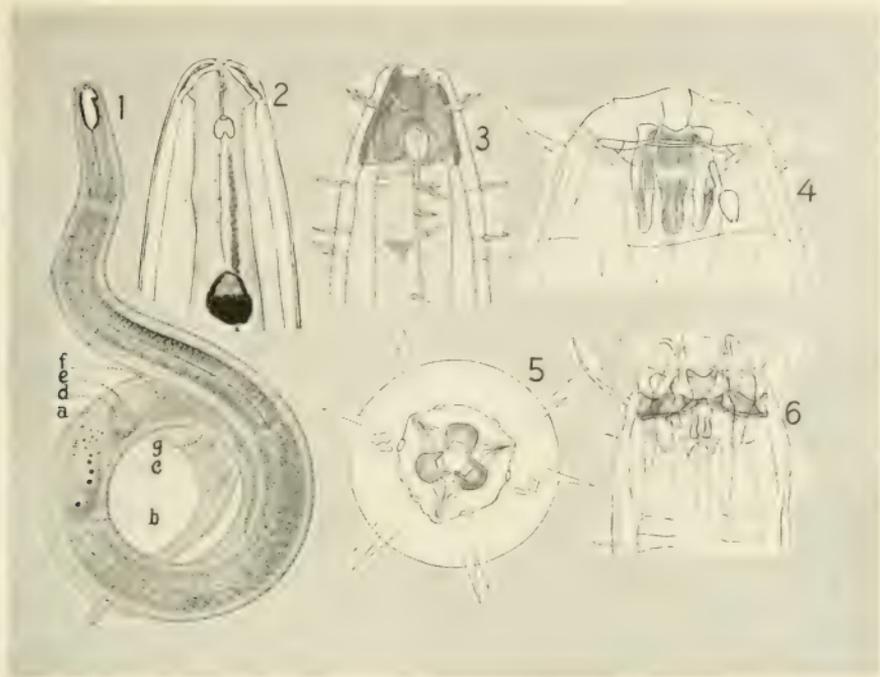
- PL. 6, FIG. 52. *Theristus setosus* (Bütschli). One can see the large vestibulum, the chitinous ring supporting the esophagus, and the spiral amphids. Note the supporting rods of the vestibulum. After Filipjev, 1929.
- FIG. 53. *Sphaerolaimus hirsutus* Bastian. The chitinous ring of the mouth capsule becomes very large, giving place to a spacious mouth capsule inside; the rods in the walls of the vestibulum are better developed. After de Man, 1907.
- FIG. 54. *Comesoma stenocephalum* Filipjev. Note the huge spiral amphid, the six labial and six cephalic papillae, and the four cephalic setae, followed by subcephalic ones. After Filipjev, 1918.
- FIG. 55. *Linhomoeus lepturus* de Man. Note the thin cuticle, the feebly developed chitinous ring of the mouth capsule, and the round, thick-walled amphid, or what might be called a spiral one in one turn. After de Man, 1907.
- FIG. 56. *Linhomoeus lepturus* de Man, showing the spicules strongly curved and with a double backward-pointing gubernaculum; this is characteristic of all the members of the family Linhomoeidae. After de Man, 1907.
- FIG. 57. *Dorylaimopsis perfectus* (Cobb), showing the double spicules; the gubernaculum is typical. After Cobb, 1920.
- FIG. 58. *Dorylaimopsis perfectus* (Cobb), showing a side view. After Cobb, 1920.
- FIG. 59. *Axonolaimus setosus* Filipjev, showing the head. The vestibulum and the mouth capsule are strongly developed; both branches of the horseshoe-shaped amphid are closely pressed together. After Filipjev, 1918.
- FIG. 60. *Diplopeltis cirrhatus* (Eberth), showing the horseshoe-shaped amphid surrounded by a strongly chitinized plate. After Filipjev, 1918.

#### Order ANGUILLULATA

- PL. 7, FIG. 61. *Rhabditis elegans* Maupas. Note the elongate mouth capsule, the preneural esophageal swelling, and the true cardiac bulb with the masticatory apparatus. After Maupas, 1900.
- FIG. 62. *Rhabditis elegans* Maupas, showing the spicules and bursa in ventral view. After Maupas, 1900.
- FIG. 63. *Rhabditis elegans* Maupas, a side view. After Maupas, 1900.
- FIG. 64. *Diplogaster fictor* Bastian, showing a dorsal view of the head. Note the folds of the lips, the teeth of the mouth capsule, and the amphids. After Cobb, 1914.
- FIG. 65. *Diplogaster fictor* Bastian, showing the esophagus separated into two parts with the preneural and cardiac bulbs. After Cobb, 1914.
- FIG. 66. *Bunonema ditlevseni* Micoletzky. The mouth capsule and the esophagus are distinctly rhabditoid, the asymmetrical cuticular knobs and head appendages are very distinctive. After Micoletzky, 1925.

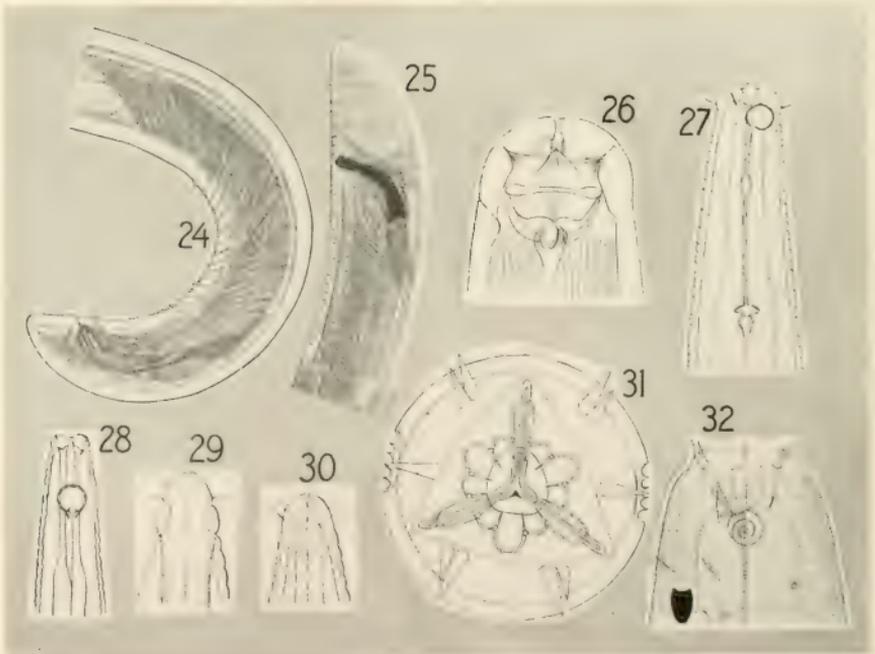
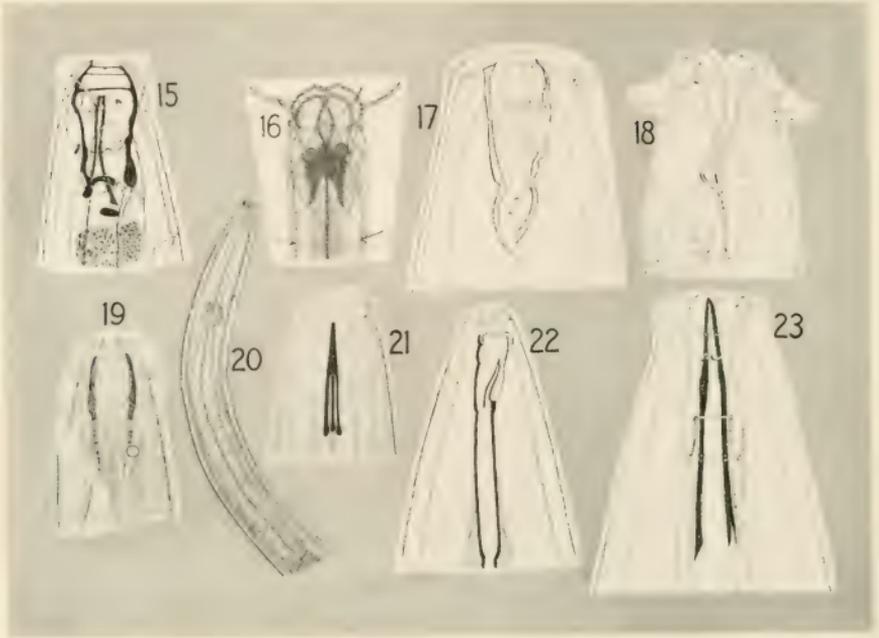
- PL. 8, FIG. 67. *Paratylenchus nanus* Cobb, a representative of a highly specialized genus of the Tylenchidae; the triple spear is very large, the preneural bulb is the only one that retains its musculature, the cardiac bulb being composed of gland cells only. After Cobb, 1925.
- FIG. 68. *Iota octangulare* Cobb, another highly specialized form of the same family. Note the huge spear and the scalelike differentiation of the cuticle. After Cobb, 1914.
- FIG. 69. *Rhabdias sphaerocephala* Goodey. Note the remnants of the preneural bulb, characteristic of the Anguillulata; in other species of the genus there are no more hints of it in the syngonic generation, but it is always very clear in the bisexual one. After Goodey, 1924.
- FIG. 70. *Cylichnostomum auriculatum* Looss, showing the bursa of the male, characteristic of the males of all the members of the family Strongyloidea to which it belongs; it could be explained as a specialization of the bursa of some form of *Rhabditis* (compare figs. 62 and 63). After Looss, 1901.



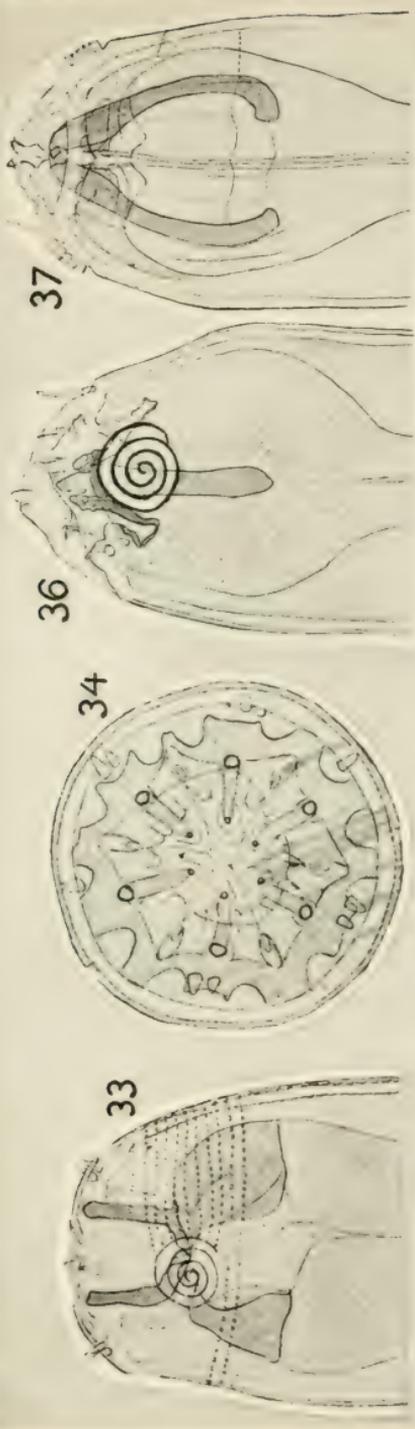


**FREE-LIVING NEMATODES**

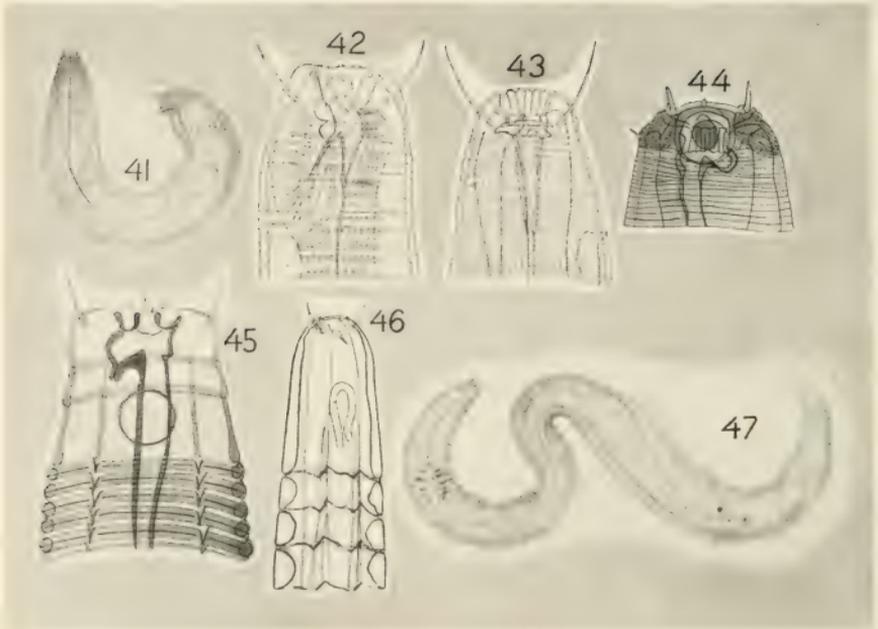
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**FREE-LIVING NEMATODES**  
(For explanation, see pages 59, 60)

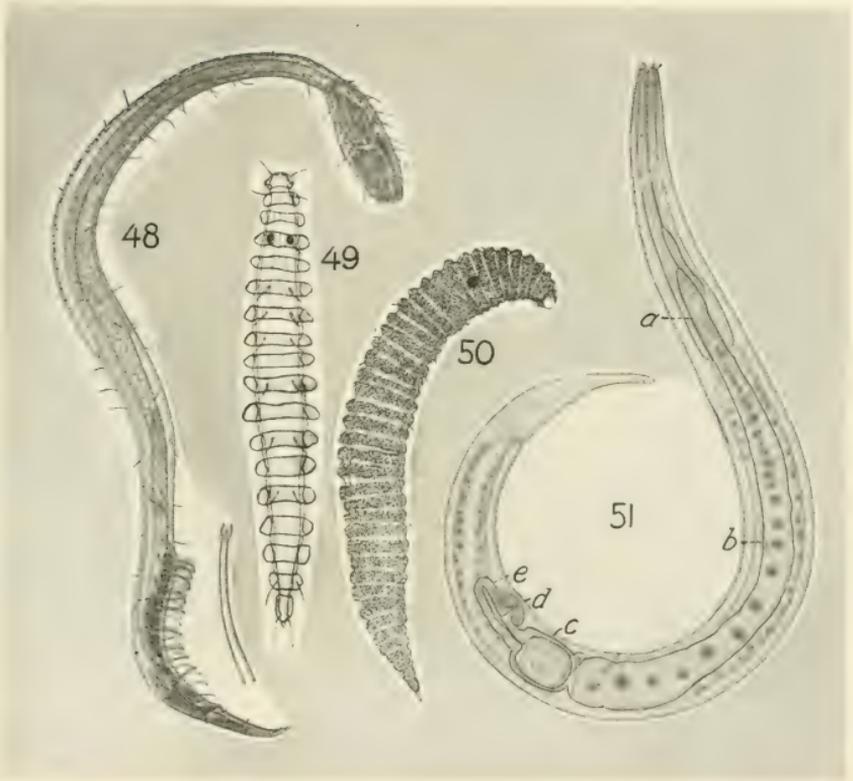


FREE-LIVING NEMATODES  
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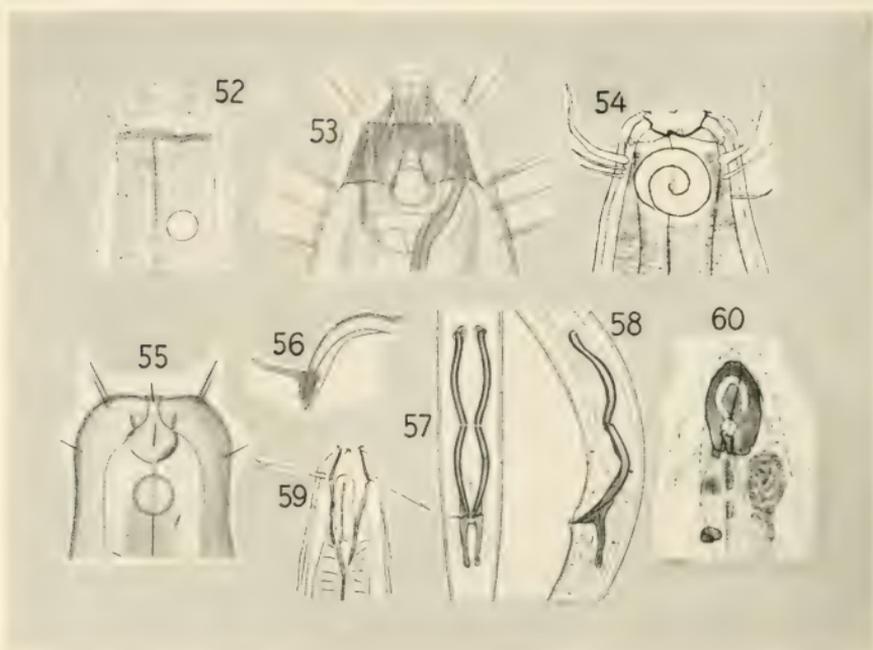
**FREE-LIVING NEMATODES**

(For explanation, see pages 60, 61)



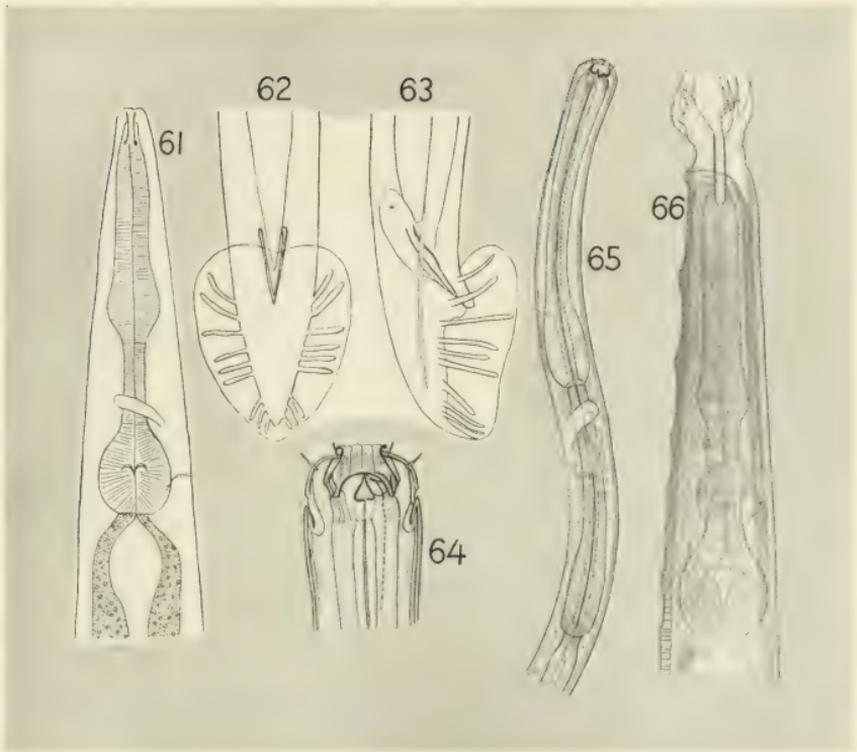
**FREE-LIVING NEMATODES**

(For explanation, see page 61)

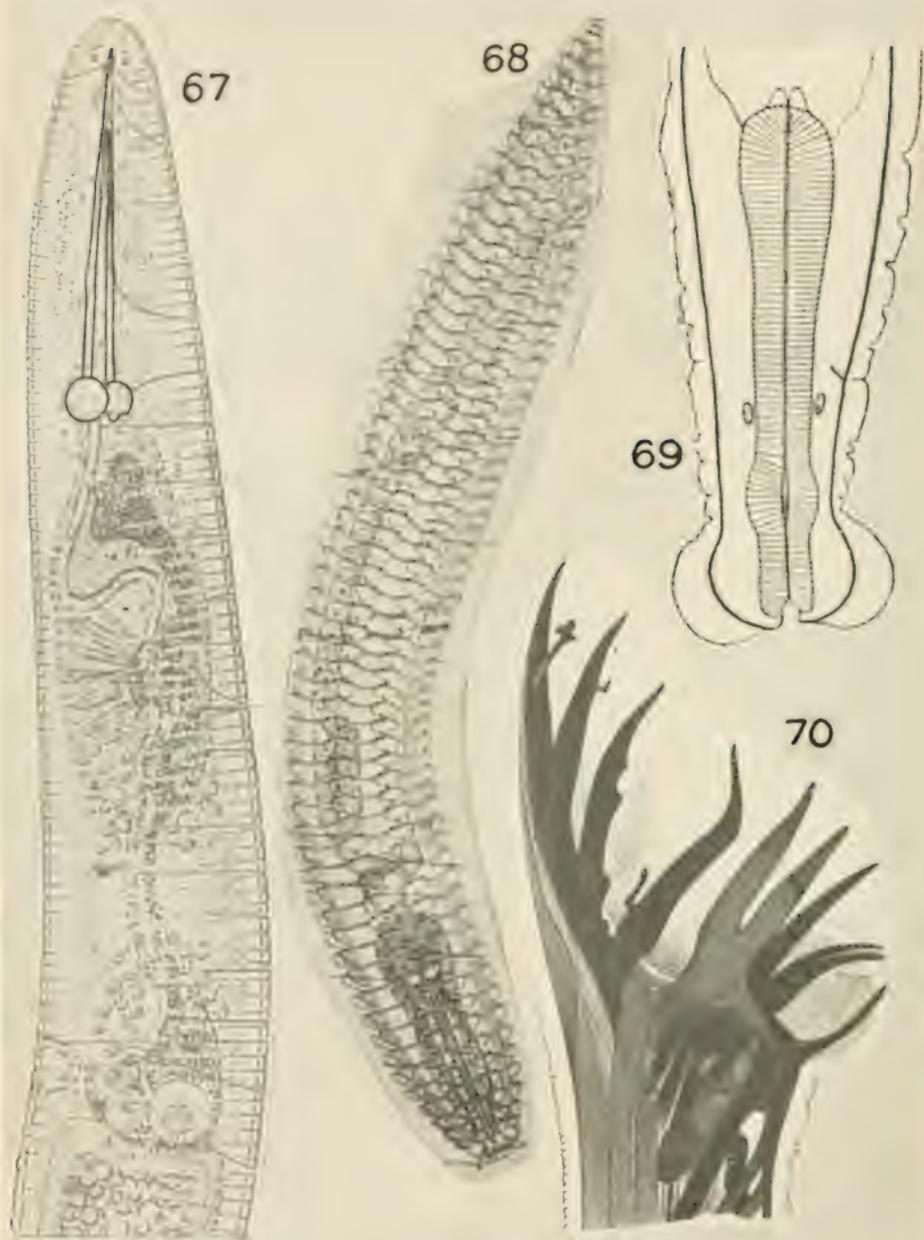


**FREE-LIVING NEMATODES**

(For explanation, see page 62)



**FREE-LIVING NEMATODES**  
(For explanation, see page 62)



**FREE-LIVING NEMATODES**  
(For explanation, see page 63)

SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 89, NUMBER 7

EVIDENCE OF INDIAN OCCUPANCY IN  
ALBEMARLE COUNTY, VIRGINIA

(WITH 11 PLATES)

BY  
DAVID I. BUSHNELL, JR.

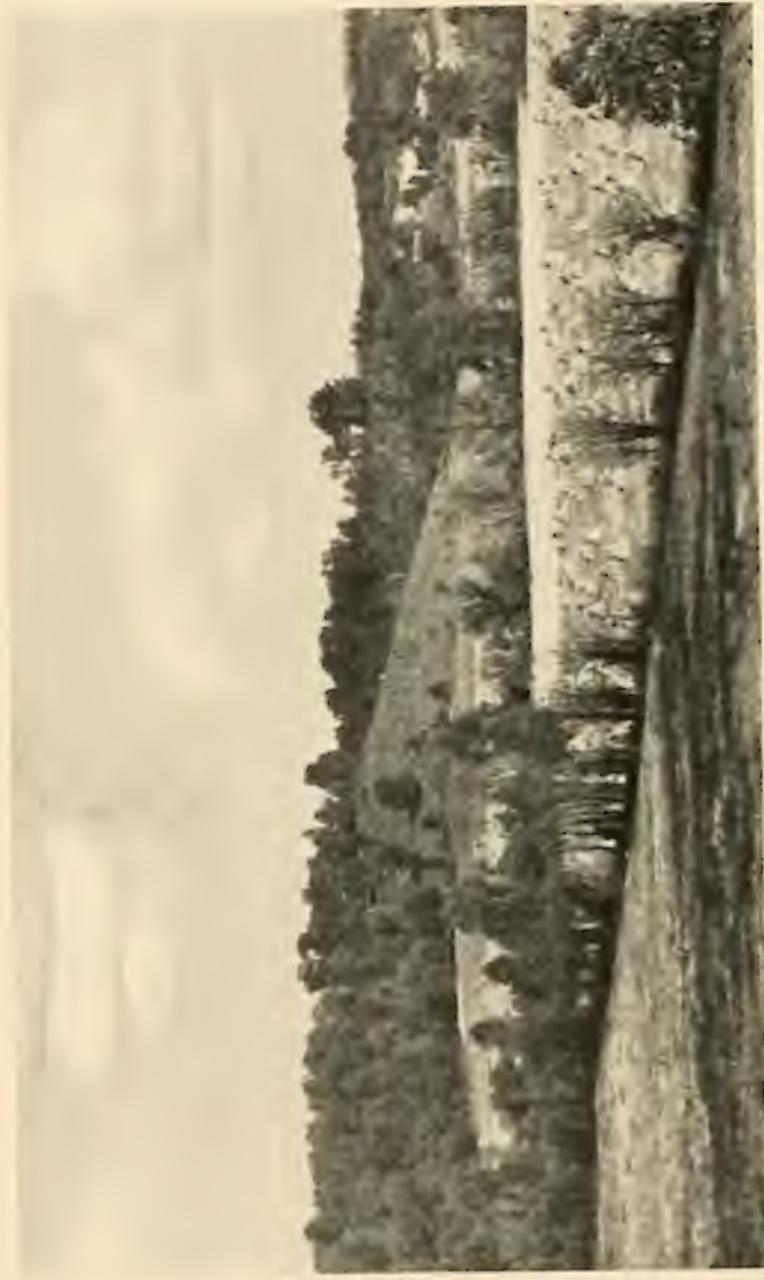


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Looking eastward from the cliffs south of the Rivanna, over part of the site of Monaskepatonough.

## EVIDENCE OF INDIAN OCCUPANCY IN ALBEMARLE COUNTY, VIRGINIA

By DAVID I. BUSHNELL, JR.

(WITH 11 PLATES)

Early in the seventeenth century, when English colonists reached Virginia, that part of the valley of the James which extends westward from the falls to the mountains was claimed by the several tribes of the Monacan confederacy. These belonged to the Siouan linguistic family, inveterate enemies of the Algonquian tribes whose villages stood along the course of the stream from its mouth to the border of the Monacan territory.

Soon after the settlement of Jamestown, late in the spring of 1607, the colonists learned of the existence of five towns or tribal centers occupied by this Siouan group, but not until the autumn of the following year, 1608, did they enter the country of the Monacan.<sup>1</sup> During that season a large party of the English ascended the James to the falls, the site of the present city of Richmond, where they left their boats and continued some miles beyond. They discovered two of the native towns, Mowhemcho and Massinacak, both located on the right bank of the James west of the falls and some 14 miles apart. The English did not advance far beyond Massinacak but soon returned to Jamestown.

It is believed the remaining three towns were never visited by Europeans and that all had been abandoned before the region was entered by white settlers. The three villages to which this refers were Rassawek, at the junction of the James and Rivanna Rivers, probably the most important of the settlements; Monahassanugh, on the James between present Norwood and Wingina in Nelson County, believed to have been the Tutelo of early narratives; and Monasukapanough, on the banks of the Rivanna north of the University of Virginia, in Albemarle County, identified as the ancient settlement of the Saponi. The three native villages thus stood at the angles of a roughly triangular area bounded on two sides by the rivers and on the third by mountains. The evidence of Indian occupancy of this region forms the subject of the present sketch.

<sup>1</sup> Bushnell, David I., Jr., *The five Monacan towns in Virginia, 1607*. Smithsonian Misc. Coll., vol. 82, no. 12, 1930.

The valley of the Rivanna and southward to the James is a country of much natural beauty. It is traversed to the westward by the Blue Ridge, which attains an elevation of more than 3,500 feet, sloping to the foothills and rolling land to the east. Here are many streams fed by innumerable springs of clear, cold water. A great part of the surface remains heavily timbered. Game was plentiful during the days of Indian occupancy, and deer, bear, and the smaller animals were here in vast numbers. Buffalo are known to have reached the valleys by coming through the gaps in the mountains, but they may never have been very numerous. A region so plentifully supplied by nature attracted the Indian hunter, and the many arrowheads found in all parts, on low ground and on mountain sides, prove that game was sought here during a long period. This must have served as a hunting ground for the people of the three ancient Monacan towns, the last of the native tribes to occupy this part of Virginia, as well as for others who had preceded them.

Although Siouan tribes were occupying villages on the banks of the James and Rivanna Rivers at the beginning of the seventeenth century, they are believed not to have been there many years; consequently all the small camp sites and numerous objects of native origin discovered in the region should not be attributed to the Monacan. Algonquian tribes may have preceded them as occupants of the same territory. The latter had evidently been pushed eastward by the Siouan people coming from the direction of the Ohio, and the pressure was still being exerted in the year 1607, at which time Powhatan related to Captain Newport "that the *Monanacah* was his Enmye, and that he came Downe at the fall of the leafe and invaded his Countrye." With these continued invasions the Algonquian villages near the falls would soon have been abandoned, thus enabling the Monacan to have advanced still farther eastward.

Conditions of the country immediately above and below the falls were very similar. Strachey wrote (p. 27):<sup>2</sup> "Pokotawes, which the West Indians (our neighbours) call maiz, their kind of wheat, is here said to be in more plentye then below, and the low country fructs grow here. It is supposed that the low land hath more fish and fowle, and the high land more number of beasts. The people differ not much in nature, habit, or condicion, only they are more daring upon us; and before we erected our forts amongst them, there was ever enmity, and open warrs, betweene the high and lowe

---

<sup>2</sup> Strachey, William, *The historie of travaile into Virginia Britannia*. Hakluyt Society, London, 1849.

country, going by the names of Monocans and Powhatans." Thus it would appear that the people of the two groups had much in common and did not differ greatly in manners or ways of life.

If the belief that the Siouan tribes moved eastward from the Ohio is correct, they must necessarily have crossed the valley of the Shenandoah—the Valley of Virginia—before entering the piedmont where they were established when first encountered by Europeans, but the rich and fertile region just west of the Blue Ridge, one which would have appealed to the hunter if he were unmolested, was not occupied by any native tribe when it first became known to the colonists. War parties of the northern Iroquoian tribes traversed the land, and evidently the fear of their coming had caused the less warlike to abandon the region and to seek new homes elsewhere. Thus it is believed the Siouan groups crossed the Blue Ridge and occupied the piedmont country, in turn pushing the Algonquian tribes before them. That such were the actual conditions appears to be proved by later events. During the months of June and July, 1744, a great gathering of the Six Nations met Commissioners of Virginia and Maryland at Lancaster and there concluded a treaty of much importance to the colonies. Present at the treaty-making were "The Deputies of the *Onandagoes, Senecas, Cayogoes, Oneidas* and *Tuscaroraes*."<sup>3</sup> On the afternoon of June 27 one of the Indians, Tachanoontia, addressed the gathering and said in part: "All the World knows we conquered the several Nations living on *Sasquahannah, Cohongoronta*, and on the Back of the Great Mountains in *Virginia*; the *Conoy-uch-such-roona, Coch-now-was-roonan, Tohoa-irough-roonan*, and *Connutskin-ough-roonaw*, feel the Effects of our Conquests, being now a Part of our Nations, and their Lands at our Disposal. We know very well, it hath often been said by the *Virginians*, that the *Great King of England*, and the People of that Colony, conquered the *Indians* who lived there, but it is not true." On the following day one of the Commissioners replied to the foregoing: "If the *Six Nations* have made any Conquest over *Indians* that may at any Time have lived on the West-side of the Great Mountains of *Virginia*, yet they never possessed any Lands there that we have ever heard of. That Part was altogether deserted, and free for any People to enter upon, as the People of *Virginia* have done, by Order of the Great King, very justly. . . ."

The conquest of the region by the northern tribes had probably occurred only a few years before the coming of the English colo-

<sup>3</sup> Colden, Cadwallader, *The history of the Five Indian Nations of Canada*, 2d ed., London, 1750.

nists, and it is believed that the last of the Siouan tribes living beyond the mountains, in the direction of their earlier habitat, were then compelled to move eastward to the lands which they occupied in 1607.

#### COMING OF THE COLONISTS

It is not known when a European first entered the region now embraced within the bounds of Albemarle County, but the earliest patents for land in parts of Albemarle "on the far side of the mountains called Chestnut," were taken out June 16, 1727. Within the next few years several large grants were secured in the southern section of the county, bordering on the left bank of the James and extending some miles up the valley of the Rockfish, including the extensive soapstone quarries which had been worked by the native tribes. And during the year 1735 Thomas Moorman was granted 650 acres extending from the branches of Meadow Creek to the South Fork of the Rivanna "including the Indian Grave low grounds,"<sup>4</sup> so designated by reason of the large burial mound which was then standing on the low ground a short distance from the right, or south bank of the stream. Some years later the mound was carefully examined and described by Jefferson in his "Notes on the State of Virginia."

A few Indians may have been living in Albemarle County two centuries ago, but nothing definite is known concerning them. However, it is within reason to believe that small scattered groups, one or more families, would have been encountered throughout the surrounding country, all of which they had, so short a time before, claimed and occupied.

About this time Indians are known to have been living on the banks of the Rapidan, some miles below Orange Court House, as is revealed in an order made by the County Court in 1730. This is in part: "William Bohannon came into court and made oath that about twenty-six Sapony Indians that inhabit Colonel Spotswood's land in Fox's neck go about and do a great deal of mischief by firing the woods, more especially on the 17th day of April last whereby several farrows of pigs were burnt in their beds, and that he verily believes that one of the Indians shot at him the same day. . . ."<sup>5</sup> Fox's Neck, mentioned in the order of the court, is a narrow spur of land, nearly a mile in length and bordered by the left bank of the

<sup>4</sup> Woods, Rev. Edgar, Albemarle County in Virginia. Charlottesville, 1901.

<sup>5</sup> Scott, W. W., A history of Orange County, Virginia. Richmond, 1907.

Rapidan, immediately up the stream from Germanna bridge, the site of the settlement of Germanna. The Indians may have been some who had formerly lived at Fort Christanna. The fort was abandoned by the Colony in 1718, but the "Sapponey Indian Town" nearby was recognized as late as 1728 as belonging to the Saponi and allied tribes, and white settlers were not permitted to acquire

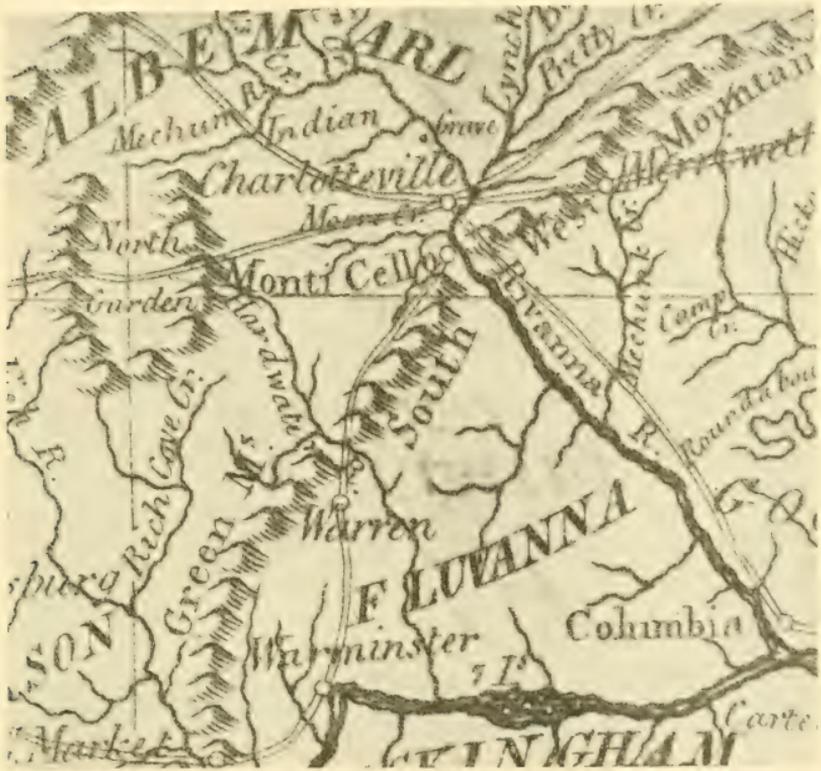


FIG. 1.—Section of "A Map of the State of Virginia, compiled for Rawle's Hot-pressed Edition of Jefferson's Notes." Philadelphia, June 1801. Showing the "Indian Grave," on the right bank of the Rivanna north of Charlottesville.

the land. It is not known when the Indians were finally dispersed, but it is believed that not all left at the same time; they probably drifted away in small groups to seek new homes elsewhere. Not long after this a party of Indians visited the burial mound, "the Indian Grave," on the low ground of the Rivanna and, as related by Jefferson, "staid about it some time, with expressions which were construed to be those of sorrow." The mound, long since destroyed,

is believed to have been the burial place belonging to the Saponi village, Monasukapanough, which occupied the level ground on both sides of the Rivanna, as described in "The Five Monacan Towns", but which must again be mentioned. Although the mound may have disappeared by the beginning of the last century, it had been remembered and was clearly indicated on the map of the State of Virginia that accompanied the 1801 edition of Jefferson's Notes. A small section of the map is reproduced in figure 1. The "Indian Grave" is placed near the right bank of the Rivanna, a little west of north of Charlottesville, on the site of the ancient settlement. A view looking northward from the cliffs south of the right bank of the river, over a section of the village site, is shown in plate 1. The course of the Rivanna is indicated by the line of trees beyond the cultivated

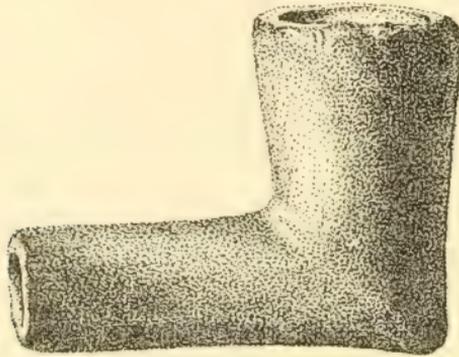


FIG. 2.—Pipe made of greenish steatite, found in contact with human remains on the site of ancient Monasukapanough, on the right bank of the Rivanna, near where the "Indian Grave" formerly stood. Natural size. (U.S.N.M. No. 364594.)

field on the extreme right in the picture. The mound stood within this cultivated area, but its exact position is not known. The rising ground in the distance is on the left bank of the Rivanna and was occupied by part of the native village.

Some years ago the owner of the land, while plowing the low ground bordering the right bank of the stream, encountered a single burial, and, although very near the surface, the bones were in a good state of preservation. Associated with the remains was a small soapstone pipe, figure 2, but no other object was noticed. The burial had been made in the stratum of sand and clay that had been deposited on the site after the abandonment of the village and should, therefore, be attributed to some of the wandering parties of Indians who visited the spot during the early part of the eighteenth century or even later.

## EVIDENCE OF AN EARLY PERIOD OF OCCUPANCY

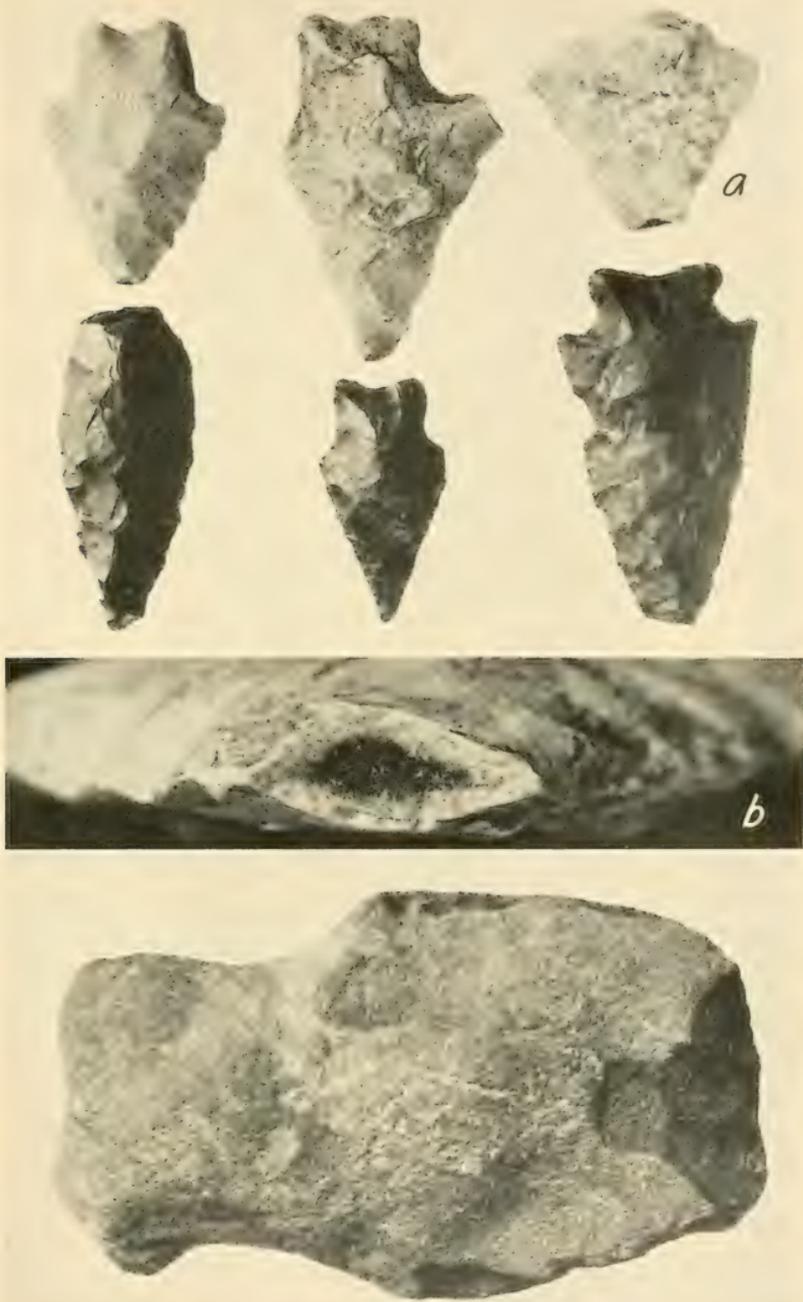
As previously stated, it is evident that several distinct groups of tribes, belonging to different linguistic families, entered and became established in the piedmont country during late prehistoric times, the centuries immediately preceding the arrival of the European colonists. This may be termed the late, or recent, period of occupancy by native tribes, and many of the artifacts now encountered scattered over the surface of village and camp sites in the valleys of the James, the Rivanna, and streams northward, were undoubtedly produced during this period. Some of the objects made of chert and diabase have become slightly weathered, but others reveal the flaking as fresh, and the edges as sharp, as when newly chipped. However, other specimens discovered on the same area and under identical conditions are deeply weathered, appear to be much older, and consequently are believed to have been made and used during an earlier period of occupancy. The approximate age of the objects attributed to the early period can only be estimated by considering the appearance and density of the weathering of the surfaces. Unfortunately, no stratified accumulation of ancient camp refuse has been encountered. All objects have been recovered from the surface and under similar conditions, so that they would have been equally exposed to, and affected by, the elements.

The gradual wearing away of the outside of a specimen, as a result of the weathering, tends to smooth and reduce the sharpness of the fractured edges and chipped surfaces. In some instances the weathering has been so great that it is now difficult to determine the exact extent to which an object had been flaked when originally produced from a pebble or bit of rock.

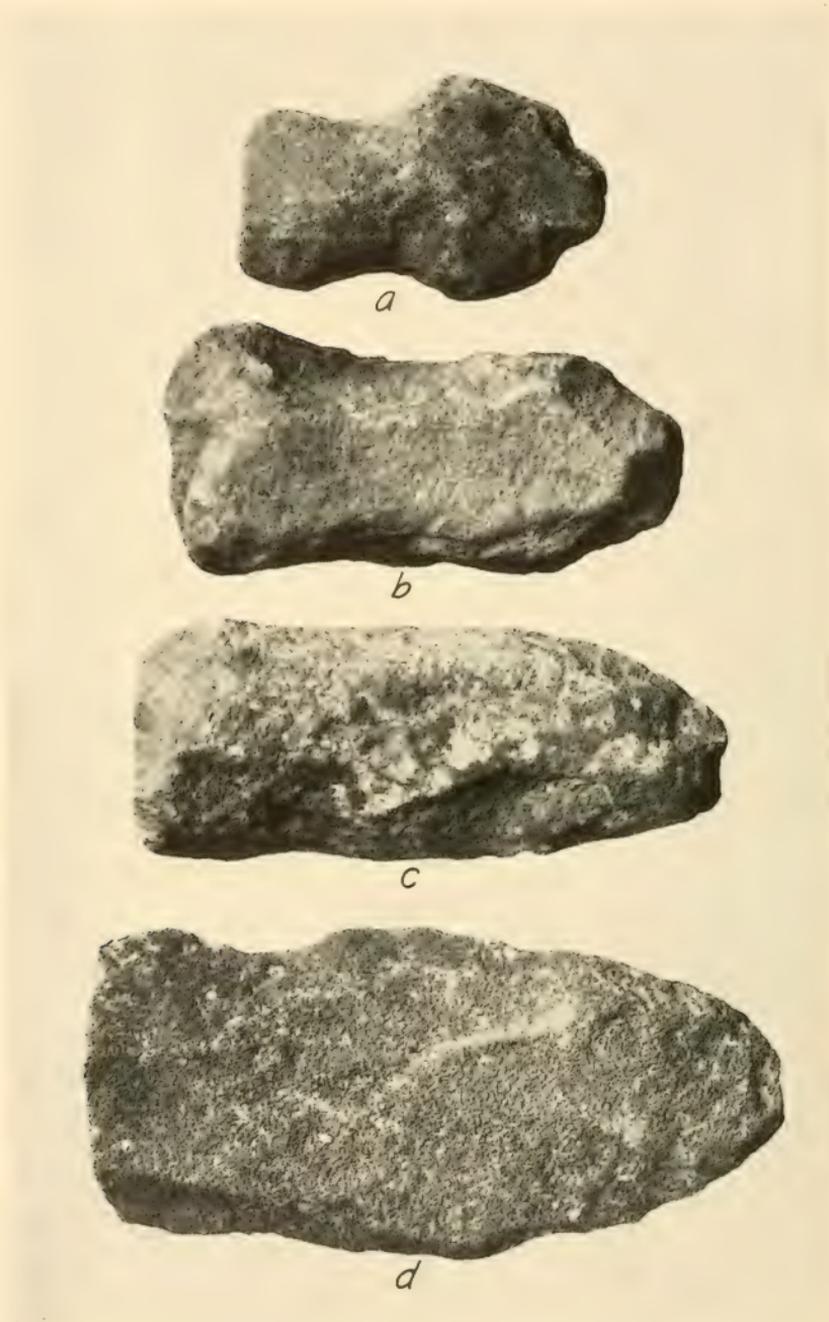
One specimen was discovered in 1928 which proves conclusively and indisputably the existence of two distinct and long separated periods of occupancy in that part of Virginia. It is an axlike object made of diabase, so plentiful in the region, and was recovered from the surface of a cultivated field near the remaining portion of a very large burial mound, believed to mark the site of the Manahoac town of Stegara, on the right bank of the Rapidan, in Orange County, a short distance east of the Greene County line. A photograph of this interesting specimen is reproduced in plate 2, lower figure. When the artifact was newly made, the surface was a lustrous black, and the position of each flake was clearly defined. Now, however, the greater part of the surface is deeply weathered, and it has changed to a light brownish color. The surface has been worn away to such

an extent that it is difficult to discern signs of the chipping by which the piece of rock was reduced to the desired form. But in one respect the specimen may be unique. It is evident that at some later time, after the original flaked surface had become greatly weathered, the object was found and partly rechipped, making it again a serviceable implement or weapon. The removal of flakes during the process of rechipping exposed the black rock, and, as clearly shown in the photograph, large flakes were removed in the endeavor to sharpen the cutting edge. Rechipping of the edge of the object continued as far as the beginning of the groove. The surface exposed by the later, or secondary, chipping has become only slightly changed, contrasting strongly with the deep weathering of the originally flaked portion, but conforming in appearance with many specimens made of the same material and believed to have been produced during the recent period of occupancy. If so slight a change has resulted after exposure to the elements for not less than two and one-half centuries, the very great age of the specimen becomes apparent. Centuries, during which time the surface became weathered and worn away, must necessarily have elapsed between the making of the implement, later to be lost or abandoned, and the time it was found, resharpened, and again used. Evidence of very early occupancy is thus revealed. Considering conditions known to have prevailed on other parts of the continent 1,500 or 2,000 years ago, it is within reason to believe that nomadic bands had even before that time penetrated into the wilderness eastward from the mountains and reached the valleys of the streams flowing into the Atlantic.

Innumerable arrowheads and various forms of small chipped implements are encountered throughout the piedmont region, a large proportion of them having been made of quartz or quartzite, materials which do not show the effect of exposure to the action of the elements. Some, however, were chipped from small pieces of black chert, the source of which has not been discovered. Six of the latter specimens, all found on the Oliver site, located near the center of Albemarle County and described in detail later in this article, prove to be of great importance, as they present additional proof of two distinct periods of occupancy in that part of Virginia. A photograph of the six pieces is reproduced in plate 2, upper figure. The three specimens below do not show weathering, although they were exposed, as was the ax in its rechipped condition, for not less than two and one half centuries. The surfaces of all are as black and fresh, and the edges as sharp, as though recently chipped. Compare



Above, six specimens discovered on the Oliver site, all made of black chert. Natural size. (U.S.N.M. No. 364579.) *b*, fractured surface of *a*.  $\times 5$ . Below, implement found on the site of Stegara, showing rechipping.  $\frac{2}{3}$  natural size. (U.S.N.M. No. 350166.)



Objects attributed to the early period.  $\frac{1}{2}$  natural size. *a, b*, found in Albemarle County. *c, d*, found in Louisa County. (U.S.N.M. Nos.: *a*, 350163; *b*, 350162; *c*, 365372; *d*, 365371.)

this condition with that of the three specimens shown above. All six are believed to have been made of the same black chert, and all were found in similar surroundings. The three above are bleached and weathered, and the edges are worn away and have become smooth. These unquestionably belonged to the early period of occupancy; the former were made and used during the late or recent period. The older specimens likewise differ in form from those of the later period. The extreme point of the specimen on the right of the upper row, *a*, has been broken, thus revealing the natural black chert unaltered and showing the depth of the weathering. An enlarged view of the fractured surface is reproduced in *b*. Some of the crudely made quartz and quartzite points may have been produced during the early period, but, as already mentioned, the material would not have become weathered and so present evidence of great age.

Four implements which are believed to have been made and used during the early period are shown in plate 3. Above are two rather small specimens, *a* and *b*, which were found on the high ground near the right bank of the Rivanna, opposite the mouth of the North Fork of that stream. Both are made of diabase. Below are two crude specimens, *c* and *d*, found some miles eastward in Louisa County, north of Louisa, near a small stream which flows into North Anna River. The larger specimen, *d*, made of a large flake of diabase which had been shaped by the removal of smaller flakes, is deeply weathered and its appearance suggests great age. The smaller specimen, *c*, differs from all others in having been made of a quartzite pebble which has not weathered, but is greatly discolored.

The weathering of the two small specimens from the vicinity of the Rivanna, *a* and *b*, resembles that of the originally chipped surface of the ax discovered near the Rapidan. The relatively great age of these and of the two examples found in Louisa County is apparent. The black chert points, so greatly weathered, are believed to have belonged to the same early period. Centuries have passed since they were made and used.

The specimens illustrated in plates 2 and 3 have been examined, and the materials identified, by Dr. R. S. Bassler, Dr. W. F. Foshag, and E. P. Henderson, of the Department of Geology, United States National Museum. All agree that the deep weathering of the rock is indicative of the long exposure of the chipped surfaces, in turn proving the great age of the implements or weapons fashioned by man.

There has ever been a degree of mystery attached to the extensive soapstone quarries existing in the piedmont. When and by whom they were operated are questions that have never been answered. No reference is known to the use of soapstone by historic tribes. Fragments of the material are seldom encountered on the village or camp sites, and consequently there is no evidence to prove its use by the Monacan, Manahoac, or other tribes belonging to the later period of occupancy. The lack of evidence of the use of the stone in recent times suggests that the quarries were opened by the earlier occupants of the country—those by whom the crude stone implements, now so weathered and revealing great age, were made and used.

It is believed that proof or indications of an early period of occupancy will eventually be recognized over a wide region, extending from the New England States southward through Virginia, with the extreme bounds difficult to determine. This belief is partly suggested by the discovery in the Connecticut Valley of specimens similar in form, material, and degree of weathering to those just described and illustrated in plates 3 and 4. Many examples now in the United States National Museum were found in or near an ancient soapstone quarry not far from Portland, Middlesex County, Conn., and are believed to have been implements used in working the steatite. Similar objects have been encountered just northward in Hartford County (U.S.N.M. Nos. 34260 and 5860). The discovery of the implements in the vicinity of ancient quarries tends to strengthen the belief, as previously expressed, that the Virginia specimens were fashioned by the tribe or tribes who occupied the piedmont, and there opened the soapstone quarries, long before the coming of the Siouan groups from their earlier habitat beyond the mountains.

#### SITES, AND THE DISTRIBUTION OF VARIOUS OBJECTS

Traces of Indian occupancy are plentiful throughout the region, many of the sites being small, others very extensive. The finding of great numbers of arrowpoints within a rather restricted area is believed to indicate that such a place had been a favorite hunting ground, a region where game had been more easily taken than elsewhere. Several such localities have been discovered about midway between the James and Rivanna Rivers, and undoubtedly other sites as interesting and as rich in material of Indian origin as those already encountered remain hidden in the forest-covered country, on the banks of streams, in the vicinity of springs, or occupying the

summits of projecting elevations that had formerly been bordered by marshy land. And although many interesting localities may not as yet have been revealed, it is certain that others of equal importance have been destroyed by natural causes. In a country of this nature the native camps and villages usually stood on or near the banks of streams, very often on the bordering low grounds which were frequently overflowed. Two centuries and more have now passed since large encampments stood on the banks of the Rivanna, and during the intervening years the stream has often flooded the adjacent lands. Several freshets of unusual volume during the past century are known to have caused radical changes in the appearance of the surface of the areas thus inundated; gullies were formed, some parts of the surface were entirely washed away, and other sections were covered with sand and soil brought down by the currents. Under such conditions all evidence of native camps and villages would have been obliterated. However, such parts of some camp sites as had occupied higher ground, approaching the bordering hills, and had thus escaped the floods, may now be discovered. Traces of such sites, preserved under these conditions, have been encountered on the banks of the Rivanna both above and below the ancient site believed to have been last occupied by the Saponi—the village of Monasukapanough. Undoubtedly, many similar sites remain to be discovered along the course of the Rivanna and other streams.

The material discovered on this extensive site has been described, and very little can be added to the account as already given. However, as evidence of two distinct periods of Indian occupancy may now be recognized in this region, it is believed that certain crudely made implements, deeply weathered and worn, which have been found on the site should be attributed to the early period, antedating by centuries the coming of the Siouan tribes to whom much of the pottery and many of the more finished stone implements should probably be ascribed.

During the autumn of 1931 a ditch was dug across the site of the ancient settlements in the endeavor to discover a deposit of camp refuse, but, unfortunately, without success. The ditch extended from the left bank of the river to the foot of the rising ground, a distance of approximately 100 yards. It was near the middle of the low ground—as distinguished from the encircling hills—and followed the left bank of a natural ravine or gully, through which water had flowed from a large spring that issues from the foot of the cliffs. Some of the most interesting specimens recovered from the site have

been found on the surface near the point where the ditch was dug. Nothing, however, was discovered beneath the surface, nor was there any indication of disturbance of the earth. Conditions may be different on other parts of the site, but that remains to be determined at some future time.

Other discoveries and localities of special interest will now be described.

#### THE SOURCES OF HARDWARE RIVER

Red Hill is a small station on the Southern Railway about 15 miles south of the Rivanna. A few hundred yards beyond the station the right of way crosses the North Fork of Hardware River just below the junction of the South Branch and North Branch, which here unite to form the main stream. Westward from this point the country is open and rolling and rises gradually to the foothills of the Blue Ridge about 3 miles in a direct line beyond. The entire area is drained by small branches which eventually reach the Hardware, and these are fed by innumerable springs, some of them large, ever-flowing springs of clear, cold water. It is a beautiful country, where wild game was formerly abundant; it had attracted the Indian hunter long before it was traversed by the white man two centuries ago. Across the divide to the westward, beyond Israel Gap, the drainage is into Mechum River, one of the two streams which unite to form the South Fork of the Rivanna.

Eastward from the crossing of the railway the Hardware flows through a very narrow valley with heavily timbered hills rising on both sides, but a mile or more beyond, after passing Dudley Mountain, the country becomes more open on the left, or north side, although steep hills continue on the south. The entire region was formerly covered by a dense forest, much of which remains.

Although the name "Hardware" is now applied to the stream, it was evidently called "Hardwater" during the days of Jefferson and was so designated on the map which accompanies the edition of "Notes on the State of Virginia," issued in Philadelphia in 1801.

#### THE BERKELEY CACHE

Just north of the left bank of the main stream of Hardware River, and about  $1\frac{1}{2}$  miles south of east from the Red Hill station, is the farm of Francis L. Berkeley. It covers part of the southeastern slope of Dudley Mountain, which continues several hundred yards and reaches the left bank of the river. The stream is rather narrow, rapid in places, and the bed is rocky. Canoes could not

have been used this far up, although they could have ascended some distance from the mouth of the river. According to tradition an ancient trail followed the course of the stream.

Very few arrowheads have been found on the Berkeley farm, although they appear to be comparatively numerous on broken ground nearer the Hardware. But as a very large proportion of the region is exceedingly rough, rocky, and heavily timbered, it is not possible to examine the surface carefully or satisfactorily. No trace of a camp site has been discovered.

About 200 feet south of the Berkeley residence, near the public road, is a slight depression in which it is said a spring formerly flowed. A large cedar is now growing on the eastern edge of the depression. Within 20 feet of the cedar, eastwardly, many quartzite blades have been discovered within a limited space of not more than 4 or 5 feet. These undoubtedly constituted part of a cache of blades which had been deposited just below the surface, lost or forgotten, later to be disturbed and scattered by the plow. Fifty or more specimens have been found during the past few years, 24 of which are now in the United States National Museum (U.S.N.M. No. 339706.) All are of the same general form, although some are rather more elongated than others. Typical examples are shown in plate 4, together with a view of the spot where the cache occurred. The material is grayish brown quartzite, probably derived from pebbles and boulders found in the vicinity.

The Indians of Virginia often secreted their possessions in some secure, secluded spot, away from their habitations, where they would remain until desired. Strachey mentioned this custom among the natives with whom he came in contact and with whose manners and customs he became familiar. He wrote (p. 113):<sup>6</sup> "Their corne and indeed their copper, hatchetts, howses, beades, perle, and most things with them of value, according to their owne estymacion, they hide, one from the knowledge of another, in the grownd within the woodes, and so keepe them all the yeare, or untill they have fitt use for them . . . and when they take them forth, they scarce make their women privie to the storehowse." The cache of quartzite blades just mentioned undoubtedly owes its origin to the custom recorded by Strachey.

One other cache is believed to have been discovered, but the specimens were not seen by the writer. This was said to have consisted

<sup>6</sup> Strachey, William, *The historie of travaile into Virginia Britannia*. Hakluyt Society, London, 1849.

of a number of white quartz arrowheads found deposited in a fissure in the rocky cliff on the right bank of the Rivanna about 1 mile above the site of Monasukapanough and just below the bridge spanning the river. It was probably as described.

HUNTING GROUNDS AND CAMP SITES BETWEEN THE JUNCTION OF THE BRANCHES OF HARDWARE RIVER AND THE MOUNTAINS

OLIVER SITE

A short distance south of west of Red Hill station, near the center of Albemarle County, begins a high, rolling tract of land, near the eastern extremity of which is the home of W. R. Oliver. The house is on the highest part of the farm, a small plateau which slopes gradually to the south and southwest and ends rather abruptly a few hundred feet northeast of the dwelling near the junction of, and between, the South Branch and the North Branch of the North Fork of Hardware River. The so-called Middle Branch of the same stream flows into the North Branch just above the mouth of the South Branch. Thus within a very small space the three branches, coming from different directions, unite to form a stream which joins the James some 20 miles away. An ancient trail led up the valley of the Hardware and is believed to have continued along the course of the Middle Branch, on through the present Israel Gap, and thence to have crossed the mountains westward over Rockfish Gap to the valley beyond. The three branches, now small streams, were undoubtedly somewhat larger in the past, when they were bordered in many places by marshy tracts which have now been changed through cultivation, following the clearing of the forests. The entire region appears to have been a hunting ground for the Indians, and, although rather small, isolated sites have been encountered where some objects of stone and many bits of pottery have been found on the surface, no evidence of a large village has been revealed.

Great numbers and varieties of projectile points have been recovered from the surface of the Oliver farm and from the adjacent lands surrounding the junction of the three branches, and in describing the material the area must be treated as a whole.

Quartzite pebbles occur on the slope facing the junction of the North and South Branches, and between 400 and 500 yards westward are outcroppings of white quartz *in situ*. These may have been the sources of materials of which many of the objects discovered on the site were made. Innumerable chips, some very small and others

quite large, scattered over the ground prove that much work was actually done here, and great numbers of arrowheads and other small chipped objects have been discovered during the past few years. The variety of forms is equally remarkable, and practically every type found on other sites is represented, together with some which have not been encountered elsewhere in the region. Although the great majority were made of quartz and quartzite, easily obtained nearby, other small objects were made of jasper, chert, and varieties of quartzite not known to occur here, but some of which may, however, have been found in the streams—pebbles brought down by the current. The latter class of specimens appears to be more plentiful on the southern slope and on the adjoining low ground than on the summit plateau. Traces of several small encampments have been encountered on the slope, from which small fragments of pottery vessels and some very crude stone implements have been recovered. Such camp sites are believed to have been occupied by one or more families when, during the hunting season, they would leave their permanent villages to seek game elsewhere. As Strachey wrote (p. 75): "In the tyme of their huntings, they leave their habitations, and gather themselves into companyes, as doe the Tartars, and goe to the most desart places with their families, where they passe the tyme with hunting and fowling up towards the mountaines, by the heads of their rivers, wher in deed there is plentye of game, for betwixt the rivers the land is not so large belowe that therein breed sufficyent to give them all content."

A view looking south from the Oliver farm over the adjoining lands is reproduced in plate 5, figure 1. Hardware River, as it appears about 2 miles below the junction of the three branches, is shown in plate 5, figure 2.

Arrowheads have been found in such quantities scattered over the surface throughout the country, that they are seldom accorded the interest they deserve and are often regarded as being too plentiful, too commonplace, to occupy a prominent position in a collection. However, in time, as much importance will probably be attributed to them, as a factor in determining the movements of the tribes by whom they were made, as is now attributed by some to designs on bits of pottery recovered from widely dispersed sites.

Capt. John Smith wrote of the natives of tidewater Virginia, the Algonquian tribes with whose manners and ways of life he became well acquainted, but at no time did he have much intercourse with the Monacan. However, it is evident that many customs of the peo-

ple of the two groups were very similar, and undoubtedly all hunted the deer in the same way; consequently Smith's account would apply equally well to the people of the Siouan and Algonquian tribes. He wrote in part, first mentioning the distance an arrow would carry (p. 365):<sup>7</sup> "Fortie yards will they shoot levell, or very neare the marke, and 120 is their best at Random.

"Having found the Deere, they environ them with many fires and betwixt the fires they place themselves. And some take their stands in the midsts. The Deere being thus feared by the fires and their voyces, they chase them so long within that circle that many times they kill 6, 8, 10, or 15 at a hunting. They use also to drive them into some narrow poynt of land, when they find that advantage: and so force them into the river, where with their boats they have *Ambuscadoes* to kill them."

The high ground on the Oliver farm, with the plateau sloping to the south, east, and north to the marshy borders of the two small streams, would have been well suited for hunting as described, and this is believed to explain the occurrence of such quantities of arrowheads found scattered over the surface. It was a great hunting ground, and nearby are indications of small camps that had been reared by the hunters in the primeval forest.

Here, as elsewhere throughout the country, the discovery of vast numbers of projectile points affords an interesting subject for study, and it is evident that the facility with which an Indian hunter could replenish his supply explains the occurrence of such quantities. Smith, who had undoubtedly witnessed the making of stone points, referred to a hunter when he wrote (p. 68): "His arrow head he quickly maketh with a little bone, which he ever weareth at his bracer, of any splint of a stone, or glasse in the forme of a hart; and these they glew to the end of their arrowes. With the sinewes of Deare, and the tops of Deares hornes boiled to a jelly, they make a glew that will not dissolve in cold water." With these simple means an ordinary point would probably have been made in a few minutes, and material was plentiful.

More than 2,500 arrowpoints and other small chipped objects have been collected during the past three years from an area of about half a mile square, at the junction of the branches of the Hardware, including the Oliver farm and adjoining lands. These vary in form and material, but the vast majority are of quartz and quartzite, much of which had undoubtedly been secured nearby. Typical examples are shown in plates 6, 7, and 8, and may be briefly described.

<sup>7</sup> Smith, Capt. John. Works. 1608-1631. Arber ed. Birmingham, 1884.



1. The cedar near which the cache was discovered. Carter Mountain in the distance.



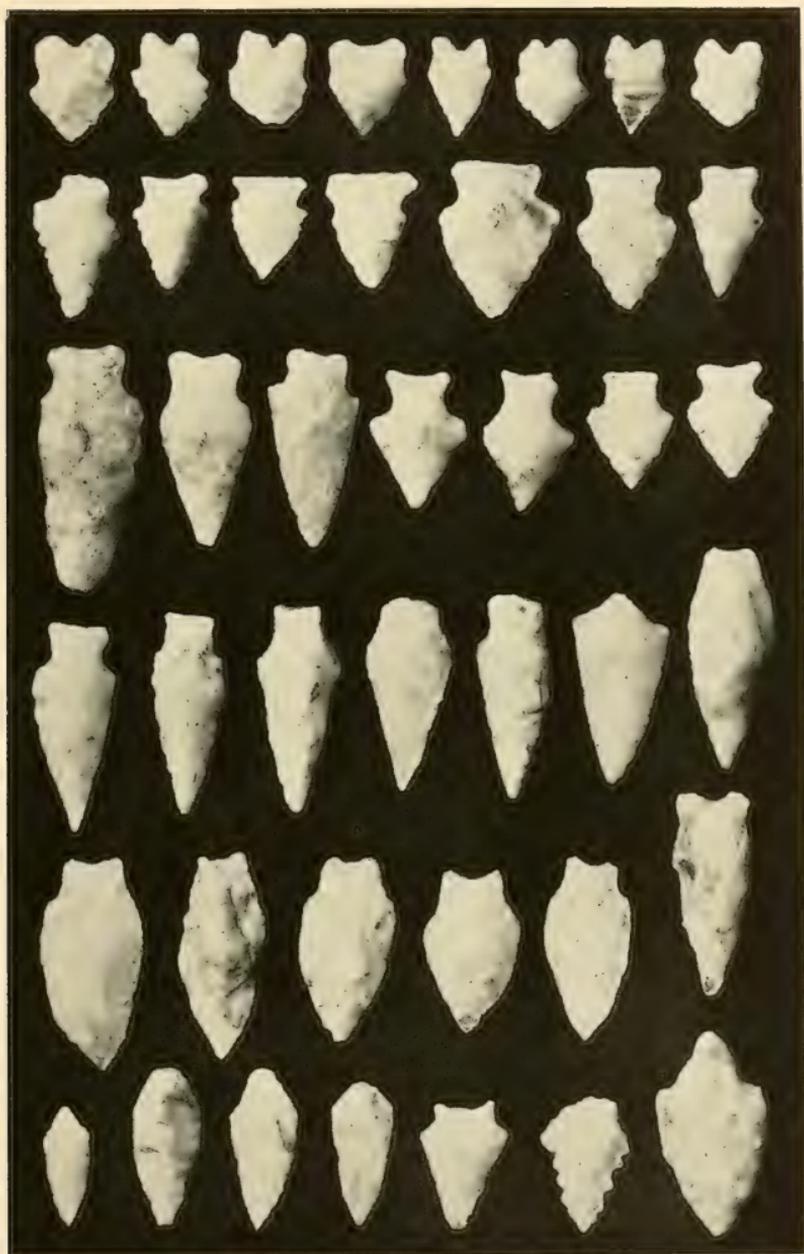
2. Typical blades from the Berkeley cache.  $\frac{2}{3}$  natural size.  
(U.S.N.M. No. 339706.)



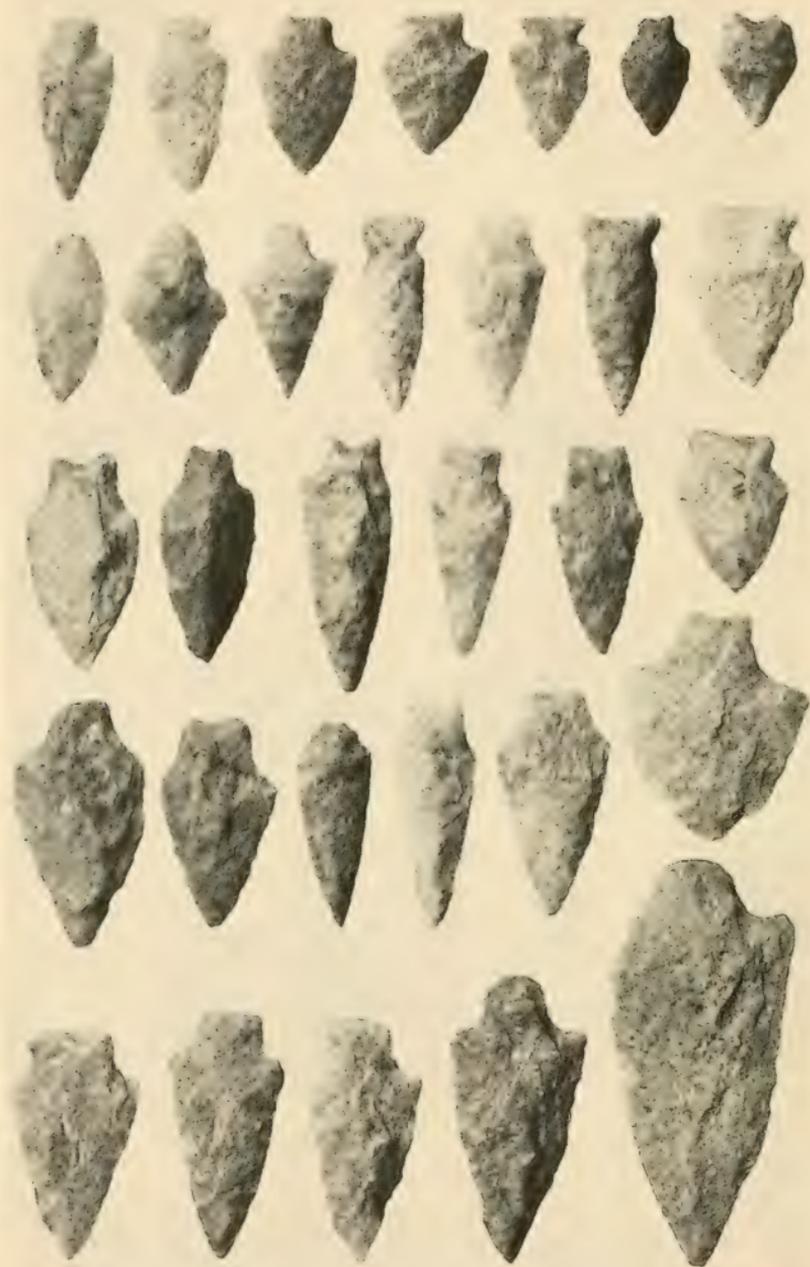
1. Looking south over the Oliver farm, with Gay Mountain beyond.



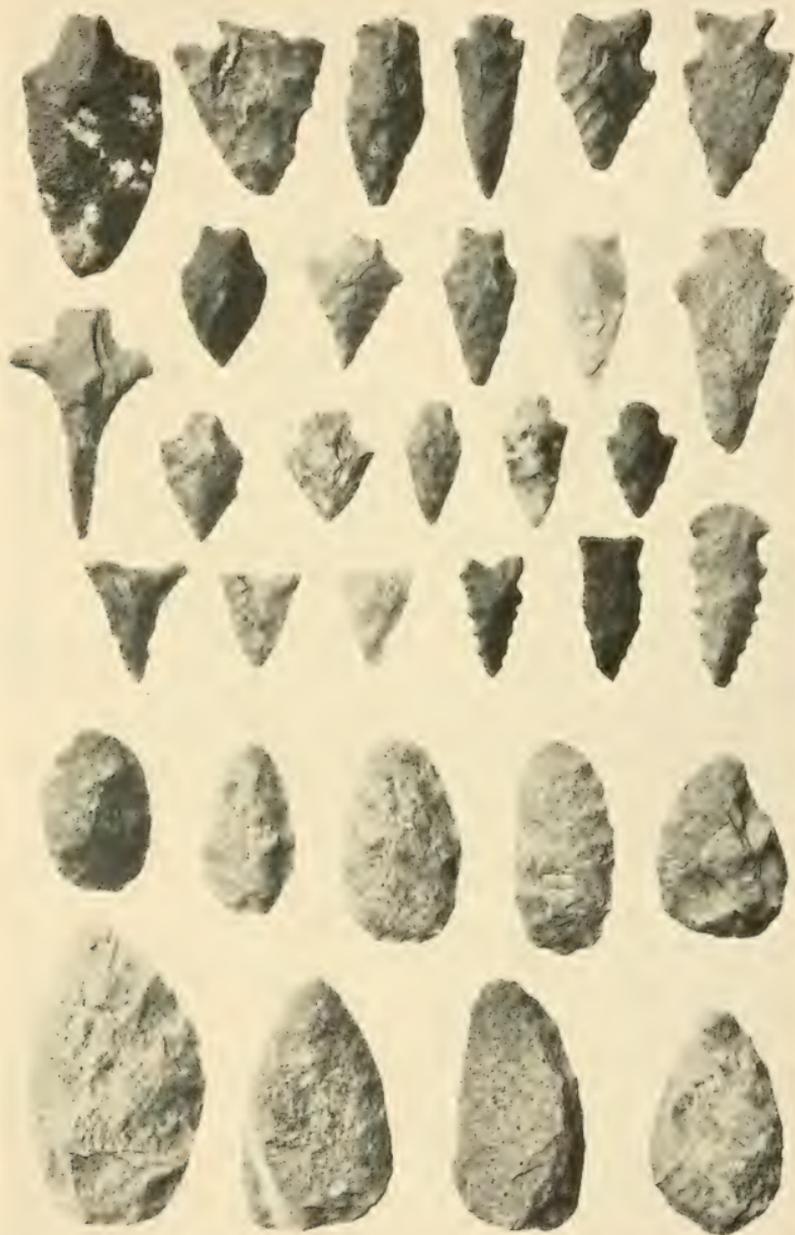
2. Hardware River, near the crossing of the old Lynchburg road, showing a primitive suspension footbridge high above the water.



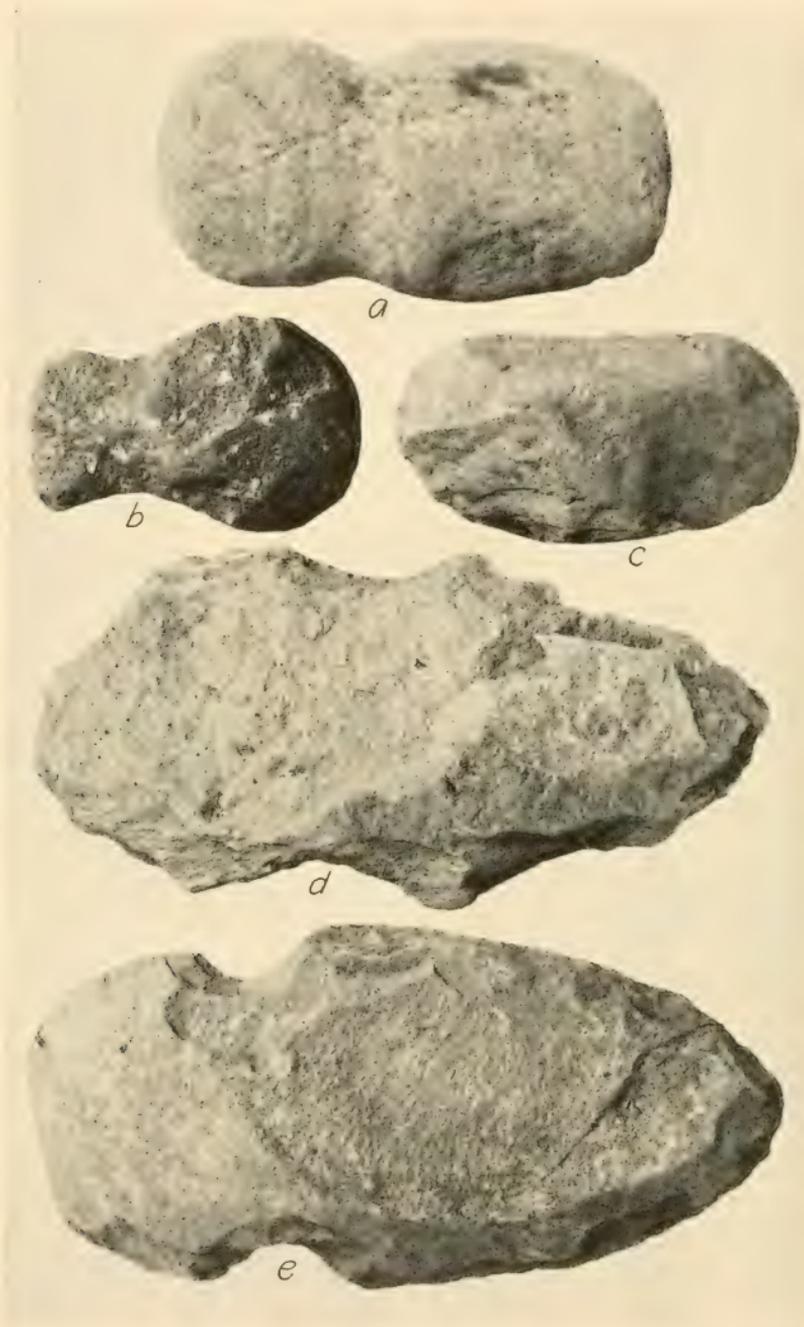
Objects found on the surface, Oliver site.  $\frac{1}{2}$  natural size.  
(U.S.N.M. No. 364575.)



Objects found on the surface, Oliver site.  $\frac{1}{2}$  natural size.  
(U.S.N.M. No. 364576.)



Objects found on the surface, Oliver site.  $\frac{1}{2}$  natural size.  
(U.S.N.M. Nos. 364577, 364578.)



Objects found on the surface, Oliver site.  $\frac{1}{2}$  natural size.  
(U.S.N.M. Nos. 364580-364584.)



Objects found on the surface, Sutherland site.  $\frac{1}{2}$  natural size.  
(U.S.N.M. No. 364595.)



1. The Burruss site in the foreground, looking northeast.



2. Specimens found on the surface, Burruss site.  $\frac{2}{3}$  natural size.  
(U.S.N.M. Nos. 364586, 364587.)

*Plate 6.*—All the objects shown on this plate are made of white quartz, which is found *in situ* throughout this part of Virginia. A large variety of forms are represented, characteristic and typical of piedmont Virginia, but as yet not a single example of a simple triangular point made of this material has been discovered on the extensive site. Some 15 miles northward, on the village site bordering the banks of the Rivanna which is believed to have been occupied by the Saponi town, Monasukapanough, more than one half—40 or 50 in number—of the white quartz points found were of the triangular type. This is significant, and if the country surrounding the branches of the Hardware was a great hunting ground, as it is believed to have been, it is evident that triangular points were not employed by hunters; otherwise some would undoubtedly have been discovered intermingled with the great number of other forms.

The specimen shown in the lower right corner of plate 6 is the only example found of that type made of white quartz; however, the material is banded and appears to be different from the quartz occurring in the vicinity.

Many small chipped objects, usually termed projectile points, were probably used for other purposes. Some undoubtedly served as knives, some as scrapers, and others as drills. Very little is known of the arts and customs of the people during the days when stone implements were made and used, before the coming of Europeans and the introduction of iron. Wood was probably worked more extensively than is generally supposed, and many stone tools would have been used.

Very often a so-called arrowpoint will be encountered on which the edge of the base and the edges of both notches will be quite smooth and polished, while the two edges continuing from the shoulders to the point will be rough and sharp as though recently chipped. An example made of white quartz, found on the Oliver site, illustrating this peculiar feature is shown in figure 3. This may have been a knife, mounted in such a manner that the edge of the base became worn and smooth, while it was necessary from time to time to resharpen or rather rechip the cutting edges. Specimens similar to this are found in other parts of the country.

*Plate 7.*—This plate shows typical examples of projectile points, and possibly some knives, all made of brownish quartzite. The quartzite of which the great majority were made resembles the material of the objects of the Berkeley cache, plate 4, and may, like the

latter, have been obtained nearby. The specimens illustrated on this plate are very characteristic of the region.

*Plate 8.*—Arrowpoints of chert, jasper, and other materials are shown in the upper part of the plate. They include a large variety of forms, and it is believed that many of these were brought from a distance; probably very few were made here. A drill and several pieces that may have been knives are included. Three triangular points are shown at the left on the lower line, these being the only examples of this type discovered on the site. Of the three, two are made of chert and one of a light-colored, fine-grained quartzite. As mentioned elsewhere, it is evident that points of this type were not used by hunters, and the belief that they may have tipped the arrows of the warrior rather than those of the hunter is suggested by the discovery, made some years ago, of a human vertebra in which a chert point of this

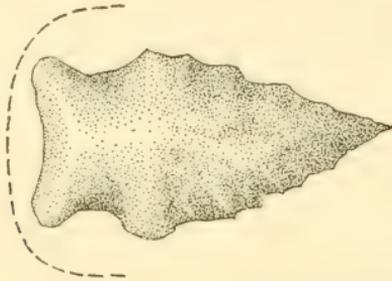


FIG. 3.—Specimen made of white quartz, from the Oliver site. Natural size. Surface and edges within the broken line are smooth and polished. (U.S.N.M. No. 364575.)

form is deeply embedded. Similar specimens have been found in other parts of the country. This was recovered from a grave near Gala, Botetourt County, Va., about 1893 (U.S.N.M. No. 169663).

Nine small quartzite blades are shown at the bottom of the plate. Several of these may have been used as scrapers.

Evidence of a small encampment has been revealed on the slope a hundred yards or more from the left bank of the South Branch of the Hardware, about midway between the junction of the branches and the Red Hill School. This is within the area referred to as the Oliver site. In addition to numerous arrowpoints and other small chipped objects found nearby were several axes, two of which are shown in plate 9, *a* and *e*. Both are typical specimens, although the latter, *e*, is exceptionally well proportioned and very symmetrical and shows no effect of use. Another object, one of great interest, was discovered on the site. It is part of a large bannerstone and was found a few

inches below the surface in a garden, but whether it had been intentionally buried or had been on the surface could not be determined. The specimen had been broken and the fractured edges of the original perforation, which had passed through the middle, were later smoothed

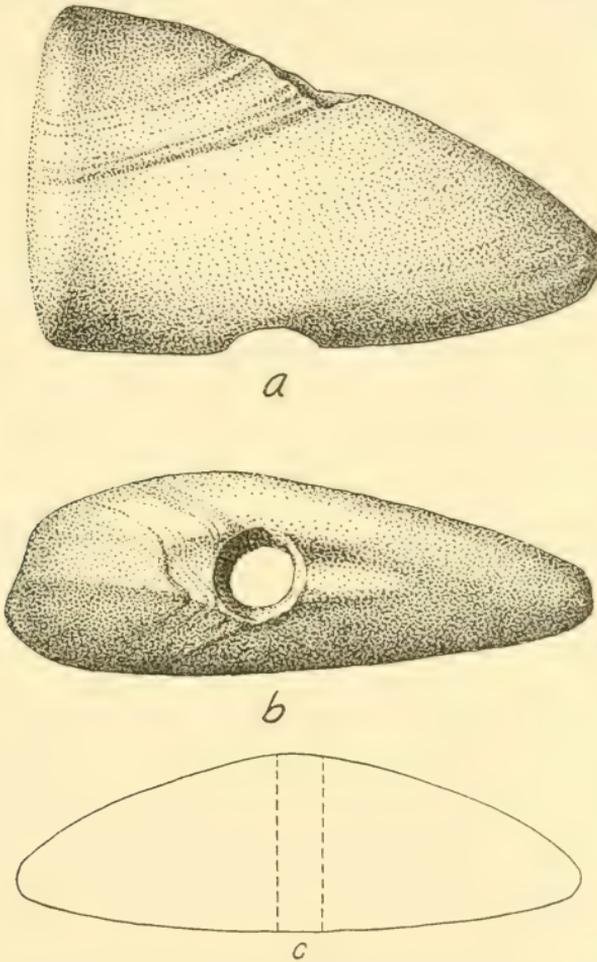


FIG. 4.—*a* and *b*, two views of part of a large bannerstone made of banded slate, found near Red Hill School, Albemarle County. After being broken, this half had been perforated and the fractured edges polished. Natural size. *c*, probable outline of the bannerstone as originally made, before being broken.  $\frac{1}{2}$  natural size. (U.S.N.M. No. 364588.)

and polished. In this restored condition it continued to be used. Two views of this interesting object are given in figure 4. The material is banded slate, light gray in color, which does not occur in this part of the country, and it is believed that the specimen came originally from

the far north or northwest, in the vicinity of the Great Lakes. Two other examples, very similar to this, are in the collections of the United States National Museum. One is from North Carolina and the other from Ohio. In the latter the new perforation had been started but not completed, and the edges of the fractured end had not been smoothed. These curious objects, of unknown use, had evidently been treasured by their owners. No fragments of pottery have been found on the site just mentioned.

Southwest of the Oliver residence, near the foot of the slope a short distance from the left bank of the South Branch, are traces of either a more extensive camp or, what is more probable, a site that had been frequently occupied. A spring formerly issued from the side of the hill just above the site, and the water flowed through a narrow channel to join the branch a few hundred feet away. This would have been a beautiful location for a camp, on the southern slope of a well-wooded hill which afforded protection against the north and west winds, and with a good supply of pure water. The land has been cultivated for many years, the gully filled, and the spring covered.

Arrowheads are numerous on the slope and adjacent low ground, and here they are more varied in form and in material than are those on the plateau above, where the more common types made of quartz and quartzite, occurring in the region, predominate. A few hammerstones, a pestle or clublike object, several pitted stones and extremely rough axes, one of which is shown in plate 9, *d*, all very crude, have been found here. One small fragment of a soapstone vessel and many bits of pottery have been recovered from the surface. The pottery is so weathered and the surface so disintegrated that it is seldom possible to determine the marking on the outer face; some fragments reveal the imprint of small twisted cords, but no impression of woven cloth has been recognized as such, although some few suggest the imprint of rigid basketry. The fragments resemble those found on the site of Monasukapanough, bordering the Rivanna.

About a third of a mile west of north of the Oliver house, on both sides of a small stream which flows into the Middle Branch just before the latter unites with the North Fork of the Hardware, are traces of a camp. The ground is very low, often marshy, and consequently difficult to examine. Many fragments of pottery have been recovered from a restricted area, besides a few arrowpoints and the two implements shown in plate 9, *b* and *c*. The pottery is similar to

that found on the site previously described; all is weathered and worn away on the surface.

Undoubtedly many other small camp sites similar to the three just mentioned are to be found along the courses of the several streams which unite to form the Hardware. All were probably temporary camps, occupied during the hunting season, when, as is well known, many families would leave their permanent village, often travel far, and "passe the tyme with hunting and fowling up towards the mountaines."

#### SUTHERLAND SITE

The road running in a northwesterly direction through North Garden and Crossroads and passing the mountain at Israel Gap is one of the oldest in Albemarle County. There is reason to believe a trail once followed the same general course. On the south side of this road, a mile or more southeast of the gap and about 3 miles in a direct line west of the Oliver site, is another locality very similar to that site. Here a long, narrow tongue of land projects due southeast from the higher ground, a spur from the south side of the gap. Small streams fed by many springs flow on both sides of the ridge and unite just below to form the principal fork of the South Branch of Hardware River, which, some miles beyond, bounds the Oliver site on the south. The ground on either side of the spur was formerly very marshy, overgrown, and consequently difficult to pass. The high land, rising thus above its marshy borders on three sides, was evidently well suited to the hunting of deer as described by Capt. John Smith, and that it was a favorite hunting ground is indicated by the vast quantities of arrowheads which are known to have been gathered from the surface. Now, after the land has been cultivated for more than a century, many are yet found which resemble those from the Oliver site. A few chipped implements, very rough and crudely made, which may be termed axes, are found in the vicinity, usually on the low ground. Three examples are shown in plate 10. This was undoubtedly a long-frequented hunting ground, as no trace of a permanent village has been discovered.

#### BURRUSS SITE

This small but very interesting site was discovered near the source of Jumping Branch, a small stream which flows south and soon joins the South Fork of Hardware River. It is near the old road, already mentioned, which extends from North Garden to

Crossroads, and about 1 mile west of south from the Red Hill School. Here is a comparatively level area a few acres in extent and sloping down to the left bank of the stream, with a steep hill rising from the opposite side. Many arrowpoints are now—and have been in the past—collected from the surface. The majority are made of white quartz and the usual grayish brown quartzite, similar to those recovered from the sites previously described, but others are made of materials less common, including jasper, chert, and argillite, as well as varieties of quartzite seldom encountered in the region. A view across the site is reproduced in plate 11, together with some of the more unusual specimens found on the surface. The specimen at the bottom of the plate, termed either celt or chisel, has a ground cutting edge at the right and shows the effect of much use.

Restricted areas, such as the one just described, where great numbers of projectile points are scattered over the surface, are frequently encountered near springs or on the banks of small streams in this part of Virginia. The scarcity of material other than arrowpoints and the total lack of pottery or any indications of a camp makes it evident that such sites were merely small hunting grounds where game was sought.

#### COOK SITE

An ancient trail of great importance led from James River up the valley of the Rockfish and thence over the mountain through Rockfish Gap to the Shenandoah. Another trail is believed to have led from Rockfish Gap across the intervening ridges and valleys to Israel Gap, near the Sutherland site, and to have continued down the course of the Hardware eastwardly, as has been mentioned elsewhere in these notes.

The coming together of several important trails necessarily made this a place of considerable interest.

The site to which reference is now made occupies the summit of a rounded knoll at the end of a ridge, rising a short distance east of the North Fork of Rockfish River, in Nelson County. It is on the farm of Charles B. Cook, and is about  $1\frac{1}{8}$  miles west of south of Avon post office. In one respect it is very unusual, for although it appears to have been a camp of rather more permanent nature than many, it occupied this exposed site, which, however, commanded a wide view of the surrounding country, including the gap through the mountains several miles away. No pottery was discovered on the site. Stone implements were numerous, including several hammerstones, broken arrowpoints, and some beautiful specimens made of

black chert which had probably been brought from the valley. Two club-shaped objects were of unusual interest. One of these is shown in figure 5; this may have been a primitive form of weapon rather than an implement. A fragment of a similar object was found on the camp site on the south of the Oliver site.

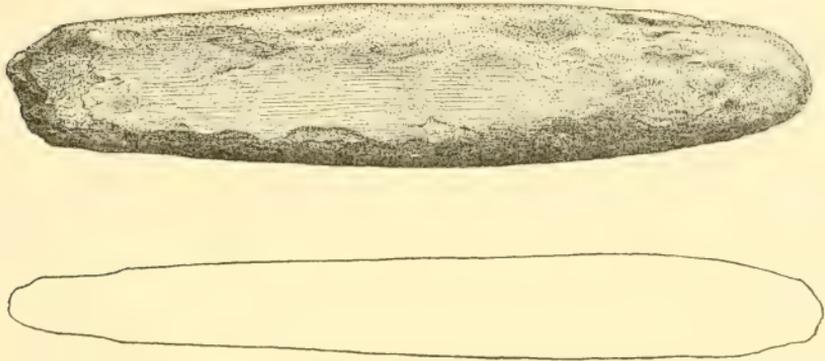


FIG. 5.—Club-shaped object made of greenstone, found on a camp site east of the North Fork of Rockfish River, south of Avon, Nelson County.  $\frac{1}{2}$  natural size. (U.S.N.M. No. 364596.)

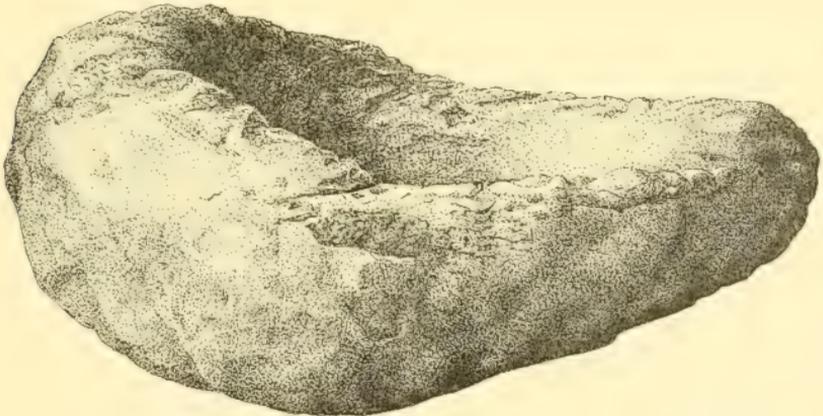


FIG. 6.—Mortar made of a block of amphibolite, found in Browns Cove, near the foot of the Blue Ridge, Albemarle County. About  $\frac{1}{3}$  natural size. (U.S.N.M. No. 337375.)

The secluded, protected spots along the foot of the mountains were often occupied by small groups, probably hunters, traces of whose camps are frequently revealed. A few objects of stone may be found, but seldom is any piece of special interest discovered. A massive mortar, formed from a piece of amphibolite, found in

Browns Cove, near the foot of the Blue Ridge, in Albemarle County, is shown in figure 6. It had probably been made and used near the spot where it was discovered; nothing similar has been found on the village or camp sites encountered in other parts of the county.

It is to be regretted that a more complete, more exhaustive archeological survey of the region could not have been made, and the same statement may be applied to the entire piedmont country. However, the few scattered sites described at this time are believed to be characteristic of the entire region, and if this be true, the examination of additional localities and the gathering of more material of the same nature would not tend to add greatly to what is now known concerning the manners and ways of life of the native tribes who once occupied the country. Two important investigations, however, remain to be carried on: One is to bring together and sift the evidence of a very early period of occupancy in piedmont Virginia; the other is to determine the route followed by the Siouan tribes from their ancient habitat beyond the Ohio to piedmont Virginia, to the land they claimed and occupied in 1607.





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# MORPHOLOGY OF THE INSECT ABDOMEN

## PART II. THE GENITAL DUCTS AND THE OVIPOSITOR

BY

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Bureau of Entomology,

U. S. Department of Agriculture



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INTRODUCTION

Mythologies usually begin with the bringing of order out of chaos. From this, however, it should not be hastily concluded that the results of all attempts to establish order where confusion has prevailed belong to the realm of mythology, even though they may deal with things by their nature unknowable. Particularly, the writer hopes, at least, that there may be seen some ground of plausibility in the scheme set forth in this paper, and in others of the same series that have preceded it.

for analyzing an insect in an orderly way from one end to the other. Incidentally it should be observed that the results come out the same regardless of which end is taken first, and this in itself is presumptive evidence of the soundness of the proposed solution. Of course, it may not be claimed that an orderly concept of the structure of an animal has, in itself, greater claim to truth than one that is prolix, unless it can be demonstrated that orderliness, and consequently simplicity is a fundamental law of animate nature. It is possible that the value of simplicity has been overestimated, and that too much confidence is raised in its favor by its mere reputation. We may concede that simplicity is the soul of wit, the essence of art, a distinguishing mark of virtue, etc., but when simplicity comes to be regarded even as an index of truth itself, we must look upon its claims with some suspicion. Simplicity, however, does have in all things a convincing manner.

Segmented animals, as every zoologist admits, are composed of a series of segments, and there is no dispute that the segments were most probably at one time alike. Hence, it follows that each segmentally composite section of the animal's body has the same basic and fundamental structure, a principle which also no one denies. Diversities of opinion concerning the correspondence of parts in different body sections, then, are merely matters of difference of interpretation.

In the study of insect anatomy entomologists have examined the insect's head as if it were a thing in itself, having only a cervical continuity with the rest of the body; they have minutely explored and topographically mapped the thorax, but have for the most part looked upon it also as a discrete entity; they have painstakingly investigated the abdomen, but without giving much thought to aligning its parts with those of the thorax and the head. Students in entomology are taught in this sectional manner, textbooks are written in the same disjointed style. In short, the first principle of insect anatomy is that an insect is *divided* into head, thorax, and abdomen. As a consequence, ideas concerning the unity of the insect are vague at best, and collectively are little short of chaotic.

For a number of years the writer has been attempting to discover the basic plan of arthropod organization that is repeated through the segments, and to see how the special modifications in the several body regions of the insect may conform with the structure of a theoretically generalized segment. The results are quite simple, and are derived from following the horizontal constructional lines through the entire segmental region of the trunk. This scheme for studying the insect

as a whole recognizes dorsiventrality as a primary factor in structural differentiation, and accepts the series of limb bases along the sides of the body as marking the anatomical distinction between dorsum and venter. The plan, in the abstract, can scarcely be questioned as morphologically sound. It is only in its practical application that questions of interpretation come up, and if, as applied by the writer, the scheme here and there conflicts with current local interpretations based on former opinions, justification for the interpretive alterations proposed must be found in the degree of improvement given to the general or perspective view of insect structure as a whole. The application of the plan, as carried out in this series of papers, will at least open a way by which the teacher in entomology may conduct his students at once straight through the insect without giving the impression that the head, the thorax, and the abdomen are each a region foreign to the others; if followed in descriptive entomology it would furnish a basis for a common nomenclature. The plan gives at once a unified and a simplified concept of insect morphology, and many facts unquestionably are in its favor; but there is no pretense here made to decree that order and simplicity in any particular pattern are synonymous with truth.

### I. GENERAL STRUCTURE OF THE ABDOMEN

In the study of the abdomen it is highly important to be able to identify the several morphologically distinct surface regions. These regions are the *dorsum* (fig. 1 A, B, D) lying above the region of the primitive limb bases; the *venter* (*V*) lying below the limb bases, and the *podial*, or *pleural*, *regions* (*P*) which are the areas of the limb bases themselves (*LB*). The dorsum is separated from the pleural region by the *dorso-pleural line* (*a-a*); the pleural region is separated from the venter by the *pleuro-ventral line* (*b-b*). Much confusion exists in descriptive works on entomology because the positions of these lines have not been clearly perceived, and, as a consequence, names have been applied to certain parts that do not properly belong to them. By observing whatever landmarks are present, however, it is usually possible to determine the limb base areas on the abdominal segments; the rest of the surface is then apportioned to the dorsum and to the venter.

The dorso-pleural line (fig. 1 B, *a-a*), beginning on the head (fig. 2 A), separates the lower edge of the cranium from the bases of the gnathopods (mandibles and maxillae); on the thorax (figs. 1 C, 2 B), it goes dorsal to the subcoxal plates of the leg bases, dipping down between them where necessary to pass beneath the spiracles;

on the visceral region of the abdomen it extends below the series of spiracles (fig. 1 C) and above the limb bases where the latter are present (fig. 2 C); and finally it runs out above the bases of the gonopods, pygopods, and uropods, or cerci (figs. 1 C, 2 D, E, F).

The pleuro-ventral line (fig. 1 B, *b-b*) begins anteriorly between the bases of the gnathopods and the ventral wall of the head (fig. 2 A); on the thorax (figs. 1 C, 2 B) it separates the leg bases from the true venter; on the abdomen it runs ventrad or mesad of the limb bases,

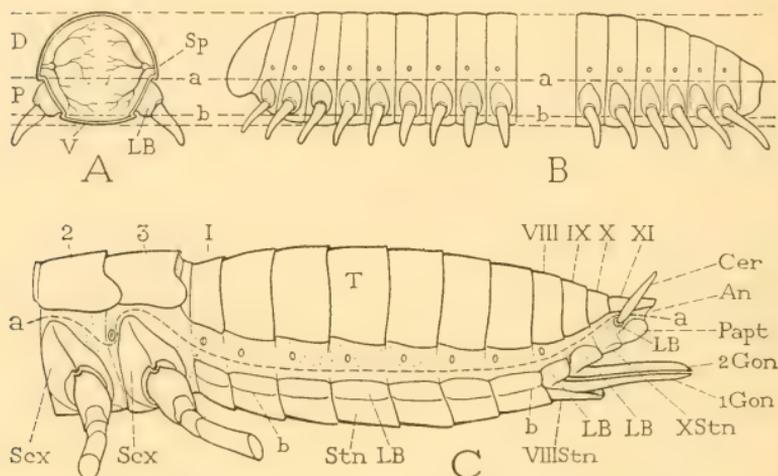


FIG. 1.—Diagrams showing the lengthwise division of the body surface of an insect into dorsal, ventral, and podial regions by the series of limb bases along the sides.

A, cross section, B, lateral view, of theoretically primitive condition in which the podial, or pleural, region of the body (*P*) consists of the segmental areas containing the limb bases (*LB*), the dorsum of the region (*D*) above the dorso-pleural line (*a-a*), and the venter (*V*) of that below the pleuro-ventral line (*b-b*).

C, generalized structure of thorax and abdomen of an adult female insect, with position of dorso-pleural line as indicated (*a-a*), and in which the limb bases form the coxae and subcoxae (*Scx*) of thorax, but unite with the sterna of abdomen, except in the genital segments (*VIII*, *IX*) and the eleventh segment (*XI*).

where the latter are distinct (fig. 2 C, D, E, F), but where appendages are absent it must be assumed to follow the line of fusion between the limb bases and the primitive sterna (fig. 1 C).

*Surface regions of the abdomen.*—The dorso-pleural line is frequently marked on the abdomen by a distinct longitudinal fold or groove of the integument running ventrad of the spiracles (fig. 1 A, *a-a*), the dorso-pleural nature of which is shown by the fact that the area above it corresponds with the dorsum of the thorax containing the tergal plates and the paratergal wing bases, while the area

immediately below it (*P*) corresponds with the region of the subcoxal pleural plates of the thorax (*Scx*). The pleuro-ventral line of the abdomen is also frequently indicated by the presence of a groove or other structural feature, as in certain Thysanura and in some holometabolous larvae. Where abdominal limb rudiments are present, their bases always occupy the areas between the folds or grooves marking the dorso-pleural and pleuro-ventral lines; but in most adult insects in which the abdominal appendages have been entirely suppressed, the limb base areas are continuously sclerotized with the primitive sterna in the definitive sternal plates, and, unless styli or other representatives of the free parts of the appendages are present, there is usually no indication in the definitive structure as to the primitive position of the pleuro-ventral line.

The dorsum of an abdominal segment may be occupied by a single tergal plate, which in some insects encloses the spiracles laterally, though the spiracles often lie in membranous paratergal areas; or the sclerotization of the dorsum may consist of a principal dorsal sclerite, and of one or more lateral paratergal sclerites. The abdominal pleural areas contain the appendage bases, where appendages are present, but the limb bases are commonly reduced to plates or lobes forming a part of the body wall, or they are entirely suppressed as individual structures, and their areas then become merely a part of the general pleural integument. In the last case the limb base area may be entirely membranous, or it may contain one or more pleural sclerites; when fully sclerotized, it is usually continuous with the primitive sternal sclerotization in a pleurosternal definitive sternum. The venter is the lower surface between the bases of the appendages, and contains the primitive sternal plates. The latter may retain their individuality, but, as just noted, the primitive sternum of each abdominal segment is more commonly united with the pleural sclerotizations. The definitive sternal plate thus formed, finally, may be still further enlarged by a fusion with paratergal plates on each side of the dorsum. It becomes evident, therefore, that the sclerotization of the abdomen is not necessarily an index to the primary regional divisions of the abdominal surface.

*The abdominal appendages.*—The appendages of the insect abdomen fall into three principal groups, namely, those of the pregenital, or visceral, segments, those of the genital segments (or segment), and those of the postgenital segments. The pregenital appendages take on such a variety of shapes and functions that it is impossible to give them collectively a distinctive name. The genital appendages are the *gonopods*. The postgenital appendages are the *pygopods* on the tenth

somite, represented by the postpedes of certain holometabolous larvae, and the *uropods*, or *cerci*, of the eleventh somite.

The pregenital appendages occur as distinctly appendicular organs principally in the Apterygota and in pterygote larvae. They never take the form of the thoracic pereiopods, but in a few cases they are multiarticulate and suggest that they are derived from jointed legs. Each appendage, when well developed, consists of a basis (fig. 2 C, *LB*) and of a movable appendicular part (*Sty*), and the basis frequently bears, mesad of the latter, an eversible and retractile vesicle (*Vs*). The appendicular process, which commonly takes the form of

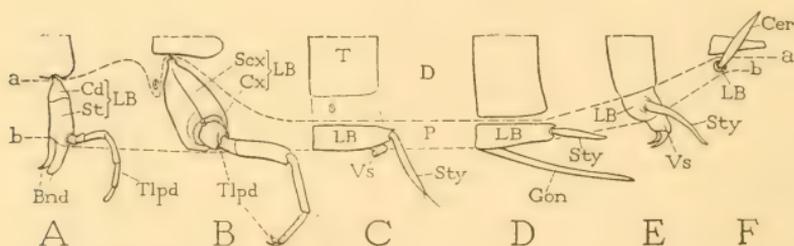


FIG. 2.—Diagrams suggesting the homologies of the basal parts of the appendages and the position of the dorso-pleural and pleuro-ventral lines (*a-a*, *b-b*) relative to them.

A, a head appendage, with basis subdivided into cardo and stipes (*Cd*, *St*), the latter bearing a pair of endites (*Bnd*) and the telopodite (*Tlpd*).

B, a thoracic appendage, with basis divided into subcoxa and coxa (*Scx*, *Cx*), the latter bearing the telopodite (*Tlpd*).

C, a thysanuran abdominal appendage, with limb basis undivided, and bearing a stylus (*Sty*) and vesicle (*Vs*).

D, a typical gonopod, with undivided basis (valvifer) bearing a stylus (*Sty*) and gonapophysis (*Gon*).

E, a generalized larval appendage of tenth segment (pygopod) or of other segments, bearing a stylus and vesicle.

F, a cercus (uropod) of eleventh segment, with small or rudimentary basis, and unsegmented distal shaft.

a stylus, a gill, or a tapering process, is usually provided with muscles, and the muscles always have their origins in the basis. The vesicle may be a small eversible sac, as in the Thysanura, a gill-bearing tubercle, as in certain sialid larvae, or a lobe serving for locomotor purposes, as in the larvae of Lepidoptera and chalastogastrous Hymenoptera; it also is provided with muscles, which in Thysanura arise within the limb basis, but which in the other forms may take their origins on the dorsum of the body wall. The limb basis usually has the form of a plate or lobe broadly implanted in the pleural area of its segment; it is generally immovable, but in the Thysanura and in the genital segments of female Pterygota it is provided with muscles arising on the body wall.

The gonopods in their more generalized form (fig. 2 D) resemble the pregenital appendages of the Thysanura (C), but they lack eversible vesicles, and each is characterized by the presence of a genital process, or *gonapophysis* (D, *Gon*) arising from the proximal mesal angle of the basis. Typically the distal process, or stylus (*Sty*), and the gonapophysis (*Gon*) are each movable by muscles arising in the basis; and the basis is movable on the body by muscles arising on the tergum of the supporting body segment. In the female, the bases of the gonopods (fig. 1 C) become the supporting plates of the ovipositor (first and second valvifers), and retain their dorsal muscles arising on the eighth and ninth abdominal terga. The female gonapophyses form the first and second valvulae (*1Gon*, *2Gon*), the basal muscles of which persist in Thysanura, but are generally lost in Pterygota. The distal processes (styli) of the gonopods are retained in Thysanura and on the second gonopods in some of the more generalized Pterygota.

The pygopods, or appendages of the tenth abdominal segment, are always absent in postembryonic stages of exopterygote insects, though they may be present in the embryo. In many endopterygote larvae, however, they are well developed as the "anal legs", or postpedes (fig. 2 E), which usually resemble the appendages of the pregenital segments. The distal process (stylus) is retained on the pygopods only in certain Neuroptera, but in some Neuroptera and in Lepidoptera and chalcidogastrous Hymenoptera the vesicle (*Vs*) forms a retractile lobe generally provided with claws.

The uropods, or cerci (fig. 2 F, *Cer*), belong to the eleventh abdominal segment. Each appendage arises typically from a membranous area behind the tenth tergum between the basal angles of the epiproct and the paraproct. In certain orthopteroid insects, the principal part of the cercus is supported on a small but distinct basal segment (*LB*). Most of the muscles that move the cercus are muscles of the tenth segment, but in some insects a muscle of the cercus arises on the epiproct. The cerci never have muscles arising on the paraprocts.

From this brief review of the various forms of appendages that occur on the insect abdomen it will be seen that the appendages all have a common type of structure, and that the gonopods differ from the others only in the presence of proximal processes (the gonapophyses) arising from the mesal angles of their bases. The bases of the abdominal appendages form a series of lobes, plates, or integumental areas occupying the pleural region on each side of the abdomen, which is continuous anteriorly with the regions of the limb bases on the thorax and the head.

## II. MORPHOLOGY OF THE GONADS AND THE GENITAL DUCTS

The embryonic genital ducts of insects are simple mesodermal tubes continuous with the mesodermal walls of the gonads. The primitive ducts had separate openings to the exterior of the body, the apertures in the male being located probably on the tenth abdominal segment, those of the female on the seventh. In the majority of modern insects, however, a median ectodermal exit apparatus, together usually with accessory structures, has been added to the primitive ducts, and in many cases the latter even are largely replaced by ingrowths from the ectodermal parts. The definitive median exit duct of the male (except possibly in *Collenbola*) opens in the ventral membrane between the ninth and tenth abdominal segments, which membrane probably belongs to the ninth primary somite. The definitive median egg passage of the female varies in its extent and point of opening from the posterior part of the seventh abdominal segment to the posterior part of the ninth, or it may open in common with the rectum into a small cloacal pouch on a terminal segment of the abdomen representing the combined ninth and tenth somites.

The gonads are mesodermal structures developed in the dorsal parts of the splanchnopleure as ridges of the latter extending continuously through several abdominal segments to enclose the germ cells here finally located. The gonadial ducts arise from ridges of cells extending posteriorly from the gonads. The subsequent compound structure of the gonads results from a secondary subdivision of each organ into a series or group of egg tubes or sperm tubes. There is no evidence from ontogeny that these gonadial tubes ever had separate openings or ducts to the exterior, and yet much theoretical speculation has been based on the idea that the component tubes of the ovaries and testes represent primitively segmental organs. The following discussion of the subject, therefore, may not be superfluous as an introduction to a study of the appendicular structures associated with the definitive genital apertures.

*Early history of the germ cells.*—In many insects, representing widely separated groups, the germ cells and the somatic cells are differentiated at the time of cleavage; and in such cases the germ cells are distinguishable when the blastoderm is formed as a group of special cells at the posterior end of the germ band. From this position the germ cells later migrate into the interior of the embryo, and are eventually associated with the dorsal part of the splanchnic wall of the mesoderm in the abdominal region of the body. Since it is not possible in all cases to recognize the germ cells as such prior to their enclosure in the abdominal mesoderm, some of the earlier, otherwise reliable

works on insect embryology contain explicit descriptions of the supposed origin of the germ cells from the mesoderm.

The most detailed account of the history of the insect germ cells after their appearance in the mesoderm is that given by Heymons (1892) in his description of the development of the female reproductive organs of *Blattella* (*Phyllodromia*) *germanica*. The germ cells of *Blattella*, according to Heymons, appear as a few large cells scattered in the posterior parts of the mesoderm at the time when the germ band consists only of ectoderm and a simple underlying mesodermal layer. At the time the appendages are formed the germ cells are arranged in two lateral series behind the first segment of the abdomen, and most of them occur above the intersegmental grooves. With the development of the coelomic sacs, therefore, the germ cells are situated in the dorsal parts of the dissepiments between the coelomic cavities. They extend now from the first to the seventh abdominal segments.

Within the coelomic septa the germ cells multiply, and soon, Heymons says, many of them are crowded out posteriorly into the coelomic cavities. The extruded cells remain in contact with the coelomic walls and migrate posteriorly upon them to the splanchnic walls of the sacs. Here they penetrate between the epithelial cells, and thus become again imbedded in the mesoderm. Wheeler (1893) has observed that at this stage in *Conocephalus* (*Xiphidium*) some of the germ cells may become detached and fall into the coelomic cavities.

*Origin of the gonads.*—The surface of the splanchnic epithelium, where the latter is penetrated by the migrating germ cells, becomes broken, and its cells grow out irregularly about the germ cells (fig. 3 A), which eventually they enclose in a loose mesodermal covering. The germ cells of *Blattella*, Heymons says, now form a continuous series on each side of the body, extending from the second into the sixth abdominal segment, the cells that remained in the dissepiments filling the gaps between those that were extruded and which later took a position in the segmental areas of the coelomic walls. The series of germ cells and their mesodermal coverings, projecting slightly into the body cavity, constitute the *genital ridges* of the embryo, which are the primitive rudiments of the gonads.

Wheeler (1893), in his study of the development of the gonads in *Conocephalus*, was not able to distinguish the germ cells from the mesodermal cells until the germ cells are clustered in segmental groups in the splanchnic walls of the coelomic sacs, where they are partially covered by a mesodermal epithelium. In *Conocephalus* at this stage the paired gonad rudiments occur in the first to the sixth abdominal

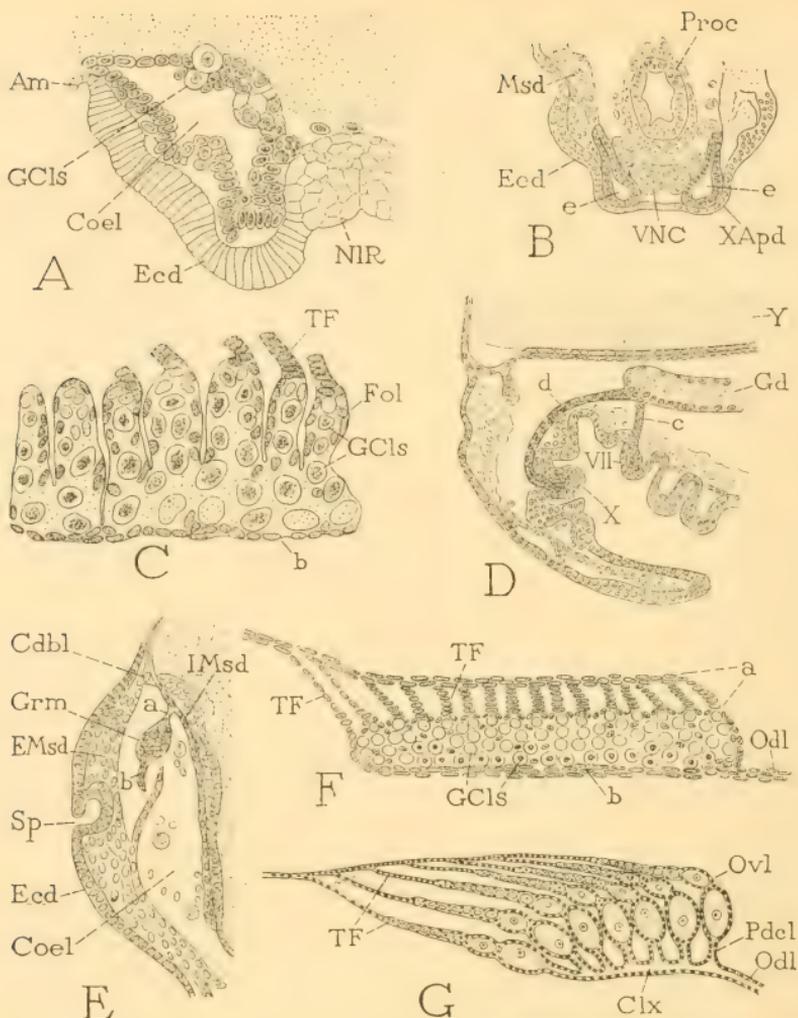


FIG. 3.—Development of the gonads and the genital ducts of insects.

A, cross section through an abdominal coelomic sac of *Blattella germanica* (from Heymons, 1892), showing group of germ cells (*GCLs*) in splanchnic wall of mesoderm.

B, section through posterior end of embryo of *Conocephalus* (from Wheeler, 1893), showing termination of male genital ducts in ampullae (*e*) in appendages (*XApd*) of tenth segment.

C, differentiation of female gonad of *Blattella* into ovarioles (from Heymons, 1892).

D, showing branching of the gonadial duct (*c, d*) in embryo of *Forficula* to seventh and tenth segments (from Heymons, 1895).

E, section through a coelomic sac of *Leptinotarsa* (from Wheeler, 1889), showing embryonic gonad differentiated into a dorsal suspensorium (*a*) attached to splanchnopleure (*IMsd*), a germinal region (*Grm*), and a ventral strand (*b*) continuous with the duct.

F, later stage in development of female gonad of *Blattella* (from Heymons, 1892), with dorsal suspensorium (*a*) differentiated into terminal filaments (*TF*), germ cells (*GCLs*) in undivided middle part, and ventral strand (*b*) continuous with duct (*Odl*).

G, subsequent stage in development of ovary of *Blattella* (from Heymons, 1892), with gonad completely divided into ovarioles (*Ovl*).

segments, and Wheeler points out that "the reproductive organs of *Xiphidium* are therefore truly metameric in their origin." Later, however, with the rapid multiplication of the germ cells, the successive gonad rudiments on each side of the body elongate and unite, resulting in the "formation of a continuous strand of germ cells with their accompanying epithelial cells".

The recent account by Lautenschlager (1932) of the development of the female gonads in *Solenobia triquetrella* (Psychidae) is in essential agreement with the observations of earlier writers on Orthoptera. The paired segmental groups of germ cells, lying in the fourth, fifth, and sixth abdominal segments, condense and unite on each side into a single group having the position of the definitive gonad in the fifth segment. Here each composite group of germ cells becomes enclosed in a layer of small mesodermal cells. The latter form a thin sheath about the germ cells dorsally and laterally, but ventrally they form three thick cellular masses, which later give rise to the ovarial pedicles and the lateral ducts of the ovaries. According to Lautenschlager the follicle cells of the definitive egg tubes of *Solonobia* also take their origin from the cells of the mesodermal sheaths of the gonads.

Seidel (1924), on the other hand, finds that in *Pyrrhocoris apterus* the segmental groups of germ cells, formed at an early embryonic stage, become surrounded individually by mesodermal epithelium, and remain thus, up to a relatively late period of development, as a series of distinctly separated gonadial rudiments segmentally distributed on each side of the body in somites *II* to *VIII* of the abdomen. Eventually, the posterior rudiments migrate forward until all are assembled in segments *II* and *III*, where those of each lateral group develop directly into the seven genital tubes of the adult organ. The only union that takes place between them is in the lower tubular parts of the primary elements, which unite to form the lateral duct. Seidel claims that this condition in *Pyrrhocoris apterus* demonstrates the direct origin of the definitive genital tubes from the segmental gonadial rudiments of the embryo. However, since the case appears to be exceptional, and since the Hemiptera are in many ways specialized insects, the suspicion is created that the facts observed are to be interpreted as the result of elimination in some of the earlier stages of development. Yet, as we shall see, there is evidence to suggest that the definitive egg tubes and sperm tubes were first formed as segmental outgrowths from continuous gonads produced by the union of the primitive segmental gonads.

With most of the higher insects the reproductive organs appear from the beginning as continuous genital ridges. In the honey bee, as

described by Nelson (1915), the genital ridges of the female at first extend along the splanchnic walls of the mesodermal tubes from the second to the seventh abdominal segments, inclusive. Later they become shorter and thicker, and finally reach only from near the anterior end of the fourth abdominal segment into the anterior end of the seventh.

Beyond the region of the germ cells the genital ridges are continued posteriorly, but they are here much reduced in size and consist of simple cellular strands. These parts of the ridges will form the mesodermal parts of the lateral genital ducts. It has been observed in many insects that the primitive ducts of the female in embryonic and larval stages turn downward posteriorly and are attached to the ectoderm at the posterior end of the ventral wall of the *seventh* abdominal segment. The male ducts of Orthoptera, as described by Heymons and Wheeler, extend into the *tenth* segment and are here similarly attached to the ectoderm.

*Comparison with Annelida.*—The early segregation of the germ cells in *Blattella* into groups within the dorsal parts of the intercoelomic septa is highly suggestive, as Heymons (1892) points out, of the similar arrangement of the germ cells in many adult Annelida, in which the gonads are simple swellings of the dissepiments, retaining the germ cells beneath a thin mesodermal epithelium. The gonads of Annelida, however, may occur on almost any part of the coelomic walls, but wherever they are formed, the germ cells are not long retained within them, being soon thrown out into the body cavity, where they mature, and from which they are eventually discharged through the nephridia, through special genital ducts, or by way of a pore or rupture in the body wall. The liberation of the germ cells into the body cavity in Annelida, Heymons claims, is represented in *Blattella* by the extrusion of the germ cells from the dissepiments before their reentrance into the mesoderm, the only difference being that in the cockroach the germ cells are not detached from the mesoderm, but migrate upon its surface to their definitive positions in the genital ridges. In *Conocephalus*, however, Wheeler (1893) observed that some of the primitive germ cells of the segmental clusters "show a tendency to leave the wall of the somite and to drop into the coelomic cavity." These cells, he says, "sometimes enlarge considerably, become vacuolated and take on the appearance of young ova."

If the condition described by Heymons in *Blattella* is truly a primitive one, it becomes evident that the definitive gonad of the Arthropoda is a secondary structure produced by the enclosure of the previously liberated germ cells in folds of the splanchnic mesoderm, which folds

close over the germ cells and afford them a protected coelomic space in which to complete their development. A similar mesodermal envelope surrounds the gonads in some of the Annelida, and may be continuous with an exit duct. On the other hand, if the condition described by Wheeler in *Conocephalus* is primitive, it would appear that the segmental clusters of germ cells in the splanchnic mesoderm are the primary gonads; and even in *Blattella* Heymons observes that some of the germ cells remain within the intercoelomic septa, where they become later a part of the continuous series of germ cells contained in the genital ridges. In most other insects in which the origin of the reproductive organs has been studied, it is found that the gonads are formed as mesodermal ridges which from the beginning contain the germ cells.

By whatever method the germ cells may become aggregated in the coelomic walls, it is clear, at least, that the primary paired gonads of insects are segmentally arranged, and that the continuous genital ridges later formed are secondary structures resulting from the fusion of the series of primitive gonads on each side of the body. It would seem scarcely probable, therefore, that the subsequent division of the genital ridges into a series of ovarial or testicular tubes can represent a primitive segmental structure of the reproductive organs, though in a few adult apterygote insects and in the embryo of *Pyrrhocoris apterus* the tubes do coincide with abdominal segments. In some of the other Apterygota, and in Protura, the mature gonad is a single, elongate sac continuous posteriorly with the duct, as it is also in most other members of the Arthropoda. In such cases, however, the gonadial sac has the structure of a single secondary tube and not that of a primitive genital ridge.

*Origin of the gonadial tubes.*—The definitive ovaries and testes of the majority of insects consist each of a series or group of diverticula arising from the common lateral duct (fig. 3 G). The ovarian tubes are free and end in terminal filaments, which are generally united in a cluster at their distal ends. In the male the testicular tubes usually lack terminal filaments, and those of each organ are generally bound together in an investing sheath; otherwise they do not differ from the egg tubes of the female.

The differentiation of the secondary continuous genital ridges into a tertiary series of tubes has been minutely followed by Heymons (1892) in the female of *Blattella*, and most other accounts of the development of the reproductive organs show that the process is essentially the same in both the female and the male of insects having compound gonads. By a multiplication of the cells along the bases

of the genital ridges each gonad in the female comes to be suspended from the splanchnopleure by a cellular sheet (fig. 3 E, *a*). This suspensorial sheet Heymons calls the *Endfadenplatte*, since it is destined to form the terminal filaments (*Endfäden*) of the ovarioles. A thickening of the fold along the lower border of the ridge forms a *ventral strand* of the gonad (*b*), which gives rise to the ovariole pedicles and the calyx of the oviduct; posteriorly it is continuous with the free part of the lateral duct. The middle part of the gonad (*Grm*) between the suspensorial dorsal plate and the ventral strand contains the germ cells, and is therefore the germarium, or region of the primitive ovary from which are formed the egg tubes of the definitive organ.

The germ cells at this state, as described by Heymons in *Blattella*, are evenly distributed throughout the length of the median part of the gonad, and the organ increases in thickness owing to a multiplication of the germ cells. The dorsal plate now separates from the wall of the body cavity, and its flat, elongate cells become arranged in about 20 vertical rows (fig. 3 F, *TF*). These columns of cells form the terminal filaments of the definitive ovarioles. The first appearance of the egg tubes is indicated by a series of dorsal swellings of the middle region corresponding with the columns of filament cells. Then the swellings are converted into definite ovarial lobes by a deepening of the grooves between them (*C*), until finally the gonad is cut vertically into separate compartments as far as the ventral strand. The compartments are the ovarial tubes, each of which is covered by an epithelial layer of mesodermal cells, and contains a number of egg cells (*GCl's*). In the larva of *Cloëon dimidiatum*, Lubbock (1863, 1866) observed that the ovaries are at first long cylindrical organs, each consisting of a central body with short lateral lobules. By the end of larval life the lobules have enlarged and have taken on the form of typical ovarial tubules. The developmental processes in these comparatively generalized insects would seem more probably to represent a primitive condition than that described by Seidel in the specialized hemipteron *Pyrhrocoris apterus*, in which the definitive genital tubes are said to be developed directly from independent segmental gonadial rudiments.

The exit apparatus of the egg tubes is formed from the ventral strand of the gonad, which becomes cleft between the attachments of the tubes upon it, and thus divided into the rudiments of the ovariole pedicles (fig. 3 G, *Pdcl*). The undivided part of the ventral strand and its posterior continuation become the lateral oviduct (*Odl*), the anterior end of which supporting the pedicles is widened to form the calyx (*Clx*). By a shortening of the calyx, the egg tubes of the

roach become horizontal and the ovary assumes its definitive form and position. In many insects, however, as in Ephemera, Dermaptera, Plecoptera, Phasmidae, and Acrididae, the ovarioles preserve their more primitive serial arrangement on the elongate calyx, as at an immature stage of the cockroach (G).

The development of the testes does not differ materially from that of the ovaries. The sperm tubes usually lack terminal filaments, and the division of each testis into compartments is not always apparent externally, and is sometimes incomplete. In the Lepidoptera, according to the studies of Zick (1911) on *Pieris*, the lumen of the testis is undivided until about the time of hatching, when there begins the formation of the septa which will divide the organ into four tubular sections. The septa are infoldings of the testicular wall, which grow inward toward the posterior ventral part of the organ where the duct arises.

*The lateral ducts.*—The primitive mesodermal exit tubes of the gonads become the lateral oviducts in the female and the vasa deferentia in the male, except in so far as they may be partially replaced by branches of the ectodermal median duct. Since the mesodermal ducts are derived from the coelomic walls, they probably originate as channels between epithelial folds continuous with the epithelial covering of the germ cells, which eventually close to form tubes. The idea that the reproductive ducts of Arthropoda are modified nephridial tubes is purely theoretical, and there is nothing to suggest that they are not, from the beginning, canals of the mesoderm formed specifically for the conduction of the germ cells to the outside of the body. Such ducts exist in some of the Annelida, and they may even unite distally in a common outlet tube (Hirudinea).

The primary mesodermal oviducts of insects undoubtedly opened to the exterior on the seventh abdominal segment, since in embryos and in young nymphal and larval stages of many modern insects they are attached to the ectoderm at the posterior end of the venter of the seventh segment. Heymons and Wheeler were the first to call attention to this condition in the more generalized insects, and the same thing has since been observed in representatives of most of the higher orders by various subsequent investigators. The subject has been so well reviewed by Nel (1930) that nothing further can be added here to substantiate the general conclusion. Nel quotes authorities to show that the termination of the mesodermal oviducts in the seventh segment is now known to occur in Thysanura, Ephemera, Odonata, Dermaptera, Orthoptera, Hemiptera, Coleoptera, Lepidoptera, Hymenoptera, and Diptera. Though some writers say that the openings

are *on* the seventh sternum, and others state that they are *between* the seventh and eighth sterna, the fact probably is the same in each case, since the "intersegmental" membranes of the abdomen are the posterior parts of the primary segments. The mesodermal oviducts retain in the adult stage the primitive position of their openings on the seventh venter, or between the seventh and eighth sterna, only in Ephemera. The paired female gonopores of the Ephemera are in some species widely separated, while in others they are approximated and open into a slight median depression of the intersegmental fold. In Dermaptera, however, the lateral oviducts open into a short median ectodermal pouch between the seventh and eighth abdominal sterna.

The history of the male genital ducts of insects has been less studied than that of the female ducts, but according to the elaborate embryological studies of Heymons (1890, 1895) and Wheeler (1893), the mesodermal vasa deferentia in the Orthoptera are first attached to the ectoderm of the ventral wall of the tenth abdominal segment. Paired male gonopores are retained in Ephemera and in some Dermaptera, but they are situated on intromittent organs, or on a single organ in some Dermaptera, which appear to be evaginations of the ventral wall of the ninth segment. According to Palmén (1884) the vasa deferentia in half-grown ephemerid larvae are attached to the posterior border of the ninth abdominal venter, and the penes are formed later as evaginations of the body wall at the points of attachment of the ducts. Palmén believed that the definitive ducts opening on the penes are the ends of the primitive vasa deferentia, but Wheeler (1893) found in *Blasturus* that a considerable length of each exit tube is lined by an intima which is shed during ecdysis attached to the exuviae of the penis and the body wall. In Dermaptera it is generally conceded that the mesodermal vasa deferentia terminate in ectodermal ejaculatory ducts. In all the higher insects the vasa deferentia come together in a single, median ejaculatory duct of ectodermal origin opening on the posterior part of the ninth venter.

*The median ducts.*—In all insects but Ephemera and male Dermaptera the lateral genital ducts discharge through a median outlet tube. In the male the median duct (ductus ejaculatorius) opens on the posterior part of the ninth abdominal segment, usually on an evagination forming an intromittent organ. In the female the opening of the median duct is variable: in some insects (Dermaptera) it is located on the posterior part of the seventh abdominal segment, in others on the eighth, and in still others on the ninth segment. The nature of the median female duct and the relation of the median genital open-

ing to the paired gonopores and the paired ducts have been matters of discussion and diversities of opinion for more than a century. A historical survey of the subject from 1815, when Herold first showed that a part of the female duct system is of ectodermal origin, is given by George (1929).

In the Dermaptera, as we have seen, the lateral oviducts open into a short median ectodermal ingrowth between the seventh and eighth abdominal sterna. Several writers have asserted that the same condition exists in Mantidae and Blattidae, but, as will later be shown, this idea is based on an erroneous interpretation of the anatomical facts in the adult insects of these families. Many insects, however, in their embryonic or postembryonic development, recapitulate the primitive condition found in Dermaptera, in that the first rudiment of the common oviduct appears as a median ingrowth on the posterior part of the seventh venter, with which the approximated lateral ducts become united.

The variable position of the female genital opening in different groups of insects has created a perplexing morphological problem, but the recent work of Nel (1930) on Acrididae, and of George (1929) and Metcalfe (1932a) on the hemipteron *Philaenus* leaves no doubt that the primitive position of the median gonopore in female insects is on the posterior part of the seventh abdominal segment behind the seventh sternum, and that the definitive opening, whether on the eighth or the ninth segment, is a subsequent formation. These writers are not entirely in accord as to how the egg duct is extended from the seventh to the eighth or ninth segment, but their observations lead to the same essential conclusions.

It is agreed that the first rudiment of the median duct is formed in a late embryonic or an early nymphal stage as an ectodermal invagination on the posterior part of the venter of the seventh abdominal segment (fig. 4 A, *Odc'*). According to Nel and George the primitive gonopore (*Gpr'*) here located in Acrididae and *Philaenus* runs out into a median groove on the eighth venter. Later, the edges of this groove, beginning anteriorly, grow together and convert the channel into a cuticle-lined tube. In this way the primary opening on the seventh segment (A, *Gpr'*) is lost as the median duct is extended through the eighth segment (B, *Odc*) and acquires its definitive opening (*Gpr*) behind the sternal plate of this segment.

A second invagination is formed in most insects at the posterior end of the eighth abdominal segment, which gives rise to the sperm receptacle, or *spermatheca* (B. *Spt*). Hence, with the posterior extension of the oviduct, the gonopore and the spermathecal opening come

to lie in close proximity, and the eggs may be readily fertilized as they issue from the former. Then the two openings, in the majority of generalized insects, are carried inward by the formation of a copulatory pouch, the *bursa copulatrix*, or *genital chamber* (C, *GC*), invaginated above the eighth sternum.

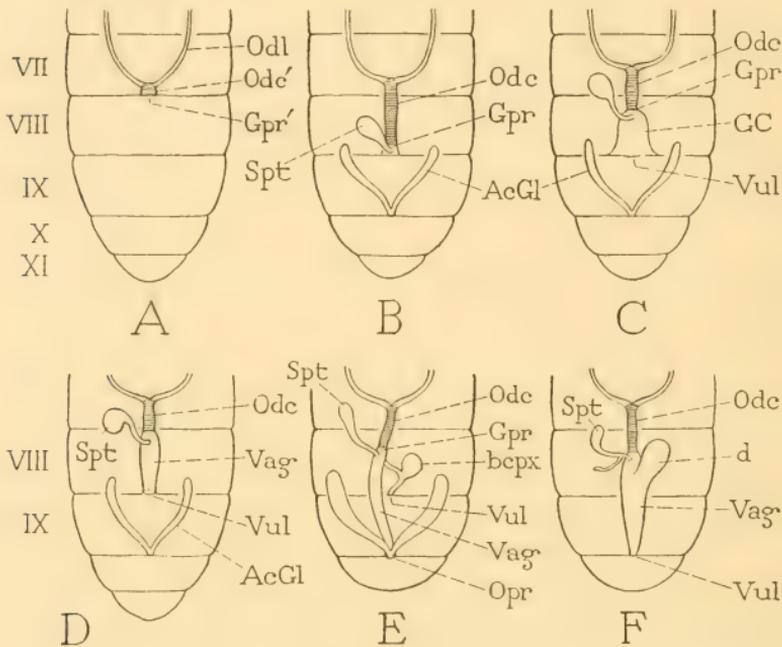


FIG. 4.—Diagrams showing the development of the median oviduct, and the evolution of the secondary copulatory structures added to the duct.

A, origin of primitive median oviduct on seventh abdominal segment.

B, extension of oviduct to end of eighth segment.

C, formation of genital chamber (*GC*) behind eighth sternum to form a copulatory and fertilization pouch receiving the oviduct and the spermatheca.

D, genital chamber having form of a tubular vagina (*Vag'*).

E, vagina extended to ninth segment, where it opens, but retains the original copulatory opening (*Vul*) on eighth segment.

F, vagina opening only on ninth segment.

*AcGl*, accessory glands; *bcpx*, copulatory pouch of genital chamber; *d*, diverticulum of vagina; *GC*, genital chamber, or bursa copulatrix; *Gpr*, gonopore; *Gpr'*, primary median gonopore; *Odc*, oviductus communis; *Odc'*, primary median oviduct; *Odl*, oviductus lateralis; *Opr*, oviporus; *Spt*, spermatheca; *Vul*, vulva, ostium vaginae.

The posterior opening of the genital chamber thus becomes both a copulatory entrance, and the final exit for the fertilized eggs. It therefore may be termed the *vulva* (*Vul*). The true gonopore (*Gpr*) is still the opening of the oviduct into the genital chamber. The genital

chamber, finally, may take the form of an elongate sac or a slender tube continuous with the oviduct (D). In such cases the median egg passage consists of an anterior part (*Odc*), which is the *true oviduct* (Eiergang), since it serves only for the conveyance of the eggs, and of a posterior section appropriately distinguished as the *vagina* (*Vag*). The two parts are separated approximately by the opening of the spermatheca into the anterior end of the vaginal region of the tube.

On the venter of the ninth abdominal segment there is commonly formed a third median invagination, which gives rise to the *accessory glands* (fig. 4 B, *AcGl*). The opening of these glands may be included in the genital chamber by the posterior extension of the eighth sternum, but it always lies between the bases of the ovipositor blades of the ninth segment when an ovipositor is present.

The observations of Metcalfe (1932a) on the manner by which the median oviduct becomes extended from the seventh to the eighth segment in *Philaenus* are somewhat different from those of George (1929) on the same insect and of Nel (1930) in Acrididae. According to Metcalfe there is formed primarily in *Philaenus spumarius* an oviducal invagination behind the seventh sternum, and a "uterine" invagination behind the eighth sternum. The second extends forward and overlies the first. Then the anterior opening becomes closed, and the opposing walls of the two invaginations come into contact, unite, and eventually break down, thus establishing a continuous median passage opening posteriorly through the primary "uterine" aperture behind the eighth sternum. The anterior end of the "uterine" invagination, which does not unite with the oviduct, becomes the functional sperm receptacle of the adult. It seems probable that the "uterine" invagination observed by Metcalfe represents both the true spermathecal rudiment and the genital chamber invagination of orthopteroid insects, which latter may become a vaginal section of the definitive egg passage.

In all Orthoptera and Hymenoptera and probably in most Hemiptera and Diptera, the egg exit is the secondary opening of the median oviduct established on the eighth segment, or in the intersegmental membrane behind the eighth sternum. This opening, the true gonopore, however, is usually concealed by an extension of the eighth sternum, or of the seventh sternum; and it may be carried inward within a copulatory invagination having the form of an open genital chamber, or of a tubular vagina, in which case the functional genital aperture is the vulva, that is, the external opening of the genital chamber or vagina.

In many of the other orders, however, the egg passage is subject to a further extension in a posterior direction, and its opening may then come to be on the venter of the ninth segment behind the ninth sternum. Thus, in Panorpidae, most Trichoptera and Lepidoptera, all Coleoptera, and apparently in some Hemiptera and Diptera, the median egg passage extends into the ninth segment and has an opening on the venter of this segment in common with that of the accessory glands, if these glands are present. When the egg passage is thus continued from the eighth segment into the ninth, the added part becomes an extension of the genital chamber, or of its derivative, the vagina, having its opening, the vulva, transferred from the venter of the eighth segment to that of the ninth. The primary oviduct remains unaltered; but the vaginal region of the exit tract now receives both the spermatheca and the accessory glands, and in most cases serves as a copulatory pouch.

The morphology of the extension of the efferent passage from the eighth to the ninth segment is not so clear as that of the extension of the oviduct from the seventh to the eighth segment. The ontogenetic processes involved are less simple, and it is difficult to give them a uniform interpretation.

An intermediate condition in the transference of the functional genital aperture from the eighth segment to the ninth occurs in Lepidoptera (fig. 4 E), where, in the majority of families, there is retained a copulatory opening on the eighth segment (*Vul*) leading into a copulatory pouch (*bcp*) and the spermatheca (*Spt*), while, on the ninth segment (or the combined ninth and tenth somites) there is established a posterior vaginal opening (*Opr*) in common with the aperture of the accessory glands (*AcGl*). The copulatory opening (*Vul*) on the eighth segment is the vulva of orthopteroid insects. The tubular passage in the eighth segment leading to the vagina, with its diverticulum known as the bursa copulatrix (*bcp*), and the part of the vagina receiving the spermatheca, together represent the genital chamber invagination of the eighth segment. The rest of the vaginal tube (*Vag*) is a secondary extension through the ninth segment. Since the posterior opening serves only for the discharge of the eggs it may be distinguished as the *oviporus* (*Opr*).

According to the account given by Jackson (1889) of the development of the female ducts and associated organs in *Vanessa io*, the definitive egg passage of Lepidoptera is formed, as we should expect, from three sections. The second and third have independent ectodermal origins; the first is formed as an outgrowth from the second. Prior to the appearance of the first rudiment, which is that of the

true oviduct, there are produced by invagination of the ectoderm two median bilobed "vesicles", one on the venter of the eighth abdominal segment, the other on the venter of the ninth segment. The lips of the anterior depression grow out in the form of two longitudinal folds, which unite to form a tube. This is the middle section of the future median passage. Its anterior end is then extended as a cellular growth into the seventh segment, where it unites with the lateral mesodermal ducts. This part becomes the anterior section (the true oviductus communis) of the definitive egg passage. The anterior vesicle gives rise also to the bursa copulatrix and to the spermatheca. The posterior section of the egg passage appears first as a groove on the venter of the ninth segment extending from the anterior vesicle to the vesicle of the ninth segment, which latter forms the accessory colleterial glands. There is thus eventually formed a continuous passage from the lateral oviducts to the ninth segment, communicating with the exterior on the eighth segment through the bursa copulatrix, and having a posterior opening at the end of the ninth segment in common with that of the accessory glands. The spermatheca opens into the dorsal wall of the tube opposite the bursa copulatrix.

In Coleoptera the female genital opening is situated on the venter of the ninth abdominal segment of the adult. According to Heberdey (1931), the rudiments of the unpaired duct and associated organs of *Hydroporus ferrugineus* appear first in a young larval stage as median invaginations on the posterior parts of the seventh and eighth abdominal segments. The bifurcate anterior ingrowth unites with the lateral oviducts ending in the seventh segment, and its median posterior part constitutes the first section (Eiergang) of the definitive outlet passage. The second section (vagina) is formed first as a groove beneath the invagination of the eighth segment, which becomes continuous with the opening of the anterior invagination, and which, by closure of its lips, produces a tube extending posteriorly from the lateral ducts, with the posterior invagination arising as a pouch from its dorsal wall. When the ninth sternal plate is formed it lies anterior to the rear opening of the tube, which latter thus comes to be on the posterior part of the ninth segmental venter. By a peculiar development in *Hydroporus*, as described by Heberdey, the median tube is divided lengthwise into an upper part (*bursa copulatrix* and *receptaculum seminis*) and a ventral part (*vagina*), the two opening separately on the ninth segment.

The development of the median female duct in *Tenebrio molitor*, as described by Singh Pruthi (1924), is somewhat different from that in *Hydroporus*, described by Heberdey. In a young pupa of *Tenebrio*,

Singh Pruthi says, the median oviduct ("uterus") begins as an invagination at the posterior margin of the eighth sternum, and a "spermathecal" invagination is formed on the ninth sternum. "Gradually the walls intervening between the two organs (the mid-ventral region of the spermatheca and the mid-dorsal of the uterus) disappear so that their cavities freely communicate with each other." Thus the "uterus", Singh Pruthi says, comes to open "into the spermathecal rudiment and communicates with the exterior through the opening of the latter, behind the ninth sternite". The development of the anterior section of the oviduct from the seventh segment is evidently not recapitulated in *Tenebrio*.

The clear account of the development of the exit apparatus of the female genital system in Coleoptera as given by Metcalfe (1932)

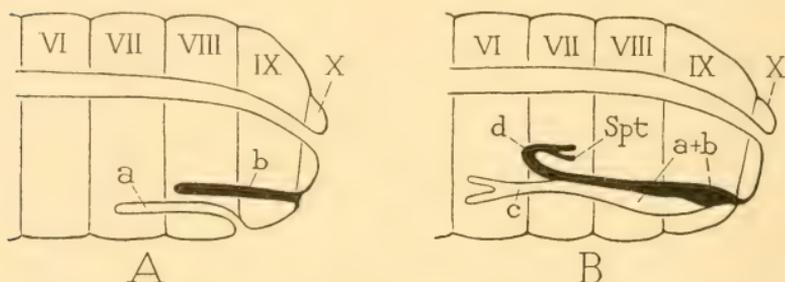


FIG. 5.—Diagrams showing the development of the female exit apparatus in Coleoptera (from Metcalfe, 1932).

A, prepupal stage of *Sitodrepa* with anterior invagination (*a*) behind eighth sternum, and posterior invagination (*b*) behind ninth sternum.

B, union of the two invaginations to form the definitive copulatory pouch and egg passage (*a + b*), with spermatheca (*Spt*) opening into diverticulum (*d*) of its anterior end.

is in essential agreement with that of Singh Pruthi. In *Sitodrepa*, *Gastroides*, *Anthonomus*, and *Rhagium*, Metcalfe finds that there are formed in the prepupal period two tubular genital invaginations of the body wall (fig. 5 A, *a*, *b*), one opening between the eighth and ninth abdominal sterna, the other behind the ninth sternum, the second lying immediately dorsal to the first. The anterior, ventral tube (*a*) bifurcates at its anterior end, and the mesodermal oviducts eventually unite with its two arms. The posterior, dorsal tube (*b*) gives off diverticula anteriorly which develop into the sperm receptacle and "accessory" glands of the adult beetle. Finally, during the early part of pupation, the two tubes unite with each other for most of their length (B), the intervening walls disappear, and the opening of the anterior tube on the eighth venter is closed. The definitive

egg passage thus comes to be a single median tube opening behind the ninth sternum, receiving the lateral oviducts into its bifurcate anterior section (*c*), and having a dorsal diverticulum (*d*) shortly behind the branches, into which open the sperm receptacle (*Spt*) and associated glands later formed.

If the ontogenetic development of the female exit apparatus in Coleoptera as given by Singh Pruthi and by Metcalfe represents the phylogenetic course of evolution in this order, it would appear that the sperm receptacle of Coleoptera is not homologous with the spermatheca of other insects, which always (except possibly in Diptera) takes its origin at the posterior margin of the eighth segment, and is subsequently associated with the genital chamber invagination found here. There is little in the adult structure of the female organs in Coleoptera, however, to suggest that the exit apparatus in this order is in any way fundamentally different from that of other insects. The large vaginal tube or sac (fig. 4 F, *Vag*) opening on the ninth segment usually has a dorsal pouchlike diverticulum (*d*), generally called the "bursa copulatrix", which it probably is in function. The sperm receptacle opens either into the anterior part of the vagina (fig. 4 F), or into the diverticulum of the latter (fig. 5 B). Accessory glands are usually absent. Since the genital tract in the mature condition has only the single opening on the ninth segment, this aperture becomes in a functional sense the vulva (*Vul*), though anatomically it corresponds with the oviporus of Lepidoptera (fig. 4 E, *Opr*).

In Diptera it is usually said the female genital opening lies on the venter of the eighth segment behind the eighth sternum, and it apparently does have this position in most families. According to Metcalfe (1933), however, the opening occurs on the ninth segment in the cecidomyid *Dasyneura leguminicola*. The development of the female efferent system in this insect, moreover, is shown by Metcalfe to be closely parallel with that found in Coleoptera. The definitive egg passage, she says, is the product of a union between an ectodermal invagination arising posterior to the eighth abdominal sternum, and another formed posterior to the ninth sternum. The first branches anteriorly, and its arms unite with the mesodermal oviducts; the anterior end of the second gives rise to the spermathecae and the accessory glands. By a closure of the anterior opening, the secondarily continuous passage has its exit through the posterior opening on the ninth segment. Thus, in *Dasyneura*, as in Coleoptera, it would appear that the sperm receptacles are derived from the invagination of the ninth segment, and not from that of the eighth, as in other insects.

When the vaginal opening lies behind the ninth sternum it may come into juxtaposition with the anal opening, particularly when the terminal segments of the abdomen are reduced or partly suppressed, and in some cases, as in Lepidoptera and certain Trichoptera, the vagina and rectum open together into an ectodermal depression, or *cloaca*, which constitutes the extreme posterior extension of the median egg passage.

The position of the functional female genital opening of pterygote insects is now seen to be so variable in different orders, and even within a single order (Hemiptera, Lepidoptera, Trichoptera, Diptera), that it can be given little value as a character for determining the relative positions of groups in classification. Thus, as shown by Busck (1931) in the Lepidoptera, several of the more generalized families in both the Jugatae and the Frenatae have only the posterior opening on the ninth segment, while all the otherwise more specialized families retain the anterior opening on the eighth segment together with an opening on the ninth.

*The genital openings of Collembola and Protura.*—The unusual positions of the genital openings in Collembola and Protura produce conditions in these groups which are different from those in any of the other Hexapoda.

The abdomen of Collembola contains not more than six segments, and the median gonopore, in both the male and the female, is situated on the posterior part of the fifth segment, or between this segment and the sixth. The Collembola, therefore, in this respect, present either a condition having no relation to that in the other insects, or one produced secondarily by specialization. If we assume that the small number of segments in the collembolan abdomen is the result of a suppression of segments in both the pregenital and postgenital regions, the problem of the position of the genital opening presents no special difficulties. On the other hand, if the six segments of the abdomen represent the maximum abdominal segmentation ever attained in this group, then the common genital opening may be a primitive subterminal aperture. But again, if the Collembola are descended from insects having the usual number of somites in the abdomen, and the posterior segments have been suppressed, then we must assume that the genital apertures have undergone an anterior migration. The general structure of the Collembola suggests a high degree of specialization on a low plane of insect organization.

The Protura present a different kind of problem, relative to the genital openings, from that presented by the Collembola, for here the gonopores, situated in both sexes between the eleventh and twelfth

abdominal segments, are evidently the primitive paired openings of the lateral genital ducts, which remain separate in the male, but unite in a median exit in the female. The position of the gonopores in this group might be taken as indicating that at some remote time in the phylogenetic history of the Hexapoda the lateral mesodermal ducts of both sexes opened just before the terminal body segment, as they do in Chilopoda. In this event, the paired openings on the tenth and seventh segments of insects are phylogenetically secondary, and, if so, it becomes an interesting subject for speculation as to how they may have been established on these segments.

*Theoretical considerations.*—Tillyard (1930) has pointed out that under the term "opisthgoneate" there is included within the Hexapoda a variation of six segments in the position of the genital openings, one extreme being represented by the Collembola with the gonopore on the fifth abdominal segment, the other by the Protura with the gonopores on the eleventh segment. The discrepancy is somewhat exaggerated, however, by including the Collembola, since the collembolan gonopore is a median genital opening, which, as we have seen, is secondary and subject to migration. The variation of the primitive lateral gonopores in Hexapoda is thus only from the seventh to the eleventh segments—a distance of four somites. To account for this variation, and for the greater variation in other arthropods that brings about the "progoneate" condition, Tillyard proposes the assumption that the primitive arthropods had segmentally paired gonads, and that each gonad had an individual segmental duct. The second part of this assumption finds little support in the known facts of the embryonic development of the insect gonads or their ducts. The investigations of Heymons (1892) and of Wheeler (1893), as shown above, have made it clear that the only stage in which the reproductive elements have a segmental arrangement is that in which the germ cells become segmentally arranged in the dorsal part of the splanchnic mesoderm. But at this stage there are no exit ducts. The condition is in every way parallel with that in the Annelida, and it is only at this early ontogenetic period that a comparison can be made between the Annelida and the Arthropoda with respect to the reproductive organs. The definitive gonads and the genital ducts of most insects are formed as continuous mesodermal structures, and the later subdivision of the gonads into tubules is generally a secondary process in ontogenetic development. Though the tubules may take a segmental arrangement, they never have separate, segmental ducts to the exterior of the body.

According to Wheeler's (1893) concise account of the development of the genital ducts in *Conocephalus*, the embryonic male ducts end

in hollow enlargements, or terminal ampullae, situated at first in the appendage rudiments of the tenth abdominal segment (fig. 3 B, *c*); the female ducts, which likewise terminate with ampullae, end in the appendage rudiments of the seventh abdominal segment. The female, however, Wheeler observes, has also a pair of ampullae in the tenth segment appendages, which appear to be homologues of the male ampullae. The account given by Heymons (1890, 1895) of the genital ducts in Dermaptera, Blattidae, and Gryllidae is essentially in agreement with that of Wheeler for *Conocephalus* in so far as the male ducts are described as terminating in mesodermal ampullae in the tenth segment, and the female ducts in ampullae of the seventh segment. According to Heymons, however, there is evidence of a primary branching of the ducts in each sex to both the seventh and tenth segments. Wheeler, on the other hand, believes that male insects never have ampullae or branches of the genital ducts in the seventh segment. Heymon's illustration of *Forficula* (fig. 3 D) gives a convincing example of the branching of a genital duct to the two segments, but his identification of the posterior branch (*d*) as the definitive oviduct is evidently wrong, since the definitive female ducts in Dermaptera open on the seventh segment.

From the above we might deduce, as a plausible explanation of modern conditions, the theory that at some period in the phylogenetic history of insects, the mesodermal ducts of the gonads opened in each sex on the bases of the appendages of the tenth abdominal segment, and that later the ducts in the female developed branches to the seventh appendages and lost the primitive connections with the tenth appendages. The reverse assumption, namely, that the openings on the seventh segment are primitive in both sexes, and those to the tenth segment secondary in the male, would appear to be disqualified by the subterminal position of the genital apertures in both sexes of Onychophora, Chilopoda, and Protura. It seems scarcely necessary to accept the view of Heymons (1890) that primitive insects were hermaphroditic. The theory of the branching of the genital ducts offers a possible explanation of the differences in position of the dual genital openings among the Insecta, and makes it possible to derive this condition from the more primitive condition retained in Chilopoda and Protura. The theory at least is in accord with the known facts of embryonic development.

### III. THE OVIPOSITOR OF THYSANURA

Among the Apterygota an ovipositor is well developed in the Thysanura. In Dicellura and Collembola the organ is entirely absent; and the female genital armature of the Protura can scarcely be sup-

posed to have any relation to the egg-laying organ of the true Insecta, since it arises from between the eleventh and twelfth segments of the abdomen. No structure homologous with the insect ovipositor occurs in any arthropods other than the insects.

The thysanuran ovipositor is composed of four processes arising from the stylus-bearing lobes of the eighth and ninth abdominal segments. These lobes, commonly designated "plates", are generally conceded to be the bases ("coxites") of true abdominal limbs. The pterygote ovipositor differs from that of the Thysanura only in its greater complexity; an essential part of its structure consists of four basal lobes, or plates, that appear without question to be direct homologues of the bases of the thysanuran gonopods. Hence, on the evidence of the limb origin of the component parts of the ovipositor in Thysanura, the parts of the pterygote ovipositor must have had the same origin. Considering, therefore, the many respects in which the Thysanura, particularly the Lepismatidae, show that they are more closely related to the Pterygota than are any other of the apterygote forms, we may reasonably assume that the ovipositor had its inception in the common ancestors of these two groups of insects, and that it has been formed by special modifications of the appendages of the eighth and ninth abdominal segments.

The Machilidae are in many respects more primitive in their structure than are the Lepismatidae; the structure of the abdomen in Machilidae is more generalized even than in any other family of the Apterygota. The relatively primitive condition of the machilid abdomen is shown particularly in the well-known fact that the bases of the appendages, throughout the visceral and genital regions, are distinct from the small median sterna. The abdominal limb bases form a double series of large, stylus-bearing plates intervening between the terga and the sterna, though the two plates of each segmental pair are usually united with each other in the median line posterior to the sternum. Each so-called "plate", however, is really the ventral wall of a flattened lobe, the membranous dorsal wall of which is reflected into the intersegmental membrane between its segment and the segment following. The stylus is borne in a notch on the distal apical margin of the lobe, and the stylus muscles arise on the anterior margin of the ventral plate. Mesad of the stylus the limb base lobe of most of the pregenital appendages bears on its distal margin also one or two retractile and eversible vesicles, the muscles of which take their origins on the ventral plate. Vesicles are never present on the gonopods.

That the stylus-bearing plates of the Machilidae are the bases of the abdominal appendages is here taken for granted, and is made the

basis for all subsequent discussions in this paper on the morphology of the ovipositor. The assumption seems to have ample support from embryology; but, if the plates in question should be shown to be something else than the basal elements of appendages, it will be necessary only to change their names; their relations to structures evolved from them in the Pterygota will not be altered. The abdominal styli of the Thysanura support the abdomen and play an active part in the locomotion of the insect. The writer has elsewhere (1931) discussed the evidence bearing on the morphology of the styli, showing that, while there is much reason for believing that the styli and their homologues in various pterygote larvae are the rudimentary telopodites of the abdominal segments, the question cannot be regarded as settled; the styli may be basal epipodites of the appendages, from which the telopodites have entirely disappeared.

The writer has not been able to make an exact study of the abdominal musculature in the Thysanura, but even with poorly preserved specimens it can easily be seen that each stylus-bearing plate of the abdomen is amply provided with lateral muscles that take their origin on the abdominal terga. In fact, it appears that all the dorsoventral muscles of the abdomen in the Machilidae are attached ventrally on the stylus-bearing plates, there being no muscles of any kind connected with the small median sternal plates. It would thus seem that in the Thysanura the lateral body musculature of the abdomen is formed entirely of the tergal musculature of the limb bases. In studying the abdomen of pterygote insects the writer (1931) was led to make the statement that no evidence was found suggesting the derivation of the lateral abdominal musculature from the muscles of the limb bases; and this is true, since in exopterygote larvae that preserve distinct limb base lobes on the abdomen, none of the body muscles is attached directly on the limb bases. The diversification of the muscle attachments in adult Pterygota, in which some of the lateral muscles may be tergopleural and others tergo-sternal, cannot be taken as evidence of a primitive condition, since it is evidently an adaptation to the mechanism of respiration and of other body movements. Likewise, in endopterygote larvae a secondary specialization in the musculature may obscure the primitive muscle pattern. The condition in the Machilidae, however, is perhaps more significant; it might be interpreted as indicating a derivation of the lateral body musculature from the primitive leg muscles, though the extreme reduction of the sterna must be taken into account as a factor bringing about a secondary transposition of some of the body muscles to the expanded limb bases.

The gonopods, or appendages of the eighth and ninth abdominal segments, differ in female Thysanura from the appendages of the pregenital segments in that they lack eversible vesicles, and that each is provided with a long genital process, or gonapophysis (fig. 6 B, C,  $1Gon$ ,  $2Gon$ ). The basal plates of each segmental pair of gonopods also are not united with each other. The gonapophysis is a slender hollow extension from the dorsal aspect of the median proximal angle of the basis of the gonopod (fig. 7). Its sclerotic wall is continuous

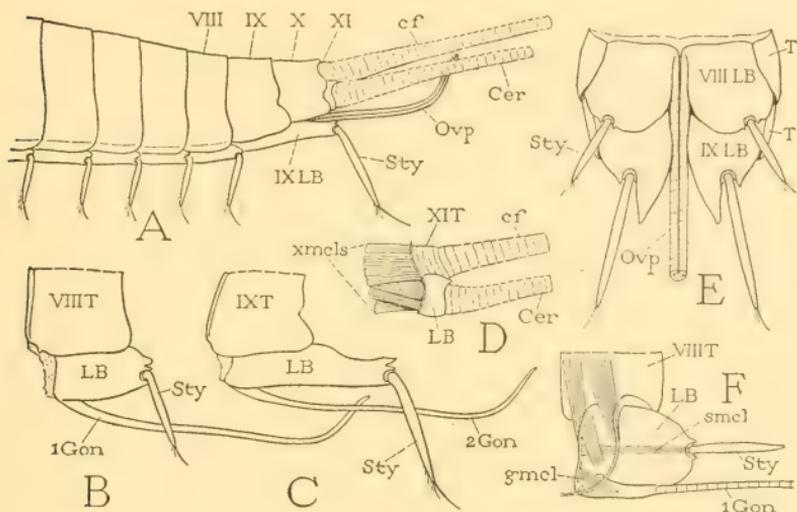


FIG. 6.—The ovipositor and terminal structures of female Thysanura.

A, abdomen of *Machilis*, showing the styli (*Sty*) in position in life.

B, C, genital segments of *Machilis*, showing gonapophyses (*Gon*) arising from limb base plates (*LB*).

D, bases of caudal filament (*cf*) and cercus (*Cer*) of *Machilis*, with muscles of tenth segment.

E, genital segments and base of ovipositor of *Thermobia*, ventral view.

F, diagrammatic figure of the principal muscles of first gonopod of *Thermobia*.

with that of the ventral plate of the basis, and the genital process is thus not articulated with the latter, as in the stylus; but, being flexible at its base, the gonapophysis is movable, and it is provided with short muscles (A, *gmcl*) arising on the basal plate mesad of the longer muscles of the stylus (*smcl*). In some of the Thysanura, as in *Nesomachilis* (fig. 7), the four gonapophyses of the ovipositor are individually free structures, except that those of the ninth segment (B) are united at their bases; in others, however, as in *Thermobia* (fig. 6 E), the gonapophyses of the second pair are fused with each other throughout the length of the ovipositor, and only those of

the first pair are free processes. The length and shape of the ovipositor vary somewhat in different Thysanura; in *Machilis* (fig. 6 A) the distal part of the organ is abruptly bent upward.

The morphological origin of the gonapophyses cannot be determined from the evidence at hand. The structures are treated in this paper as being processes of the gonopod bases having the nature of endite lobes. Some writers prefer to regard them as the true telopodites of the genital appendages, but their limitation to the gonopods, their origins from the proximal parts of the latter, their special func-

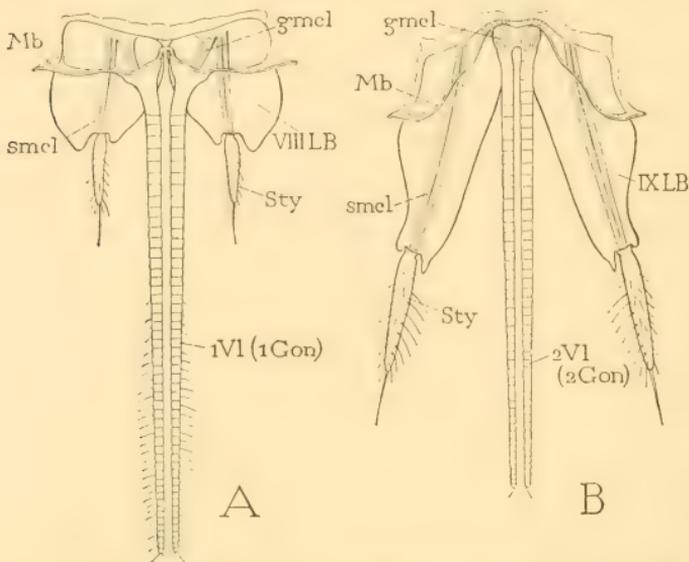


FIG. 7.—Female gonopods of *Nesomachilis maoricus*, dorsal view.

Note in each appendage muscles from basal plate to stylus (*smcl*) and to gonapophysis (*gmcl*).

tion, and the fact that they never show a leglike form seem to be suggestive, rather, that the gonapophyses are secondary structures developed on the appendages of the eighth and ninth abdominal segments in adaptation to the special function these appendages have assumed.

The bases of the thysanuran gonopods, in conformity with the bases of the pregenital appendages, are well equipped with muscles arising on the terga of their respective segments (fig. 6 F). Some of these muscles of each appendage are inserted on the plate forming the ventral wall of the limb basis, and others at the inner margin of its membranous dorsal wall. Smaller groups of median, longitudinal

fibers, apparently intersegmental muscles, are attached near the base of the gonapophysis and evidently act as protractors and retractors of the latter. An exact study of the gonopod musculature could not be made on the material at hand, but there is no doubt that each gonopod, as indicated somewhat diagrammatically at F of figure 6, is movable as a whole by the tergal muscles inserted on its base (*LB*). The gonapophysis, on the other hand, is movable individually on the basis by the group of short fibers (*gmcl*) arising in the latter, and inserted within its proximal end. The stylus (*Sty*), being set in a membranous socket on the distal margin of the basis, is freely movable by its long muscles (*smcl*) arising on the proximal margin of the basal plate. In *Thermobia* the gonapophysis of the ninth segment is attached directly to a small sclerite lying in a notch of the base of the large stylus-bearing plate, but the small sclerite is evidently a secondary subdivision of the larger one.

The postgenital segments of the Thysanura are more generalized in some members of the group than they are in any of the Pterygota. The tenth segment is a complete annulus (fig. 6 A, X), but it lacks appendages in postembryonic stages, as it does in all the more generalized Pterygota. The small eleventh segment (A, XI) is normally concealed within the tenth segment, but it bears the cerci (*Cer*) and the long median caudal filament (*cf*). In *Nesomachilis* the body of the eleventh segment, when removed from the tenth (D), is seen to consist of a dorsal arch (*IXT*) produced into the caudal filament (*cf*), of two lateral lobes (*LB*), evidently the bases of the cercal appendages (*Cer*) which they support, and of a narrow, membranous venter bearing the two paraproctal lobes. The cerci appear to have no muscles arising in their own bases, but the tenth segment is filled with a mass of intersegmental fibers (D, *xmcls*) attached posteriorly on the anterior margin of the eleventh segment. Some of these fibers, inserted at the bases of the cerci, serve to move the cerci. The twelfth segment, or periproct, is practically obliterated, but in some species of Thysanura there is a small, fleshy dorsal lobe beneath the base of the caudal filament, possibly a remnant of the lamina supra-analis of the telson.

In order better to compare the structure of the pterygote ovipositor with that of the ovipositor of Thysanura, we may briefly summarize the principal features of the simple thysanuran ovipositor as follows:

1. The thysanuran ovipositor consists of two pairs of processes (the first and second gonapophyses), and of two pairs of basal plates belonging to the eighth and ninth abdominal segments, respectively.

2. The gonapophyses are continuous with the mesal proximal angles of the basal plates, and each is provided with a short muscle arising on the supporting plate.

3. The basal plates of the ovipositor are evidently the bases of the appendages (gonopods) of the eighth and ninth abdominal segments. Each bears a gonapophysis proximally and a stylus distally, and is equipped with dorsal muscles arising on the tergum of its segment.

4. The styli of the thysanuran gonopods do not form a part of the ovipositor, but serve to support the end of the abdomen, and are active in the locomotion of the insect. Each is movable by muscles arising proximally in the basal plate on which it is borne.

#### IV. GENERAL STRUCTURE OF THE PTERYGOTE OVIPOSITOR AND ASSOCIATED ORGANS

There appears to be little doubt that the pterygote ovipositor is an organ formed of the appendages of the eighth and ninth abdominal segments, and that it is, therefore, homologous with the ovipositor of the Thysanura. If, in the embryonic development, the blades of the pterygote ovipositor appear to arise directly from the ventral walls of the genital segments, it is probable that the apparent venter of each segment includes the areas of the limb bases and the sternum. In the definitive condition the limb bases are always distinctly differentiated from the sterna. Associated with the base of the ovipositor are typically three internal organs formed by median invaginations of the ectoderm. The first is the *median oviduct*, the second is the *spermatheca*, the third is a pair of *accessory glands*. Finally, there may be formed cavities at the base of the ovipositor, covered by a posterior extension of the eighth sternum, and of the seventh sternum. These cavities are the *genital chamber* above the eighth sternum, and the *vestibulum* above the seventh sternum.

#### THE GENITAL INVAGINATIONS

The three median genital invaginations of female insects, namely, the oviduct, the spermatheca, and the accessory glands, have anatomically metameric relations to one another, since primarily they are developed on successive segments (fig. 8 A); but it has not been shown that there is any morphological significance in this fact.

The oviductus communis, as shown in section II, first appears in the embryo, nymph, or larva of many insects as a median ingrowth on the posterior part of the venter of the seventh abdominal segment, or in the intersegmental membrane between the seventh and eighth sterna.

We may assume, therefore, that the first of the three median genital invaginations occurred primitively on the posterior part of the seventh venter, and that, by union with the mesodermal oviducts (fig. 8 A, *Odl*), it became the primary median outlet tube of the ovaries, or *oviductus communis* (*Odc'*). The duct retains the primitive position of its opening in adult insects only in Dermaptera.

The second median genital invagination is formed on the posterior part of the venter of the eighth abdominal segment (fig. 8 A, *Spt*), and gives rise to a pouch for the reception of the spermatozoa. This invagination is the *spermatheca*, or *receptaculum seminis*. The spermatheca is usually a single organ, though it may be double or triple. A diverticulum of its duct commonly forms a tubular spermathecal gland.

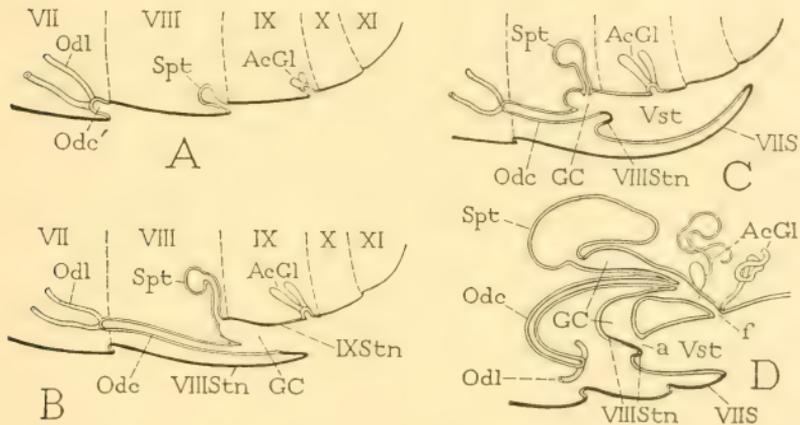


FIG. 8.—Diagrams showing positions of ducts and associated structures of the female genital apparatus.

A, primitive condition, with median oviduct (*Odc'*) opening on seventh segment, spermatheca (*Spt*) on eighth segment, and accessory glands (*AcGl*) on ninth segment.

B, usual condition, with oviduct (*Odc*) extended to end of eighth segment, where it opens together with spermatheca (*Spt*) in a genital chamber (*GC*) formed above eighth sternum.

C, genital chamber (*GC*) enclosed in a vestibulum (*Vst*) formed above seventh sternum (*VIIS*), accompanied by a reduction of eighth sternum (*VIIIStn*).

D, unusual structure in *Magicicada*, in which genital chamber (*GC*) opens from vestibulum by the primary copulatory aperture (*a*), but discharges the eggs through a secondary posterior opening (*f*).

The third median genital invagination is formed on the venter of the ninth abdominal segment (fig. 8 A, *AcGl*). It is typically bifurcate, and gives rise to the *accessory glands* of the female genital apparatus. These glands usually have a colleterial function, since they

discharge a substance for attaching the eggs to a support, or for agglutinating the eggs to one another, but the secretion may also be used to form an egg covering, or an egg capsule, and in the stinging Hymenoptera one of the glands produces an irritant or toxic liquid. In some insects the accessory glands are absent, and their function may be assumed by special glandular parts of the oviducts.

The median oviduct and the spermatheca have no homologues in the male insect; but it seems possible, as some writers claim, that the male ejaculatory duct and mucous glands are derived from the same invagination of the ninth segment that forms the accessory glands of the female.

The oviductus communis, in all insects but Dermaptera, becomes extended posteriorly. In most insects the definitive opening of the median oviduct (fig. 8 B, *Odc*) is carried back to the posterior part of the eighth segment, and comes to lie just before the opening of the spermatheca (*Spt*) behind or above the eighth sternum.

Insects having the aperture of the definitive egg passage situated on or behind the ninth abdominal segment include some species of Hemiptera, Parnorpidæ, and Diptera, most Trichoptera, and all Lepidoptera and Coleoptera. An opening on the eighth segment in conjunction with that on the ninth is retained in most adult Lepidoptera, and, as we have seen, occurs in immature stages of Coleoptera. A similar opening on the eighth segment is present also in species of Cicadidæ in which the genital chamber opens posteriorly on the ninth segment. The trichopterous families Limnophilidæ and Phryganiidæ preserve the more primitive condition in that the female genital aperture is on the eighth abdominal segment just behind the eighth sternum. In *Panorpa* the oviductus communis, the spermathecal duct, and the duct of the accessory glands discharge into an open cavity in the ventral part of the ninth segment. This cavity is a simple invagination of the body wall widely open laterally and posteriorly above and behind the edges of the somewhat enlarged sternal plate of the ninth segment, and its lumen corresponds with the genital chamber of more generalized insects, though it is closed below by the *ninth* sternum. The anus of *Panorpa* lies on the ventral surface of the very small eleventh segment of the female. In trichopterous forms having the female genital aperture behind the ninth sternum, the oviduct, the spermatheca, and the accessory glands open likewise into a common chamber, but the latter is here entirely enclosed within the body, and has a small aperture at the base of the terminal (tenth) segment in common with the rectum. In Coleoptera the part of the

egg passage beyond that formed of the true median oviduct takes the form of a vaginal tube, and may be produced into a large copulatory pouch.

The egg duct in all Lepidoptera opens at the end of the ninth abdominal segment, or on a terminal segment which is evidently the united ninth and tenth somites. The statement made by Petersen (1900) that the single genital aperture in *Hepialus* and other Jugatae is on the eighth abdominal segment has not been substantiated by subsequent investigators. It has recently been shown by Busck (1931) that the posterior aperture is always on the ninth segment (or on the combined ninth and tenth somites) and that the single, posterior opening is a feature not only characteristic of the Jugatae but occurring likewise in several of the lower families of the Frenatae. It is thus somewhat surprising to find that in the Lepidoptera the more primitive, anterior opening has been suppressed in the more generalized families, but the explanation lies in the fact that the posterior position of the oviporous is correlated with the tubular extension of the abdomen to form an "ovipositor". There is no clear distinction in the egg passage of the Lepidoptera between the true oviducal part of the tube and the vagina, but the opening of the spermatheca into the tube probably marks the anterior end of the secondarily added vagina.

#### THE GENITAL CHAMBER AND THE VESTIBULUM

The formation of external cavities at the base of the ovipositor concealing the gonopore and the opening of the spermatheca, and sometimes the opening of the accessory glands, results from the invagination of the body wall at the base of the ovipositor, usually accompanied by a posterior extension of the eighth or of the seventh sternum. The sternum concealing the cavity is known as the *subgenital plate*; in some insects it is the eighth, in others the seventh.

The cavity here defined as the *genital chamber*, or *bursa copulatrix* (fig. 8 B, *GC*) is that formed by an invagination of the part of the body wall above the end of the eighth sternum in which are situated the openings of the median oviduct and the spermatheca. The ventral wall of the genital chamber may contain the reflected posterior part of the eighth sternum. The oviductus communis (*Odc*) opens either on the floor of the genital chamber or into its anterior end. The spermatheca (*Spt*) opens typically in the dorsal wall of the chamber, morphologically posterior to the gonopore. The actual relation of the two openings to each other, however, varies on account of the variable position of the gonopore, the latter, when located on the floor of the

genital chamber, being below and often behind the point at which the spermatheca opens into the dorsal wall of the chamber.

In some insects the spermatheca appears to arise from the dorsal wall of the median oviduct, but it is probable that in all such cases the part of the median egg passage receiving the spermathecal duct is formed as an extension of the genital chamber. There can be no doubt, for example, that the copulatory pouch of the cicada (fig. 32, *GC*) or of the honey bee (fig. 44 B, *b*), into which the spermatheca opens, is a part of the genital chamber, and it seems equally certain that the so-called "uterus" of viviparous Diptera is likewise a special compartment of the genital chamber. Since in most cases the genital chamber receives the male organ during mating, it is functionally a "bursa copulatrix". When the genital chamber, or an anterior part of it, however, takes the form of a tubular passage leading back from the true oviduct, it should be called the *vagina*, as by Demandt (1912, Korschelt, 1924) in *Dytiscus*, and by Imms (1930), Heberdey (1931), and others, to distinguish it from the true *oviductus communis* (Eiergang). Much confusion exists in descriptive works as to the distinction between median oviduct and genital chamber, or vagina. A safe rule to follow is that the oviduct lies anterior to the mouth of the spermatheca, and the genital chamber (*vagina*, or "uterus") posterior to it.

Morphologically the terminus of the *oviductus communis* in the genital chamber, or vagina, should be distinguished from the posterior opening of the latter to the exterior. The opening of the oviduct is the true *median gonopore*, whether exposed externally, or concealed in the genital chamber; when the genital chamber is converted into a copulatory pouch or a vaginal tube with a narrowed exit, its posterior opening, whether on the eighth or the ninth segment, is the *ostium vaginae*, or *vulva*.

When the seventh sternum is extended beyond the eighth sternum (fig. 8 C), the latter (*VIII Stn*) is generally reduced in size, and may become rudimentary, or it is retained only as a small plate on the floor of the genital chamber containing the gonopore. This condition is characteristic of Termitidae, Blattidae, Hemiptera, and Hymenoptera.

The extension of the seventh abdominal sternum beyond the eighth produces a second cavity (fig. 8 C, *Vst*) lying above the seventh sternum, which becomes an antechamber to the primary genital chamber (*GC*), or a continuation of the latter, and may be distinguished as the *vestibulum*.

With insects that retain a generalized structure in the genital segments, the base of the ovipositor usually lies in the genital chamber,

and the eggs discharged from the gonopore located on the floor of the chamber are passed into the channel of the ovipositor between the bases of the first valvulae. This condition is well illustrated in Acrididae, Tettigoniidae, and Gryllidae. Since the first valvifers, however, are always distinct from the eighth sternum, they may be displaced posteriorly to such an extent that the ovipositor base lies entirely posterior to the genital chamber. This condition is found especially in insects in which the seventh sternum is prolonged, for in such cases the eighth sternum is generally reduced (fig. 8 C, *VIIIStn*) and the genital chamber (*GC*) becomes a mere pocket of the anterior wall of the vestibulum (*Vst*). An unusual condition, to be described in detail later, occurs in some of the Cicadidae, in which the highly developed genital chamber has a second posterior opening on the ninth venter (fig. 8 D).

#### THE OVIPOSITOR

An ovipositor formed from appendicular processes of the abdomen is in general present only in insects having the female genital opening on the eighth abdominal venter, or between the eighth and ninth sterna. With the transposition of the genital opening to the ninth segment, the ovipositor has been suppressed in all cases (except in Cicadidae having two genital openings, in which the egg passage leads directly into the channel of the ovipositor; and it should be noted also that the female exit apparatus of the Homoptera in general is not well understood). Apparent rudiments of the gonopods of the ninth segment, however, may be retained, as in Panorpidae and Coleoptera. A comparative study of the plates and appendicular structures associated with the female genital opening in Colcoptera has been made by Tanner (1927), who claims that the terminal hooks or spurs are styli; but the general structure and musculature of the organs does not correspond closely with that of the parts of a typical ovipositor belonging to the ninth segment. The principal groups of pterygote insects in which an ovipositor is well developed are the Orthoptera, Hemiptera, Thysanoptera, and Hymenoptera. In various other orders, however, an ovipositor may be present in some members, either as a fully developed organ or in a rudimentary form. The fundamental structure of the ovipositor is always the same, and the wide occurrence of the organ suggests that an ovipositor formed of the appendages of the eighth and ninth abdominal segments was a character of the common ancestors of the Thysanura and Pterygota.

The pterygote ovipositor, in its typical form, consists of a shaft and a basal mechanism, and usually includes a pair of accessory lobes.

The shaft is composed generally of two pairs of bladelike processes, the *first* and *second valvulae* (fig. 9, *1VI*, *2VI*). The basal mechanism consists essentially of four lobes or plates, the *first* and *second valvifers* (*1Vlf*, *2Vlf*), associated with the eighth and ninth segments of the abdomen, together with their connected muscles. The accessory lobes, or *third valvulae* (*3VI*), are borne at the posterior ends of the second valvifers. In some insects the basal structure of the ovipositor includes median sclerites lying between the second valvifers, known as the *inter-valvulae*, and also muscles inserted on these sclerites. The first and

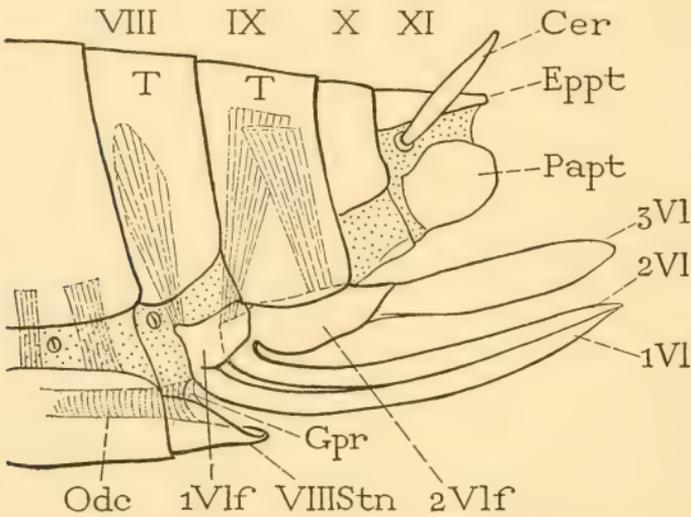


FIG. 9.—Diagram of the basic structure of the pterygote ovipositor.

Each gonopod consists of a basal plate, or valvifer (*1Vlf*, *2Vlf*), and a gonapophysis, or valvula (*1VI*, *2VI*); each valvifer provided with muscles arising on the tergum of its segment; the basis of second gonopod produced distally in a free lobe, the third valvula (*3VI*); gonopore (*Gpr*) at base of ovipositor above eighth sternum.

second valvulae arise from the anterior ends of the first and second valvifers, respectively. The third valvulae, arising from the posterior ends of the second valvifers, are usually free lobes, but in most Orthoptera they form a third pair of blades in the shaft of the ovipositor. The first valvifers in the Hemiptera are closely associated with the lower margins of the eighth tergum, though they are united by mesal extensions with the ninth tergum; in Orthoptera and Hymenoptera they become more or less displaced posteriorly, and articulated with the ninth tergum, or with the second valvifers. The second valvifers are always associated with the ninth tergum. The dorsal muscles of the first valvifers, regardless of the position of the plates themselves,

invariably take their origin on the eighth tergum (fig. 9); the dorsal muscles of the second valvifers arise on the ninth tergum.

From this sketch of the more generalized structure of the ovipositor in pterygote insects it is clear that the organ may be derived theoretically from a pair of genital appendages having the same structure and the same relations to the eighth and ninth segments of the abdomen as have the female gonopods in the Thysanura. Thus we may conceive that the parts of the pterygote ovipositor belonging to the eighth segment (fig. 10 A) represent the limb bases (LB) of a pair of gonopods, which become the first valvifers (B, *1Vlf*), and a pair of corresponding gonapophyses (A, *Gon*), which become the first valvulae (B, *1VI*). The styli of the first gonopods (A, *Sty*) are

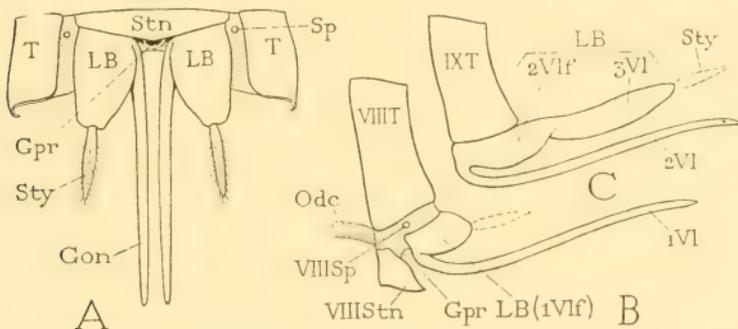


FIG. 10.—Analytical diagrams of the morphology of the pterygote ovipositor.

A, ventral view of theoretical generalized structure of eighth segment and gonopods (cf. fig. 6 E, fig. 7 A).

B, lateral view of generalized eighth segment and first gonopod; stylus absent in all pterygote insects.

C, lateral view of generalized ninth segment and second gonopod; basis of gonopod (LB) subdivided into second valvifer (*2Vlf*) and third valvula (*3VI*), stylus (*Sty*) sometimes present.

absent in all pterygote insects (B). The gonopore (A, *Gpr*) is located typically behind or above the posterior margin of the primitive sternum of the eighth segment (*Stn*), but between the proximal ends of the limb bases. It is, then, but a secondary matter if the limb base plates, or valvifers, of the eighth segment become more or less dissociated from the eighth segment (B) and variously connected with the ninth tergum or with the second valvifers. As above noted, the first valvifers, regardless of their displacement, retain their muscle connections with the eighth segment. The parts of the pterygote ovipositor belonging to the ninth segment may be supposed in the same way to represent corresponding parts of the second gonopods of Thysanura, the second valvifers (fig. 10 C, *2Vlf*) being limb bases, and the second valvulae (*2VI*) the second gonapophyses.

The terminal lobes of the second valvifers (figs. 9, 10 C, 3VI) might suggest by their usual position that they are the styli of the second gonopods; but, as will be shown presently, it is certain that they are secondary outgrowths of the gonopod bases. They are here termed "third valvulae" because in the Orthoptera they resemble the first and second valvulae, and form a third pair of blades in the shaft of the ovipositor. Usually the third valvulae ensheath the distal part of the ovipositor between their concave inner surfaces.

The sclerites termed intervalvulae, lying between the bases of the second valvifers, evidently belong to the venter of the ninth segment, and probably represent sclerotic remnants of the ninth sternum.

A review of the history of opinion concerning the morphology of the insect ovipositor would occupy more space than its value would justify. The theory here elaborated is essentially that now current with students of insect anatomy, except that it has not been generally recognized that the first valvifers are the bases of the first gonopods. Some writers have claimed that these plates bearing the first valvulae are derived from the eighth sternum, and others that they are a part of the ninth tergum. The difference of opinion has arisen probably from the fact that the position of the first valvifers relative to the surrounding parts differs considerably in different insects according to the mechanism of the ovipositor. In some insects the plates clearly belong anatomically to the eighth segment, since they lie in the pleural areas of this segment between the tergum and the sternum; in others they are dissociated from the eighth segment and are hinged to the second valvifers; in still others they are definitely articulated with, or attached to, the ninth tergum. If, therefore, the first valvifers appear to be derived in their development from the eighth sternum, the ontogenetic facts mean simply that at an early stage the bases of the first gonopods are not distinguishable from the true sternal area of this segment; on the other hand, if the first valvifers appear to be cut off from the ninth tergum, it is probable that their phylogenetic history is not fully recapitulated in their ontogenetic development. The invariable origin of the muscles of the plates in question on the eighth tergum leaves no doubt that the plates belong to the eighth segment, and the fact that the plates always carry the first valvulae would seem to be proof that they are the bases of the first gonopods.

The term "valvifer" was first introduced into the nomenclature of the ovipositor by Crampton (1917) to designate the sclerite here called "first valvifer" supporting the first, or ventral, valvula, and is so used by Walker (1919). A small plate at the base of the first valvula Crampton called the "basivalvula". In a later paper containing a

more extensive comparative study of the ovipositor, however, Crampton (1929) repeatedly confused the valvifer and the basivalvula because he did not base his identifications of these sclerites on their relations to the rest of the mechanism of the ovipositor. His "valvifer" in *Grylloblatta*, *Ceuthophilus*, *Gryllus*, and Hymenoptera, for example, is the sclerite he calls "basivalvula" in Hemiptera, while in *Periplaneta* he gives the name "valvifer" to a sclerite that belongs to the ninth tergum. The sclerite designated *first valvifer* in the present paper, therefore, is the "valvifer" of Crampton as he applied the term in Grylloblattidae, Tettigoniidae, Gryllidae, and Hymenoptera, and the homologous sclerite in other insects as determined by its muscle attachments and its relation to the first valvula. In his hypothetical diagrams Crampton (1929, figs. 1-4) derives the valvifer from the ninth tergum, probably because the sclerite he calls "valvifer" in Blattidae is a part of the ninth tergum, but he gives it no connection with the first valvula, though this is its most distinguishing and characteristic feature in the mechanism of the adult ovipositor in all insects. Crampton's diagrams, however, do not represent actual anatomical conditions, and it is only by a detailed dissection of the parts in question that the true identities of the various basal elements of the ovipositor can be determined.

Since the term *valvifer* is a very appropriate one when consistently used, inasmuch as it signifies literally a sclerite supporting a valvula, the writer here introduces the innovation of extending it to both pairs of valvula-bearing plates, distinguishing those that carry the first valvulae as the *first valvifers*, and those that carry the second and third valvulae as the *second valvifers* (usually called "coxites" of the ninth segment). The term *basivalvula* fittingly signifies the small sclerites that sometimes occur at the bases of the first valvulae, so named by Crampton (1917, 1929) in *Grylloblatta*, Tettigoniidae, and Gryllidae.

The leading facts in the ontogenetic development of the ovipositor are too well known to be given here more than a brief review. All investigators agree that a pair of processes grow out from the under surface of the eighth abdominal segment, and a second pair from the under surface of the ninth segment, and that each of the processes of the second pair typically becomes double by dividing lengthwise, or by budding an inner lobe from its mesal surface. The processes of the eighth segment in most cases become the first valvulae; the outer processes of the ninth segment form the second valvifers, including the terminal lobes of the latter, while the inner processes become the second valvulae. It is claimed by Nel (1930) that the definitive first valvulae of Odonata and Orthoptera are not the gonapophyses of the

first gonopods, but the bases of these appendages. Nel's studies were made principally on Acrididae, in which the ovipositor differs in many respects from that of other Orthoptera, and it is hence possible that his interpretation applies only to this family. His statement concerning the Odonata is based on the observation of George (1929) that there is an inner lobe developed from each of the ovipositor processes on the eighth segment of *Agrion*, which Nel would interpret as being the true gonapophyses of the first gonopods, though George, himself, makes no suggestion that they are other than secondary outgrowths.

While, in general, there is no dispute concerning the ontogenetic development of the first valvulae, the origin of the basal plates, or first valvifers, in connection with them has not been so definitely observed, and, as already noted, these sclerites have been variously ascribed to the eighth and ninth segments. An examination of a nymphal cicada in the last instar shows quite clearly that the genital processes of the eighth segment (fig. 11 A, 1Gon) arise from a broad plate (VIII LB) lying behind the gonopore (Gpr) and the small true eighth sternum (VIII Sn). This plate bearing the first gonapophyses, which is incompletely divided into lateral halves, can scarcely be anything else than the limb bases of the first gonopods united with each other behind the eighth sternum. It is, on the other hand, clearly the nymphal representative of the first valvifers of the adult (fig. 31 A, 1Vlf), though this identity could not be verified in the specimens studied by the writer because the imaginal parts were already retracted forward far in advance of the nymphal parts.

The splitting of the primary genital processes of the ninth segment, or the budding of inner lobes from their mesal surfaces, represents the development of the second gonapophyses from the bases of the second gonopods. The result is the formation of four processes on the ninth segment (fig. 11 B). The outer processes (IX LB) are the true limb bases, which in the adult are differentiated into the second valvifers and their terminal lobes, or third valvulae (fig. 31 B, 2Vlf, 3VI); the inner processes (fig. 11 B, 2Gon) are the second gonapophyses, or the second valvulae of the adult (fig. 31 B, 2VI). The true ventral region of the ninth segment lies between the limb bases, concealed by the second gonapophyses. In some insects it contains remnants of the ninth sternum forming intervalvular sclerites.

There is not much evidence from ontogeny as to the nature of the distal lobes, or "third valvulae", borne by the second valvifers in the higher insects, but the development of the ovipositor as described by Walker (1919) and others in Blattidae and by Crampton (1927) in *Grylloblatta* appears to show conclusively that the third valvulae

are not styli, as is suggested anatomically by their lack of muscles. In a female nymph of a cockroach small processes occur on the ends of the limb base lobes of the ninth segment, which almost certainly are true styli (fig. 25 B, *Sty*); they persist, Walker says, until the last molt, but they are not retained in the imago. In the adult roach, however, the outer processes (limb bases) of the ninth segment are clearly differentiated into a basal part, which is the second valvifer (fig. 24 C, D, *2Vlf*), and into a large, free distal lobe, or third valvula (*3Vl*). In *Grylloblatta* Walker thinks the length of the dorsal valvulae indicates that these processes include the styli, which are distinctly appendicular in the nymph; but Crampton says that the styli of the ninth "coxites" are lost in the adult female, and that, with the suppression of the styli, "the elongate coxite of the nymph becomes the

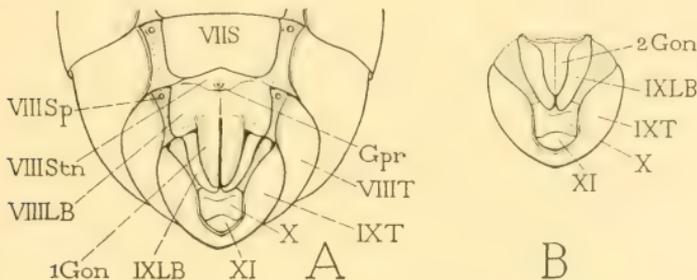


FIG. 11.—Female nymph of *Magicicada septendecim*.

A, ventral view of end of abdomen, showing first gonapophyses (*1Gon*) arising from limb base plates (valvifers) of eighth segment (*VIII LB*) behind small eighth sternum (*VIII Stn*).

B, ninth and following segments detached from eighth segment, showing second gonapophyses (*2Gon*) arising from bases of second gonopods (*IX LB*).

dorsal valve of the adult." It is probable that small processes borne on the third valvulae in the adult stage of some of the lower insects, as in Odonata, are true styli.

From the above evidence we may conclude that the limb bases of the second gonopods in most adult female insects lose their primitive styli, and that in the Pterygota each becomes secondarily differentiated into a proximal second valvifer and a distal third valvula (fig. 10 C). In an adult cicada the limb basis of the ninth segment is distinctly separated into valvifer and third valvula (fig. 31 B, *2Vlf*, *3Vl*), but in the mature nymph the outer ovipositor lobes of the ninth segment are undivided (fig. 11 B, *IX LB*), yet they are mostly occupied by the imaginal third valvulae.

The late, usually postembryonic, development of the external genital processes, often after a complete and prolonged suppression of the

embryonic abdominal appendages, as in the larvae of Hymenoptera, is to be regarded merely as a case of retarded development in organs that are used in their secondary function only in the adult stage of the insect. The genital structures in such cases are developed from "imaginal disks", which are rudiments of primitive limbs. Evidence that the "law" against rehabilitation of a lost structure does not apply in ontogeny seems to be clearly demonstrated by the Acarina, in which, it is said, the fourth pair of legs, present in the early embryo, are suppressed long before hatching, and are fully restored in a late nymphal stage. In some of the lower insects the genital processes, as described by Wheeler (1893) in *Conoccephalus*, are derived directly from the persistent rudiments of the abdominal appendages.

The characteristic features of the pterygote ovipositor and the probable correspondence between the parts of the pterygote and thysanuran ovipositors are briefly summarized in the following paragraphs:

1. The pterygote ovipositor consists of two or three pairs of processes (the first, second, and third valvulae), and of two pairs of basal plates (the first and second valvifers) belonging to the eighth and ninth abdominal segments, and sometimes includes intervalvular sclerites of the ninth segment.

2. The first and second valvulae are attached to the anterior ventral angles of the first and second valvifers, respectively; they correspond with the first and second gonapophyses of the Thysanura, and in some insects each has a short muscle inserted on its base, which arises in the corresponding valvifer. The shaft of the ovipositor in most insects is formed of the first and second valvulae alone, but in most of the Orthoptera the third valvulae enter into the composition of the shaft.

3. The first valvifers belong to the eighth segment of the abdomen, and are provided with dorsal muscles arising on the eighth tergum. Typically they are located in the pleural areas of the eighth segment between the tergum and the sternum, but usually they are more or less displaced posteriorly, and may be more closely associated with the ninth tergum, or with the second valvifers. The first valvifers correspond with the stylus-bearing plates of the eighth segment of Thysanura, and are therefore the bases of the first gonopods; in pterygote insects they always lack styli.

4. The second valvifers belong to the ninth abdominal segment, and are provided with muscles arising on the ninth tergum. They are always located between the lower edges of the tergum and the narrow median venter of the ninth segment. The second valvifers, together with the third valvulae, correspond with the stylus-bearing plates of the ninth segment of Thysanura, and are therefore derived from the

bases of the second gonopods. In most pterygote insects each primitive limb base of the ninth segment becomes differentiated into a proximal second valvifer, and a free distal lobe, or third valvula. In some of the lower insects the third valvulae bear small terminal styli, which are usually lost in the adult stage.

5. The third valvulae are secondary differentiations of the limb bases of the second gonopods, forming free lobes at the distal ends of the second valvifers. Usually they ensheath the distal part of the ovipositor between their apposed inner surfaces, but in most of the Orthoptera they resemble the gonapophyses, and form a third pair of blades in the shaft of the ovipositor.

6. The intervalvular sclerites are remnants of the ninth abdominal sternum; in some insects they give insertion to tergo-sternal and other muscles.

#### DEFINITIONS

The following terms applied to the ovipositor and associated structures are here defined as used in this paper in order to make the application clear, and to avoid the confusions of synonymy.

*Oviductus laterales (Odl)*.—The paired oviducts, formed primarily from the mesodermal strands continuous with the mesodermal sheaths of the ovaries, but their posterior parts may be of ectodermal origin, and in some cases the entire mesodermal ducts are said to be replaced by ectoderm. The ducts are attached to the ectoderm at the posterior border of the seventh segment in young stages of many insects, and open at this position in adult Ephemera, but in other adult insects they are confluent in the anterior end of the median oviduct.

*Oviductus communis (Odc)*.—The median oviduct, of ectodermal origin, opening in Dermaptera just behind the seventh abdominal sternum, but in other insects extended to the eighth segment.

*Female gonopore (Gpr)*.—Any of the true oviducal apertures, paired or median. The paired gonopores of Ephemera and the median gonopore of Dermaptera are on the posterior part of the seventh abdominal segment; the single female gonopore of other insects is on or just behind the eighth sternum, where it is either exposed externally or concealed in the genital chamber (copulatory pouch, or vagina).

*Spermatheca, receptaculum seminis (Spt)*.—An ectodermal invagination, usually single, but often double, and sometimes triple, serving for the reception of the spermatozoa; primarily formed on the posterior part of the eighth abdominal segment, opening into the anterior end of the genital chamber, or vagina, when this organ is present.

*Accessory glands (AcGl).*—Typically a bifurcate or paired invagination on the venter of the ninth segment, usually forming glands having a colleterial function.

*Gonopods (Gp).*—The appendages of the eighth and ninth abdominal segments. Each gonopod, when complete, consists of a *basis (Lb)* bearing a proximal, medial *gonapophysis (Gon)*, and a distal *stylus (Sty)*.

*Ovipositor (Ovp).*—The egg-laying organ formed of the gonopods.

*First valvifers (1Vlf).*—The basal plates or lobes of the ovipositor supporting the first valvulae; derived from the bases of the first pair of gonopods, and provided with muscles arising on the eighth tergum.

*Second valvifers (2Vlf).*—The basal plates or lobes of the ovipositor supporting the second valvulae; derived from the bases of the second gonopods, and provided with muscles arising on the ninth tergum. (Usually called "coxites" of the ninth segment.)

*First valvulae (1Vl).*—The gonapophyses of the first gonopods, forming the ventral blades of the ovipositor.

*Basivalvulae (bv).*—Small sclerites sometimes differentiated at the bases of the first valvulae.

*Second valvulae (2Vl).*—The gonapophyses of the second gonopods, forming usually the dorsal blades of the ovipositor, but the inner blades in Orthoptera having a third pair of valvulae.

*Third valvulae (3Vl).*—The distal lobes of the second valvifers, derived with the latter from the bases of the second gonopods; usually forming a sheath for the shaft of the ovipositor, but in most Orthoptera a third (dorsal) pair of blades in the ovipositor.

*Intervalvulae (iv).*—Sclerotic remnants of the ninth sternum between the second valvifers.

*Egg guide.*—A median process sometimes present on the end of the eighth sternum behind the invaginated gonopore, serving to direct the eggs into the channel of the ovipositor between the bases of the first valvulae.

*Genital chamber (GC).*—An inflection of the body wall at the base of the ovipositor above the end of the eighth abdominal sternum, forming a pouch containing the gonopore and the opening of the spermatheca; in Panorpidae the genital chamber is closed below by the ninth sternum and opens above the latter.

*Vestibulum (Vst).*—A cavity formed by inflection of the body wall above the seventh sternum when the latter is prolonged beyond the eighth, thus concealing the true genital chamber above the usually reduced eighth sternum.

*Subgenital plate*.—The exposed sternal plate beneath the genital apparatus; primarily the eighth abdominal sternum, but the seventh when the latter underlies and conceals the reduced eighth sternum, or the ninth sternum when the vaginal opening is transferred to the ninth segment.

*Vagina (Vag)*.—The genital chamber when the latter takes on a pouchlike or tubular form with a narrowed posterior opening; in some insects extended into the ninth segment to open on or behind the ninth sternum.

*Ostium vaginae, or vulva (Vul)*.—The external opening of the copulatory pouch or vagina, on either the eighth or the ninth abdominal segment, serving usually both for copulation and for the discharge of the eggs.

*Bursa copulatrix*.—Any cavity of the female serving for the reception of the male organ of copulation; usually the genital chamber or its derivative, the vagina; in most Lepidoptera a diverticulum of the genital chamber invagination on the eighth abdominal segment.

#### V. THE OVIPOSITOR OF ORTHOPTERA

The ovipositor of orthopteroid insects presents three types of structure. It occurs in a reduced and in some cases a more or less modified form in Phasmidae, Mantidae, and Blattidae; it is normally developed in Grylloblattidae, Tettigoniidae, and Gryllidae, and attains its greatest mechanical perfection in the last family; finally, it is most specialized and modified in structure in Acrididae and Tridactylidae. For a general account of the ovipositor in these several families the student is referred to the paper by Walker (1919) on the terminal structures of orthopteroid insects; the comparative musculature of the ovipositor is described by Ford (1923). The morphology and mechanism of the organ will be illustrated here from studies made on *Blatta* and *Gryllus*, forms representing the first and second types of structure noted above; a description of the specialized acridid type will be reserved for a future paper.

The ovipositor of Grylloblattidae, Tettigoniidae, Gryllidae, and Acrididae differs from the ovipositor of other insects in that the third valvulae enter into the formation of the shaft of the organ, which thus consists of three pairs of appendicular blades or lobes, which are the first, second, and third valvulae as here named. Because of their usual positions relative to one another in the Orthoptera, the three pairs of blades are distinguished by Walker (1919) as *dorsal, ventral, and inner valvulae*, or correspondingly by Chopard (1920) as *valves*

*supérieures, inférieures* and *internes*. The ventral pair are the first valvulae, as designated in the present paper, the inner pair the second valvulae, and the dorsal pair the third valvulae. In Gryllidae and Acrididae the inner, or second, valvulae are rudimentary, and the functional part of the ovipositor thus consists of only two pairs of valvulae. Hence, it must be observed that the four-valve ovipositor of these insects differs from the four-valve ovipositor of Thysanura, Hemiptera, and Hymenoptera in that the shaft is formed of the first and third valvulae, while in the latter groups it consists of the first and second valvulae. The first valvifers are always displaced posteriorly in the Orthoptera and closely associated with the ninth segment; the second valvifers are never distinctly differentiated from the third valvulae.

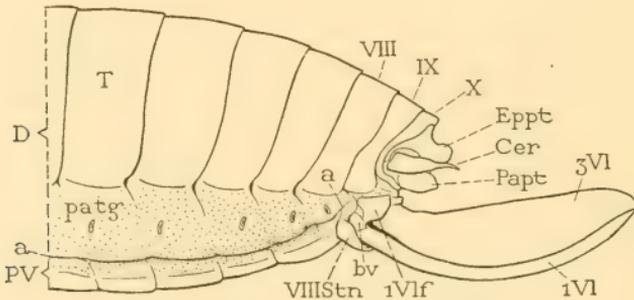


FIG. 12.—Female nymph of *Scudderia*.

Dorso-pleural line of abdomen marked by a fold (*a-a*); ovipositor with small basalvalvular sclerite (*bv*) at base of first valvula (*1VI*); epiproct (*Eppt*) partially surrounding base of cercus (*Cer*).

The six-valve type of ovipositor is typically developed in Grylloblattidae and Tettigoniidae, but the basal parts of the organ are somewhat weak in these families, and in structure they are scarcely representative of that of the highly perfected basal mechanism of the ovipositor of Gryllidae. A brief study of a typical form, such as *Scudderia*, however, will serve as an introduction to the more detailed description of *Gryllus* to follow.

The abdomen of *Scudderia* (fig. 12) presents a wide membranous area on each side in which the spiracles are located. A prominent groove traversing the lower part of the membrane marks the dorso-pleural line (*a-a*), which posteriorly extends above the basal plates of the ovipositor. The spiracles lie in the laterodorsal, or paratergal, region of the membrane (*patg*) above the dorso-pleural line. The eighth, ninth, and tenth terga are distinct, and the epiproct (*Eppt*) is well developed. The eighth sternum (*VIIIStn*) forms a small

subgenital plate underlapping the base of the ovipositor. The first valvifers (*1Vlf*) are displaced posteriorly, and are thus entirely separated from the tergum of the eighth segment, though they are in closer association with the eighth sternum. The broad ovipositor shows only the first and third valvulae externally (*1VI*, *3VI*), the second valvulae being concealed between the outer blades.

The mature ovipositor of *Scudderia* is strongly upcurved, and its free margins are toothed (fig. 13 C). The mechanical relations of the parts of the organ to one another can be studied only in fresh specimens, or in specimens preserved in liquid; the parts are best seen when the entire ovipositor is removed from the body. Each of the first, or ventral, valvulae (*1VI*) is attached to a small, oval lateral plate at the base of the ovipositor (*1Vlf*), which is the first valvifer ("pileolus" of Chopard, 1920). The first valvifer and its valvula are continuous, but they are flexible on each other by reason of the narrowness of their union (*c*). The upper end of the valvifer is connected, also by a flexible union (*b*), with the basal part of the broad third, or dorsal, valvula (*3VI*), the side of which it overlaps ventrally. From an angle on the anterior margin of the first valvifer there projects internally a strong apodeme (*c*), on which muscles are attached. If the first valvifer is revolved upward on its flexible dorsal attachment (*b*), the ventral valvula is retracted. In some of the Tettigoniidae the proximal part of the first valvula is more or less distinctly differentiated as a basal sclerite, or *basivalvula*, shown in the nymph of *Scudderia* (fig. 12, *bv*).

Each of the dorsal, or third, valvulae of *Scudderia* (fig. 13 C, *3VI*) is somewhat thickened at its base where the first valvifer is attached, there being differentiated here an area (*2Vlf*) that evidently corresponds with the second valvifer of an ovipositor having a more typical structure (figs. 10 C, 31 B), in which each limb base element of the ninth segment becomes divided into a valvifer (*2Vlf*) and a distal lobe (*3VI*). The muscles inserted on this basal part of the dorsal valvula in *Scudderia* and other tettigoniids are those of the second valvifer in other insects. The area in question is sometimes called the "basivalvula" of the dorsal valvula, but the term is unnecessary and misleading since the area so designated does not correspond morphologically with the basivalvula of the ventral valvula. A strong apodeme (fig. 13 C, *g*) projects from the anterior margin of the valvifer area. This apodeme is the *superior apophysis* of Walker (1919).

The dorsal and ventral valvulae are rather weakly connected with each other in *Scudderia*, but in the Tettigoniidae and Gryllidae gen-

erally the two on each side are interlocked by dovetailing grooves and ridges on their opposing margins (fig. 20), so that they may freely slide upon each other without being separated. Judging from the

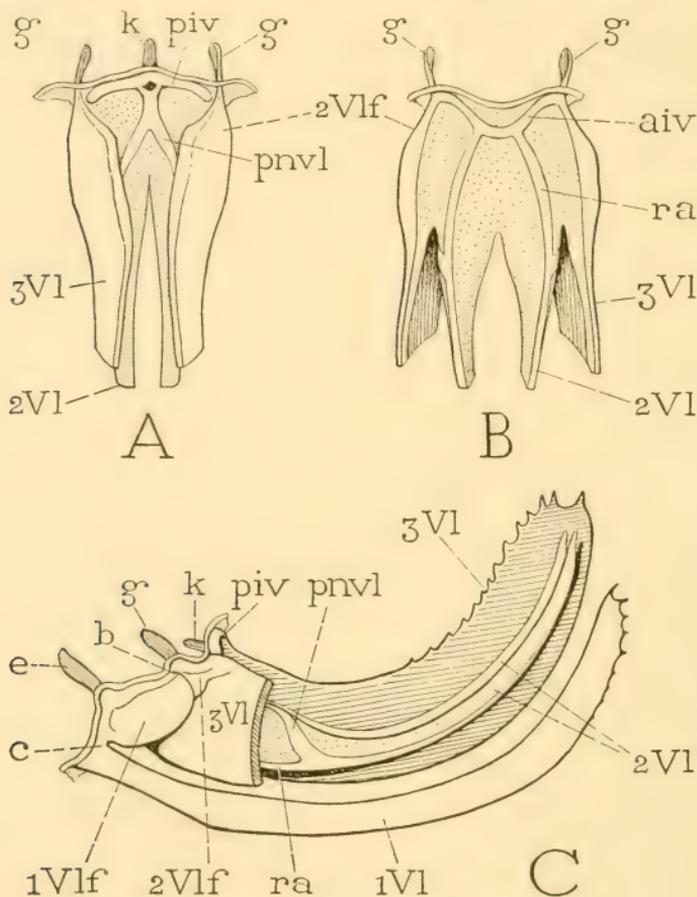


FIG. 13.—Ovipositor of adult *Scudderia*.

A, dorsal view of base of ovipositor.

B, ventral view of same.

C, lateral view of ovipositor, with left third valvula removed near base.

*aiv*, anterior intervalvula; *b*, articulation of first valvifer with second valvifer; *c*, attachment of first valvula to first valvifer; *e*, apodeme of first valvifer; *g*, apodeme of second valvifer; *k*, apodeme of posterior intervalvula; *piv*, posterior intervalvula; *pnv1*, pons valvularum; *ra*, ramus of second valvula; *1V1*, first valvula; *2V1*, second valvula; *3V1*, third valvula; *1Vlf*, first valvifer; *2Vlf*, second valvifer.

mechanism of the ovipositor in *Scudderia* it would appear that the principal mobile elements are the ventral valvulae, which are movable by the muscles of the first valvifers.

The inner, or second, valvulae of *Scudderia* are narrow, closely appressed blades (fig. 13 C, *2Vl*), upcurved between the broad third valvulae. Their thickened bases are united medially with each other (B, *2Vl*) and laterally with the inner faces of the basal valvifer areas (*2Vlf*) of the third valvulae. The lower edges of the weak inner valvulae are strengthened by narrow sclerotic bands in their walls, the proximal continuations of which, termed by Walker (1919) the *rami* (fig. 13 B, C, *ra*), are united with a transverse intervalvular bar (B, *aiv*) between the ventral margins of the second valvifers. From the ramus of each inner valvula a sclerotic tongue extends upward in the lateral wall of the valvula (C, *pnvl*) into the dorsal wall of the common base of the two inner valvulae (A), and here the two from opposite sides are confluent in a median stem that unites with a dorsal intervalvular bar (*piv*). This Y-shaped dorsal sclerotization in the base of the inner valvulae Walker (1919) calls the *pons valvularum* (*pnvl*).

The dorsal and ventral intervalvular bars above mentioned (fig. 13 A, B, *piv*, *aiv*) are the "superior intervalvula" and "inferior intervalvula" of Walker (1919). These terms are appropriate in the Tettigoniidae where one intervalvula is dorsal to the other, but the sclerites both belong to the ventral wall of the ninth segment, and are hence morphologically posterior and anterior, as they are anatomically in Gryllidae (fig. 18, *piv*, *aiv*). For this reason the writer terms the intervalvular sclerites the *anterior intervalvula* (*aiv*) and the *posterior intervalvula* (*piv*), the first being the "inferior" intervalvula according to Walker, the second the "superior". The posterior intervalvula of *Scudderia* bears a prominent median apodeme (fig. 13 A, C, *k*).

The musculature of the ovipositor in Tettigoniidae and Gryllidae is more complex than in Hemiptera and Hymenoptera. The dorsal muscles of the eighth segment are inserted on the first valvifers; those of the ninth segment on the second valvifers, and on the intervalvulae, the first being tergopleural, the second tergoventral. Besides these there are muscles connecting the first valvifers with the second valvifers and with the posterior intervalvula. In *Scudderia* a large bundle of fibers arises on the inner face of the second valvifer and is inserted on the outer wall of the corresponding inner valvula between the ramus and the arm of the pons. The musculature of the ovipositor and the terminal segments of the abdomen will be fully treated in the description of *Gryllus assimilis*.

The ovipositor of *Grylloblatta*, judging from the descriptions of Crampton (1917, 1927) and Walker (1919), is very evidently of the

tettigoniid type. Walker says that "in the external form of the valvulae and their connections with neighboring sclerites *Grylloblatta* is remarkably like a primitive Tettigoniid, such as *Ceuthophilus*." The three pairs of valvulae are well developed, but the dorsal and ventral pairs are not connected, and the median pair is exposed between them. The basivalvulae form distinct sclerites between the bases of the ventral valvulae and the eighth sternum. Crampton believes that the basivalvulae are derived from the "coxites" of the eighth segment of the nymph, but he gives no evidence that the sclerites in the nymph are limb base elements. The presence of well-developed styli on the ends of the dorsal valvulae in the nymph of *Grylloblatta*, which are lost in the adult, is a primitive feature retained likewise in the young of Blattidae.

#### GRYLLUS ASSIMILIS FABRICIUS

Since the cricket is a good subject for school laboratory work, it is here selected for a detailed study of the orthopteroid abdomen and ovipositor. The abdomen of the cricket gives a fairly generalized example of the typical structure of the abdominal part of the insect body. The ovipositor, however, is by no means generalized; it is specialized in the way the ovipositor of all Orthoptera is specialized, and in addition it is one of the most highly perfected egg-laying mechanisms found among the insects.

*The visceral region of the abdomen.*—The pregenital segments of the cricket's abdomen are all well developed in both the male and the female (fig. 14 A), and contain distinct tergal and sternal plates. The terga (*T*) are separated from the sterna (*Stn*) by a wide membranous or coriaceous area on each side of the body, containing the spiracles. Running lengthwise through each of these membranous areas, below the spiracles, is a prominent lateral fold (*a-a*). The relations of the parts of the abdomen above and below the lateral fold to each other and to the corresponding parts of the thorax attest that the fold marks the site of the dorso-pleural line. The membranous area above the fold, containing the spiracles, is, therefore, the laterodorsal region, or paratergal area of the dorsum (*Id*), and that below the fold is the true pleural area (*P*). Anteriorly it is seen that the line of the dorso-pleural fold on the abdomen extends into the thorax dorsal to the thoracic pleural plates, or subcoxae (*Scx*), and that the pleural area continued from the abdomen here expands between the metathoracic tergum and sternum (*T<sub>3</sub>, Stn<sub>3</sub>*) to include the thoracic pleura, or subcoxal parts of the leg bases. Posteriorly the line of the dorso-pleural fold extends, in the female (*B, a*), between the tergum of the ninth

segment (IX) and the basal plates of the ovipositor (*Ovp*). This relation is more clearly shown if the dorsum of the abdomen is separated from the pleurosternal parts (C), the dorso-pleural line (*a-a*) being theoretically carried out above the bases of the cerci (*Cer*). It is thus to be seen that the basal plates of the ovipositor (*C*, *1Vlf*, *2Vlf*) belong to the pleural area of the abdomen (*P*), and that, there-

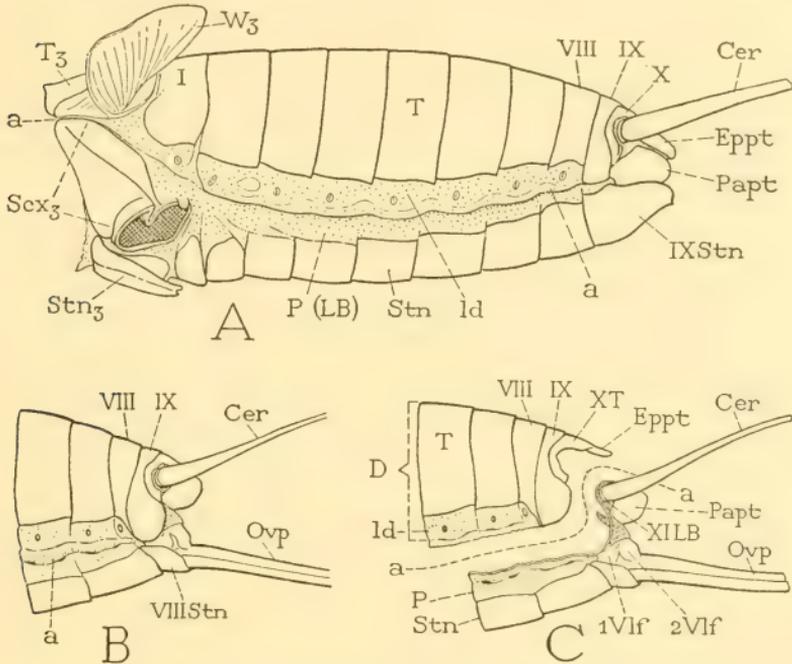


FIG. 14.—Abdomen of *Gryllus assimilis*.

A, lateral view of male abdomen and metathorax, showing groove (*a-a*) along dorso-pleural line above thoracic subcoxae and limb base, or pleural, region (*P*) of abdomen.

B, end of abdomen of female, showing relation of base of ovipositor to eighth and ninth segments.

C, same part of abdomen separated along dorso-pleural line (*a-a*).

fore, they correspond in position, at least, with the subcoxal plates of the thoracic leg bases (A, *Scx*).

A closer study of the membranous lateral areas of the visceral region of the abdomen (fig. 15 A) shows that the dorso-pleural fold (*a-a*) on each side is bordered above by an undulating series of slender sclerotizations, and below by a similar series of somewhat thicker sclerotizations. The upper series evidently marks the lower edge of the dorsum (*D*), and the lower series the upper edge of the pleuro-

ventral region (*PV*). The sclerotic thickenings form attachment points for muscles on the inner abdominal wall (*B*).

The musculature of the visceral segments in the abdomen of *Gryllus* comprises the usual *dorsal*, *ventral*, *lateral*, *transverse*, and *spiracular* muscles. The following muscles may be distinguished in an individual segment, such as the fifth or sixth, shown at *B* of Figure 15.

The *dorsal muscles* consist of two sets of longitudinal fibers, both of which apparently belong to the internal system, since no muscles

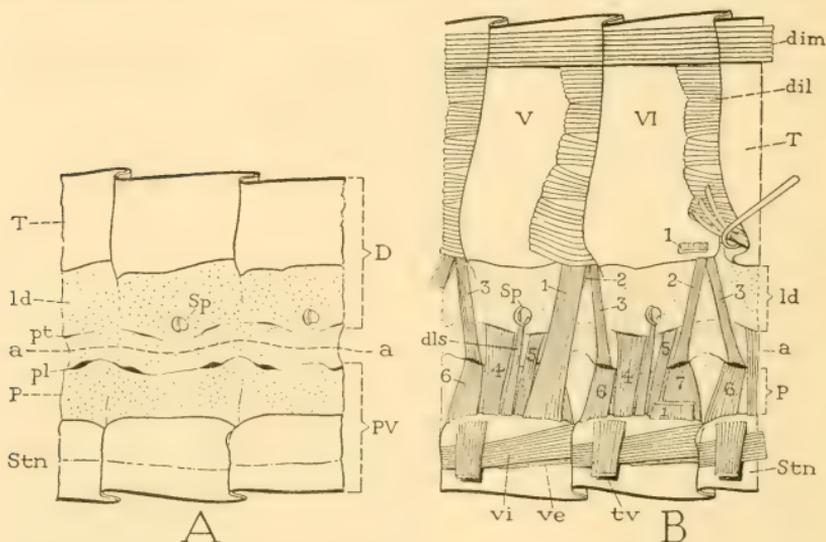


FIG. 15.—Relation of the musculature to the integumental areas in the abdomen of *Gryllus assimilis*.

*A*, lateral and ventral parts of two consecutive segments, with separation between dorsum (*D*) and pleuroventral region (*PV*) indicated by dorso-pleural line (*a-a*).

*B*, musculature of right half of segments *V* and *VI*.

*a-a*, dorso-pleural line; *D*, dorsum; *ld*, laterodorsal area; *P*, pleural region; *pl*, series of pleurites; *pt*, series of paratergal sclerotizations; *PV*, pleuroventral region; *Stn*, sternae; *T*, terga.

lie external to them. The fibers of one set, the median dorsals (*dim*), form in each segment a narrow band of segmental length on each side of the median line of the back, attached to the anterior margins of successive terga. The fibers of the other set, the lateral internal dorsals (*dil*), occupy the wide lateral parts of the terga, but they are confined to the posterior parts of the segments, since they arise behind the middle of the tergal plate before the one on which they are inserted.

The *ventral longitudinal muscles* comprise internal ventrals (*vi*) of segmental length located laterally on the sternae, and external ven-

trals (*vc*) lying beneath the others, where they arise near the middle of each sternal plate and are inserted posteriorly on the anterior margin of the sternum following. The *transverse ventrals* consist of wide bands of fibers (*tv*) crossing the anterior parts of the segments internal to the longitudinal ventrals, and attached laterally on the edges of the sternal plates. The last transverse ventral in the female is that of the seventh segment (fig. 19 A, *tv*).

The *lateral muscles* include tergo-sternal, tergo-pleural, paratergo-sternal, and pleurosternal muscles. In each segment there is a large tergo-sternal lateral muscle (1) arising on the posterior lateral part of the tergum external to the lateral dorsals, and inserted on the posterior lateral margin of the sternum. Just behind this muscle, and external to it, are two tergo-pleural muscles (2, 3) taking their origin on the lower edge of the tergum. The first (2) is attached ventrally on the pleural margin of the same segment; the second (3) is intersegmental since it is attached on the pleural margin of the following segment. The paratergo-sternal muscles comprise two bands of fibers (4, 5) on the middle of each segment, one before, the other behind the spiracle dilator (*dls*). The pleurosternal muscles include likewise two bands of fibers, one (6) in the anterior part of each segment, the other (7) in the posterior part.

The *spiracular muscles* are the usual antagonistic pair inserted on the manubrium of the anterior movable wall of the spiracular atrium. One is a very small occlusor arising on the posterior atrial wall; the other is a large dilator (*dls*) arising ventrally on the edge of the sternum between the attachments of 4 and 5.

The somatic muscles of the visceral region of the cricket's abdomen are used by the female principally for respiratory purposes, since oviposition is accomplished by the muscles of the genital segments, and ordinarily involves few movements in the rest of the abdomen. The mechanical relation of the lateral muscles to the skeletal parts of the abdomen is shown diagrammatically at A of figure 16. It is to be noted that the muscles can produce only a contraction of the abdomen, brought about mostly by a lifting of the sternal plates, since there is no antagonistic mechanism capable of dilating the abdomen, either dorso-ventrally or longitudinally, such as that developed in the Acrididae. Inspiration with the cricket, therefore, must be accomplished by a passive expansion of the abdominal parts compressed by muscular force.

*The genital segments and the ovipositor.*—The genital segments of the female cricket (fig. 14 B, I, VIII, IX) are somewhat reduced by comparison with the eighth and ninth abdominal segments of the

male (A). The shortened eighth tergum (B, *VIII*) ends below in a point separated by the dorso-pleural fold from the small eighth sternum (*VIIIStn*), which projects beneath the base of the ovipositor as a small subgenital plate. The ninth tergum (*IX*) is narrowed above, but is widened on the sides, and extends downward to the base of the ovipositor. The venter of the ninth segment is not visible externally; it is the narrow, membranous ventral wall of the segment between the basal halves of the ovipositor, containing anteriorly and posteriorly

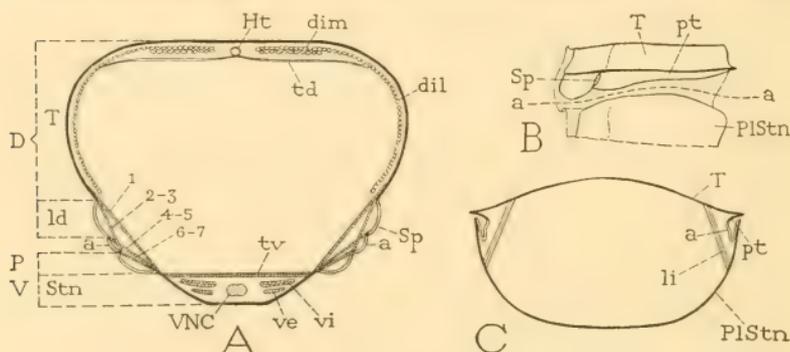


FIG. 16.—Abdominal structures of *Gryllus* and *Blatta*.

A, diagrammatic cross-section through abdomen of *Gryllus assimilis*, showing relation of integumental areas and muscles illustrated in Figure 15.

B, lateral parts of abdominal segment of *Blatta orientalis* with dorsal and ventral plates separated to expose the dorso-pleural fold (*a-a*).

C, diagrammatic cross section of abdomen of *Blatta*, showing infolded dorso-pleural membrane (*a*), and position of lateral muscles (*li*).

the sclerotic intervalvular bridges (figs. 17 H, 18, *aiv*, *piv*). In the male the ninth sternum is fully exposed, and forms a large subgenital plate (fig. 14 A, *IXStn*). The inner surfaces of the eighth and ninth terga of the female (fig. 18) are enlarged by thin apodemal extensions from their anterior margins, giving attachment to muscles of the ovipositor. The ninth tergum has a strongly developed antecosta (*Ac*), which terminates in a ventral process bearing a socket (*a*) for articulation with the basal part of the ovipositor.

The musculature of the genital segments is mostly adapted to the mechanism of the ovipositor. The dorsal muscles, however, conform with those of the visceral segments, and in the eighth segment there are one or two pairs of weak lateral muscles inserted below near the margins of the eighth sternum. The other lateral muscles in both genital segments are highly developed as muscles of the ovipositor (fig. 17 E). Ventral muscles are absent in the eighth segment, and those of the ninth segment are of doubtful homology with the ventral muscles of the visceral segments.

The ovipositor of the cricket consists of a small basal part, attached to the ninth abdominal segment (fig. 14 B), and of a long, slender shaft terminating in a sharp-pointed enlargement (fig. 17 B). The shaft is formed of the first and third valvulae (figs. 17 A, E, 18, *1VI*, *3VI*), which are respectively ventral and dorsal in position relative to each other. The second valvulae are reduced to a pair of small, membranous lobes (figs. 17 E, G, 18, *2VI*) arising from the venter of the ninth segment between the bases of the dorsal valvulae. The base of the ovipositor consists of the first and second valvifers (figs. 14 C, 17 A, *1Vlf*, *2Vlf*), and the anterior and posterior intervalvulae (fig. 17 H, *av*, *piv*). The two valvifers on each side are closely associated with the lower edge of the ninth tergum, but their true segmental relations are shown by the origins of their dorsal muscles (fig. 17 E), those of the first valvifer (3) arising on the eighth tergum, those of the second valvifer (6, 7) on the ninth tergum. The connection of the first valvifers with the ninth tergum is evidently a secondary association, since it is clearly an adaptation to the special mechanism of the orthopteroid type of ovipositor.

The first valvifer is an irregularly triangular plate (fig. 17 A, F, *1Vlf*). Its only connection with the eighth segment is by the pleural membrane uniting the eighth tergum and sternum; otherwise its associations are entirely with the ninth segment, except for its musculature. By a strongly developed condyle near the middle of its dorsal margin (F, *a*), the first valvifer freely articulates with the lower extremity of the antecosta (*Ac*) of the ninth tergum. Its anterior end is produced into a tapering process (*e*) for the attachment of muscles. At its posterior angle it has a narrow, flexible external connection with the second valvifer (*A*, *b*), internal to which is a deep notch (F, *d*) by which the first valvifer articulates with a condylar surface (G, *h*) of the second valvifer (figs. 17 H, *2I*, *dh*). Ventrally the first valvifer is continuous by a narrow, flexible tongue (fig. 17 A, F, *c*) with the first, or ventral, valvula (*1VI*). From the inner face of the first valvifer, above the inner articulation with the second valvifer, there arises a large flat apodeme (F, H, *f*), giving attachment to a thick, cylindrical muscle (E, H, *g*) from a median apodeme (*k*) of the posterior intervalvula (*piv*).

The second valvifer (fig. 17 A, G, *2Vlf*) is of a more irregular shape than the first, and its ventral part is directly continuous into the third, or dorsal, valvula (*3VI*). Its posterior end, just before the base of the valvula, is produced upward in a broad dorsal arm (G, *i*), which terminates in an apodeme, the superior apophysis, projecting within the ninth tergum (*A*, *i*). The anterior extremity of the second

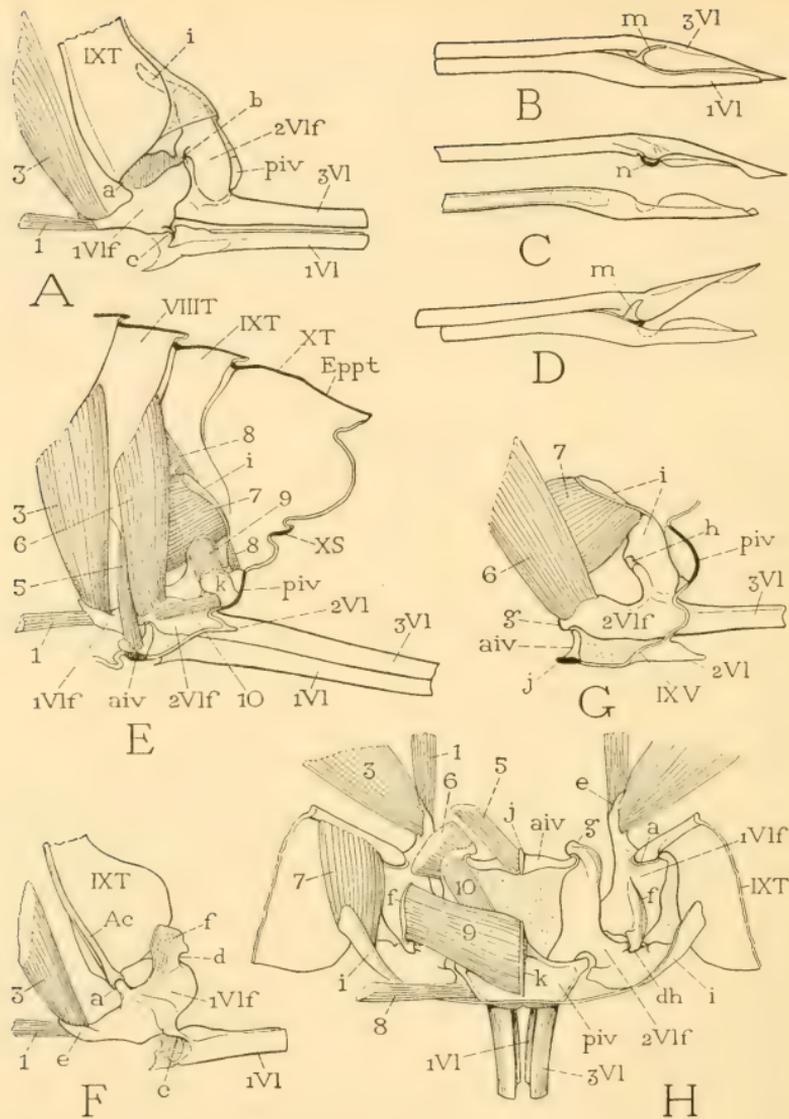


FIG. 17.—Details of structure and musculature of ovipositor of *Gryllus assimilis*.

A, base of ovipositor, showing articulation of first valvifer (*1Vlf*) at *a* with ninth tergum, and at *b* with second valvifer.

B, C, D, apical structure of shaft ovipositor.

E, inner view of genital and tenth segments, with right half of base of ovipositor and muscles of same side.

F, inner view of right first valvifer, showing its articulation (*a*) with ninth tergum, its anterior muscles, and connection (*c*) with first valvula.

G, inner view of right second valvifer and its muscles (*6*, *7*), together with anterior intervalvula (*aiv*), rudimentary second valvula (*2Vl*), and base of third valvula (*3Vl*).

H, dorsal view of valvifers and intervalvulae, and their muscles; first valvifers (*1Vlf*) articulated dorsally (*a*) to ninth tergum (*IXT*), posteriorly (*dh*) to second valvifers (*2Vlf*); second valvifers connected anteriorly by anterior intervalvula (*aiv*) and posteriorly by posterior intervalvula (*piv*).

valvifer forms a second strong process, the inferior apophysis (G, H, *g*). The articular condyle by which the second valvifer is hinged to the first is located on the inner face of the anterior margin of the dorsal arm (G, *h*). The second valvifer of the cricket has no direct connection with the ninth tergum.

Two intervalvular sclerites are well developed in *Gryllus*. The first, or anterior intervalvula (fig. 17 H, *aiv*), is a transverse bar between the anterior processes (*g*) of the second valvifers. Medially it bears a small apodeme (*j*). The second, or posterior intervalvula (*piiv*), is a broad, externally convex plate exposed above the bases of the dorsal valvulae (A, *piiv*). By its produced lateral extremities it articulates with the second valvifers at the deeply notched angles between the dorsal arms of the latter and the bases of the dorsal valvulae (H). Medially the posterior intervalvula bears a high, plate-like apodeme (E, H, *k*). In a lengthwise section of the abdomen (figs. 17 E, 18) it is clearly seen that the two intervalvulae (*aiv*, *piiv*) belong to the venter of the ninth abdominal segment, and that they have the status of anterior and posterior sternal sclerites lying between the second valvifers. Tergal muscles of the ninth segment are inserted on each of the intervalvulae.

The reduced eighth sternum, which forms a free subgenital plate (fig. 18, *VIIIStn*) beneath the base of the ovipositor, conceals a small genital chamber (*GC*) above its dorsal wall, between the bases of the valvulae. Into the anterior end of the genital chamber the short median oviduct (*Odc*) opens between two membranous folds (fig. 19 B, *l*) on the dorsal surface of the subgenital plate. Dorsal to the opening of the oviduct, the anterior dorsal wall of the genital chamber before the anterior intervalvula (*aiv*) forms a deep pouch (*t*) projecting into the body cavity above the oviduct. The pouch contains a strongly sclerotized, spoutlike organ (*u*) reflected from its anterior wall, which is transversed by the terminal part of the spermathecal duct (*SptD*). The deflected distal extremity of the spout, containing the opening of the sperm duct, projects into the genital chamber a little beyond the opening of the oviduct. The eggs issuing from the gonopore are thus, evidently, fertilized just before entering the channel of the ovipositor between the bases of the valvulae.

The shaft of the ovipositor consists of the slender, elongate first and third valvulae. The two valvulae on each side are firmly but freely interlocked by a ridge with an expanded margin on the lower edge of the dorsal third valvula (fig. 20) that is held in a groove on the apposed surface of the ventral first valvula. The valvulae of opposite sides are not united. The inner walls of the dorsal valvulae are

strongly sclerotized throughout, and each is strengthened by a high internal ridge. The ventral valvulae are membranous and flexible on their mesal surfaces, and the inner wall of each is thrown into a longitudinal fold.

*The muscles of the ovipositor.*—The musculature of the cricket's ovipositor is strongly developed, but is not particularly complex. It includes the ventral muscles of the seventh abdominal segment, and the principal lateral and ventral muscles of the eighth and ninth seg-

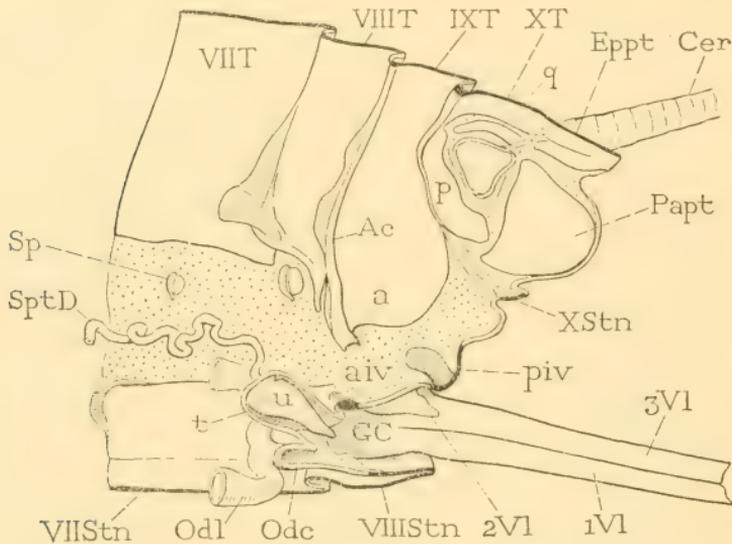


FIG. 18.—Inner view of right half of genital and postgenital segments of *Gryllus assimilis*.

Note genital chamber (*GC*) at base of ovipositor above eighth sternum (*VIIIStn*), with opening of median oviduct (*Odc*) anteriorly, and opening of spermathecal duct (*SptD*) through a spoutlike process (*u*) in a dorsal pouch (*t*) of genital chamber.

ments. The muscles attached on, or associated with, the ovipositor are the following, indicated by arabic numerals on figures 17 and 19 A.

1. *Retractors of the ovipositor* (fig. 19 A).—Origin anteriorly on anterior apodemes of seventh sternum; insertion posteriorly on anterior extremities of first valvifers (fig. 17 A, E, F, H). These muscles of the ovipositor fall directly in line with the internal ventrals of the pregenital segments anterior to the seventh (fig. 19 A, *vi*), and are clearly the corresponding muscles of the seventh segment, though here attached posteriorly on the valvifers of the eighth segment instead of on the eighth sternum.

2. *Retractors of the spermathecal pouch* (fig. 19 A).—Origins anteriorly on seventh sternum external to 1; convergent posteriorly to insertions on spermathecal pouch (*t*). These muscles clearly represent the external ventrals of the preceding segments. (Described by Du Porte, 1920, and Ford, 1923, as inserted on the median oviduct.)

3. *Tergal muscles of the first valvifers* (fig. 17 A, E, F, H).—The largest muscles of the ovipositor. Origins on anterior lateral apodemes and anterolateral surface of eighth tergum (E); insertions ventrally on anterior ends of first valvifers. These muscles, on the assumption

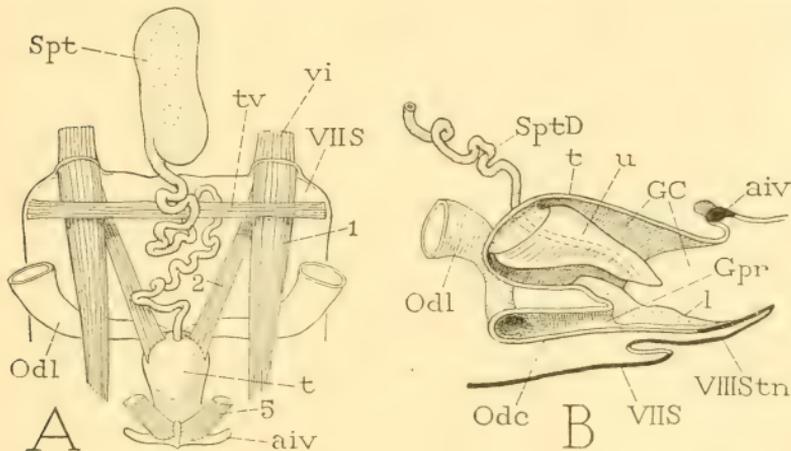


FIG. 19.—The spermatheca and associated structures of *Gryllus assimilis*.

A, dorsal view of spermatheca, lateral oviducts, and base of seventh sternum.

B, median section of genital chamber, spermathecal pouch, and median oviduct.

*aiv*, anterior intervalvula; *GC*, genital chamber; *Gpr*, gonopore; *l*, fold of membrane at side of gonopore; *Odc*, oviductus communis; *Odl*, oviductus lateralis; *Spt*, spermatheca; *SptD*, spermathecal duct; *t*, spermathecal pouch of genital chamber; *tv*, transverse ventral muscle of seventh segment; *u*, spermathecal spout; *vi*, internal ventral muscle of seventh segment; *1*, muscle from seventh sternum to first valvifer; *2*, muscle from seventh sternum to spermathecal pouch.

that the first valvifers are the bases of the first gonopods, are tergo-pleural muscles of the eighth segment.

4. *Ventrolateral dilators of the rectum*.—A group of slender, branching fibers arising on inner face of each first valvifer behind articulation with ninth tergum; inserted ventrolaterally on rectum. (Not shown in figures.)

The four following pairs of muscles arise on the lateral parts of the ninth tergum. Two of them (fig. 17 E, 5, 8), inserted ventrally on the intervalvulae, are anterior and posterior tergo-sternal muscles; the other two (6, 7), inserted on the second valvifers, are tergo-pleural muscles.

5. *Tergal muscles of the anterior intervalvula* (fig. 17 E, H).—A slender muscle on each side arising on anterior margin of lateral part of ninth tergum; the two converging ventrally to insertions medially on anterior intervalvula (*aiv*).

6. *Anterior tergal muscles of second valvifers* (fig. 17 E, G, H).—A pair of large vertical muscles, arising on anterior lateral apodemes of ninth tergum, internal to 5; insertions ventral on anterior processes (inferior apophyses) of second valvifers (G, H).

7. *Posterior tergal muscles of second valvifers* (fig. 17 E, G, H).—A pair of large, flat, horizontal muscles; each arising anteriorly on anterior margin of ninth tergum (H), external to 6 (E); inserted posteriorly on posterior dorsal apodeme (superior apophysis) of second valvifer (E, G, H, i).

8. *Tergal muscles of posterior intervalvula* (fig. 17 E, H).—A pair of relatively slender muscles, arising on lateral parts of ninth tergum (E) above 5 and external to upper ends of 6; extend ventrally and posteriorly, ectad of 7, to insertions in membranes laterad of posterior intervalvula (E, H, *piv*), with a few fibers attached on the latter.

The next two pairs of muscles have a ventral position and connect the valvifers with the posterior intervalvula, but their homology with muscles of the pregenital segments is not clear. They are described by Ford (1923) as primary and secondary "outer sternal muscles" of the ninth segment. An "inner sternal muscle" of the ninth segment, she says, extends from the first valvifer to the paraproct, but the writer did not observe this muscle in the female of *Gryllus*, which, according to Du Porte (1920), occurs in the male only.

9. *Intervalvular muscles of the first valvifers* (fig. 17 E, H).—A pair of short, thick, cylindrical muscles arising on sides of median apodeme (*k*) of posterior intervalvula (*piv*); extending laterally and a little forward to posterior internal apodemes of first valvifers (H, *f*).

10. *Intervalvular muscles of second valvifers* (fig. 17 E, H).—Origins medially on apodeme of posterior intervalvula (*k*), ventral to 9; diverge anteriorly to insertions on anterior ends of second valvifers.

Muscles pertaining to the rudimentary second, or inner, valvulae the writer did not find in *Gryllus*, but Ford (1923) describes a pair of such muscles having their origins on the anterior intervalvula and their insertions in the tips of inner valvulae. In *Scudderia* the well-developed muscles of the inner valvulae have their origins on the inner faces of the second valvifers.

*The mechanism of the ovipositor.*—The eggs of *Gryllus* are laid in the ground. Before inserting the ovipositor the female often clears

a small space on the surface of the earth selected as the oviposition site. The clearing operation is a strenuously performed task, the insect hurriedly scratching away loose surface material with her fore feet as if in desperate haste to prepare the spot, from which she may remove in her jaws pellets and pebbles as large as her body. This done, she reverses her position and jabs the ovipositor at the clearing, or, at least, such is her evident intent, but often as not the aim miscarries, quite unperceived by the impetuous cricket, and the subsequent insertion of the ovipositor is then made at a place entirely untouched in the work of preparation.

At the beginning of oviposition the *Gryllus* female elevates herself on her hind legs, thus raising the abdomen, and depresses the ovipositor until its shaft is directed posteriorly and downward at an angle of about 45 degrees to the surface of the ground, as the tip is inserted

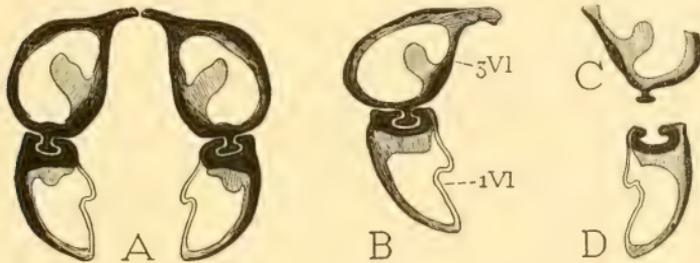


FIG. 20.—Sections of the shaft of the ovipositor of *Gryllus assimilis*, showing groove-and-ridge connections between the first and third valvulae.

into the latter. Within the space of a minute, when working in soft soil, the ovipositor is buried to full length, and the terminal part of the abdomen comes in contact with the ground. During the insertion process the two valvulae of each side glide rapidly back and forth a short distance on each other, the corresponding blades of opposite sides apparently working in unison. The egg enters the channel of the ovipositor at the bases of the valvulae, passes along the entire length of the shaft, and is extruded from the tip into the bottom of the excavation. During the withdrawal of the ovipositor, the organ is repeatedly thrust down into the cavity at successively shorter depths, evidently to pack the soil above the egg. When the ovipositor is fully extracted, the insect gives no further attention to the place where the egg has been intrusted to the earth. These observations on *Gryllus* were made on individuals in confinement. *Nemobius* scratches over the surface where the egg has been deposited before leaving it; *Occanthus* plugs each egg cavity she makes in a twig with bark chew-

ings mixed with a gluey discharge from the ovipositor. As is the usual habit with crickets, *Gryllus* deposits but one egg in each boring.

The movements of the ovipositor made by *Gryllus* during egg laying in soft soil are thus seen to be very simple ones, and there is scarcely any accompanying motion of the abdomen, such as the contortions made by *Oecanthus* while drilling into wood. The ovipositor of *Gryllus* is lowered preparatory to its insertion into the ground, its penetration is accompanied by the rapid back-and-forth movement of the valvulae on each other, and after withdrawal it is elevated again to the usual position. The entire organ is probably capable of a slight protraction and retraction.

The fixed points of movement in the basal parts of the ovipositor are the articulations of the first valvifers with the lower edges of the ninth abdominal tergum (fig. 17 A, F, 21, *a*), the outer and inner articulations of the two valvifers on each side with each other (fig. 17 A, *b*, fig. 21, *dh*), and the weak, flexible unions of the first valvulae with the lower angles of the first valvifers (*c*). Otherwise the ovipositor has a free movement on the abdomen by means of its membranous connections with the latter.

The movements of depression and elevation of the ovipositor affect not only the shaft but the entire basal parts of the organ, and the fulcra are the articulations of the first valvifers with the lower angles of the ninth tergum (figs. 17 A, 21, *a*). The muscles that accomplish these movements are clearly the anterior and posterior lateral muscles of the ninth tergum (figs. 17 E, H, 21, 5, 8), the first of which are inserted ventrally on the anterior intervalvula (*aiv*), the second on or near the posterior intervalvula (*piv*). The insertion points of these muscles are anterior and posterior to the articulations of the first valvifers on the ninth tergum (*a*), and pulling upward on these points correspondingly depresses or elevates the ovipositor. Morphologically the levators and depressors of the ovipositor are the tergoabdominal muscles of the ninth abdominal segment.

The alternating opposite movements of the dorsal and ventral valvulae on each other depend on the articulation of the first valvifers with the ninth tergum (fig. 21, *a*), and on the inner articulation of the two valvifers of each side with each other (*dh*). A depression of the posterior end of either of the first valvifers (B) causes the corresponding ventral valvula, which is flexibly attached to the ventral angle of the first valvifer, to slide proximally on the lower edge of the dorsal valvula. But, since the first valvifer rocks on the fulcrum (*a*) of the ninth tergum, its posterior end, when depressed, describes a short arc of a circle in a downward direction

(indicated by the curved arrow on the right), and this movement bears down on the second valvifer and gives this valvifer a thrust posteriorly, which causes the dorsal valvula to slide backward on the ventral valvula while the latter is moving forward. The opposite movement of the first valvifer (indicated by the curved arrow on the left) reverses the movement of the valvulae on each other. Thus, by a simple rocking motion of the first valvifer on its articulation with the ninth tergum, the two valvulae of the same side move lengthwise on each other alternately in opposite directions. This action can easily be demonstrated on a dissected specimen. But also it will be observed that a rocking motion of the second valvifer on its articulation with the first valvifer (*dh*) imparts the same movements to

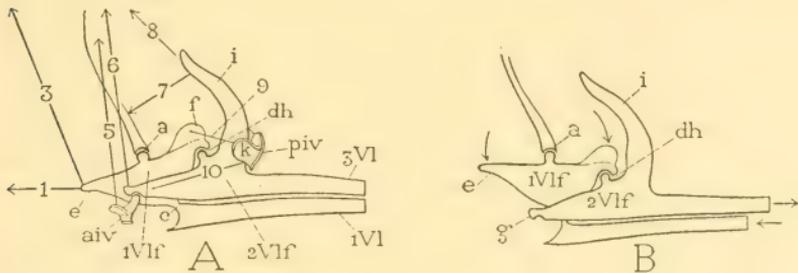


FIG. 21.—Diagrams of the basal mechanism of the ovipositor of *Gryllus assimilis*.

*a*, articulation of first valvifer with ninth tergum; *aiv*, anterior intervalvula; *c*, attachment of first valvula to first valvifer; *dh*, inner articulation between first and second valvifers; *e*, anterior apodeme of first valvifer; *f*, posterior apodeme of first valvifer; *g*, anterior apodeme of second valvifer; *i*, posterior apodeme of second valvifer; *k*, median apodeme of posterior intervalvula; *piv*, posterior intervalvula; *1Vl*, first valvula; *3Vl*, third valvula; *1Vlf*, first valvifer; *2Vlf*, second valvifer.

the two valvulae, and increases the degree of movement in the dorsal valvula. The mechanism is extremely delicate, and the least motion, either of the first valvifers on the ninth tergum, or of the second valvifers on the first valvifers, produces the sliding movement of the valvulae on each other. The dorsal valvulae are the stronger of the two pairs of blades forming the shaft of the ovipositor, and end in sharp points which normally project beyond the thin, truncate tips of the second valvulae (fig. 17 B, C).

The muscles that bring about the movement of the valvulae on each other are the three pairs of large lateral muscles inserted on the valvifers (fig. 17 E, H, 3, 6, 7). These muscles, morphologically, are the tergopleural muscles of the eighth and ninth abdominal segments. The first on each side (3), arising on the eighth tergum and inserted

on the anterior end of the first valvifer, depresses the posterior end of this valvifer by pulling upward on its anterior end (fig. 21 A, B). The muscle, however, has no antagonist inserted on the first valvifer, so that its contraction simply retracts the ventral valvula and protracts the dorsal valvula (B). After this, the principal movement of the valvulae on each other evidently results from the motion of the second valvifer on the first, and there can be no doubt that the muscles effecting this action are those of the ninth tergum inserted on the second valvifers (fig. 17 E, G, H, 6, 7). The first of these two muscles (6) is attached on the anterior apophysis (*g*) of the second valvifer; the second (7), having a horizontal position, is attached on the posterior dorsal arm (*i*) of the same valvifer. The two muscles thus oppose each other from opposite sides of the articular surface (G, *h*) by which the second valvifer rocks on the first valvifer. If the ovipositor were a rigid structure, this mechanism apparently could only move the distal shaft of the ovipositor up and down on the fulcral point (*h*), but as already noted, the demonstrable effect of the rocking of the second valvifer on the first valvifer is an opposite back-and-forth movement of the two valvulae of the same side on each other.

The two pairs of ventral muscles of the ovipositor (fig. 17 E, H, 9, 10) uniting the first valvifers and the second valvifers, respectively, with the posterior intervalvula (*piw*), must be tensors in function, since their contraction could only produce a compression of the basal parts of the ovipositor. The muscles of the seventh sternum (fig. 19 A, 1), inserted on the anterior ends of the first valvifers (fig. 17 A, E, F, H, 1), are evidently retractors of the ovipositor.

During oviposition, the egg passes through the entire length of the ovipositor in the channel between the valvulae. It appears that the movement of the valvulae on each other is the cause of the progress of the egg, but it is not evident how the effect is produced, since the inner surfaces of the valvulae are smooth and give no suggestion of the means by which the movement of the egg is controlled.

The distal end of the ovipositor is somewhat enlarged and forms a lanceheadlike termination of the shaft with the acute apex slightly depressed (fig. 17 B). The tips of the valvulae are capable of opening upon each other by reason of a hingelike membranous area (*m*) at the base of the enlarged terminal part of each of the dorsal valvulae. In handling narcotized specimens, the observer may be surprised to see the ends of the valvulae suddenly gape widely apart (D), as they sometimes do. There are no muscles in the terminal parts of the ovipositor; the opening of the distal extremities of the blades is pro-

duced automatically by an extreme retraction of the dorsal valvulae, which brings a pair of knobs (*C, n*) on their under surfaces against abruptly rising areas on the upper surfaces of the ventral valvulae, with the result that the distal parts of the dorsal valvulae, beyond the membranous hinges (*m*) at their bases, are suddenly thrown upward (*D*). The opening apparatus probably enables the cricket to hold the egg in the tip of the ovipositor so that it may be thrust securely into the bottom of the hole where it is deposited. This use of the ovipositor the writer has clearly observed in the case of *Nemobius* ovipositing against the wall of a glass jar.

*The postgenital segments.*—The tenth and eleventh segments of the abdomen together form a conical end piece of the body, which supports the cerci laterally and encloses the anus between its distal lobes (fig. 22 A).

The tenth tergum and the epiproct (fig. 22 A, *XT, Eppt*) are united in a composite supra-anal plate, but the boundary separating the two component parts of the plate is quite evident. The narrowed anterior lateral angles of the dorsal part of the tenth tergum are continued into abruptly widened lateral plates (fig. 18, *p*), which are produced ventrally on the sides of the tenth segment, before the bases of the cerci, to the lower angles of the paraprocts (*Papt*). The venter of the tenth segment is mostly membranous, but it contains a narrow, transversely elongate sternal sclerotization (fig. 22 C, *XStn*). Internally the anterior margin of the tenth tergum is strengthened by a strong antecosta (*Ac*). The dorsal part of the tenth tergum is separated from the base of the cercus on each side by a wide membranous area containing a small crescentic sclerite (*A, q*).

The tergum of the eleventh segment, or epiproct, consists of the distal lobe of the supra-anal plate (fig. 22 A, *Eppt*). Its marginal parts (*s*) are separated from the median shield-shaped region by a narrow, weakly sclerotized or membranous area on each side. The marginal band (*s*) appears to end anteriorly at the transverse folds extending outward from the posterior edge of the tenth tergum to the bases of the cerci. Considering, however, that the cerci belong to the eleventh segment, and observing that in *Scudderia* (fig. 12) the basal angles of the epiproct (*Eppt*) are produced into slender arms extending forward and downward *anterior* to the bases of the cerci, there is reason to believe that the marginal band of the epiproct in *Gryllus* is morphologically continued anteriorly in the narrow crescentic sclerites (fig. 22 A, *q*) lying mesad of the bases of the cerci, which appear to belong to the dorsum of the tenth segment. When the area about the base of the cercus is stretched and flattened out

(B), there is brought to view a weakly sclerotic connection between the sclerites *s* and *q*, and, moreover, there is exposed a distinct third sclerite (*r*) intervening between *q* and the base of the cercus (*LB*), which by an anterior process articulates with the inner margin of the

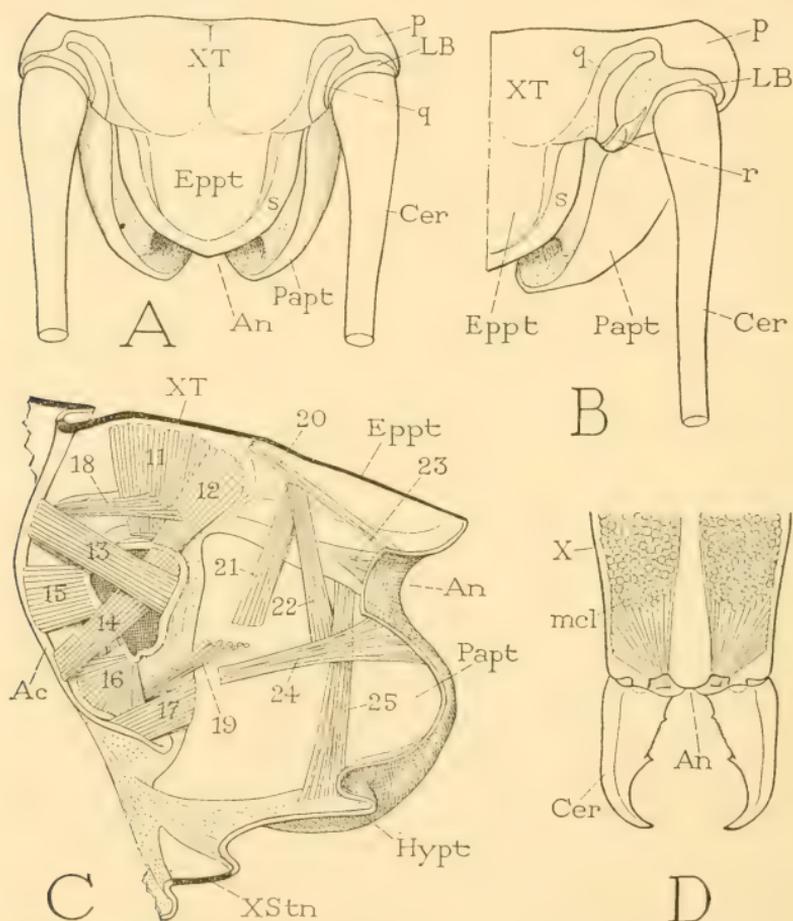


FIG. 22.—Structure of postgenital segments of *Gryllus assimilis*, and muscles of cerci of *Heterojapyx gallardi*.

A, dorsal view of postgenital segments of *Gryllus*.

B, right half of same with membranous parts stretched to show hidden sclerites.

C, muscles of right half of postgenital segments of *Gryllus*.

D, cerci and muscles in tenth segment of *Heterojapyx*.

latter. It is to be seen, therefore, that a broken sclerotic continuity exists between the base of the cercus and the epiproct.

The paraprocts (figs. 18, 22 A, B, C, *Papt*) are large, half-oval sclerites occupying the ventrolateral parts of the eleventh segment

behind and below the bases of the cerci and the lower ends of the lateral plates of the tenth tergum (fig. 18). The dorsal edges of the paraprocts are connected by membrane with the lateral margins of the epiproct (fig. 22 A, C), and their lower edges are united to each other by a median ventral membrane, the posterior edge of which forms a small median flap, or hypoproct (C, *Hyppt*). The posterior margins of the several lobes of the eleventh segment are inflected in the circumanal membrane, which is possibly to be regarded as a remnant of the periproct, and which is directly continued into the walls of the rectum.

The cerci are implanted on membranous areas (fig. 18) surrounded by the laterodorsal crescentic sclerites (*q*) above, the lateral plates (*p*) of the tenth tergum anteriorly and ventrally, and the paraprocts (*Papt*) behind. Each cercus has a distinct though narrow annular basis (fig. 22 B, *LB*), which, as already observed, articulates by its inner margin with the anterior arm of the small oval sclerite (*r*) attached to the posterior end of the crescentic dorsal sclerite (*q*). The appendage is provided with six muscles arising on the tenth tergum (C).

The musculature of the postgenital segments has little resemblance to that of the genital and visceral segments and gives little evidence bearing on the morphology of the terminal parts of the abdomen. The tenth segment muscles are mostly inserted on the bases of the cerci; the muscles of the eleventh segment connect the epiproct and paraprocts, and go to the circumanal membrane. The postgenital complex is movable on the rest of the abdomen by the dorsal muscles of the ninth segment inserted on the antecosta of the tenth tergum, and in the male there is a strong ventral muscle on each side from the anterior lateral angle of the ninth sternum to the inner face of the paraproct.

The muscles arising on the tenth tergum include the muscles of the cerci, two pairs of rectal muscles, and a pair of muscles to the paraproct. Du Porte (1920) describes and figures for *Gryllus* a dorsal longitudinal muscle lying "near the median line of the suranal plate, stretching from the anterior to the posterior borders of the sclerite": but the writer could find no such muscle present, and no corresponding muscle is mentioned by Ford (1923). The muscles of the tenth and eleventh segments, illustrated at C of Figure 22, are the following:

11.—A broad, flat, transverse muscle arising medially on tenth tergum; inserted on anterior arm of the small sclerite (B, *r*) articulating with dorsal margin of base of cercus.

12.—Origin posterior to 11 on extreme posterior part of tenth tergum; crosses internal to outer end of 11 to insertion on dorsal margin of base of cercus. This muscle Ford (1923) regards as a muscle of the epiproct which has shifted forward to the tenth tergum, since the corresponding muscle in some other Orthoptera arises on the epiproct.

13.—Origin anterior on antecosta of tenth tergum above level of cercus; goes posteriorly and downward to insertion on inner (posterior) edge of base of cercus.

14.—Origin on antecosta of tenth tergum before lower end of cercal base; extends upward and posteriorly, ectad of 13, to insertion on posterior dorsal angle of base of cercus.

15.—A short muscle arising on antecosta of tenth tergum between 13 and 14; insertion on anterior (outer) margin of base of cercus.

16.—A short, fan-shaped muscle arising on ventral part of tenth tergum; fibers converging dorsally to insertion on ventral angle of base of cercus.

The number of muscles arising in the tenth segment inserted on the bases of the cerci might seem to discredit the embryonic evidence that the cerci are appendages of the eleventh segment. We can only suppose that the muscles which function as motors of the cerci are morphologically the dorsal intertergal muscles between the tenth and eleventh segments that have secondarily become attached on the bases of the cerci. The same assumption must be made for all other insects, except with regard to the cercal muscles from the epiproct, but in the Thysanura it is quite evident that the cercal muscles are the normal longitudinal muscles of the tenth segment (fig. 22 D).

Three muscles take their origin in the tenth segment of *Gryllus* that are not attached on the cerci.

17.—A short intersegmental muscle arising on ventral end of tenth tergum (fig. 22 C); inserted posteriorly on anterior margin of para-proct.

18.—Dorsolateral muscle of the rectum, arising dorsally on tenth tergum above 13.

19.—Ventrolateral muscle of the rectum, arising ventrally on tenth tergum in angle between 16 and 17.

The following muscles are confined to the eleventh segment:

20.—A pair of slender, median, dorsal muscles, arising on anterior end of epiproct (fig. 22 C); inserted posteriorly on extremity of dorsal wall of rectum. (The supra-anal muscles of Ford.)

21, 22.—Two lateral muscles on each side, arising together on anterior lateral part of median plate of epiproct; diverging downward to insertions on inner face of upper half of paraproct.

23.—A very small muscle arising in membrane between epiproct and paraproct; inserted on extremity of rectum laterally.

24.—Origin anteriorly on inner face of paraproct; insertion posteriorly on circumanal membrane above posterior end of paraproct.

25.—Origin dorsally on upper edge of paraproct posterior to 22; insertion ventrally on membrane between lower edges of paraprocsts at base of hypoproct.

#### BLATTA ORIENTALIS LINNAEUS

The Blattidae, the Mantidae, and the Termitidae show a most interesting relationship to one another, especially with respect to the female genital apparatus. The termites are very much like the cockroaches in many of their general features, and particularly in the structure of the ovipositor, though they are placed in a separate order, while, as Walker (1919) says, "in the cockroaches we find many of the peculiarities of the Mantidae in a more pronounced form, as well as special characteristics of their own". In each of the three families the eighth abdominal sternum of the female is reduced, and the seventh sternum is prolonged backward as a large subgenital plate concealing the eighth sternum and, in the Blattidae, the entire ovipositor as well. In the mantids the seventh sternum forms a troughlike structure with mobile, valvular terminal lobes for manipulating the material of the egg case; in the blattids the lobes of the seventh sternum (fig. 24 A, *VIIISL*) enclose a large, distensible vestibular chamber (fig. 23, *Vst*) in which the ootheca is formed, and in some species retained a varying length of time. Hence, we find in the Mantidae, as pointed out by Chopard (1920), "almost the same structure as in the blattids of the subfamily Blattinae, though the rôle of the valves in the two cases may be very different according to the mode of oviposition". The formation of the egg case in the Mantidae is described by Bugnion (1923).

The definitive female gonopore in both the Mantidae and the Blattidae is located on the reflected dorsal surface of the reduced eighth sternum (fig. 23, *Gpr*), and therefore has the same position as in other members of the Orthoptera. The statement frequently made that the female gonopore in these families lies between the seventh and eighth sterna is based on an error of anatomical interpretation, as will presently be shown. Above the eighth sternum is the true genital chamber

(*GC*) into which opens the spermatheca (*Spt*). The genital chamber of the roach, however, has the appearance of being a mere pocket in the anterior wall of the large vestibulum (*Vst*) lying above the seventh sternum (*VIIS*) and the terminal lobes of the latter (*VIISL*). The accessory glands (*AcGl*) open into the dorsal wall of the vestibular chamber in the region of the ninth venter. The female genital invaginations in the mantids and roaches, therefore, are of the type of structure shown diagrammatically at C of figure 8.

The ovipositor has many points of resemblance in the Mantidae, Blattidae, and Termitidae; it is of small size as compared with the

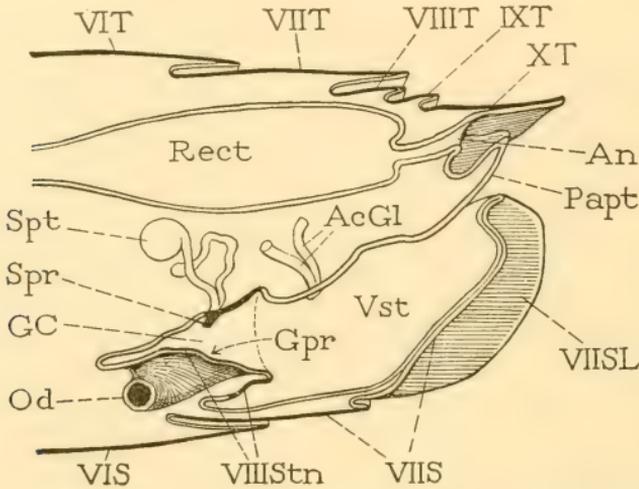


FIG. 23.—Diagrammatic median section through the distal abdominal segments of *Blatta orientalis*.

Note large vestibulum (*Vst*) formed within lobes of seventh sternum (*VIISL*), concealing small genital chamber (*GC*) at its anterior end above invaginated eighth sternum (*VIIIStn*), gonopore (*Gpr*) and spermathecal pore (*Spr*) in walls of genital chamber, and accessory glands (*AcGl*) opening into vestibule.

usual ovipositor of other orthopteroid insects, and in some respects it appears to be degenerate, while at the same time, especially in the Blattidae, it shows unusual specializations that obscure the generalized structure of the organ.

The visceral region of the abdomen has a simpler mechanism in the Mantidae and Blattidae than in the Tettigoniidae and Gryllidae, allowing much less play between the dorsal and ventral plates. The spiracles are contained in deflected marginal sclerites (fig. 16 B, *Sp*), which belong to the dorsum and are therefore paratergites (*pt*), and not "pleurites" as they are sometimes called.

In *Blatta orientalis* the dorso-pleural line of the abdomen (fig. 16 B, *a-a*, C, *a*) is contained in the narrow, infolded lateral membrane uniting the paratergites (*pt*) and the large ventral plates. Since in the male roach the ventral plate of the ninth segment bears a pair of styli, it is probable that the definitive sterna of all the abdominal segments are composite pleurosternal plates (*PlStn*) formed of the limb base areas and the primitive sterna. The lateral abdominal muscles of the roach are all functionally tergosternal (fig. 16 C), though some may be morphologically tergopleural. Two muscles of each segment are attached above on the median tergite (*T*), and one on the paratergite (*pt*), the last being described by Ford (1923) as a "pleural" muscle. The three are attached below on the lateral parts of the large, strongly convex sternal plate (*PlStn*). The roaches do not make any perceptible breathing movements of the abdomen under ordinary conditions. The well-known diagram by Plateau (1884) purporting to show the respiratory movements of *Blatta orientalis* undoubtedly depicts the kind of movements a roach can bring about between its dorsal and ventral abdominal plates; but since Plateau's subjects were induced to make them after being pinned down by the edges of the prothorax, with the legs and wings cut off, and the abdomen propped up on a bent pin, there is reasonable doubt that the observed contractions and expansions of the abdomen represent normal respiratory movements.

The genital segments of female Blattidae are almost entirely concealed within the seventh segment (fig. 24 A). Beyond the seventh tergum, and above the large terminal lobes of the seventh sternum, is the proctiger carrying the cerci laterally, projecting from the concealed ninth segment (B). The dorsal plate of the proctiger (*XT*) is evidently the tenth tergum alone, as claimed by Walker (1919), the epiproct being represented only by the membranous fold beneath its base. The muscles of the cerci take their origin on the proximal part of the plate, but the weakly developed muscles of the paraprocts are attached dorsally in the ventral membrane. The writer in a former paper (1931), without examining the paraproctial musculature, regarded the terminal dorsal plate of the cockroach as formed of the combined tenth tergum and epiproct, and Crampton (1929) makes the same interpretation. Walker (1919) points out, however, that "the disappearance of the supra-anal plate (epiproct) in the blattids and its substitution by the tenth tergite is the more complete expression of the same tendency indicated in the mantids, where the true supra-anal plate, though present, is reduced and entirely covered by the tenth tergum." In Tettigonidae, Gryllidae, and Acrididae, on the

other hand, the epiproct is retained and forms the terminal plate of the abdomen.

The tergum of the seventh segment (fig. 24 A, *VIIIT*) does not differ from the terga preceding it. The seventh sternum (*VIIIS*), how-

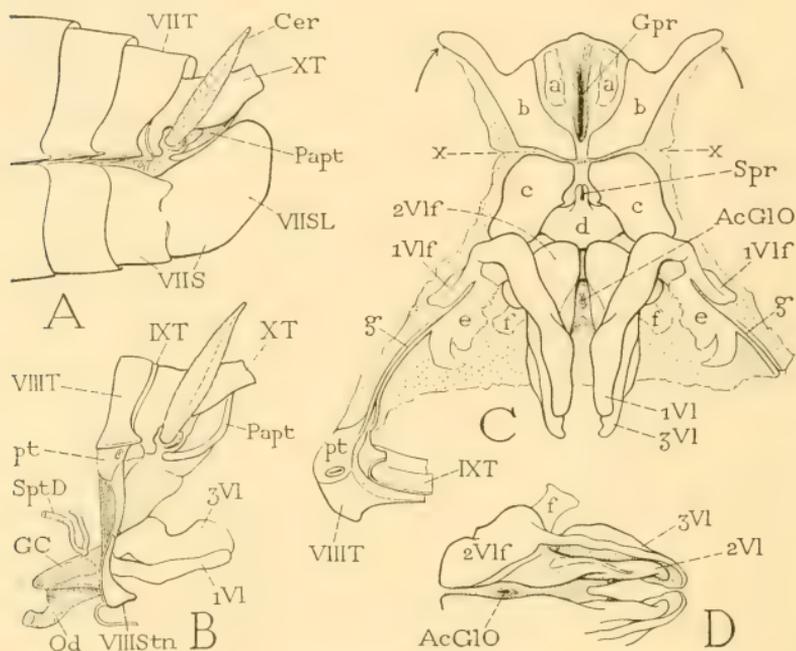


FIG. 24.—The genital segments and the ovipositor of *Blatta orientalis*.

A, end of abdomen, showing large valvular lobes of seventh sternum concealing vestibulum, ventral parts of eighth segment, genital chamber, and ovipositor.

B, genital and postgenital segments detached, showing eighth sternum as small fold beneath entrance to genital chamber (*GC*) into which opens the oviduct (*Od*) and spermathecal ducts (*SptD*).

C, ventral view of ovipositor and associated parts: floor of genital chamber containing gonopore (*Gpr*) turned forward along line *x-x*, exposing sternal sclerites (*a, b*) of eighth segment; spermathecal pore (*Spr*) in median plate (*d*) of roof of genital chamber, flanked by two lateral plates (*c, c*); opening of accessory glands (*AcGLO*) in venter of ninth segment between second valvifers (cf. fig. 23).

D, ventral view of parts of ovipositor belonging to ninth segment.

*a, b*, sclerites of eighth sternum in floor of genital chamber associated with gonopore; *c, d*, secondary sclerites in dorsal wall of genital chamber associated with spermathecal pore; *e*, ventral part of ninth tergum; *f*, lobe of second valvifer; *g*, intersegmental groove between ventral ends of eighth and ninth terga; *x-x*, line across anterior extremity of genital chamber on which floor of genital chamber is turned forward (C).

ever, is highly modified and specially developed. It consists of a basal, semiannular plate resembling the preceding sterna, and of two large, oval, distal, lateroventral, valvelike lobes (*VIIISL*) forming a hood-like cap concealing the ovipositor. The median ventral edges of these

lobes are united by a wide inflected membrane, and from their inner surfaces there are produced laterally two high membranous folds. The space between these folds can be greatly expanded by the extension of the ventral membrane, thus forming a pocket in which the ootheca is lodged. All this extension and modification of the seventh sternum is clearly an adaptation for the formation and retention of the egg case. In the structure of the female genital apparatus, therefore, the roach is highly specialized. The oothecal pocket is a part of the vestibulum (fig. 23, *Vst*), at the anterior end of which is the small true genital chamber (*GC*) above the reduced eighth sternum (*VIIIStn*).

When the seventh segment is removed there are exposed dorsally the narrow eighth and ninth terga (fig. 24 B, *VIIIT*, *IXT*), though the ninth tergum is mostly concealed beneath the eighth. The eighth tergum is somewhat widened laterally, where on each side it forms a sharp marginal ridge as do the preceding terga, and it is then deflected in a small paratergal sclerite (*pt*) enclosing the eighth spiracle. From the paratergite a fold of the integument extends downward and mesally to the lateral arms of the eighth sternum (*VIIIStn*). A lateral tergo-sternal muscle of the eighth segment lies just within the fold uniting the tergum with the sternum.

The sternum of the eighth segment is the sclerotization in the wall of a short fold produced posteriorly from the anterior wall of the vestibulum (figs. 23, 24 B, *VIIIStn*). At the margin of the fold the sternum is reflected dorsally and anteriorly on the dorsal wall of the fold. The fold itself, therefore, is the venter of the eighth segment, and its reflected dorsal wall forms the floor of the genital chamber (fig. 23, *GC*). Upon the latter is situated the gonopore (*Gpr*), a long, narrow, median opening (fig. 24 C, *Gpr*). In *Blatta* the floor of the genital chamber contains four sclerites composing the eighth sternum; two are small median plates (*C, a, a*) lying at the sides of the gonopore, and two are large lateral plates (*b, b*) produced upward on the sides as a pair of arms on which the tergo-sternal muscles of the eighth segment are attached (B). This group of sclerites associated with the gonopore is termed the "vaginal plate" by Vogel (1925). The view of the genital parts given at C of figure 24 shows the roof of the genital chamber and vestibulum, together with the ovipositor, as seen from below; but the floor of the genital chamber is turned forward (as indicated by the arrows) along the transverse line (*x-x*) at its anterior end.

The roof of the genital chamber contains two large, irregularly oval lateral sclerites (fig. 24 C, *c, c*) and a median sclerite (*d*). These plates must be secondary sclerotizations between the eighth and ninth

segments. The median sclerite bears the opening of the spermathecal tubes (*Spr*) on a small projection from its anterior margin (fig. 23, *Spr*), suggestive of the spermathecal spout of *Gryllus*, similarly situated except that it is contained in a pouch of the genital chamber (fig. 18, *u*). The eggs of *Blatta* must be fertilized in the genital chamber, and then passed out between the processes of the ovipositor into the vestibulum, where they are enclosed in the ootheca. The roof of the vestibulum contains the basal parts of the ovipositor (fig. 24 C), between which is the median opening of the large accessory glands (*AcGIO*). An account of the histological structure of these glands, together with a study of their contents, is given by Bordas (1909), and the formation of the ootheca in the vestibular chamber has been described by Kadyi (1879).

The morphology of the female genital segments of the Blattidae as given above, and as interpreted by Miall and Denny (1886), Walker (1919), Ford (1923), Crampton (1929), and Imms (1930), is so strictly in accord with that of the genital segments of other Orthoptera that it is difficult to see why certain recent investigators have not acceded to it. Vogel (1925), Nel (1930), and Heberdey (1931), for example, follow Bordas (1909), who accepted the statement of Peytoureau (1893) that "l'overture du vagin se trouve entre le septième et le huitième" urosternites. Vogel, therefore, disposes of the sclerites of the genital surface (fig. 24 C, *a*, *b*) surrounding the gonopore (collectively termed the "vaginal plate") as secondary sclerotizations of the membrane between the seventh and eighth segments, and regards the median plate in the dorsal wall of the genital chamber (*d*), bearing the opening of the spermathecal ducts, or situated behind the latter in some species, as the true eighth sternum. Nel (1930) adopts the same idea, and as a consequence is forced to conclude that the sperm receptacles of Blattidae, since they open on the "seventh" intersternal membrane, are not homologous with the spermatheca of other insects. In describing *Blattella* he says: "The common oviduct is short and opens by means of the gonopore on a raised fold of the floor of the genital cavity very near its anterior end. This raised fold is due to a pocket of the genital cavity extending beneath the part carrying the gonopore. The gonopore is thus on the reflexed inner surface of the seventh sternum, the seventh intersternal or so-called intersegmental membrane." Further, he says of the spermathecal ducts that they open into a short dorsal groove on the fold carrying the gonopore, and he then observes that the position of the spermathecal openings, which are thus on the "seventh intersternal membrane", constitutes an "aberrant and secondary condition." When

it is seen, however, that the fold bearing the gonopore is a part of the eighth sternum, there is then no discrepancy between the Blattidae and other Orthoptera, either with regard to the position of the gonopore or that of the spermathecal opening.

Any doubt that the sclerite (or group of sclerites) on the fold bearing the female gonopore in the Blattidae represents the true eighth sternum is dispelled by observing the muscle connections with the seventh sternum and the eighth tergum. Ford (1923) says convincingly "the sclerite is clearly eighth sternal", because her statement is based on the fact that the sternal muscles from the seventh segment are inserted on its anterior margin, and that tergo-sternal muscles of the eighth segment are attached upon it laterally. Hence, the female gonopore of adult Blattidae has the same morphological position as in other adult Orthoptera. It is probable that the female gonopore originates in the Blattidae on the posterior part of the seventh venter behind the seventh sternum, as it is known to do in various other insects, and that the position of the definitive opening is secondary. A migration of the gonopore in the roaches, however, has not been observed. Nel's (1930) statement that the median oviduct of *Blattella* originates on the seventh intersegmental membrane is based on his view that this membrane forms the fold bearing the gonopore, which is here interpreted as the eighth sternum. The female gonopore of adult Blattidae has the usual location on the posterior part of the eighth segment, and is not situated either on the seventh segment, or between the seventh and eighth sterna.

The ovipositor of *Blatta* is reduced and its parts are of irregular form as in other members of the Blattidae, but it retains all the elements of a typical orthopteroid ovipositor, including two pairs of valvifers and three pairs of valvulae.

The first, or ventral, valvulae (fig. 24 C, *IVl*) are widely divergent proximally, where they are connected with a pair of small basal plates (*IVlf*). These basal sclerites, though separated by a considerable space from the eighth sternum, are clearly the first valvifers since upon them are inserted muscles from the tergum of the eighth segment, and because they are directly continuous with the ventral valvulae. Each valvifer, however, is fused with an irregular sclerite (*e*) behind it, which belongs to the ninth segment, as shown by the fact that it lies posterior to the intersegmental groove (*g*) and is continuous with the ninth tergum (*IXT*) by a slender sclerotic strip on the posterior margin of the fold. This sclerite (*e*) Crampton (1925, 1929) calls the "valvifer", but it is not the homologue of the sclerite he terms "valvifer" in Gryllidae and Tettigoniidae; it is evidently the

lowermost extremity of the ninth tergum, to which the first valvifer is attached, as it is in most other insects. The eighth tergum has a small paratergal sclerite (B, C, *pt*) enclosing the eighth spiracle, which is extended ventrally (C) in a narrow sclerotic band on the anterior lip of the intersegmental fold (*g*).

The two valvulae of each side belonging to the ninth segment (fig. 24 D, *2VI*, *3VI*) arise from a common base (*2VIf*) representing the second valvifer. A small extension (*f*) of the valvifer apparently corresponds with the base of the posterior dorsal arm of the second valvifer in *Gryllus* (fig. 17 G, H, *i*), since it gives attachment to a muscle from the ventral plate (*e*) of the ninth tergum. The large accessory glands of *Blatta* open medially on the ninth venter between the second valvifers (fig. 24 C, D, *AcGIO*).

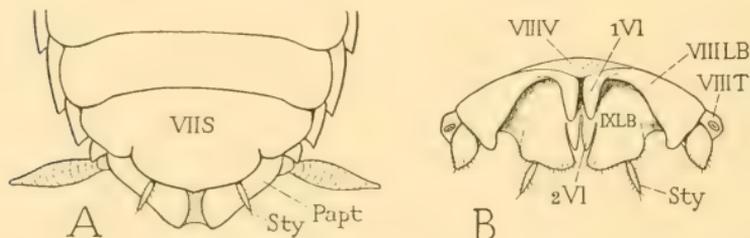


FIG. 25.—Young female nymph of *Blatta orientalis* with styli on ninth segment.

A, ventral view of terminal part of abdomen.

B, eighth and ninth segments exposed from below by removal of seventh sternum, showing styli (*Sty*) borne on basal plates (*IXLB*) of gonopods of ninth segment.

The close correspondence in fundamental structure between the ovipositors of *Blatta* and *Gryllus*, notwithstanding the great differences in size and form of the parts, scarcely needs to be pointed out. Walker (1919) has shown that the ovipositor of the Blattidae is developed in the usual manner from lobes of the eighth and ninth somites. It is particularly interesting to observe that the basal plates of the second gonopods in the female nymph bear small but distinct styli (fig. 25, *Sty*) which, though lost in the adult female, correspond with the styli of the male borne on the definitive sternal plate of the ninth segment.

The female genitalia of the termites, as described by Crampton (1920, 1923, 1929), appear to be the same as those of the Blattidae, except that the parts are more simple in form. In a female soldier of *Mastotermes darwinensis*, Crampton (1920) shows a small subgenital lobe of the seventh sternum underlapping the median part of the eighth sternum, beyond which is the ninth sternum bearing a pair of lobes

(limb bases) supporting distally the short styli and basally the rudiments of a pair of inner valvulae. In a winged adult female (Crampton, 1923) the three usual pairs of valvulae are well developed, but the styli, present in the soldier form, apparently are lost. Below the ovipositor the seventh sternum is produced as a subgenital plate, or "hypogenum", and the reduced eighth sternum forms a small lobe beneath the base of the ovipositor. In other termites the ovipositor is rudimentary or completely suppressed. Walker (1919) describes in *Termopsis* a pair of small lobes arising from the eighth sternum, representing the ventral valvulae, but the valvulae of the ninth segment are entirely absent.

## VI. THE OVIPOSITOR OF HEMIPTERA

The genital segments and the ovipositor of the Hemiptera present the following characteristic features:

1. The shaft of the ovipositor is formed of the first and second valvulae, the first being external and ventral, the second internal and dorsal. The second valvulae are generally united with each other, either for a part or for most of their length.

2. The sternum of the seventh abdominal segment forms the subgenital plate of the female, and encloses a small vestibular chamber at the base of the ovipositor.

3. The eighth segment is exposed dorsally, but its lateral and ventral parts are mostly concealed within the seventh segment.

4. The first valvifers have a pleural position below the tergum on the sides of the eighth segment, though their posterior angles may be flexibly attached to the ninth tergum. The dorsal muscles of the first valvifers arise on the eighth tergum.

5. The sternum of the eighth segment is rudimentary, being represented generally by a mere fold of the integument below the base of the ovipositor at the anterior end of the vestibulum. The genital chamber is correspondingly reduced in most cases to a small pocket beneath the gonopore; in some of the Cicadidae, however, the genital chamber forms a large pouch into which open the median oviduct and the spermatheca.

6. The first valvulae have each two proximal rami. The outer ramus is flexibly attached to the ventral angle of the first valvifer; the inner ramus expands in a small plate solidly united with the anterior ventral angle of the ninth tergum. A muscle extends from the inner face of the first valvifer to the basal plate of the inner ramus.

7. The ninth tergum is exposed, and usually large. Its anterior ventral angles are produced forward as extensions to which are united the inner rami of the first valvulae.

8. The second valvifers have a pleural position on the sides of the ninth segment beneath the lateral margins of the ninth tergum. Each is movably articulated with the tergum at a point near the middle of its dorsal margin, and is provided with antagonistic muscles from the ninth tergum inserted before and behind the fulcrum.

9. There are generally no intervalvular sclerites in the ninth venter, and tergo-sternal muscles are absent in the ninth segment.

10. The second valvulae are attached proximally, each by a single arcuate ramus, to the anterior end of the second valvifer, and the ramus slides on the concave margin of the inner ramus of the corresponding first valvula.

11. The third valvulae are well differentiated from the second valvifers; they form a pair of lobes ensheathing the distal end of the shaft of the ovipositor; rarely they are absent.

12. The mechanism of the hemipterous ovipositor is very simple as compared with that of the gryllid ovipositor; its only muscles are those of the first and second valvifers, and the pair of muscles from the first valvifers to the inner rami of the first valvulae.

13. An unusual condition bringing about the discharge of the eggs directly into the channel of the ovipositor exists in some of the Cicadidae, in which the genital chamber forms a large pouch opening above the rudimentary eighth sternum, and has a second posterior exit between the bases of the second valvulae. The relation of this structure to the usual structure in other Hemiptera is not understood, and it appears that the morphology of the terminal parts of the female genital ducts in the Hemiptera is a subject in need of further investigation.

As between the Heteroptera and the Homoptera there is no essential difference in the structure of the ovipositor. In each group, also, the ovipositor is well developed in some forms, and reduced or absent in others. According to the comparative studies of Ekblom (1926, 1930), an ovipositor is present among the Heteroptera in the families Saldidae, Nabidae, Lygaeidae, Veliidae, Gerridae, Mesoveliidae, Corixidae, and Coreidae, and is best developed in the Saldidae and Nabidae; but the organ is well developed also in Notonectidae and Coreidae. The structure of the hemipterous ovipositor will be shown in this paper by examples taken from the Saldidae, Coreidae, Cicadellidae, and Cicadidae. In connection with a study of the ovipositor it is important to understand the segmentation of the abdomen, since students of the Hemiptera are most frequently at fault concerning

the identity of the abdominal segments, on account of the partial or complete suppression of the first segment. In order to understand the morphology of the parts of the ovipositor described and figured by Ekblom, the following description of a saldid species, *Pentacora ligata*, is given as an introductory example.

PENTACORA LIGATA SAY

The abdomen of *Pentacora* (fig. 26 A) is broad and flattened, but the genital region, including the seventh, eighth, and ninth segments, forms a terminal enlargement supporting the ovipositor (*Ovp*). The

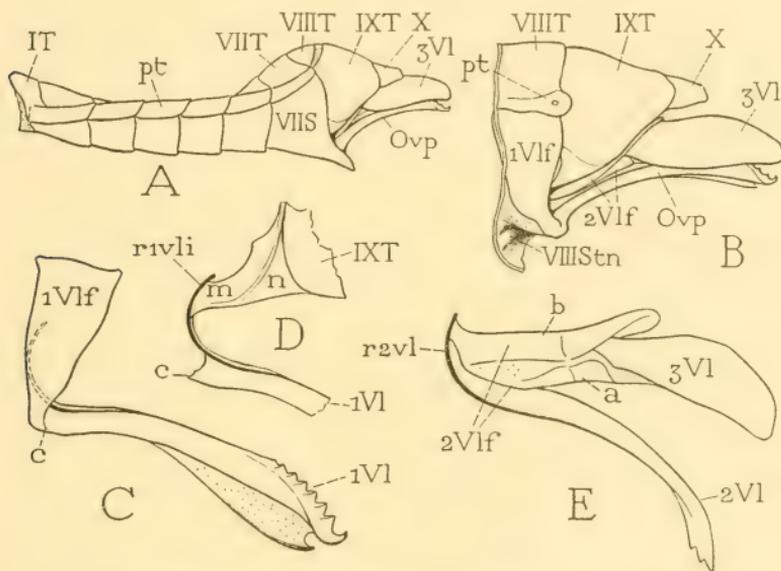


FIG. 26.—Abdomen and ovipositor of *Pentacora ligata* (Saldidae).

- A, entire abdomen.  
 B, genital and postgenital segments and ovipositor, showing rudimentary eighth sternum beneath gonopore.  
 C, first valvifer and first valvula.  
 D, attachment of inner ramus of first valvula to ninth tergum.  
 E, second valvifer with second and third valvulae.

first tergum (*IT*) is well developed, its anterior margin forming a free fold overlapping the narrow notum and postnotum of the metathorax; but the sternum of the first segment is either suppressed or indistinguishably united with the second. Segments *II* to *VII* have large paratergal plates (*pt*) forming the lateral margins of the wide pregenital region of the abdomen. The spiracles of these segments are situated ventrally in the lateral borders of the sternal plates, but those of the eighth segment lie in the paratergal lobes of the dorsum

(B, *pt*). The abdomen ends with the small tenth segment, or proctiger (*X*), from beneath which project the wide third valvulae (*3Vl*) with the shaft of the ovipositor (*Ovp*) between them.

The seventh segment is funnel-shaped, expanded posteriorly. Its large sternum (fig. 26 A, *VIIIS*) projects ventrally in a median lobe beneath the base of the ovipositor, and its posterior margin is inflected to form the ventral and lateral walls of a vestibulum concealing the lower anterior parts of the eighth and ninth segments, and the base of the ovipositor.

The eighth segment is mostly concealed within the seventh (fig. 26 A). When removed from the latter (B) it is seen to consist of a complete annulus, though the ventral part is reduced and membranous. Dorsally the segment presents a tergal plate (*VIIIT*), with small paratergal lobes (*pt*) containing the eighth spiracles; its lateral walls are formed by large, triangular pleural plates, which are the first valvifers (*I'Vlf*); the membranous ventral part forms a small fold (*I'VIIIStn*) at the base of the ovipositor, representing the rudimentary eighth sternum. The genital opening appears to be situated above the sternal fold between the bases of the first valvulae, but its existence here could not be positively determined in the dried specimens examined.

It is of particular interest to note that the first valvifer (fig. 26 B, *I'Vlf*) has a true pleural position on the side of its segment. Crampton (1929) mistakes the valvifer of the eighth segment in Hemiptera for a basivalvula, but the identity of the plate in question is shown without doubt by its musculature, and by the fact that the first valvula is directly connected with its ventral angle (C). The first valvula, however, has an inner ramus (D, *r1vli*) which curves upward from its dorsal margin and is connected with a small plate (*m*) attached to an extension (*n*) of the lower anterior margin of the ninth tergum (*IXT*). This basal sclerite (*m*) of the inner ramus of the first valvula might be regarded as a part of the valvula, inasmuch as it is continuous ventrally with the latter by a fold of the connecting membrane, or it might be supposed to be a part of the ninth tergum; but it is more probable that it is a part of the ramus itself, since there is inserted upon it a short thick muscle arising on the inner face of the valvifer, which would appear to represent the basal muscle of the gonapophysis in Thysanura (fig. 6 F, *gmcl*). In any case, the structure of the first valvifer, and the inner connection of the first valvula with the ninth tergum, as shown in *Pentacora*, are features characteristic of all the Hemiptera. The movements

of the first valvula are produced in the usual manner by muscles of the first valvifer arising on the eighth tergum.

The ninth segment has a large tergal plate (fig. 26, A, B, *IXT*) covering the back and sides of the segment; its anterior ventral angles are extended anteriorly within the seventh segment, and, as just noted, they are here fused with the basal plates of the inner rami of the first valvulae (D). Below each lateral margin of the ninth tergum is an elongate lobe (B, *2Vlf*), the outer wall of which is not continuously sclerotized, but presents a dorsal and a ventral plate (E, *a*, *b*). The lobe, however, is unquestionably the second valvifer (*2Vlf*), since it carries the second and the third valvulae (*2VI*, *3VI*). The second valvula is attached to the anterior end of the second valvifer by an arcuate basal ramus (*r2vl*), which slides on the concave margin of the inner ramus of the first valvula. The large third valvula (*3VI*) arises from the distal end of the second valvifer; the third valvulae form two broad free lobes embracing the distal end of the shaft of the ovipositor between their concave mesal surfaces. The second valvifer is articulated at a point near the middle of its dorsal margin to the lower edge of the ninth tergum, and muscles arising on the latter, inserted anteriorly and posteriorly on the valvifer, rock the latter up and down and impart a back-and-forth movement to the second valvula attached to its anterior end. The two second valvulae probably work in unison because of their connection with each other. The true sternal region, or venter, of the ninth segment is the narrow membranous wall between the two second valvifers.

According to the terminology used by Ekblom (1926, 1930) for naming the parts of the hemipterous ovipositor, the dorsal plate of the second valvifer (fig. 26 E, *b*) is the "parasternite" of the ninth segment; the small ventral plate (*a*) supporting the third valvula is "sternite *a*" of the ninth segment; and the third valvula is "sternite *b*" of the ninth segment.

The shaft of the ovipositor of *Pentacora* is formed of the first and second valvulae, the first being external, the second internal. Each first valvula consists of a strong outer part (fig. 26 C, *1VI*) with coarse teeth on the upper margin of its distal part, and of an inner membranous fold. Basally, as already observed, the first valvula is connected externally with the lower angle of the first valvifer (C, *c*), and mesally by an arcuate inner ramus with the lower anterior angle of the ninth tergum (D). The second, or inner, valvulae (E, *2VI*) are united with each other for most of their length by a narrow membrane between their dorsal margins; their distal parts, however, are

free, decurved, and toothed at their extremities. Basally each second valvula is connected by a single curved ramus (*rvl*) with the anterior end of the corresponding second valvifer. The second valvulae are moved back and forth by the rocking motion of the second valvifers on their points of articulation with the ninth tergum. The mechanism of the hemipterous ovipositor will be more fully explained in the account of the two homopterous species to be described.

#### ANASA TRISTIS (DEGEER)

The abdomen of female Coreidae consists of 10 segments, all of which are visible and distinct from above (fig. 27 A), though the first tergum is united with the second. The sternum of the first segment, however, is absent (B), and the first ventral plate (II), therefore, is the second sternum. It bears laterally a pair of spiracles. The segments following, to the seventh, present no special modifications, and the spiracles are located in the lateral parts of their ventral surfaces. The seventh segment of *Anasa tristis* has a broad tergal plate, emarginate posteriorly (A, VII). The seventh sternum (B, VII) is deeply emarginate, and bears medially a pair of small lobes (*a*), at the bases of which is a prominent transverse groove. The terga of the eighth and ninth segments are distinct though narrow plates as seen from above (A, VIII, IX); their lateral parts appear ventrally (B) as two pairs of marginal lobes at the sides of the genital region. The true sternal parts of these segments are covered by a pair of large triangular plates (B, *IVlf*), which, as will presently be shown, are the valvifers of the eighth segment. The tenth segment (X) projects beyond the genital segments in the form of a short tube containing the anal opening.

The description of the abdomen of *Anasa tristis* by Tower (1913) is wholly misleading, and has been the cause of considerable confusion to systematists in Hemiptera. In the first place, the numbering of the abdominal segments as given by Tower is at fault because the first segment is entirely disregarded, though it is represented by a distinct tergal plate (fig. 27 A, IT). The last pregenital segment, therefore, is segment VII, not the sixth; and the first pair of subgenital plates (B, *a*) are lobes of the sternum of this segment (VII). The second and larger pair of genital plates (*IVlf*), apparently the "eighth sternum" of Tower, are the valvifers of the eighth segment. The ventral parts of the ninth segment are concealed, and the proctiger, mistaken for the ninth segment by Tower, is the tenth segment, numerically, though anatomically it may represent segments X and XI.

The ovipositor of *Anasa tristis* is small, and is ordinarily concealed beneath the large first valvifers (fig. 27 B, *1Vlf*). When the valvifers are spread apart, however, the lobes of the ovipositor are exposed (D), and between the bases of the first pair is seen the large, open genital chamber (GC), into which the oviduct discharges anteriorly. The ovipositor has the typical hemipterous structure, except that the first valvifers are relatively very large, and the third valvulae are ab-

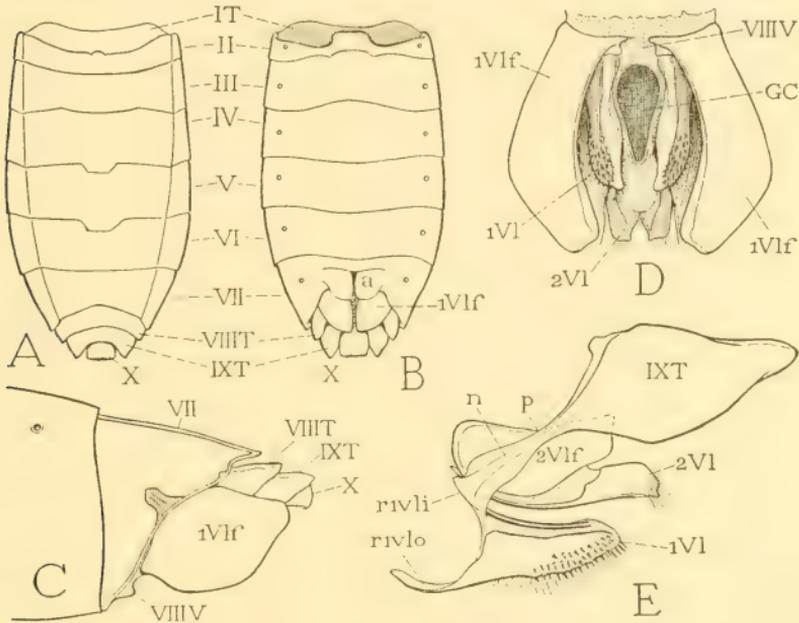


FIG. 27.—Abdomen and ovipositor of *Anasa tristis* (Coreidae).

A, entire abdomen, dorsal view.

B, same, ventral view.

C, lateral view of genital segments, with left wall of segment VII removed.

D, ventral view of genital region, with valvifers (*1Vlf*) spread apart, showing lobes of ovipositor (*1VI*, *2VI*), and large genital chamber (GC) opening between anterior pair.

E, left side of ovipositor and ninth tergum, with first valvifers removed, showing basal union of first valvula (*1VI*) with arm (*n*) of ninth tergum.

sent. The four lobes associated with the opening of the genital chamber are the first and second valvulae (D, *1VI*, *2VI*).

The first valvifers, as we have seen, are large triangular plates lying like a pair of valves (fig. 27 B, *1Vlf*) beneath the lobes of the ovipositor. Their bases are attached to the membrane behind the seventh segment (C) ventral to the eighth tergum. On the anterior margin of each valvifer is a strong apodeme for muscle attachments. The venter of the eighth segment is entirely membranous, and is repre-

sented only by the membranous bridge between the bases of the first valvifers and the first valvulae anterior to the opening of the genital chamber (C, D, *VIIIV*).

The first valvula is a thick lobe (fig. 27 D, E, *IVl*) about two thirds the length of the first valvifer. In its outer surface is a plate provided distally with short spines. The proximal ventral angle of the plate is prolonged as the outer ramus of the valvula (E, *rIVlo*), and is attached to the lower basal angle of the first valvifer (B, C, *IVlf*), thus leaving no doubt of the identity of the latter. The dorsal proximal angle of the first valvula forms the inner ramus (E, *rIVli*), which is attached, in the manner characteristic of Hemiptera, to a process (*n*) from the ninth tergum (*IXT*). The dorsal surface of the first valvula contains two parallel sclerotic ridges, between which is a groove into which fits a ridge on the ventral surface of the corresponding second valvula.

The second valvifer is an oblong plate (fig. 27 E, *2IVlf*) lying mesad of the ventral arm (*n*) of the ninth tergum, and articulated to the ninth tergum at a point (*p*) near the middle of its dorsal margin. Its distal end has a free, truncate edge, representatives of the third valvulae being absent in *Anasa*, though these lobes are usually present in other Hemiptera (fig. 26 E, *3VI*).

The second valvulae are united with each other, except at their distal ends, which form two short free lobes (fig. 27 D, *2VI*). The basal part of each has a broad membranous connection with the corresponding second valvifer (E), and the ventral surface bears a strong median sclerotic ridge that slides in the groove of the first valvula.

The mechanism of this ovipositor is evidently such as to cause alternate back-and-forth movements of the upper and lower valvulae on each other. The movable articulations of the second valvifers on the ninth tergum (fig. 27 E, *p*), and the firm union of the first valvulae with the ventral arms (*n*) of the tergum assure an opposite movement in the two pairs of valvulae. The muscles arising on the ninth tergum and inserted on opposite ends of the second valvifers rock the latter up and down and thus move the attached dorsal valvulae; but the same muscles pulling on the tergum impart an opposite movement to the ventral valvulae through the leverlike arms (*n*) supporting the latter.

#### AMBLYDISCA GIGAS FOWLER

The ovipositor is well developed in the Cicadellidae, and the family is one of considerable economic importance, but since most of the species are very small it is a difficult matter to make a satisfactory

study of the egg-laying organ. The Central American species here described, however, has a length of 20 millimeters, and the structure of its ovipositor probably will be found typical of the family in general.

The abdomen of *Amblydisca* is cylindrical, and rigid except at its attachments on the thorax. The first two segments are reduced and their tergal plates are more or less united with each other and with the third tergum. The postnotum of the metathorax is strongly developed laterally, where its ventral ends are fused with the epimera, but dorsally it is reduced to a narrow sclerotic bar beneath the overhanging posterior edge of the metathoracic scutellum. It is entirely separated by membrane from the first abdominal tergum, except for a small, flexible sclerotic bridge on each side, the two points of union forming the fulcrum on which the abdomen is movable on the thorax. The sternal plates of the first two abdominal segments are narrow and are concealed in a ventral depression at the base of the abdomen. The distal part of the abdomen (fig. 28 A) is tapering, and ends with the broad tips of the third valvulae ( $3VI$ ) which normally ensheath the end of the ovipositor (*Ovp*).

The seventh segment of the abdomen is the first that is modified in relation to the genital functions. Its tergum (fig. 28 A, *VIIIT*) resembles the tergal plates of the preceding segments, which have prominent marginal paratergites (*pt*) with inflected ventral surfaces containing the spiracles. The seventh sternum (*VIIIS*) is a triangular sclerite with a free posterior margin, toothed at the apex, projecting posteriorly as a subgenital plate beneath the base of the ovipositor. Above the seventh sternum is a large vestibular cavity.

The visible part of the eighth segment consists of a principal tergal plate (fig. 28 A, *VIIIT*) exposed behind the seventh tergum, and of a large, triangular paratergite on each side containing the eighth spiracle (B, *pt*). The lower anterior angle of the paratergite is connected with the dorsal posterior angle of the first valvifer (B, *IVlf*), which is normally concealed within the lower part of the seventh segment by the invagination of the lower parts of the eighth and ninth segments within the seventh (A). The intersegmental membrane (B, *Mb*) between the seventh and eighth segments is reflected from the dorsal (anterior) margin of the second valvifer, and ventrally is continued into the membranous floor of the vestibulum over the seventh sternum. From the anterior wall of the vestibulum there projects beneath the base of the ovipositor a small liplike fold slightly thickened on its dorsal surface (B, *VIIIStn*). This fold is evidently a remnant of the eighth sternum. Above it there is

a large, slitlike opening (*a*) between the ventral, or outer, rami of the second valvulae (*rivlo*), which leads into a small cavity into which the oviduct appears to open, but the internal anatomy could not be satisfactorily studied in the dried specimens on which this description is based. As will be shown later a similar but much larger pouch in *Magicicada* is the genital chamber, receiving the openings both of the

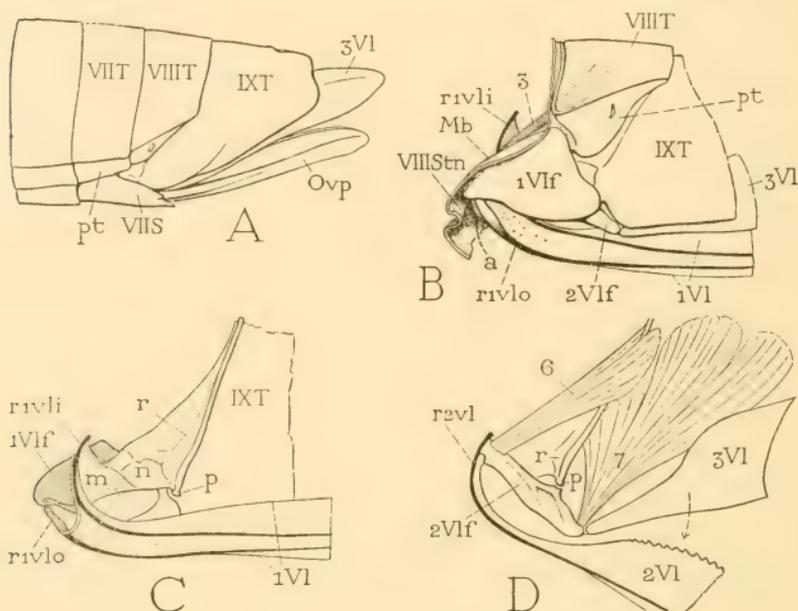


FIG. 28.—Ovipositor of *Amblydisca gigas* (Cicadellidae).

A, genital segments and ovipositor.

B, seventh segment removed, showing first valvifer in pleural position on side of eighth segment, and exposing rudimentary eighth sternum.

C, base of right first valvula, mesal view, showing connection of inner ramus (*rivli*) with ninth tergum.

D, right second valvifer and basal parts of second and third valvulae, mesal view, showing articulation (*p*) of second valvifer with ninth tergum, and tergal muscles (*6, 7*) of valvifer.

median oviduct and the spermatheca (fig. 32, *GC*). In *Magicicada*, however, there is a second, posterior opening from the genital chamber between the bases of the second valvulae. A posterior opening could not be found in *Amblydisca*, and it has not been observed in any homopteron except two species of cicadas. The structure in *Amblydisca*, therefore, so far as can be judged from dried specimens, is the same as that described for Homoptera generally by other writers. (See Holmgren, 1899; Myers, 1928; Weber, 1930.)

The exposed part of the ninth abdominal segment of *Amblydisca* (fig. 28 A, *IXT*), as in Homoptera generally, consists of the large tergum. The ventral part of the segment is membranous and deeply concave, forming a cavity in which are lodged the proximal parts of the third valvulae and the shaft of the ovipositor.

The ovipositor consists of two pairs of broad, thin valvulae, the first and the second (fig. 29 A, *1VI*, *2VI*), mostly concealed between the wide third valvulae (*3VI*). The planes of the valvulae are vertical. The first valvulae lie close against the outer surfaces of the

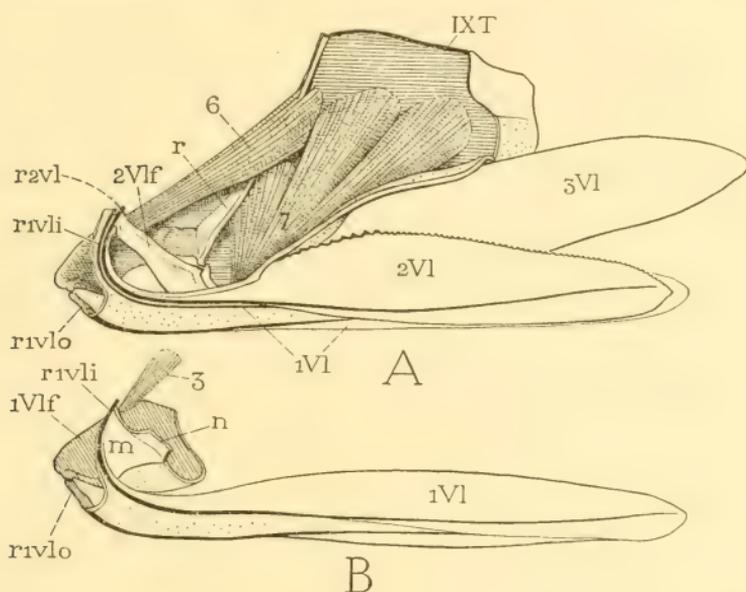


FIG. 29.—Muscles of the ovipositor of *Amblydisca gigas*.

A, right half of ovipositor and ninth segment, mesal view.

B, right first valvifer and first valvula, mesal view.

second pair, and the two on each side are firmly but movably attached by the usual interlocking grooves and ridges. The second, or inner, valvulae are conspicuously serrate along their dorsal margins (A, *2VI*); at their bases they are united with each other by a membranous fold, but for most of their length they are free, though closely appressed. Each first valvula has two proximal rami (figs. 28 C, 29 B), a ventral outer ramus (*rvlo*) attached to the anterior angle of the first valvifer (*1Vlf*), and a dorsal inner ramus (*rvli*) which expands in a small triangular plate (*m*) attached to the lower anterior angle of the ninth tergum (fig. 28 C, *n*, *IXT*). The second

valvula has a single basal ramus (fig. 28 D, *r2vl*), which is attached to the anterior end of the second valvifer (*2Vlf*), and lies against the concave margin of the inner ramus of the first valvifer (fig. 29 A).

The first valvifer (fig. 28 B, *1Vlf*) is a triangular plate attached posteriorly by membrane to the anterior margin of the paratergite (*pt*) of the eighth segment, and ankylosed with the lower anterior part of the ninth tergum (*IXT*). In the normal position it is concealed by invagination within the seventh segment (*A*). The intersegmental membrane between the seventh and eighth segments (*B*, *Mb*), therefore, extends forward from the lower end of the eighth tergum along the dorsal margin of the valvifer to the rudimentary eighth sternum (*VIIIStn*) beneath the anterior ends of the valvifers. To the anterior end of each first valvifer is flexibly attached the outer ramus of the first valvula (figs. 28 B, C, 29 A, B, *r1vlo*); the inner ramus of this valvula (figs. 28 C, 29 B, *r1vli*), as already noted, is firmly attached by a small plate (*m*) to the lower anterior angle (*n*) of the ninth tergum, mesad of the first valvula. A muscle arising on the eighth tergum (fig. 28 B, 3) is inserted on the dorsal margin of the first valvifer (fig. 29 B, 3). The first valvifers are not freely movable because of their posterior ankyloses with the ninth tergum, but they are flexible, and the contraction of their muscles evidently must elevate their anterior ends and produce a depression of the distal part of the ovipositor. A pair of short thick muscles attached laterally on the valvifers and internally on the mesal plates of the inner rami of the first valvulae, are probably antagonistic to the dorsal muscles of the valvifers.

The second valvifer (fig. 28 D, *2Vlf*) is a strong, elongate sclerite having the ramus of the second valvula (*2Vl*) attached to its anterior end, and the base of the third valvula (*3Vl*) movably articulated to its posterior end. In the normal position the second valvifer is mostly concealed, in a lateral view (*A*), by the first valvifer. The second valvifer is movably articulated at a point somewhat beyond the middle of its dorsal margin to a condyle (*D*, *p*) on the lower end of a strong anterior ridge (*r*) of the inner surface of the ninth tergum (*C*, *IXT*). Two large antagonistic muscles arising on the ninth tergum (figs. 28 D, 29 A, 6, 7) are inserted on the opposite ends of the second valvifer (*2Vlf*). These muscles evidently rock the valvifer up and down on the fulcrum of the ninth tergum, and thus impart a strong back-and-forth movement to the second valvula attached by its narrow basal ramus (fig. 28 D, *r2vl*) to the anterior end of the valvifer. The second valvulae slide freely on their tracklike

connections with the first valvulae, but since the second valvulae are united at their bases with each other, the two inner blades of the ovipositor, which are serrated on their dorsal margins (fig. 29 A, 2VI), must work in unison between the outer first valvulae. The first valvulae also may have some independent movement produced by the muscles of the first valvifers, but the writer has not observed the cicadellid ovipositor in action on a living specimen.

An interesting account of the structure of the valvulae in the cicadellid ovipositor, and their relations to one another is given by Balduf (1933). The anterior valvulae, however, are referred to the "seventh sternite", and the second or inner pair to the "eighth sternite." This error probably arises from overlooking the true first segment of the abdomen, which is partially united with the second, though in no insect are the valvulae connected with the sternal plates of their segments.

#### MAGICICADA SEPTENDECIM (LINNAEUS)

The well-developed ovipositor of the Cicadidae furnishes an easily studied example of the structure of the ovipositor typical of the Hemiptera. The 17-year cicada here described, however, has a curious and unusual development of the genital chamber, which is provided with a secondary posterior passage giving exit to the eggs directly into the channel of the ovipositor.

*General structure of the abdomen.*—There has been so much misinformation given out on the subject of the abdomen of the cicada that it will be permissible to devote a little more attention to the general abdominal structure of this insect than would be necessary otherwise in connection with a study of the ovipositor.

The general form of the female abdomen in *Magicicada septendecim* is shown at A of figure 30. At its base the abdomen is broadly but movably joined to the thorax, but the connecting parts are mostly concealed by overlapping parts of the metathorax. When the thorax and the abdomen are somewhat pulled apart, as shown at B of the same figure, it is seen that there lies in the infolded membrane between the metatergum ( $T_3$ ) and the first abdominal tergum ( $IT$ ) a well-developed though narrow postnotal plate of the metathorax ( $PN_3$ ), which bears the large third phragma, and is fused ventrally with the metapleural epimera ( $Epm_3$ ) in the usual manner. On each side of the dorsum the postnotum retains a flexible sclerotic connection ( $a$ ) with the first abdominal tergum. The latter ( $IT$ ) is a narrow, transverse plate united with the second tergum ( $IIT$ ); its lateral part

presents an enlarged oval area (*b*), which corresponds with the area of the sound-producing cymbal of the male.

The sternal plates of the first and second abdominal segments are highly modified, and they are separated by a deep inflection that forms a large ventral cavity at the base of the abdomen. This cavity is ordinarily closed to a narrow slit between the sternal plates, and is

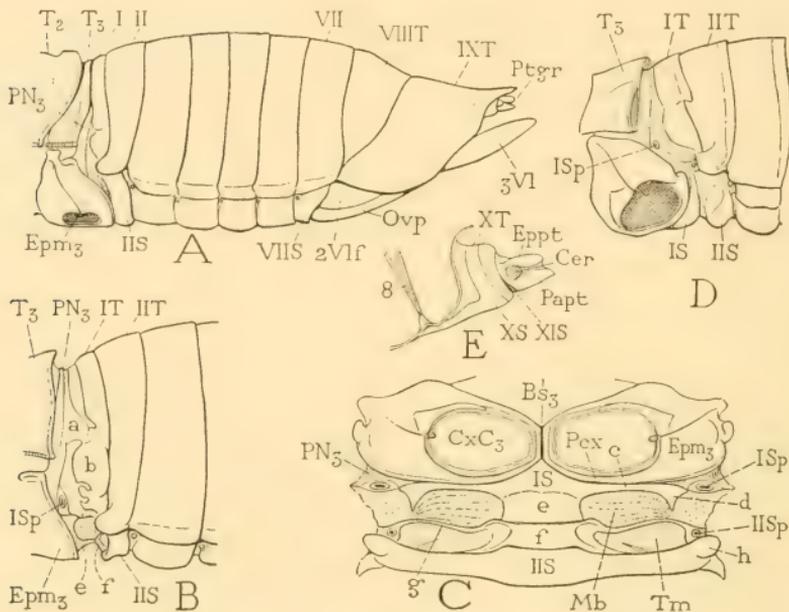


FIG. 30.—Abdomen of *Magicicada septendecim* (Cicadidae).

A, entire abdomen and base of thorax of adult female.

B, details of connection between thorax and abdomen, lateral view.

C, ventral plates of metathorax and first and second abdominal segments.

D, base of abdomen of mature nymph.

E, tenth and eleventh segments of adult.

*a*, hinge between postnotum of metathorax and first abdominal tergum; *b*, lateral area of first abdominal tergum on which cymbal of male is developed; *c*, lateral arm of first abdominal sternum with expanded end (*d*) on which tergo-sternal muscle is attached; *e*, posterior median plate of first sternum; *f*, anterior median plate of second sternum; *g*, lateral arm of second sternum forming marginal rim of tympanum (*Tm*).

but little evident in a casual examination of a dried specimen. In the male cicada the cavity is much larger than in the female and contains the so-called "resonance" membranes, or "mirrors", which are now regarded as tympana for the reception of sound vibrations, since it has been shown by Vogel (1923) that chordotonal organs, situated in the lower ends of the second abdominal tergum, are connected with their lateral extremities. The tympanal cavity can be opened and

closed by movements of levation and depression of the abdomen on the lateral hinges (fig. 30 B, *a*) between the postnotum and the first abdominal tergum, the movements being produced by the dorsal and ventral muscles of the first abdominal segment. The structure of the first and second abdominal sterna and of the tympanal cavity between them is essentially the same in both sexes, but it is more simple in the female.

The first abdominal sternum of the female cicada lies immediately behind the narrow postcoxal arms of the metathoracic epimera (fig. 30 C, *Pcx*). It consists of two parts. The first is an anterior, median, triangular plate (*IS*) having its lateral angles prolonged as a pair of arms (*c*) fused with the postcoxal bridges (*Pcx*), but each terminating in a lateral expansion (*d*), on which are attached the tergo-sternal muscles of the first abdominal segment. The second plate is a median, quadrate sclerite (*e*) flexibly hinged to the anterior plate (*IS*), and extending upward from the latter in the anterior wall of the tympanal cavity (B, *e*).

The spiracles of the first abdominal segment (fig. 30 B, C, *ISp*) are contained in peritremal sclerites fused with the lower ends of the metathoracic postnotum (*PN<sub>2</sub>*). They open directly into the great air chamber of the abdomen.

The sternum of the second abdominal segment consists, as does that of the first segment, of two parts, one part exposed, the other concealed in the tympanal cavity. The exposed part of the sternum is in this case the posterior part, which forms a narrow, transverse bridge between the lower ends of the second abdominal tergum (fig. 30 A, B, C, *IIS*), with which it is solidly continuous. The anterior part of the second sternum is a weaker median sclerite (C, *f*) turned upward on the anterior margin of the posterior sclerite in the posterior wall of the tympanal cavity (B, *f*); its dorsal margin meets the posterior plate of the first sternum (*e*) in the transverse fold of the roof of the cavity. The lateral angles of the anterior sclerite of the second sternum (C, *f*) are produced into slender bars (*g*) that extend outward to meet the lateral extremities of the posterior sclerite, where each ends in a small expansion containing one of the second abdominal spiracles (*IISp*). Between the arms (*g*) of the first sclerite and the lateral parts of the second sclerite are the oval glistening tympana (*Tm*), or so-called "mirrors". The chordotonal sense organs connected with the tympana (in the male) are said to be contained in the tubercles (*h*) located at the ventral lateral angles of the second segment where the tergum and the sternum are confluent. The thick corrugated membranes (*Mb*) in the anterior wall of the tympanal cavity are intersegmental membranes between the first and second sterna.

The description of the basal parts of the abdomen of the cicada given by Vogel (1923) in connection with his account of the chordotonal organs, though minute in detail, is not morphologically sound in every respect. The anterior plate of the second sternum (fig. 30 C, f) Vogel regards as the first abdominal sternum, and he consequently refers the tympana and the second spiracles to the first abdominal segment. The posterior sclerite of the second sternum (*IIS*), bearing the "auditory capsules" (*h*), he calls the second sternum. Much of this interpretation is clearly in error since it disregards the true first sternum and the first abdominal spiracles, which latter Vogel assigns to the thorax. The difficulty of properly disposing of the first abdominal spiracles in the cicada arises from the fact that the spiracular peritremes in the adult insect are fused with the lower posterior margins of the metathoracic postnotum (fig. 30 B, C, *PN*<sub>3</sub>), the lower ends of which are united with the epimera; but the observation that the spiracles in question lie behind the internal intersegmental ridge bearing the lobes of the third phragma shows conclusively that these spiracles belong to the first segment of the abdomen. The true relations of the basal parts of the cicada's abdomen are unmistakable in the mature nymph of *Magicicada* (D). The first abdominal sternum is here a simple triangular plate (*IS*) lying immediately behind the metathoracic subcoxae, and the first abdominal spiracles (*ISp*) lie in the membranous lateral parts of the dorsum of the first segment. The tergum and sternum of the second segment (*IIT*, *IIS*) show no particular modifications, and the ventral tympanal cavity is not developed in the nymph.

One of the most curious aberrations in entomological morphology is the tendency to regard the great air chamber of the cicada's abdomen as a part of the digestive system. The chamber is a thin-walled sac always filled with gas, but never containing liquid. Yet, the cicada's stomach may be distended with liquid food. The idea that the air sac is a diverticulum of the stomach was first proposed by Hickernell (1920) on the basis of histological sections, which seemed to show a connection between the two organs. The question was later discussed in the affirmative by Hargitt (1923) and by Myers (1928). If the air sac lacks taenidia and even a chitinous lining these points do not prove that it is not of tracheal origin, since tracheal sacs do not usually contain taenidia, and some investigators have failed to find chitin in their walls. The abdominal air sac of the cicada, as may be more clearly seen in other genera than *Magicicada*, opens directly to the exterior through the first abdominal spiracles; and in various places large, open tracheal tubes are given off from its walls. In

*Magisicada* there is a tubular extension from the sac that proceeds in the direction of the stomach, but the writer believes it goes into the filter chamber and not into the stomach lumen, though the facts could not be more closely investigated for the lack of fresh material. However, the anatomical incongruity of having a diverticulum of the stomach opening to the exterior through a pair of spiracles suggests a human error rather than a lapse of nature.

Most of the visceral organs of the cicada's abdomen, except the stomach, which lies anteriorly, are crowded into the rear part of the abdomen by the posterior extension of the air chamber, which ends in the seventh segment. The turgid form of the middle part of the abdomen (fig. 30 A), therefore, presents the shape of the air sac. The region between the second and the eighth segments contains a succession of regular tergal and sternal plates. The lateral edges of the terga are inflected to meet the sterna, which are pleurosternal plates, there being no intervening pleurites or other lateral sclerites. In the adult, the spiracles of these segments are contained in small peritremal sclerites united with the anterior lateral angles of the sterna; in the nymph the spiracles have the same position but they lie in membranous areas between the tergal and sternal plates (figs. 11 A, 30 D).

The tergum of the seventh segment does not differ from the terga preceding it. The seventh sternum (fig. 30 A, *VIIIS*), however, is shortened, but its deeply emarginate posterior edge underlaps the base of the ovipositor (*Ovp*). Above the seventh sternum is a small vestibular cavity (fig. 32 A, *Vst*), in the anterior wall of which is a large genital opening (*a*) above a small fold (*VIIIStn*), which is the posterior lip of the otherwise invaginated eighth sternum. The genital aperture may be exposed by depressing the seventh sternum, or by pulling the latter forward (fig. 31 A, *a*). It leads into a large copulatory pouch (*GC*), which, as will be shown later, is the true genital chamber.

The eighth segment is exposed dorsally but its ventral parts are normally concealed within the seventh segment. The tergum is declivous behind the seventh tergum (fig. 30 A, *VIIIT*); its lateral parts are narrowed and are widely separated from the sternal region of its segment. The anterior end of the eighth sternum appears as a small fold beneath the opening of the genital chamber (figs. 31 A, 32 A, *VIIIStn*), but most of the sternal plate is reflected anteriorly upon the floor of the chamber (fig. 32 B, *VIIIStn*) and is therefore concealed within the latter. The exposed anterior (anatomically posterior) end of the eighth sternum is connected by membranous folds

with the lower ends of the eighth tergum (figs. 31 A, 32 A). The spiracles of the eighth segment (*VIIISp*) lie in these folds behind the lower ends of the eighth tergum. The first valvifers (fig. 31 A, *1Vlf*) are entirely detached from the eighth sternum and are closely associated with the ninth tergum.

The ninth segment forms the large conical, apical part of the abdomen (fig. 30 A). The tergum (*IXT*) ends posteriorly in a median triangular rostrum projecting above the proctiger (*Ptgr*), which is is

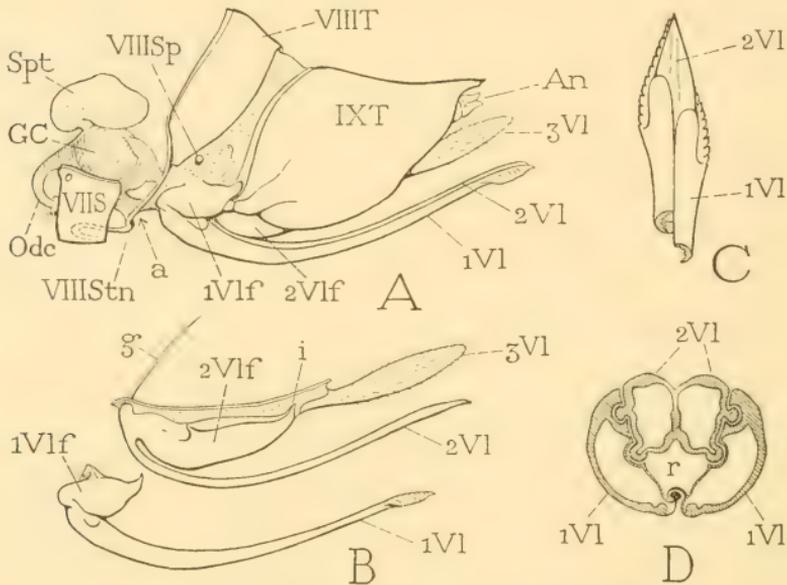


FIG. 31.—Ovipositor of *Magicicada septendecim*.

A, genital segments and ovipositor, with seventh sternum pulled forward exposing genital opening (*a*) leading into pouchlike genital chamber (*GC*).

B, parts of ovipositor separated.

C, tip of ovipositor, ventral.

D, section of ovipositor.

mostly retracted into the rear end of the ninth segment. Between the ventral edges of the ninth tergum is a deep concavity in which is concealed most of the ovipositor and the membranous ventral region of the ninth segment. The latter contains a median sclerotization with strong transverse corrugations lying between the second valvifers. The basal parts of the latter (*2Vlf*) are exposed below the anterior ventral angles of the ninth tergum.

The ovipositor is strongly developed. It consists of two pairs of valvulae (fig. 31 A, *1Vl*, *2Vl*), which are the first and second gona-

pophyses, arising respectively from the first and second valvifers (A, B, *1Vlf*, *2Vlf*). The second valvulae are fused by their inner faces (D); the first valvulae are freely movable on flanges of the shaft formed by the united second valvulae, and their lower edges are movably connected with each other. Between the four valvulae is a closed channel (*r*) for the conduction of the eggs. A pair of elongate lobes, the third valvulae (A, B, *3Vl*), arise at the distal ends of the second valvifers, and enclose the distal part of the ovipositor.

The proctiger consists of the tenth and eleventh segments. Ordinarily its tip only is visible projecting from beneath the rostrum of the ninth tergum (fig. 30 A, *Ptgr*). When exposed (E) the proctiger is seen to consist of a basal part representing the tenth segment, and of a distal part representing the eleventh segment. The dorsum of the tenth segment contains a narrow transverse tergal plate (*XT*), which is continuous ventrally with the posterior angles of a long sternal plate (*XS*). The anterior angles of the sternum are produced into a pair of small apodemal processes, on each of which is inserted a muscle (*8*) arising on the ninth tergum (fig. 34, *8*). The small eleventh segment consists of a dorsal and a ventral lobe, apparently representing the epiproct (fig. 30 E, *Eppt*) and the fused paraprocts (*Papt*) enclosing the anal opening (fig. 34, *An*). Between their bases on each side is a small, hairy lobe, evidently the rudimentary cercus (fig. 30 E, *Cer*). At the base of the ventral wall of the eleventh segment is a small sternal sclerite (figs. 30 E, 34, *XIS*). Upon it are inserted short, longitudinal, intersegmental muscle fibers (fig. 34, *9*) from the anterior part of the tenth sternum. From the latter there arise also on each side a group of fibers (*10*) that go to the terminal part of the rectum (*Rect*).

*The copulatory and egg-discharging apparatus.*—The short seventh sternum of the female cicada ends, as we have observed (fig. 30 A, *VIS*), in a free posterior margin, and if this subgenital plate is depressed there is exposed above it a large open cavity (fig. 32 A, *Vst*) extending forward into the anterior end of the sixth segment beneath the base of the ovipositor. This cavity clearly corresponds with the vestibulum of the cockroach (fig. 23, *Vst*), though the vestibular space is much larger in the latter insect because of the posterior extension of the seventh sternum (*VISL*).

In the anterior wall of the vestibulum of the cicada is a wide, thick-lipped opening (figs. 31 A, 32 A, *a*) that leads through a short passage (fig. 32 A, *b*) into a large, strongly muscular pouch (*GC*). The median oviduct (*Odc*) connects with the anterior wall of the pouch, and the spermathecal sac (*Spt*) opens by a narrow neck (*c*) into the

dorsal part of the pouch. Posteriorly the pouch has a large funnel-shaped extension (*d*) that terminates in a narrow membranous neck, which opens by a small pore (*f*) between the bases of the second valvulae of the ovipositor. From the base of the neck there arise laterally two small oval sacs (*e*) of a bright yellow color, into each of which opens a long, slender, much-coiled tube. A large, median tubular accessory gland (*h*) lies posterior to the pouch and opens at the rear aperture of the latter (B, *f*) into the channel of the ovipositor.

A section of the genital pouch (fig. 32 B) shows that the oviduct opens into the pouch lumen at the tip of a long, conical inflection

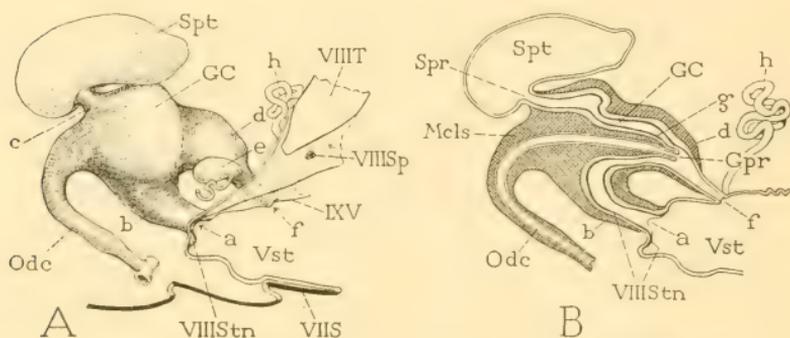


FIG. 32.—Genital chamber of *Magicada septendecim*.

A, lateral view of genital chamber pouch (GC) opening from vestibulum (Vst) by copulatory aperture (*a*), but with posterior exit (*f*) for discharge of eggs.

B, diagrammatic median section of genital chamber, oviduct, spermatheca, and vestibulum.

*a*, copulatory opening to genital chamber; *b*, entrance tube; *c*, duct of spermatheca with opening (B, *Spr*) into genital chamber; *d*, posterior exit tube for discharge of eggs; *e*, reservoir of lateral accessory gland; *f*, posterior opening of egg passage; *g*, evagination of anterior wall of genital chamber with gonopore (*Gpr*) at its extremity; *h*, median accessory gland.

of the anterior wall of the pouch (*g*), which projects into the posterior funnel-shaped passage (*d*) leading to the rear exit (*f*). Just dorsal to the base of the oviducal cone is the opening of the spermatheca (*Spr*). The cuticular lining of the pouch is irregularly thickened and corrugated, and is thrown into strong folds, the details of which are not shown in the diagrammatic section (fig. 32 B). All parts of the pouch and the entering oviduct are ensheathed in a thick layer of muscle fibers (*Mcls*), which appear to be so arranged as to force the oviducal cone into the posterior funnel (*d*).

The presence of two genital openings in the female cicada suggests the similar condition in Lepidoptera. Though the structure in the

two cases is not identical, yet it is evident that the posterior opening is a secondary one, and that it is located, as in Lepidoptera, at the aperture of the accessory gland.

The morphological nature of the genital pouch of the female cicada is clear when it is considered that it lies above the eighth abdominal sternum (fig. 32 B, *VIIISTn*), and that both the gonopore (*Gpr*) and the spermathecal pore (*Spr*) lie in its walls. The pouch can be nothing else than the genital chamber (fig. 8 C, *GC*) greatly enlarged and modified in an unusual manner. It corresponds exactly with the genital chamber of the Orthoptera (figs. 19 B, 23, *GC*). In the cicada the eighth sternum is mostly reflected forward upon the floor of the genital chamber (fig. 32 B, *VIIISTn*), but its morphologically anterior end projects as a short fold beneath the entrance of the chamber (A, *VIIISTn*). The posterior part turned forward is sclerotized as a small plate surrounding the base of the oviducal cone. The gonopore of the cicada, therefore, lies morphologically in the eighth sternum just as it does in the cockroach (figs. 23, 24 C, *Gpr*). The relation of the terminal genital structures in *Magiccicada* to the more usual structure of these parts in other insects is shown in the series of diagrams given in figure 8.

The posterior opening of the genital chamber in *Magiccicada septendecim* between the bases of the second valvulae is undoubtedly a special modification to allow the eggs to be discharged directly into the closed channel of the ovipositor. This condition is not peculiar to the 17-year cicada; the same structure was long ago described in *Dundubia (Cicada) mannifera* by Doyère (1837), but has received little or no attention since, so far as the writer can find. Doyère refers to the genital chamber as the "vestibule copulateur", and other writers have called it the "bursa copulatrix". Holmgren (1899) studied the female genital organs of various homopterous forms (Cicadarien), now classed in the families Cercopidae, Cicadellidae, and Fulgoridae, but he says that all species examined by him have but a single genital opening. Myers (1928) gives a review of literature on the female reproductive organs of Cicadidae, including Doyère's paper, and makes no mention of two openings. He describes and figures the female organs of *Carineta formosa*, but the terminal genital structures in this species must be quite different from those in *Dundubia* and *Magiccicada*. The single opening shown by Myers is at the point where the accessory glands with yellow sacs open into the "oviduct", and would therefore appear to be the posterior opening of *Magiccicada*. The writer has examined specimens of several other species of Cicadidae, which, though too

poorly preserved for reliable dissection, seem to show the same structure as described by Myers for *Carineta*.

*The ovipositor.*—The ovipositor of the Cicadidae does not differ in any essential respect from that of other Hemiptera. The shaft of the organ is formed by the first and second valvulae (fig. 31 B, *1Vl*, *2Vl*) supported at their bases by the first and second valvifers (*1Vlf*, *2Vlf*); the third valvulae (*3Vl*) are free distal lobes of the second valvifers. The second valvulae are solidly fused with each other (D, *2Vl*) except at their tips, and the first valvulae (*1Vl*) slide freely on ridges of the united second valvulae. The lower edges of the second valvulae are locked together by a fold on one that grasps a ridge on the other, and the egg passage (*r*) of the ovipositor thus becomes a closed channel. Since the cicadas deposit their eggs in the twigs of trees, the ovipositor is strong and is provided with powerful muscles.

The first valvifer lies at the base of the ovipositor (fig. 31 A, *1Vlf*) where it is normally concealed by the overlapping lateral part of the seventh sternum (*VIIStn*, pulled forward in the figure). When the seventh sternum is removed, the first valvifer is seen to be a small irregularly oval or triangular plate (B, *1Vlf*) bearing the first valvula (*1Vl*). The middle of its dorsal margin is produced into a short wide apodemal plate (fig. 33 A, *e*) for the attachment of muscles. Its somewhat elongate posterior end (*a*) overlaps the anterior part of the second valvifer, and is movably attached to the lower anterior angle of the ninth tergum (fig. 31 A). The first valvifer is separated from the eighth tergum (*VIIIT*) by a much wider space in the cicada than it is in *Amblydisca* (fig. 28 B), or particularly in *Pentacora* (fig. 26 B), owing apparently to a desclerotization of the paratergal region of the dorsum, which in the cicada is represented by the membranous area containing the eighth spiracle (*VIIISp*). The intersegmental membrane between the seventh and eighth segments is continued ventrally on the side anterior to the first valvifer, past the genital opening (*a*), to the subgenital fold formed by the eighth sternum (*VIIISTn*).

The broad base of the first valvula (fig. 33 A) is not differentiated into distinct outer and inner rami, as in the Cicadellidae, but it has the same proximal connections. Its outer wall (B, showing a mesal view) has a membranous union with the lower edge of the first valvifer (*1Vlf*), but it is articulated with the anterior angle of the valvifer (*c*) and is movable on the valvifer at this point. The dorsal wall of the valvula, corresponding with the inner ramus in *Pentacora* and *Amblydisca*, is produced upward and expanded in a small tri-

angular plate (*m*) lying mesad of the valvifer, which is fused with the lower anterior angle (*n*) of the ninth tergum (*IXT*). A thick bundle of short muscle fibers (*4*) extends from the inner face of the first valvifer to the mesal plate (*m*) of the base of the first valvula. The other muscles of the first valvifer are inserted on the dorsal apodeme (*e*). They include a lateral muscle (*C*; *1*) from the seventh

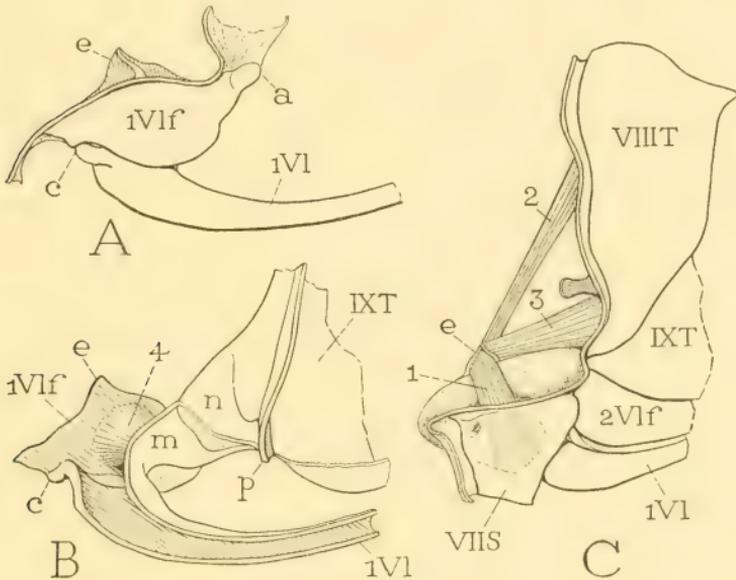


FIG. 33.—Structural details of ovipositor and muscles of first valvifer of *Magicicada septendecim*.

A, left first valvifer and base of first valvula, external view.

B, right first valvifer and base of valvula, mesal view, showing connections with ninth tergum.

C, base of ovipositor and adjoining segmental plates, with seventh tergum removed to show muscles attached on apodeme (*e*) of first valvifer.

*a*, articulation of first valvifer with ninth tergum; *c*, attachment of first valvula to first valvifer; *e*, apodeme of first valvifer; *m*, mesal plate of base of first valvula; *n*, anterior ventral part of ninth tergum attached to mesal plate (*m*) of first valvula.

sternum (*VllS*), and two dorsal muscles (*2*, *3*) from the eighth tergum (*VIllT*).

The second valvifer (fig. 31 B, *2Vlf*) is an elongate plate, or rather, a fold with a sclerotic outer wall, lying beneath and mostly overlapped by the lower edge of the ninth tergum (A). From its anterior end a slender apodeme (B, *g*) projects dorsally into the body cavity for the attachment of muscles; at its posterior end arises the third valvula (*3Vl*). The second valvula (*2Vl*) is directly continu-

ous with the anterior end of the second valvifer, there being no movement between the two parts except such as is permitted by the flexibility of the narrow base of the valvula. The inner surface of the outer wall of the second valvifer bears a strong longitudinal ridge near its dorsal margin (fig. 34, *2Vlf*). At a point on this ridge anterior to the middle of the valvifer is the articulation of the second valvifer with a fulcrum process (*p*) on the lower margin of the ninth tergum near the anterior angle of the latter (fig. 33 B). Two large antagonistic muscles (fig. 34, *6*, *7*), arising on the ninth tergum, are inserted anteriorly and posteriorly on the second valvifer at opposite sides of the tergal fulcrum. Tergosternal muscles of the ninth segment are absent in the cicada as in other Hemiptera.

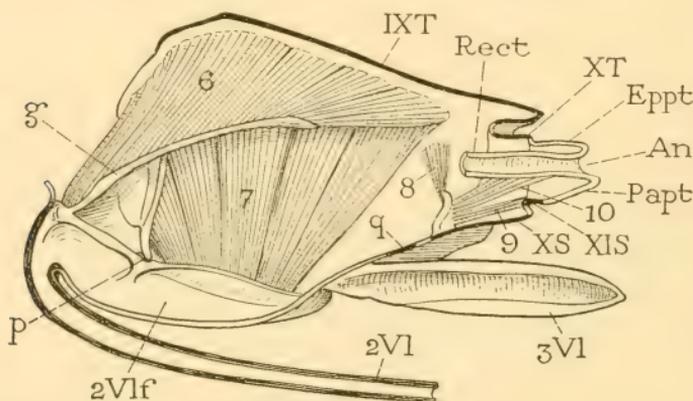


FIG. 34.—Right half of ninth and post-genital segments of *Magicicada septendecim*, mesal view, together with second valvifer and its muscles.

*g*, anterior apodeme of second valvifer; *p*, fulcrum of second valvifer on ninth tergum between insertions of anterior and posterior muscles (*6*, *7*).

The muscles of the ovipositor, or associated with it, are the following:

1. *Depressor of the first valvifer* (fig. 33 C).—A broad muscle arising on lateral part of seventh sternum; goes dorsally in membranous fold laterad of the valvifer to dorsal apodeme (*e*) of the latter. This muscle, as in *Gryllus* (figs. 17 A, 19 A, 1), is an inter-segmental ventral muscle of the seventh segment attached posteriorly, not on the eighth sternum, but on the valvifer of the eighth segment.

2. *First levator of the first valvifer* (fig. 33 C).—A long tergo-pleural muscle of eighth segment, arising dorsally on anterior margin of eighth tergum; inserted ventrally on dorsal apodeme of first valvifer. This muscle rotates the valvifer upward on its posterior articulation with the ninth segment.

3. *Second levator of the first valvifer* (fig. 33 C).—A tergo-pleural muscle of the eighth segment, arising on lower part of anterior margin of eighth tergum; inserted anteriorly on dorsal apodeme of first valvifer. This muscle is accessory to the last, and both 2 and 3 are clearly antagonistic to 1.

4. *Muscle of the first valvula* (fig. 33 B).—A thick bundle of short fibers arising on inner face of first valvifer (*IVlf*); inserted posteriorly and mesally on inner plate (*m*) of base of first valvula. This muscle appears to be antagonistic to 2 and 3, and accessory to 1.

5. *Conjunctival muscle* (not shown in the figures).—A short thick muscle arising dorsally on lateral part of eighth tergum; fibers converging downward to insertion on intersegmental membrane between eighth and ninth segments above and posterior to eighth spiracle (fig. 31 A, *VIIISp*). This muscle apparently serves to inflect the wide membrane between the segments.

6. *Anterior muscle of the second valvifer* (fig. 34).—A flat triangular sheet of strong fibers arising mediodorsally in longitudinal series on ninth tergum; insertion ventrally on anterior apodeme (*g*) of second valvifer and on extreme anterior end of the valvifer. The contraction of this muscle rotates the second valvifer upward anteriorly on the tergal fulcrum (*p*) and retracts the second valvula. It is the homologue of muscle 6 of *Gryllus* (fig. 17 E, G) and of *Amblydisca* (fig. 28 D).

7. *Posterior muscle of the second valvifer* (fig. 34).—A huge fan of several thick bundles of fibers arising dorsally on ninth tergum, laterad of 6; inserted ventrally on dorsal part of second valvifer posterior to the tergal fulcrum (*p*). This muscle is antagonistic to the anterior muscle (6), and protracts the second valvula by depressing the anterior end of the valvifer. It is the homologue of muscle 7 of *Gryllus* (fig. 17 E, G) and *Amblydisca* (fig. 28 D).

The first valvifers can respond freely to the contraction of the muscles inserted upon them because of the flexible nature of their posterior connections with the ninth tergum. The effect of the muscles inserted on the dorsal apodemes of the valvifers (fig. 33 C, 1, 2, 3) is only to elevate and depress the anterior ends of the plates. In a dissected specimen these movements of the first valvifer correspondingly depress and elevate the entire ovipositor, and there can scarcely be any question that they serve to unsheath and resheath the ovipositor preceding and following its use in oviposition. The short muscle from each first valvifer to the inner plate of the first valvula (B, 4) is apparently accessory to the depressor of the valvifer (C, 1), since, when the ovipositor is depressed, the valvifer

and the plate *m* move in opposite directions. The muscles of the first valvifers, however, must also produce independent back-and-forth movements of the first valvulae when the tip of the ovipositor is inserted into the bark of a tree. The broad, strongly serrate extremities of these valvulae (fig. 31 C) indicate that they play an important part in cutting out the egg chamber, and furthermore, the ends of the outer valvulae are often found in freshly killed specimens to be in different positions on the apex of the median shaft formed of the united inner valvulae, indicating that the outer valvulae are protracted alternately on the ridges of the median shaft (D).

The great size of the muscles of the second valvifers (fig. 34, 6, 7), particularly of the posterior muscles (7), leaves little doubt that the median shaft of the ovipositor, formed of the solidly united second valvulae, with its strong, sharp spearheadlike tip (fig. 31 C, *zVl*), is an important piercing implement of the egg-laying apparatus. Because of the union of the second valvulae, the corresponding muscles of the second valvifers on opposite sides probably work in unison.

The mechanism of the ovipositor of any insect could not accomplish the results it does if the parts of the organ were rigid. The valvulae slide lengthwise upon one another by the movement of the valvifers because they are pliable, and because of the flexibility of their basal connections. A wooden model of the cicada's ovipositor, for example, could not be made to do anything more than to move the shaft up and down at its base. The writer has elsewhere (1921) described the method by which the female 17-year cicada excavates the egg cavities in the twigs of trees in which she deposits her eggs.

Since the Hemiptera are in some respects one of the most highly specialized and individualized orders of insects, it is somewhat surprising that the ovipositor should be more generalized in its structure than in either the Orthoptera or the Hymenoptera. The only orders of insects that seem to approach the Hemiptera in the structure of the head and mouth parts are the Corrodentia and the Thysanoptera. Most of the Corrodentia have a small, simple ovipositor, but in some forms the organ is reduced or absent. Chapman (1930) says, "In *Psocus*, *Peripsocus*, and certain other genera, a distinct if not long and strongly chitinized ovipositor is present. It is composed of three pairs of gonapophyses, one pair arising from the eighth segment and two pairs from the ninth." In *Ectopsocus parvulus*, as described by Weber (1931), there are three pairs of small, soft processes surrounding the female gonopore, which appear to represent the three pairs of valvulae, since one pair arises on the eighth segment

and the others on the ninth. The genital processes hold the eggs as the latter issue from the ovipositor, but there is present no mechanism for their movement.

An ovipositor is well developed in one suborder (Terebrantia) of the Thysanoptera, but it is so minute in the ordinary species that the writer has not been able to make a detailed study of its structure. It consists of a large single dorsal piece presumably the united second valvulae, and of two strongly serrate ventral blades. The first valvifers appear to be a pair of triangular plates on the sides of the eighth segment immediately below the lateral edges of the eighth tergum. A third pair of valvulae was not observed in the species examined.

#### VII. THE OVIPOSITOR OF HYMENOPTERA

The ovipositor of the Hymenoptera, regardless of the shape, length, or function assumed by the shaft of the organ, has the same basic structure throughout the order. In its general form and in the composition of the shaft the hymenopterous ovipositor resembles the ovipositor of the Hemiptera more closely than that of the Orthoptera, but it has one particular feature, namely, the articulation of the second valvifers on the first valvifers, instead of on the ninth tergum, which is a characteristic feature of the ovipositor of Gryllidae, though the mechanism is not exactly the same in the two cases. The salient points in the structure of the hymenopterous ovipositor may be summarized as follows:

1. The subgenital plate of the female is the seventh sternum, and the base of the ovipositor is contained in a vestibular cavity.

2. The eighth tergum in lower families is a dorsal plate of the usual form exposed externally; in the bees it is entirely concealed within the seventh segment, its median part is reduced to a membranous fold over the back, and the lateral parts form a pair of small sclerites bearing the eighth spiracles.

3. The eighth sternum is completely suppressed in all Hymenoptera, though the venter of the eighth segment may be represented by a fold of membrane beneath the gonopore.

4. The first valvifers are entirely dissociated from the other parts of the eighth segment and form an intimate part of the basal mechanism of the ovipositor or sting. Their muscles, however, take their origin on the eighth tergum. Each is a small triangular plate bearing the ramus of the first valvula on its anterior end, and articulating posteriorly by its dorsal angle with the ninth tergum, and by its ventral angle with the second valvifer.

5. The ninth tergum is complete in lower families, its widened lateral parts being continuous dorsally at least in a narrow sclerotic bridge, with which the proctiger may be united; in the bees the ninth tergum consists of two large lateral sclerites, known as the "quadrate plates", but the median part of the ninth dorsum is membranous and not distinct from the proctiger.

6. The second valvifers are oblong plates bearing anteriorly the rami of the second valvulae, and posteriorly the third valvulae. Each is articulated by its dorsal margin with the ventral posterior angle of the first valvifer (not with the ninth tergum), and is provided with the usual anterior and posterior muscles arising on the ninth tergum.

7. The venter of the ninth segment is always membranous, there being no intervalvular sclerites.

8. The shaft of the ovipositor or sting is composed of the first and second valvulae, the first being ventral, the second dorsal. The second valvulae are united with each other beyond their convergent rami, either solidly or by membrane, and two pairs of muscles are inserted on their bases, one pair arising on the proximal parts of the rami, the other on the inner faces of the second valvifers. These muscles of the second valvulae are characteristic features in the mechanism of the ovipositor or sting of the Hymenoptera, but they appear to have no homologues in other insects.

9. The third valvulae are free lobes ensheathing the distal part of the shaft of the ovipositor; they vary greatly in length according to the length of the ovipositor.

10. The proctiger is always present. In lower families it consists of a dorsal and a ventral plate, and bears a pair of small appendicular processes; in the higher families it becomes reduced to a simple membranous tube or cone.

Four examples, selected from the Tenthredinidae, Braconidae, Ichneumonidae, and Apidae, will serve to illustrate the characteristic structure and some of the principal modifications of the ovipositor as the organ is developed in the Hymenoptera.

#### PTERONIDEA RIBESII (SCOPOLI)

The relatively large abdomen of the female currant sawfly contains the usual 10 abdominal segments present in the Hymenoptera. The eight pairs of spiracles are located in the lower parts of the tergal plates. The first segment is broadly joined to the thorax; its tergum is divided dorsally by a median membranous area, and the precostal region forms a narrow postnotal plate of the metathorax; the venter of the first segment is reduced and contains no sternal sclerite.

The seventh segment forms the last completely exposed annulus of the abdomen. Its tergum (fig. 35 A, *VIIIT*) resembles the terga of the preceding segments, but the sternum (*VIIIS*) is extended as a subgenital plate beneath the base of the ovipositor, and ends in two small lobes embracing the ventral valvulae. Above the seventh sternum is a vestibular cavity, in the anterior wall of which is the gonopore. The eighth tergum (*VIIIT*) has the same shape as the seventh, but its lower ends are overlapped by the posterior lateral angles of the seventh sternum. The venter of the eighth segment is represented only by the membranous integument forming the anterior wall of the vestibulum containing the genital aperture. The ninth tergum (*IXT*) is narrowed dorsally, but is expanded on the sides of the ninth segment, where its lower margins overlap the second valvifers (*2Vlf*). Between the valvifers the membranous venter of the ninth segment forms a deep concavity in which is lodged the shaft of the ovipositor. The abdomen terminates with a conical proctiger (*Ptgr*) bearing ventrolaterally a pair of slender processes (*Soc*). Beneath the proctiger the third valvulae (*3VI*) project as a pair of short, broad, dark-colored lobes, normally embracing the tip of the ovipositor (*Ovp*).

The ovipositor of *Pteronidea ribesii* is rather weak, since the eggs of the currant sawfly are deposited on the surface of the leaves of the food plant, but it has the characteristic form of the sawfly ovipositor. The shaft of the organ is composed of the broad, laterally compressed first and second valvulae (fig. 35 B, *1VI*, *2VI*), which are respectively ventral and dorsal to each other. The dorsal blades are united for their entire length by a narrow median membrane (E). The outer surface of the distal part of each valvula is crossed by a series of strong, oblique ridges (C, D); the membranous proximal part is traversed by a narrow flexible ramus (C, *r1vl*, E, *r2vl*) which curves upward to the basal attachment of each valvula with the corresponding valvifer.

The first valvifer is a small triangular sclerite lying anterior to the lower end of the ninth tergum (fig. 35 B, *1Vlf*), where it is mostly concealed beneath the lower part of the eighth tergum (A). It is definitely articulated by its dorsal posterior angle (B, C, *a*) to the ventral anterior angle of the ninth tergum, and by its ventral angle (*b*) to the dorsal edge of the second valvifer. The ramus of the first valvula is continuous with the first valvifer at the anterior angle of the latter (*c*).

The second valvifer is a large elongate plate (fig. 35 B, E, *2Vlf*) lying beneath the eighth and ninth terga (A). It is connected by membrane with the ninth tergum, but has no articulation with the latter,

its fulcrum of movement being the articulation with the lower angle of the first valvifer (B, *b*). The wide membranous proximal part of the second valvula is broadly united with the ventral margin of the anterior part of the second valvifer (E), but its ramus (*r2vl*) is attached to the anterior angle of the valvifer. Posteriorly the second valvifer bears the short, broad third valvula (A, B, E, *3VI*).

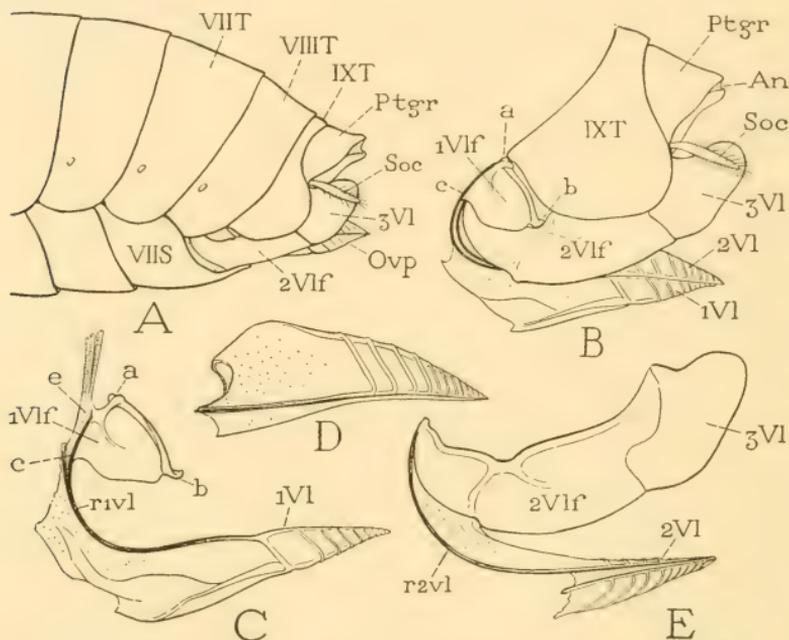


FIG. 35.—Abdomen and ovipositor of *Pteronidea ribesii* (Tenthredinidae).

A, end of abdomen with ovipositor in natural position.

B, ninth segment, with proctiger and ovipositor.

C, left first valvifer and first valvula.

D, distal part of second valvula.

E, left second valvifer and second and third valvulae, with united ends of second valvulae turned outward showing long ramus (*r2vl*) united with second valvifer.

*a*, articulation of first valvifer with ninth tergum; *b*, articulation of first valvifer with second valvifer; *c*, attachment of ramus of first valvula to first valvifer; *e*, attachment of muscle from eighth tergum on first valvifer.

The basal mechanism of the tenthredinid ovipositor brings about an opposite movement of the dorsal and ventral valvulae by the interaction of the two valvifers on each other, and of the first valvifer on the ninth tergum. A dorsal rotation of the anterior end of the second valvifer on the lower point of the first valvifer causes a rotation of the first valvifer on the ninth tergum, and vice versa, with the result that the first and second valvulae are simultaneously moved in opposite directions.

The proctiger of the lower Hymenoptera is of particular interest because of the pair of appendicular processes arising from it. In *Pteronidea* the proctiger consists of a bonnetlike dorsal plate (fig. 35 B, *Ptgr*) and of a broad, flat, membranous ventral flap, which enclose the anus (*An*) between their distal ends. The appendicular processes (*Soc*) are attached to the margin of the lower ends of the dorsal plate of the proctiger. The writer has been unable to find any trace of muscles connected with these appendages, though a large muscle extends into the proctiger from the ninth segment dorsal to the base of each process.

The proctiger of the Hymenoptera is probably a compound segment containing the tenth and eleventh abdominal somites, though there is little evidence even in the larvae of the presence of the eleventh somite. It has been shown by Nelson (1918), however, that in the embryo and young larva of the honey bee there is evidence of 11 abdominal ganglia. The newly hatched larva has nine distinct ganglionic masses in the nerve cord of the abdomen, the last of which lies in the caudal region behind the eighth segment, and contains three pairs of nerve centers, making thus a total of 11 pairs of ganglionic centers in the abdomen, which is indicative of the presence of the same number of somites. In the mature larva the composite end ganglion has united with the ganglion of the eighth somite to form the definitive terminal ganglion of the adult.

The appendages of the proctiger have usually been regarded as the cerci. If, however, we accept the embryological evidence that cerci are the appendages of the eleventh abdominal segment, it is difficult to see how these appendicular processes of the proctiger in adult Hymenoptera can be cerci, since in larval stages of the same insects the eleventh segment is absent, or represented only by the circumanal lobes of the terminal segment. The postpedes, or terminal appendages, of sawfly larvae clearly belong to the tenth abdominal segment, as do those of lepidopterous larvae, and it is claimed by Middleton (1921) that these larval appendages of *Pteronidea ribesii* give rise to protuberances of the tenth segment in the pupa within which the processes of the proctiger of the adult are developed. Though Middleton calls the adult processes "cerci" his own evidence suggests that they are identical in origin with the appendages of the tenth segment of the larva and are, therefore, not true cerci. The same argument applies to the appendicular processes of the proctiger present in adult males of some Lepidoptera, termed the *socii* by lepidopterists. The *socii* evidently are not cerci, since the eleventh abdominal segment is suppressed in the caterpillars and the last appendages in both the

larva and the embryo are those of the tenth segment. Hence, it seems probable that the proctiger of adult Lepidoptera and Hymenoptera is mostly the tenth segment of the abdomen, and that its appendicular processes, if they represent segmental appendages at all, are the appendages of the tenth segment. Likewise the processes of the proctiger in adult male Trichoptera appear to be homologues of the *socii* of Lepidoptera, and here again the terminal appendages of the larva belong to the tenth abdominal segment. The writer, therefore, tentatively designates the appendages of the proctiger in Trichoptera, Lepidoptera, and Hymenoptera the *socii*, since clearly it is more probable that they represent the pygopods, or appendages of the tenth segment, present in the larvae, than that they are the cerci, or appendages of the eleventh segment, which segment is suppressed in the larvae of all these insects.

On the other hand, the terminal appendicular processes of the abdomen of adult Mecoptera and Diptera may be true cerci. In *Panorpa* they arise from a small but distinct end piece of the abdomen beyond the tenth segment, which bears the anus on its ventral surface, and is therefore the eleventh segment. The morphology of the terminal appendages of Mecoptera and Diptera is discussed in a recent paper by Gerry (1932), who regards the structures as cerci.

#### ATANYCOLUS RUGOSIVENTRIS (ASHMEAD)

The ovipositor of this member of the Braconidae will illustrate the structure of the slender, elongate type of ovipositor characteristic of many of the parasitic Hymenoptera. The functional abdomen of a braconid, as that of all the higher families of the order, contains only nine segments, since the first abdominal segment forms the propodeum of the thorax, and there is but one postgenital segment, which is the proctiger.

The abdomen of *Atanycolus rugosiventris* (fig. 36 A) is elongate oval, rather broad, and of a pale orange color contrasting with the blackish thorax, head, and legs, and the dusky wings. The terga and sterna of the visceral region are separated by wide lateral membranous areas, and the tergal plates of segments III and IV are fused. The slender shaft of the ovipositor (*Ovp*) is nearly as long as the abdomen and thorax, and the third valvulae (*3VI*) are correspondingly lengthened and narrow. In life the third valvulae probably ensheath the ovipositor between their hollowed inner surfaces. The seventh, eighth, and ninth tergal plates of the abdomen are narrowed above (B) and separated by wide intersegmental membranes. The seventh sternum (*VIIIS*) projects posteriorly beneath the base of the ovipositor as a

large subgenital plate. There is no eighth sternum, and the venter of the eighth segment is represented only by the membrane of the anterior wall of the vestibulum beneath the gonopore. The proctiger (*Ptgr*) contains a dorsal and a ventral plate, and bears laterally a pair of small appendicular processes (*socii*).

The shaft of the ovipositor and the third valvulae project from above the seventh sternum (fig. 36 B). The dorsal second valvulae

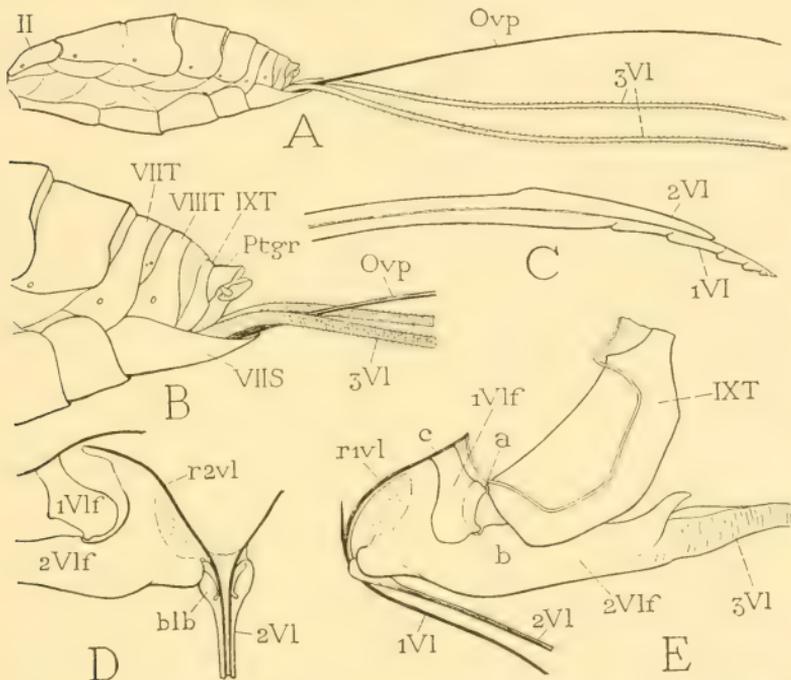


FIG. 36.—Abdomen and ovipositor of *Atanycolus rugosiventris* (Braconidae).

A, abdomen, with ovipositor separated from the ensheathing third valvulae.

B, end of abdomen and base of ovipositor.

C, distal part of shaft of ovipositor.

D, ventral view of base of united second valvulae, with ramus of right side showing union with second valvifer.

E, base of ovipositor and ninth tergum, showing articulation of first valvifer at *a* with ninth tergum, and at *b* with second valvula.

are solidly united with each other in the free part of the ovipositor (D, *2VI*), and the tip of the resulting median dorsal piece of the shaft is somewhat enlarged and slightly decurved (C). The first valvulae slide freely on the ventral margins of the second valvulae, and their distal ends (C) are strongly serrate on their lower edges. The basal ramus of each first valvula (E, *r1vl*) curves upward and posteriorly to its attachment (*c*) with the dorsal margin of the corres-

ponding first valvifer (*1Vlf*). The proximal ends of the united second valvulae (D, E, *2Vl*) present two lateral swellings which abut against the anterior ends of the second valvifers, but from each a narrow ramus (D, *r2vl*) curves upward and posteriorly against the inner face of the ramus of the first valvula of the same side, and is broadly attached to a proximal dorsal lobe of the second valvifer (*2Vlf*).

The first valvifer is a small plate (fig. 36 E, *1Vlf*) articulating between the anterior ventral angle of the ninth tergum (*a*) and the dorsal margin of the second valvifer (*b*); it gives attachment to the ramus of the first valvula (*r1vl*) by its upper margin (*c*). The lateral part of the ninth tergum (*IXT*) has the form of a sclerotic fold, the outer wall of which is deeply emarginate where the wide intersegmental membrane behind the eighth tergum is attached to it.

The second valvifer is a large, elongate plate (fig. 36 E, *2Vlf*), overlapped by the lower angle of the ninth tergum, but, as in *Pteronidea* and other Hymenoptera, having no articulation or specific point of movement on the latter; it rocks on the ventral pivot (*b*) of the first valvifer. The anterior end of the second valvifer is expanded in a dorsal lobe (D) to which the ramus of the second valvula (*r2vl*) is attached. Posteriorly the second valvifer bears the long, slender third valvula (E, *3Vl*).

The mechanism of the braconid ovipositor is the same as that of *Pteronidea*.

#### MEGARHYSSA ATRATA (FABRICIUS)

The species of the ichneumonid genus *Megarhyssa* are remarkable for the great length of the bristlelike ovipositor, which they insert into dead wood of trees in order to deposit their eggs in the burrows of wood-boring larvae on which their own larvae are parasitic.

The end of the abdomen of *Megarhyssa* is greatly enlarged and curiously modified (fig. 37 A). The modification involves the seventh, eighth, and ninth segments. The seventh segment is abruptly expanded from the end of the sixth; its sternum (*VIIIS*) is turned forward and projects downward beneath the anterior end of the seventh tergum (*VIIIT*). The eighth tergum (*VIIIT*) lies behind the seventh tergum, but its narrowed elongate, ventral ends are inflected within the lower parts of the seventh segment; the eighth sternum, as in other Hymenoptera, is completely obliterated. The ninth tergum is concealed dorsally within the overlapping eighth tergum, but its lateral parts are exposed ventrally (*IXT*) below the eighth and seventh segments. When the ninth tergum is removed

from the other segments, however, it is seen to consist of a long oval lobe on each side (B, *IXT*) having the usual relations with the valvifers of the ovipositor (*1Vlf*, *2Vlf*); its dorsal part forms a narrow median bridge between the lateral lobes, with which is ankylosed the dorsal plate of the proctiger (*Ptgr*).

The ovipositor of *Megarhyssa* is in no way different structurally from that of a braconid. The first valvifer (fig. 37 B, C, D, *1Vlf*)

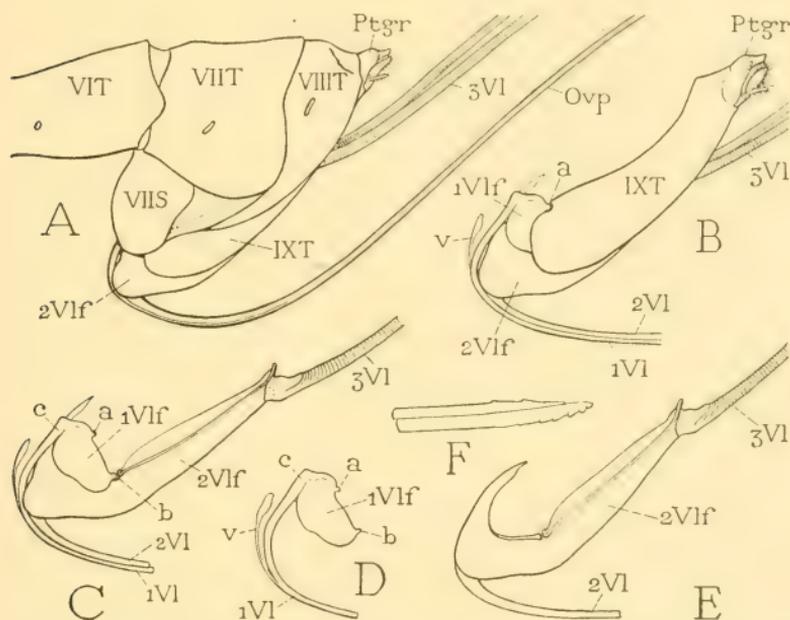


FIG. 37.—End of abdomen and structure of ovipositor of *Megarhyssa atrata* (Ichneumonidae).

- A, end of abdomen and basal parts of ovipositor.  
 B, ninth segment and proctiger with basal parts of ovipositor.  
 C, base of ovipositor, left side.  
 D, first valvifer and proximal end of first valvula.  
 E, second valvifer, with proximal parts of second and third valvulae attached.  
 F, distal end of shaft of ovipositor.

is a small oval plate articulating dorsally with the ninth tergum (B, *a*), and ventrally with the second valvifer (C, *b*). The first valvula arises from its dorsal end (D, *c*) and curves downward and posteriorly around the lower end of the second valvifer. Each first valvula has a slender but conspicuous basal branch (B, D, *v*). The second valvifer is an elongate plate (C, E, *2Vlf*) with its anterior end produced upward in a hook-shaped lobe, to which the first valvula (*1Vl*) is attached; distally it bears the long, slender

third valvula (*3lV*). The second valvifer rocks on the pivot of the lower articular point of the first valvifer (*C, b*). The curved basal rami of the two valvulae of each side are closely associated with each other, that of the second valvula lying against the inner face of the ramus of the first valvula. The two ventral first valvulae slide freely on the lower edges of the completely united dorsal second valvulae. The tip of the ovipositor (*F*) presents no unusual features.

#### APIS MELLIFICA LINNAEUS

The sting of the bee has been the subject of many anatomical studies, and the structural details of its skeletal parts are well known; the mechanism of the stinging apparatus, however, has not been fully understood, and none of the various attempts to explain how the bee stings is based on a correct dissection of the musculature. The sting of the bee is morphologically the ovipositor, but by both the worker and the queen it is used exclusively for purposes of stinging. Though structurally the organ has been but little modified to adapt it to its secondary use, it is effectively disqualified for egg-laying purposes through the obstruction of the channel of the shaft by a pair of valvular lobes arising from the first valvulae that serve for driving the poison liquid through it.

The principal feature that endows the bees and other stinging Hymenoptera with their stinging properties is the conversion of one of the accessory glands of the female genital system into a poison-secreting organ. The duct of this gland, which appears to be the right gland of a pair of accessory glands, opens into a large sac (fig. 41, *PsnSc*) that discharges directly into the proximal end of the channel of the sting. The other, much smaller, tubular gland (*BGl*), generally known as the "alkaline gland", lies to the left of the poison sac. The experiments of Carlet (1890), which seemed to show that it is only the mixture of the secretions from both glands that has maximum toxic qualities, are not generally accepted as conclusive, and Trojan (1930) has recently shown that in the honey bee the two glands do not open together, nor even at points where their products could readily mix. The alkaline gland opens ventrally in the membrane between the rami of the valvulae just before the base of the shaft of the sting, and entirely outside the channel of the latter. Nothing definite is known concerning the function of the alkaline gland, but it has been supposed that its secretion in the bee serves to lubricate the sliding parts of the sting, or to neutralize the acid secretion of the other gland when the bee has failed in an attempt

to inflict a wound. In many other Hymenoptera, however, the alkaline gland is much larger than in the honey bee, and in general it appears that this gland is best developed in the solitary bees.

*General structure of the abdomen.*—In order to understand the stinging mechanism of the bee it will be necessary to know something of the structure and musculature of the entire abdomen, since the movements of the abdomen as a whole are important in the act of stinging. The abdomen is divided at the petiole between the first and second segments (fig. 38 D). The first segment is the *propodeum*; the rest of the abdomen is called the *postabdomen*. The propodeum, however, is virtually a part of the thorax, and it is often convenient to refer to the body section beyond it as the “abdomen”, though the segments should be enumerated beginning with the propodeum. In the act of stinging, the bee not only moves the postabdomen as a whole on the propodeum, but it bends the distal segments of the former abruptly downward and protrudes the sting often in an approximately vertical direction. The general abdominal musculature of the bee has been described by Betts (1923) and by Morison (1927).

The petiolate structure of the abdomen, which brings the point of flexibility at the base between the first and second segments, gives a much freer movement to the abdomen than is possible in the more usual condition in which the play is between the metathorax and the first abdominal segment, because it allows the muscles between the first and second segments to be the effectors. With insects having the second pair of wings well developed, the dorsal muscles of the metathorax are a part of the wing mechanism; but in the higher Hymenoptera the hind wings and the metathorax are both greatly reduced, and the metathoracic muscles are in consequence so small and so cramped for space that they could have little effectiveness in giving movement to the abdomen. In the bees, the second phragma of the thorax extends backward through the metathorax into the posterior part of the propodeum (fig. 38 A, *2Ph*). A pair of muscles ( $d_2$ ) arise in lateral concavities on the posterior surface of the phragma and converge posteriorly and medially to a small median apodemal process of the dorsal wall of the propodeum just above the petiole (fig. 39,  $d_2$ ). These muscles are evidently the longitudinal dorsals of the metathorax, the posterior ends of which have migrated far backward on the tergum of the propodeum.

The propodeum of the honey bee (fig. 38 D, *I*) consists mostly of a large, strongly convex tergal plate (*T*) solidly incorporated into the thorax by a complete fusion with the upper edges of the

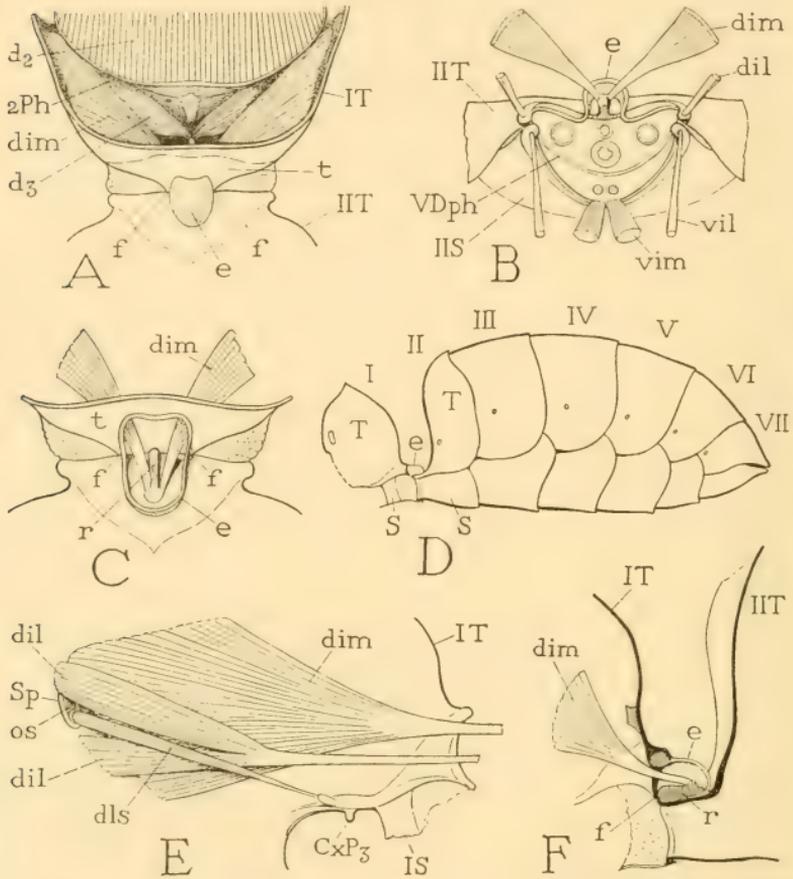


FIG. 38.—Structure of the abdominal petiole of *Apis mellifica*, worker (Apidae).

A, propodeum and petiole, dorsal view, with upper wall of propodeum removed to show muscles.

B, anterior end of petiole, showing muscle attachments on second segment.

C, dorsal view of petiole and end of propodeum, with dorsal wall of membranous pouch (*e*) removed to show insertion of levator muscles (*dim*).

D, abdomen, including propodeum.

E, dorsal muscles in right side of propodeum, mesal view.

F, levator mechanism of the petiole.

$d_2$ , dorsal muscles of mesothorax;  $d_3$ , dorsal muscles of metathorax; *dil*, lateral dorsal muscle of propodeum; *dim*, median dorsal muscle of propodeum; *dls*, dilator muscle of spiracle; *e*, membranous dorsal wall of dorsal pouch of petiole; *f, f*, fulcra of postabdomen on propodeum; *os*, occlusor muscle of spiracle; *r*, median ridge on floor of pouch of petiole; *t*, posterior triangular area of tergum of propodeum; *vil*, lateral ventral muscle of propodeum; *vim*, median ventral muscle of propodeum.

posterior parts of the oblique metathoracic pleura. The propodial sternum is reduced to a narrow, weakly sclerotic band (*S*) in the membrane between the hind coxae and the second abdominal sternum. The short petiole of the postabdomen is formed mostly of the constricted anterior part of the second abdominal segment, and involves both the tergum and the sternum of this segment. The large first abdominal spiracles are located laterally on the anterior part of the propodeum.

The posterior declivous surface of the dorsal plate of the propodeum terminates in a small triangular area above the petiole (fig. 38 A, *t*). The median apical part of the triangle is deeply excavated by a horseshoe-shaped notch, the lateral extremities of which form a pair of points (*f, f*), which articulate with the anterior margin of the second tergum, and constitute the fulcræ on which the postabdomen moves on the propodeum. The intersegmental membrane between the fulcræ is arched upward in a small dome (*e*), which extends from the propodial notch backward on the dorsal surface of the petiole. There is thus formed upon the anterior part of the petiole beneath the membrane, a small pocket communicating with the cavity of the propodeum through the notch in the dorsal wall of the latter (*C*). The floor of the pocket is strongly sclerotized and presents a small, median, dorsal ridge (*C, r*). On the posterior end of this ridge, within the pocket, are inserted the tendons of a pair of large muscles (*dim*) which take their origins on the lateral walls of the propodeum (*A*). These several correlated structures and the pair of propodeal muscles constitute the levator apparatus of the postabdomen (*F*). The insertion of the muscles on the posterior end of the petiole ridge (*r*) gives the muscles a short leverage on the abdomen distal to the fulcræ (*f*). The mechanism is thus, as noted by Betts (1923), a lever of the third order, and, considering the weight of the postabdomen, it is surprisingly effective.

The levator muscles of the postabdomen are evidently the median internal dorsals of the propodeal segment (fig. 39, *dim*). They converge from the sides of the propodeum into the dorsal pocket of the petiole (fig. 38 A, B, C). Each is a broad, fan-shaped muscle (*E, dim*) with a flat, tapering tendon. A second pair of muscles from the propodeum is inserted on the second abdominal tergum at the lateral extremities of the anterior margin of the petiole (*B, dil*), and would appear to be the lateral internal dorsals of the first segment (fig. 39, *I, dil*). Each is distinctly two-branched (fig. 38 E, *dil*), one branch arising above the propodeal spiracle (*Sp*), the other below it, the fibers of the two branches converging upon the end

of a long slender tendon. The tendons of these muscles support the lateral margins of the ventral diaphragm, which latter extends into the propodeum and is attached anteriorly on the endosternum of the pterothorax. The long slender dilator muscle of the spiracle (*dls*) lies between the two branches of the lateral dorsal muscle, and is attached posteriorly on a small process of the lower margin of the propodeum close to the pleural articular process of the metacoxa (*CxP<sub>3</sub>*). The ventral muscles of the petiole comprise two pairs of muscles arising anteriorly on the endosternum of the pterothorax (fig. 39, *I*, *vim*, *vil*). Those of the larger median pair are attached close together on the sternal margin of the aperture of the petiole (fig. 38 B, *vim*); the smaller muscles of the lateral pair (*vil*) are inserted by slender tendons on the lateral extremities of the sternal margin. The median ventrals are antagonistic to the median dorsals, but both the lateral dorsals and the lateral ventrals serve to move the postabdomen from side to side.

The postabdomen consists of six exposed segments (fig. 38 D), of which the last, or segment *VII*, has a conical shape, with a cleft on each side between the tergum and the sternum. Within the seventh segment is a large vestibular chamber in which are concealed the genital segments, the proctiger, and the sting (fig. 40).

The musculature of the postabdomen is rather simple; it is clearly adapted to produce the movements of respiration and the motions of the segments that accompany the use of the sting. The pattern of the muscle arrangement is repeated in each of the first five segments, with a few modifications in the first segment. We may, therefore, examine the musculature of the third segment of the postabdomen, which has been concisely described by Morison (1927), as an example of the musculature of segments *III* to *VI*. The names here applied to the individual muscles are those proposed by the writer (1931, p. 34) as generally applicable to the muscles of the pregenital region of the insect abdomen. They have a locational significance, and are therefore somewhat briefer than functional terms, and can be used for corresponding muscles where the action is different. The muscles found in each side of the third segment of the postabdomen (fig. 39, *IV'*), omitting the diaphragm muscles, are as follows:

*Musculus dorsalis internus medialis (dim)*.—A broad band of oblique fibers on median part of dorsum extending from the antecosta (*Ac*) of tergum *IV'* posteriorly and medially to antecosta of tergum *V*.

*M. dorsalis internus lateralis (dil)*.—A narrower band of fibers on lateral area of dorsum, attached anteriorly on tergum *IV* just behind marginal apodeme (*a*), extending posteriorly and ventrally to antecosta of tergum *V*.

*M. dorsalis externus (de)*.—A short protractor muscle. Origin on posterior margin of tergum *IV*; insertion anteriorly on marginal tergal apodeme of segment *V*. The corresponding muscles of segments *II* and *III* are more oblique or almost transverse in position. The innervation of the protractors, which according to Morison

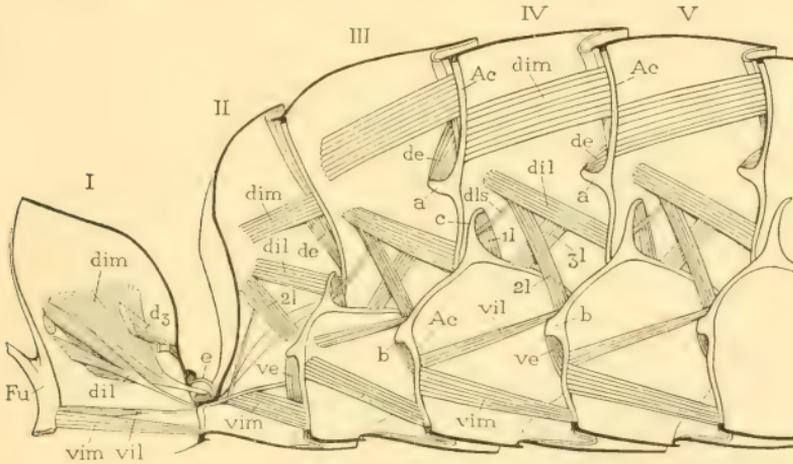


FIG. 39.—Muscles in right half of first five abdominal segments of *Apis mellifica*, worker, with muscles of dorsal and ventral diaphragms omitted.

*a*, anterior tergal apodeme; *b*, anterior sternal apodeme; *c*, lateral sternal apodeme; *d<sub>3</sub>*, dorsal muscles of metathorax attached on propodeum; *de*, external dorsal muscles; *dil*, lateral internal dorsal muscles; *dim*, median internal dorsal muscles; *dls*, dilator muscle of spiracle; *e*, dorsal wall of pouch of petiole; *il*, *2l*, *3l*, first, second, and third lateral muscles; *ve*, external ventral muscle; *vil*, lateral internal ventral muscles; *vim*, median internal ventral muscles.

is from the ganglion of the more anterior segment in each case, shows that these muscles belong to the segments giving attachment to their posterior (morphologically anterior) ends.

*M. ventralis internus medialis (vim)*.—A strong oblique muscle extending from antecosta of sternum *IV* posteriorly and medially to antecosta of sternum *V*.

*M. ventralis internus lateralis (vil)*.—A narrow lateral oblique muscle from anterior part of sternum *IV*, close to or beneath origin of *vim*, to anterior apodeme (*b*) of sternum *V*.

*M. ventralis externus (ve)*.—A short sternal protractor arising on posterior part of sternum *IV*; insertion anteriorly on anterior apodeme of sternum *V*.

*M. lateralis primus* (*1l*).—A tergo-sternal dilator of the abdomen. Origin on ventral margin of tergum *IV*; insertion dorsally on lateral apodeme (*c*) of sternum *IV*.

*M. lateralis secundus* (*2l*).—Origin dorsally on anterior lateral part of tergum *IV* external to *dil*; extends posteriorly and ventrally to insertion on posterior lateral part of sternum *IV*.

*M. lateralis tertius* (*3l*).—Origin dorsally on lateral part of tergum *IV* external to *dil*; extends ventrally and anteriorly, external to *2l*, to lateral margin of sternum *IV*. The second and third laterals are tergo-sternal compressors of the abdomen.

*M. oclusor spiraculi*.—A very small muscle between the ends of the closing valve of the spiracle. (Spiracle lies external to lateral muscles.)

*M. dilator spiraculi* (*dls*).—Origin on lateral arm of sternum; insertion on lower end of closing valve of spiracle.

The musculature of the first postabdominal segment (fig. 39, *II*) is somewhat reduced. The internal dorsals (*dim*, *dil*) are both present, though they are shorter than segmental length. The external dorsal (*de*) arises dorsally on the posterior part of tergum *II* and is inserted ventrally on the antecosta of tergum *III*. Of the sternal muscles the lateral internal ventral is absent; and there is but one lateral muscle present (*2l*), which corresponds with the second of the other segments.

The last exposed segment of the postabdomen, or segment *VII*, is conical in shape. Its basal part is largely retracted within the sixth segment; its apex forms the tip of the abdomen. The tergum and sternum are separated posteriorly on each side by a deep cleft (fig. 43 B), and the narrow posterior end of the sternum (*A*) is cut by a median notch through which the sting glides when it is protruded. The tergum (*B*, *VIIIT*) is a large bonnet-shaped plate with a prominent apodeme (*a*) projecting anteriorly from each side of the dorsal part of its anterior margin, on which is inserted a strong protractor muscle from the posterior margin of the sixth tergum. The seventh sternum (*A*, *VIIIS*) is a broad heart-shaped plate with its expanded basal lobes concealed above the sixth sternum. The body cavity in the seventh segment is greatly reduced by the invagination cavity containing the genital segments, the sting, and the proctiger (fig. 40). This cavity, formed by inflection of the integumental membrane (*bw*) from the posterior margins of the tergum and sternum of the seventh segment, is rather more than an ordinary vestibular invagination, and is generally called the *sting*

*chamber*: Its anterior wall is formed of the venter of the eighth segment, and contains the genital opening (fig. 44 A, *c*).

The eighth segment is much reduced and is mostly membranous, but in the queen it forms a distinct oval annulus (fig. 44 A, *VIIIT*, *VIIIV*) at the anterior end of the sting chamber surrounding the basal parts of the sting and the proctiger. The dorsum of the eighth segment is a weakly sclerotized fold across the back (fig. 40, *VIIIT*), but on each side it contains a large tergal sclerite, the *lamina spiracularis* (figs. 40, 44 A, *Lsp*), in which is situated the eighth spiracle. From each spiracular plate a membranous fold (fig. 44 A, *VIIIV*)

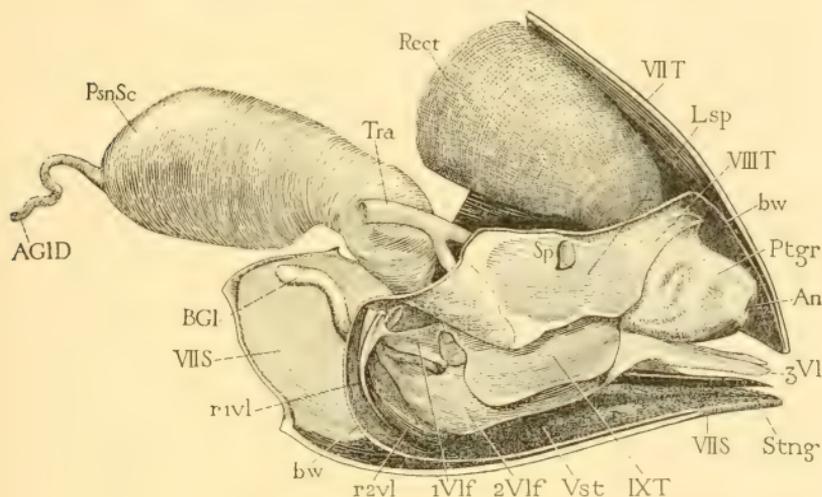


FIG. 40.—End of abdomen of *Apis mellifica*, worker, with left side removed, exposing the sting chamber containing the external parts of the stinging apparatus and the proctiger, and showing also the poison sac and a part of the rectum. (From Snodgrass, 1910.)

extends downward on the anterior wall of the sting chamber, and these folds, which are continuous ventrally beneath the genital opening, represent all that is left of the eighth venter.

The genital structures contained in the seventh segment, as well as the eighth segmental annulus itself, are much better developed in the queen than in the worker. By depressing the seventh sternum of the queen there is to be seen on the anterior wall of the sting chamber, immediately before the base of the sting, a triangular depression (fig. 44 A, *a*) between the folds of the eighth venter (*VIIIV*). Within this depression is a large, transverse median genital aperture (*c*) and, at the sides of and below the latter, two other openings (*d, d*). The median orifice leads into a large median

genital pouch (*B, b*), and the lateral openings into a pair of lateral pouches (*e, e*). The median pouch receives anteriorly the short oviductus communis (*Odc*), and dorsally at its anterior end the duct of the spermatheca (*SptD*).

The structure of the female genital apparatus in the bee has been described by Zander (1916) and by Bishop (1920). Both these writers apply the term "vagina" (or *Scheide*) to the entire passage that leads posteriorly from the confluent lateral oviducts, and appear to imply that it corresponds with the median oviduct of other insects. It is clear, however, since the spermatheca opens into the anterior end of the median pouch, that this part of the exit apparatus is derived from the genital chamber of the eighth segment, and that only the short, narrower tube anterior to the spermathecal opening is the true oviductus communis (cf. fig. 44 B with fig. 8 C). The shallow external triangular cavity containing the openings of the three genital pouches is called the "bursa copulatrix" by Bishop; but inasmuch as the common entrance cavity, the median pouch, and the lateral pouches are all parts of the genital chamber and have a copulatory function, the term "bursa copulatrix" should be applied to these parts collectively, since they are but differentiations of a single primitive invagination of the eighth segment, the genital chamber. The median pouch receives the median eversible part of the male organ during copulation and the lateral pouches the lateral lobes (pneumophyses). Bishop distinguishes two regions in the median pouch, the anterior of which contains the opening of the spermathecal duct, but in the gross anatomy of the organ this differentiation is not evident externally. Two pairs of muscles from the spiracular plates of the eighth tergum are inserted on the dorsal wall of the median pouch (fig. 44 B, *15, 16*), and a large muscle (*9*) from the antecosta of the seventh sternum (*VIIIS*) is inserted on the anterior wall of each lateral pouch.

In the worker the genital organs are greatly reduced; lateral pouches of the genital chamber are scarcely perceptible, but the common oviduct opens into a median pouch, from the dorsal wall of which arises the duct of the rudimentary spermatheca.

The lateral oviducts of the bee, according to Zander (1916), are mostly of ectodermal origin, the primitive mesodermal strands of the embryo being replaced as far as the calyces during postembryonic development by lateral branches of the ectodermal oviductus communis.

The valvifers of the eighth segment (fig. 40, *IVlf*) are entirely dissociated from the rest of the segment, since they form essential

elements in the basal mechanism of the sting, but their true segmental relations are attested by the muscles that connect them with the spiracular plates of the eighth tergum (fig. 46 D, E, 14).

The ninth segment has lost all resemblance to a segmental annulus. The median part of its dorsum is indistinguishable from the membranous wall of the proctiger (fig. 40, *Ptgr*); the lateral parts, however, form a pair of large quadrate plates (*IXT*), which are important elements of the sting mechanism. Each is overlapped dorsally by the spiracular plate of the eighth dorsum. The pleural parts of the ninth segment are represented by the oblong second valvifers (*2Vlf*), which are largely overlapped by the quadrate tergal plates. The ventral region of the segment, lying between the valvifers, is membranous and is ordinarily arched upward (fig. 45 A, *IXV*), forming beneath it a deep concavity thickly clothed with slender spinelike hairs, in which is lodged the bulbous basal part of the sting.

The proctiger, when fully protruded (fig. 40, *Ptgr*), is a membranous cone with the anal opening (*An*) at its distal end. The ventral wall of the proctiger contains a weakly sclerotized area.

*Structure of the sting.*—The stinging apparatus of the bee involves nearly all the parts that are invaginated within the seventh abdominal segment (fig. 40). These parts include the spiracle-bearing plates of the eighth tergum (*Lsp*), the lateral plates of the ninth tergum (*IXT*), the first and second valvifers (*1Vlf*, *2Vlf*), and the valvulae, which form the rami and shaft of the sting (*Stng*). The proctiger (*Ptgr*), because of its natural connections, is intimately associated with the stinging mechanism. The structure of the sting of the honey bee has been described by Sollmann (1863), Kraepelin (1873), Cheshire (1886), Snodgrass (1910, 1925, 1933), Zander (1911), Betts (1923), Leuenberger (1928, 1929), and various other writers. The well-known facts are repeated here in order to show the homologies between the parts of the sting and those of the ovipositor of other insects, and also that their description may serve as a basis for a closer study of the musculature and a better understanding of the mechanism of the sting.

Students of bee anatomy have adopted special names for the parts of the sting apparatus, which are convenient to use for descriptive purposes. The lateral sclerites of the eighth tergum bearing the spiracles are known as the *spiracular plates* (*laminae spiraculares*); the lateral sclerites of the ninth tergum are the *quadrate plates*, the first valvifers are the *triangular plates* (*Winkel* of German writers), and the second valvifers the *oblong plates*. The first valvulae are the *darts*, or *lancets* (*Stechborsten*). The structure formed by the united second valvulae

(fig. 41, 2VI) is sometimes called the sheath of the sting (Cheshire, 1886, Snodgrass 1910, 1925), or the *shaft* (Betts, 1923); but, since this part is hollowed beneath to form a channel giving passage to the poison, European writers generally term it the sting trough, or gutter (*Stachelrinne*, *fourrou-guttière*). The enlarged basal part of this organ is the *bulb* (*blb*); the slender tapering distal part we may term the *stylet* (*stl*). The third valvulae (figs. 40, 41, 3VI) are sometimes called the "palpi" of the sting, but since their chief function is, as in other Hymenoptera, to ensheath the distal part of the sting or ovipositor shaft, they are better termed the *sheath lobes* (*Stachelscheiden*),

The general structure of the bee's sting differs but little from that of the ovipositor of other Hymenoptera, and it is only in certain de-

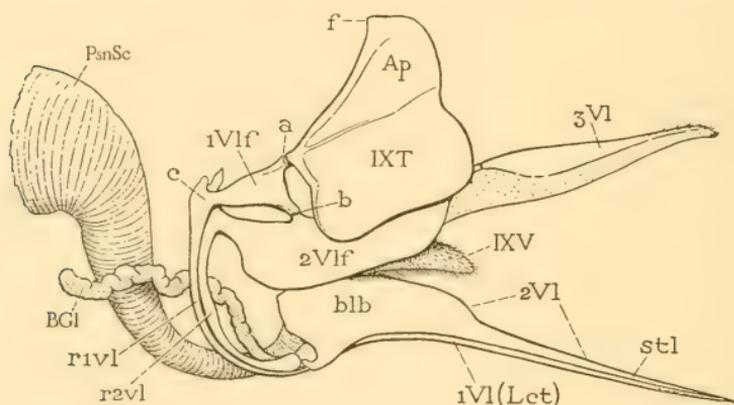


FIG. 41.—The sting and associated parts of *Apis mellifica*, worker. (From Snodgrass, 1910, but relettered in accord with the general nomenclature of the ovipositor adopted in this paper.)

tails that the sting is specialized for its specific function of ejecting the poison liquid from the reservoir of the poison gland.

The spiracular plates of the eighth tergum overlap externally the upper ends of the lateral plates of the ninth tergum (fig. 40). The spiracular plates of the worker are triangular in shape (fig. 43 B, *Lsp*), with the lower anterior angle of each produced into a process for muscle attachment. In the queen the plates are relatively larger and of irregular form (fig. 44 C). Though the spiracular plates are connected entirely by membrane with the surrounding parts, they have an elaborate musculature, which will be fully described later, but it should be noted particularly that they are anchored in position by dorsal muscles from the seventh tergum and ventral muscles from the seventh sternum (fig. 43 B). On the other hand, each spiracular plate is connected with the ninth tergal plate of the same side by two

muscles (*10*, *11*) from its upper end, and with the first valvifer by a single muscle (*14*) from its lower margin.

The quadrate plates, or lateral tergal sclerites of the ninth dorsum (fig. 41, *IXT*), are the suspensory plates of the sting mechanism. Because of their membranous dorsal connections they are freely movable on their upper angles (*f*) within the overlapping spiracular plates. Each quadrate plate is a large four-sided sclerite, articulated anteriorly with the dorsal posterior angle (*a*) of the first valvifer (*1Vlf*). Its dorsal part projects into the body cavity as a flat apodemal extension (*Ap*) on which important muscles of the sting mechanism are attached; its lower edge overlaps the second valvifer (*2Vlf*), with which it is connected by a membranous fold of the integument.

The triangular plate, or first valvifer (fig. 41, *1Vlf*), is a relatively small sclerite lying anterior to the quadrate plate. Its anterior angle (*c*) is continuous with the upper end of the ramus of the lancet, or first valvula (*1vl*), and its posterior angles (*a*, *b*) articulate respectively with the anterior angle of the quadrate plate (*IXT*) and the dorsal margin of the second valvifer, or oblong plate (*2Vlf*). The single muscle of the first valvifer, which arises on the lower margin of the spiracular plate (fig. 43 B, *14*), is inserted on the upper edge of the valvifer very near the posterior dorsal angle (fig. 42 A, *14*). In the usual position the muscle is horizontal.

The oblong plate, or second valvifer (fig. 41, *2Vlf*), lies beneath the first valvifer and the quadrate plate. Its articulation with the lower posterior angle of the first valvifer (*b*) is somewhat before the middle of its dorsal margin. Its anterior end is narrowed and continuous with the ramus of the second valvula (*2rvl*); posteriorly it supports the third valvula (*3VI*), which in the bee is a short, soft, mostly membranous appendage.

The oblong plates of opposite sides are connected medially by an ample membrane thickly clothed with hairs, which represents the venter of the ninth segment. The membrane is ordinarily arched upward above the base of the sting (fig. 45 A, *IXV*), forming below it a deep cavity in which the bulb of the sting is ensheathed, but, when the sting is depressed, the membrane is partly everted and appears as a hairy pad over the bulb (fig. 41, *IXV*).

The shaft of the sting is composed of the united second valvulae (fig. 41, *2VI*), and of the slender first valvulae, or lancets (*1VI*). The single dorsal piece, formed of the second valvulae, is enlarged basally as the bulb of the sting (*blb*); its distal tapering part is the stylet (*stl*). The lancets slide freely on the lateral ventral margins of the bulb and stylet (fig. 42 E); their lower edges are in contact,

and between the three parts of the shaft is the poison canal of the sting (*r*). In the bulb the canal expands to a large chamber, in which lie a pair of pouchlike valves borne on the upper edges of the lancets (*A*, *Vlv*) that serve to drive the poison liquid through the canal, from which it makes its exit near the tip of the sting from a ventral cleft between the lancets. The stings of the worker and the queen differ principally in the size and form of the shaft. The shaft of the queen is relatively larger and is strongly bent downward in the region of the bulb; when exerted, therefore, it curves ventrally or anteriorly according to the position of the abdomen. The poison sac opens directly into the base of the bulb (fig. 42 C, *PsnSc*). The distal end of the stylet is narrow but rounded, and in the worker it has three pairs of very small lateral barbs on its dorsal surface. The tips of the lancets are acute, and the terminal part of each lancet of the worker is strongly serrate ventrally on its outer surface by a series of 10 retrorse barbs.

The shaft of the sting is supported at its base on the rami of the valvulae (fig. 41, *r1vl*, *r2vl*). The two pairs of rami are widely divergent as they curve upward to their connections with the valvifers (*1Vlf*, *2Vlf*). A membrane stretches between the rami of the second valvulae. The two rami of each side are united by a groove-and-ridge connection continuous with that on the shaft (fig. 42 E), but since the ramus of the first valvula lies against the outer surface of the ramus of the second valvula (fig. 41), the groove of the first valvula, which follows the dorsal edge of the lancet (fig. 42 A, *d*), goes over to the inner face of the ramus (*d'*).

In order to understand an important point in the mechanism of the sting it will be necessary to give close attention to certain details of structure at the base of the bulb. Each second valvular ramus is rather broad (fig. 42 B, *r2vl*) and presents a rounded lobe (*w*) near its lower end. The direct union of the ramus with the bulb is a narrow sclerotic bar (*x*), but laterad of it a hooked process (*y*) from the base of the bulb makes a very fine connection (*z*) with the lobe (*w*) of the ramus. The muscle of the ramus (*z0*) is inserted on this process.

The basal surface of the bulb is inclined forward considerably in advance of its connections with the rami (fig. 42 C), and a membranous fold projects from it dorsally into the body cavity. In this fold there lies a Y-shaped rod, the *furcula* (*C*, *Frc*, *D*), the arms of which are connected with the base of the bulb, while the median stem curves upward and posteriorly above the latter, and above the membranous ninth venter (*IXV*). Upon the furcula are inserted a pair of large

muscles from the second valvifers (fig. 45 A, 19). These muscles serve to deflect the distal end of the shaft of the sting, since their pull is on points at the base of the bulb anterior to the articulations of the latter (fig. 42 B, C, *z*) with the lobes of the rami. The rôle of the furcular muscles in the mechanism of the sting has not generally

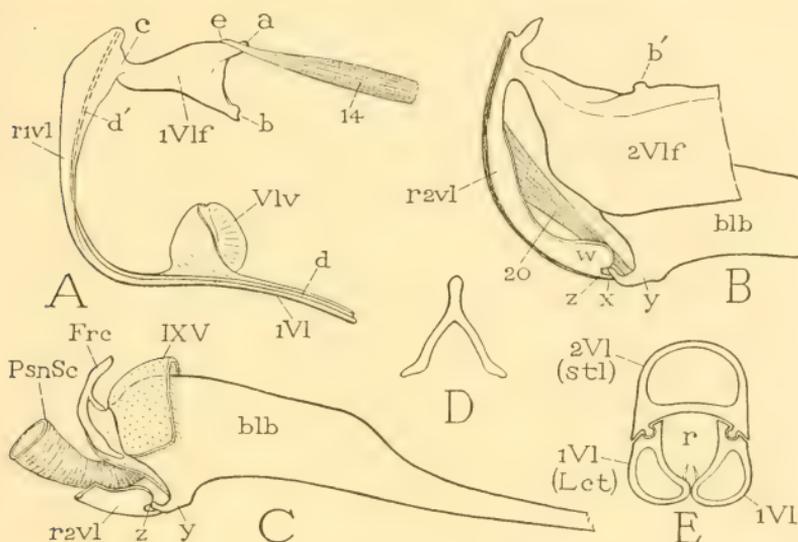


FIG. 42.—Structural details of the various parts of the sting of *Apis mellifica*, worker.

A, left first valvifer and proximal half of first valvula.

B, anterior part of left second valvifer with ramus of corresponding second valvula and basal part of bulb, showing articulation of the latter on the ramus, and the ramus muscle.

C, basal mechanism of shaft of sting and attachment of furcula.

D, furcula.

E, cross section of distal part of shaft of sting.

*a*, articulation of first valvifer with ninth tergum; *b*, articulation of first valvifer with second valvifer; *b'*, corresponding articular point of second valvifer; *c*, attachment of first valvula to first valvifer; *d*, *d'*, groove of first valvula; *e*, insertion on first valvifer of muscle (14) from spiracular plate of eighth tergum; *r*, poison canal of sting; *w*, distal lobe of ramus of second valvula; *x*, connection between ramus and bulb of second valvula; *y*, articular process of base of bulb; *z*, point of articulation between ramus and bulb of second valvula.

been understood. Zander (1911) and subsequent writers have regarded them as protractors of the sting shaft; but, as will later be shown, the outward thrust of the sting is brought about by other means, while simultaneously the shaft is depressed by the muscles inserted on the furcula.

The morphological nature of the furcula has been somewhat puzzling to students of bee anatomy, but it is evident that the furcula is

merely a movable apodeme contained in a membranous fold at the base of the bulb. The homologues of the muscles inserted upon it in the bee are attached in the braconid (fig. 45 B, 19) directly to a bulbous enlargement of the base of the ovipositor, while in the ichneumonid (C) they are inserted on a ligamentous stalk containing a small U-shaped sclerotization. The depressor mechanism of the shaft of the sting in the bee, therefore, is clearly a development from a much simpler mechanism of the ovipositor in the lower Hymenoptera, but it appears to have no counterpart in other orders of insects.

*Muscles of the seventh segment and the sting.*—Since the muscles of the seventh and genital segments cannot all be certainly identified with specific muscles of the preceding segments, they will be given descriptive names by which they may be recognized; they are designated on the figures with arabic numerals. The numbered series of muscles applies in full to the queen only, certain muscles being absent in the worker. The list of muscles here recorded for the terminal segments of the bee, 22 in all, is somewhat greater than that given by Betts (1923) and Morison (1927). Certain other discrepancies in the accounts will be noted at the appropriate points, as will also a few additions and corrections that must be made in the description of the muscles of the sting as given by Sollmann (1863), Kraepelin (1873), and Zander (1911).

The following nine muscles belong to the seventh segment:

1. *First internal dorsal muscle.*—A rather wide muscle in the worker arising anteriorly on seventh tergum (fig. 43 B); extending posteriorly and ventrally to dorsal lobe of spiracular plate. Smaller in the queen (fig. 44 C), where its insertion on spiracular plate is on dorsal margin of anterior lobe.

2. *Second internal dorsal muscle.*—Found only in the queen. A slender muscle arising dorsally on lateral part of seventh tergum; insertion ventrally on dorsal margin of spiracular plate above the spiracle (fig. 44 C). Not described by Betts or Morison.

3. *External dorsal muscle* (not shown in the figures).—A wide muscle against outer face of spiracular plate, present in both worker and queen. Origin ventrally near lower lateral margin of seventh tergum; insertion dorsally on upper margin of dorsal lobe of spiracular plate, as indicated in the figures (figs. 43 B, 44 C, 3). This muscle is a protractor between the tergal plates of segments VII and VIII.

4. *First lateral tergo-sternal muscle.*—Origin posteriorly on lateral part of seventh tergum external to spiracular plate (fig. 43 B); insertion anteriorly on lateral apodeme of seventh sternum (A, B).

5. *Second lateral tergo-sternal muscle*.—Origin dorsally above 4 on lateral part of seventh tergum (fig. 43 B); insertion ventrally on lateral margin of seventh sternum (A). In the queen there are two branches to this muscle, a short outer group of fibers arising on the seventh tergum below the spiracles being inserted on the sternum along with the fiber of the inner group.

6. *Occluser of the spiracle*.—A small muscle between ends of closing valve of seventh spiracle (fig. 43 B).

7. *Dilator of the spiracle*.—A long slender muscle arising on margin of seventh sternum just before lateral apodeme; inserted on lower end of closing valve of seventh spiracle (fig. 43 B).

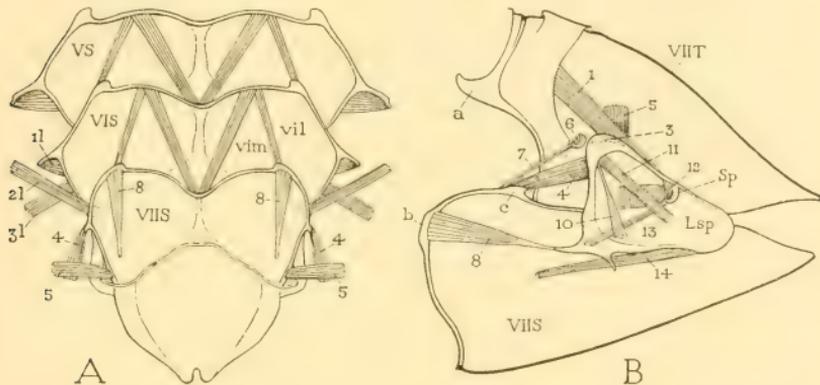


FIG. 43.—Musculature of posterior abdominal segments of *Apis mellifica*, worker.

A, muscles of fifth, sixth, and seventh sterna.

B, muscles of right half of seventh segment and of right spiracular plate of eighth segment, mesal view.

8. *Intersegmental sternotergal muscle*.—Origin on anterior apodeme of seventh sternum (fig. 43 A, B); fibers in the worker convergent posteriorly to insertion on a tendon attached to end of ventral anterior point of spiracular plate of eighth tergum (B), but in the queen (fig. 44 C) attached directly to anterior lobe of spiracular plate. This muscle cannot be homologized with any muscles of the preceding segments, since no muscle in the latter segments has corresponding connections.

9. *Median internal ventral muscle*.—Present only in the queen (fig. 44 B). A short, thick, conical muscle arising anteriorly on antecosta of seventh sternum (VIIIS) in position of the usual median ventrals (fig. 43 A, *vim*); fibers divergent posteriorly to insertion on anterior wall of corresponding lateral pouch of genital chamber (fig. 44 B, *e*). Not mentioned by other writers.

The following muscles of segment *VIII*, here enumerated as muscles *10* to *16*, are all attached on the spiracular plate of the eighth tergum:

*10. First dorsal muscle.*—A very slender muscle in the worker (fig. 43 *B*), a large muscle in the queen (fig. 44 *C*), arising dorsally

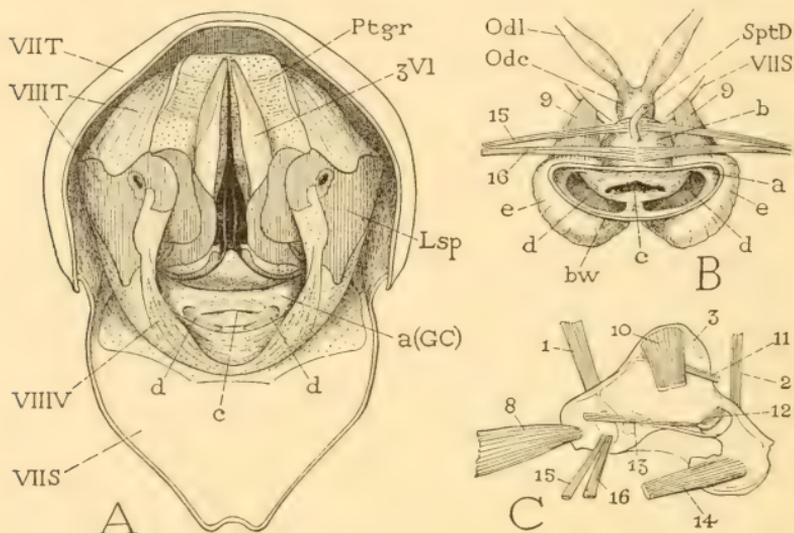


FIG. 44.—External genital apparatus, and muscles of the spiracular plate of eighth segment of *Apis mellifica*, queen.

*A*, the sting chamber opened from behind by separation of tergal and sternal plates of seventh segment, showing the complete annulus of eighth segment (*VIIT*, *VIII*), with outer depression (*a*) of genital chamber at base of ovipositor between folds of eighth venter (*VIII*).

*B*, the genital pouches and the oviducts, posterodorsal view, with wall of outer cavity of genital chamber (*a*) cut away along line *bw*, and apertures of pouches (*c*, *d*) distended.

*C*, right spiracular plate of eighth segment and its muscles, mesal view.

*a*, shallow external cavity of genital chamber; *b*, median pouch of genital chamber; *c*, aperture of median pouch; *d*, *d*, apertures of lateral pouches; *e*, *e*, lateral pouches of genital chamber.

on upper part of inner face of spiracular plate; inserted ventrally on outer surface of ninth tergal (quadrate) plate anteriorly at base of dorsal apodeme of the latter.

*11. Second dorsal muscle.*—Origin on inner face of dorsal lobe of spiracular plate (figs. 43 *B*, 44 *C*); insertion posteriorly and ventrally on posterior dorsal angle of quadrate plate of ninth tergum (fig. 45 *A*). In the worker this muscle arises just behind *10* (fig. 43 *B*); in the queen (fig. 44 *C*) it arises external and ventral to origin of *10*.

12. *Occlusor of the spiracle*.—A short, relatively broad muscle in the worker arising dorsally on marginal ridge of spiracular plate, with fibers convergent ventrally to insertion on lower end of closing valve of eighth spiracle (fig. 43 B); in the queen this muscle attached as usual to both ends of spiracular valve (fig. 44 C).

13. *Dilator of the spiracle*.—A slender muscle arising on anterior ventral part of spiracular plate, crossing the plate obliquely to insertion on lower end of closing valve of spiracle (figs. 43 B, 44 C).

14. *Tergovalvifer muscle*.—A long muscle, horizontal in the usual position. Origin posteriorly on ventral margin of spiracular plate in the worker (fig. 43 B), on inner face of posterior lobe of plate in the queen (fig. 44 C); insertion anteriorly on posterior end of first valvifer (figs. 42 A, 45 A). This muscle is the only representative in the bee of the usual tergal muscles of the first valvifer.

15. *First tergoventral muscle*.—A slender muscle, present only in the queen, arising on anterior lobe of spiracular plate (fig. 44 C); extends mesally and anteriorly to dorsal wall of median pouch of genital chamber anterior to duct of spermatheca (B).

16. *Second tergoventral muscle*.—Similar to the last and present only in the queen. Origin just behind 15 on spiracular plate (fig. 44 C); insertion on dorsal wall of median pouch of genital chamber posterior to spermathecal duct (B).

It will be observed that there are 11 muscles, including the spiracular muscles, attached on each of the spiracular plates of the eighth tergum in the queen (fig. 44 C), and eight in the worker (fig. 43 B). Morison (1927) says there are nine in the worker, but he describes a small muscle from the antero-ventral margin of the plate to the side of the quadrate plate, which was not observed by Betts (1923), and which the writer has been unable to find. It is evident that the spiracular plates are important parts of the general sting mechanism, but since the muscles from them to the parts of the eighth and ninth segments that compose the sting apparatus are all small, it is probable that they do not produce any of the major activities of the latter.

The muscles of the ninth segment include the principal muscles of the stinging mechanism, and the muscles of the proctiger. Their distribution and functions have been discussed particularly by Sollmann (1863), Kraepelin (1873), Zander (1911), and Snodgrass (1933). These muscles are as follows, on each side:

17. *Anterior tergal muscle of the second valvifer* (fig. 45 A).—A large tergo-pleural muscle composed of two distinct bundles of fibers, one dorsal (17a), the other ventral (17b). Fibers of dorsal group

arise on posterior dorsal angle of quadrate plate of ninth tergum, and cover both surfaces of dorsal apodemal part of the plate; insertion anteriorly on upper extremity of ramus of second valvifer (*r2vl*). Fibers of ventral group (*17b*) arise posteriorly on inner face of quadrate plate, and lie parallel to those of dorsal group; insertion anteriorly on anterior arm of second valvifer (oblong plate).

Much confusion has existed as to the insertion points of these muscles. Sollmann (1863) correctly gave the insertion of the upper muscle on the extremity of the ramus of the second valvula, but the lower muscle he wrongly described as attached on the first valvifer (Winkel); Kraepelin (1873), on the other hand, erroneously ascribed the dorsal muscle to the first valvifer, but correctly described the attachment of the lower one on the second valvifer. Kraepelin's error has been followed by Zander (1911), Betts (1923), and Morison (1927). The two groups of fibers in the bee very clearly correspond with the usually single anterior tergal muscle of the second valvifer (figs. 29, 34, *6*). In some Hymenoptera, as in *Megarhyssa* (fig. 45 C), they form two quite distinct muscles (*17a*, *17b*). These muscles are the *protractors* of the lancets.

*18. Posterior tergal muscle of the second valvifer.*—A broad, flat, tergo-pleural muscle covering most of the inner face of quadrate plate of ninth tergum, on which it arises dorsally and anteriorly (fig. 45 A); insertion ventrally on posterior part of dorsal ridge of second valvifer (*2Vlf*). This muscle is the *retractor* of the lancet.

In the queen a slender muscle arises dorsally on the posterior dorsal angle of the quadrate plate, and is inserted ventrally on the second valvula mesad of *18*. This muscle is described by Morison (1927) as a distinct muscle, but it is here regarded as a branch of *18*, since the two have the same insertion, and together would represent the usual posterior tergal muscle of the second valvifer (figs. 29, 34, *7*).

*19. Muscle of the furcula.*—A highly developed muscle in the bee (fig. 45 A), consisting of a wide layer of strong fibers arising ventrally on most of length of inner surface of second valvifer (oblong plate); fibers curve anteriorly, dorsally, and mesally over ninth ventral membrane (*IXV*) to insertion on stem and upper part of arm of furcula (*Frc*). This muscle is much smaller in lower Hymenoptera; in the braconid *Atanycolus* it is inserted directly on a small basal swelling of the united second valvulae (B, *19*); in the ichneumonid *Megarhyssa* (C, *19*) it is attached on a short ligamentous process arising from a hooked dorsal extension of the base of the united second valvulae; in the tenthredinid *Pteronidca*, a corresponding muscle arising on the second valvifer is inserted on a long basal process of the

second valvula. A representative of this muscle has not been found in other orders of insects.

The muscles of the furcula are usually regarded as the protractors (Vorstossmuskeln) of the sting. It was correctly observed by Kraepelin (1873), however, that they can act only in the capacity of deflecting the distal end of the shaft since they pull upward on the base of the bulb.

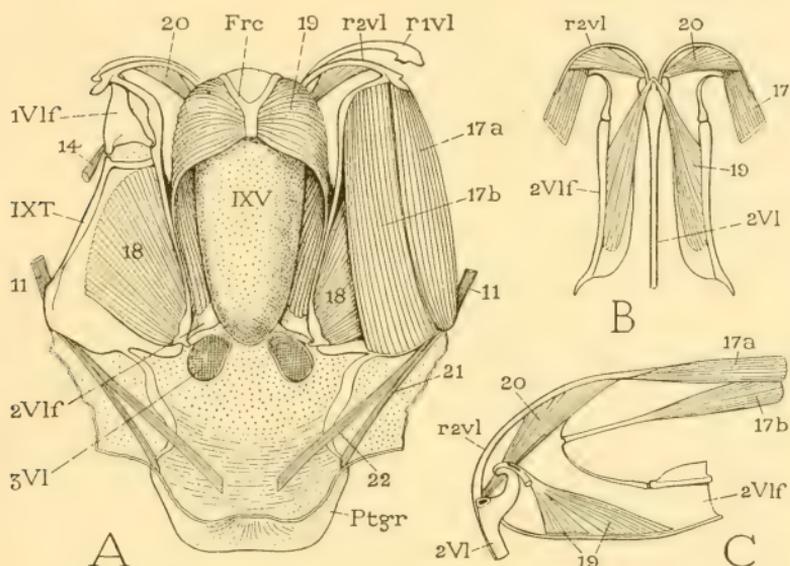


FIG. 45.—Musculature of the hymenopterous ovipositor or sting.

A, sting of *Apis mellifica*, worker, with venter of ninth segment and proctiger, dorsal view, showing muscles of the stinging apparatus.

B, second valvifers and base of shaft of ovipositor of *Atanycolus rugosiventris*, with muscles inserted on the latter, dorsal view.

C, anterior end of right second valvifer, mesal view, with right ramus and base of shaft of ovipositor of *Megarhyssa atrata*, showing anterior muscles (17) of valvifer, and muscles of the shaft (19, 20).

*20. Ramus muscle of the second valvula.*—A rather small muscle in the worker bee attached dorsally on upper part of ramus of second valvula (figs. 42 B, 45 A), and ventrally on lateral process (y) of base of bulb (fig. 42 B). In *Atanycolus* (fig. 45 B) and in *Megarhyssa* (C) this muscle is relatively larger and stretches like a bowstring between the two extremities of the strongly arched ramus. The ramus muscle appears to have no homologue in insects other than Hymenoptera.

*21, 22. Muscles of the proctiger.*—Two slender muscles arising from posterior dorsal angle of quadrate plate (fig. 45 A): extending

posteriorly and ventrally to ventral wall of proctiger, where one (21) is inserted laterally, the other (22) medially.

*The mechanism of the sting.*—When a worker bee is held securely by the thorax, preferably in a pair of forceps, her ineffectual attempts to use the sting are accompanied by a strong deflection of the end of the abdomen. The shaft of the sting is thrust out from the cleft between the tergal and sternal plates of the seventh segment, and slides back and forth in the terminal notch of the sternum. The exposure of the shaft is usually greatest as the direction of the thrust approaches a perpendicular to the axis of the body; the seventh sternum is depressed and the bulb of the sting appears in the opening above it. The third valvulae, or so-called “palpi” of the sting, are not in evidence while the shaft is probing for an object to strike, and the writer has never observed any use made of these organs by the bee to suggest that they have a tactile function, or that by means of them the bee determines where a vulnerable spot is presented for her attack, as she has been supposed and even said to do. The third valvulae do not issue from the sting chamber. The highly mobile abdomen swings around in all directions on the petiole, and the decurved tip strikes at random until an object is encountered, which, if nothing else presents, may be the body, head, or mouth of the bee herself.

The deflection of the terminal part of the abdomen is brought about by the contraction of the oblique lateral intertergal dorsal muscles (fig. 39, *dil*) and the median intersternal ventral muscles (*vim*) of the segments concerned. The accompanying movements of the abdomen as a whole depend upon the mechanism of the petiole and are produced by the muscles of the propodeum inserted upon the second segment.

The entire act of stinging involves three separate movements, or sets of movements, in the sting apparatus. The first accomplishes the outward thrust of the shaft, the second the depression of the shaft, and the third the movements of the lancets on the stylet. The first two movements are simultaneous, but each has its own mechanism, while the movement of the lancets depends on a third mechanism quite distinct from the other two.

When the bee persists in her attempts to sting an inaccessible or nonexistent object, the shaft, as we have seen, glides rapidly back and forth in the notch of the seventh sternum, and with each outward thrust is exposed for nearly its entire length. If now, while the bee is held under the microscope, the plates of the apical segment are separated with a needle or a pair of slender forceps, it is to be seen that the movements of the shaft are produced by corresponding move-

ments of the entire basal part of the sting apparatus. The latter, however, does not move back and forth horizontally in the position of repose (fig. 46 A); on the contrary, the whole structure, including the valvifers and the quadrate plates of the ninth segment, swings downward and posteriorly on the upper angles of the quadrate plates, and the shaft, which at the same time is unsheathed and depressed,

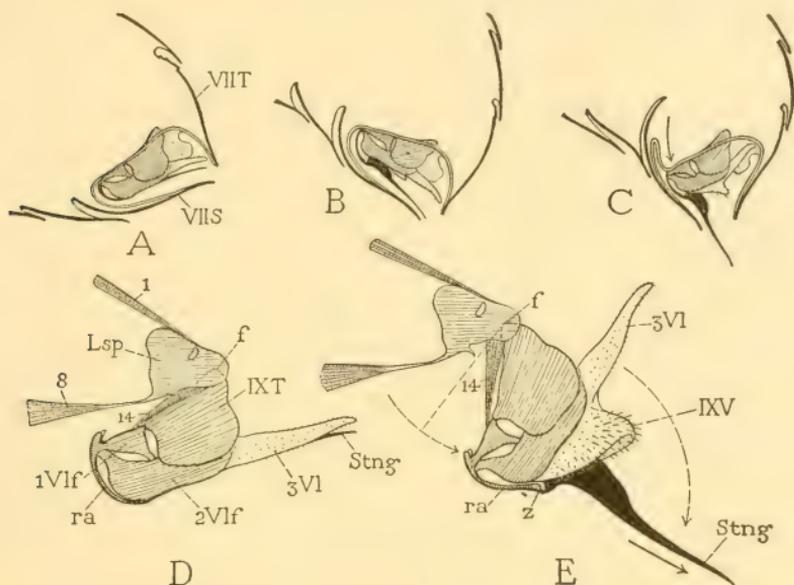


FIG. 46.—Relative positions of the parts of the sting of a worker bee, *Apis mellifica*, in repose and action.

A, sting in usual position within the sting chamber.

B, end of abdomen bent down, shaft of sting unsheathed and partly depressed ready for extrusion.

C, basal part of sting apparatus swung posteriorly as indicated by arrow, sting fully depressed and extruded.

D, usual position of basal parts of sting, ninth tergal plates, and spiracular plates of eighth segment within the sting chamber during repose.

E, position of same parts when shaft of sting is fully protruded.

is driven out from the sting chamber at the tip of the abdomen (B, C). By a reverse set of movements in the basal apparatus the sting is retracted and elevated to its initial horizontal position and ensheathed between the second valvifers and their distal lobes. Conversely, it can be demonstrated on a freshly killed specimen that back-and-forth movements of the shaft involve these same swinging movements of the basal apparatus. The free movement of the basal parts is made possible by the membranous connections of the latter with the sur-

rounding parts, and particularly by the ample length of the membranous floor of the sting chamber reflected from the seventh sternum.

The relative changes in position of the various parts of the sting apparatus before and after the protrusion of the shaft are shown at D and E of figure 46. The axis of revolution in the basal parts passes through the upper ends (*f*) of the quadrate plates (*IXT*), which are overlapped by the spiracular plates (*Lsp*) of the eighth segment. The spiracular plates themselves are but little affected by the movements of the sting, since they are held in place by their dorsal and ventral muscles (*r*, *s*). In the position of protraction (E) the sting base is almost at right angles to the lower margins of the spiracular plates, and the sheath lobes, or third valvulae (*3VI*), are pointed upward. The shaft of the sting, on the other hand, has retained its position in the direction of the thrust by a movement of depression. The depression of the shaft somewhat flattens the curve of the rami (*ra*), and is accompanied by an eversion of the membranous ninth venter, which now appears as a large hairy lobe (*IXV*) over the bulb of the sting.

The mechanism of the stinging apparatus of the bee was first studied by Sollmann (1863), who observed that the outward thrust of the shaft is produced by a backward swing of the supporting basal parts. His explanation of the movements of the latter, however, is mostly fanciful, since he attributes them to muscles that either do not exist or do not have the attachments he ascribed to them. It was later shown by Kraepelin (1873) that there are no muscles immediately connected with the sting or its basal support that can give the movements of protraction and retraction to the shaft. Accepting this fact, Kraepelin says: "Ich nehme daher keinen Anstand, als treibendes Princip für die Bewegung des Stachels im engeren Sinne die Blutflüssigkeit zu bezeichnen, welche ja auch bekanntermassen bei den Hervorstülpen des Penis und ähnlicher Körperanhänge eine so wichtige Rolle spielt. Bei jeder stechenden Biene kann man eine seitliche Annäherung der Abdominalwandungen mit Lichtigkeit beobachten, bei frisch getödeten aber genügt ein geringer Druck auf die vordern Hinterleibssegmente, um den Stachel in normaler Weise hervortreten zu lassen."

A careful examination of the bee confirms the truth of Kraepelin's statement concerning the lack of any special muscles for the protrusion and retraction of the sting, and makes it clear that the shaft is driven out of the sting chamber by pressure exerted against the membranous walls of the latter from within the body cavity of the abdomen. The rotund anterior part of the postabdomen, by a bulblike action of compression and expansion, thus swings the basal support of the sting back and forth on its points of suspension at the dorsal angles of the quad-

rate plates, and the shaft is correspondingly protruded and withdrawn. It is possible that the strong contraction of the seventh abdominal segment, which elevates the broad anterior lobes of the sternum, may cause the latter to press directly on the base of the sting, but if this is partly accountable for the sting protraction it is only a minor factor. Kraepelin's account of the mechanism of protraction and retraction of the sting seems to have made little impression on other students of the bee, for all subsequent writers appear to assume that the outward thrust of the shaft is caused by the muscles of the furcula arising on the second valvifers.

While, then, we can explain the protraction and retraction of the sting only as the result of a bulblike action of the abdomen, it is not true that any compression of the abdomen, either in a living bee or a freshly killed specimen, will exert the sting. The movement of protraction in the basal apparatus must be accompanied by a depression of the distal part of the shaft; otherwise the latter will be simply tilted upward with the sheath.

The depression of the shaft during the outward thrust and its elevation with the reverse movement are brought about by a special mechanism of the basal apparatus, which includes the furcula, the furcular muscles, the rami, the ramus muscles, and the articular points between the base of the bulb and the distal lobes of the rami. It is curious that all students of the mechanism of the bee's sting, since Kraepelin (1873), have regarded the furcular muscles as the protractors (*Vorstossmuskeln*) of the shaft. An examination of the sting structure shows at once that the shaft of the organ can have no horizontal movement between the second valvifers (oblong plates), on which the furcular muscles are attached, except what little motion might result from the flattening of the rami. Furthermore, a backward pull on the furcula in the direction of its muscles (fig. 47 B, 19) has an immediate response in the depression of the distal end of the shaft (C). The fulcrum of the vertical movements of the shaft are the points of articulation between the basal processes of the bulb and the distal lobes of the second rami (fig. 42 B, C, 47 B, *s*). When the shaft is turned down (fig. 47 C) the curves of the rami are flattened, and the ramus muscles (20), which are attached on the basal processes of the bulb distal to the fulcrum (*s*), are stretched. The ramus muscles, therefore, are the antagonists of the furcular muscles (19) and serve to elevate the shaft and to restore it to its position of repose between the second valvifers and their distal lobes.

The third set of movements in the sting apparatus, namely, the movements of the lancets on the stylet, has to do with the penetration



of the wound by the shaft after the tip of the latter has once been inserted; and incidentally these movements accomplish also the injection of the poison by motion of the valves of the lancets in the poison chamber of the bulb. The skeletal parts in the basal apparatus concerned with the movement of the lancets are the first and second valvifers and the quadrate plates; the motor elements are the anterior and posterior muscles of the second valvifers.

It will be unnecessary to review the opinions of other writers on the working of the mechanism that moves the stylets, since all investigators except Sollmann (1863) have wrongly attributed the attachment of the dorsal group of fibers of the anterior second valvifer muscles (fig. 47 A, 17a) to the first valvifers, while Sollmann on his part, besides committing various other inaccuracies, believed the ventral group of fibers (17b) to be attached on the first valvifer. Hence, all descriptions of the sting mechanism contain the error of attempting to explain the movements of the lancets as caused by muscles inserted on the first valvifers. Notwithstanding this mistake, Kraepelin (1873) is not far wrong in his account of the working of the sting, inasmuch as he deduces the correct movements of the lancets from his concept of the mechanism.

The only muscle inserted on the first valvifer (triangular plate) in the bee, as already shown, is the slender muscle from the lower margin of the spiracular plate of the eighth segment (fig. 46 D, E, 14); but this muscle is attached on the valvifer so close to the posterior end of the latter, and has such a weak support on the spiracular plate, that it seems probable its chief function is to maintain a proper relation between those two sclerites. The principal muscles that accomplish the movements of the lancets in the bee are undoubtedly the large anterior and posterior muscles of the second valvifers (oblong plates) that have their origins on the quadrate plates of the ninth tergum (fig. 47 A, 17, 18). The homologues of these muscles are readily identified in all pterygote insects; in the Hymenoptera the fibers of the first muscle are separated into two distinct groups (17a, 17b), but they are all inserted on the anterior arm of the second valvifer or on the upper extremity of the ramus of the second valvula. The posterior muscle (18) arises anteriorly and dorsally on the inner face of the quadrate plate, and its fibers converge posteriorly and ventrally to their insertion on the posterior end of the elongate second valvifer. These two sets of muscles are antagonistic to each other because the fulcrum of the second valvifer on the first valvifer (*b*) lies between their attachments on the former plate.

In most other insects the second valvifer is articulated directly to the ninth tergum, and has a simple rocking movement on the latter produced by the alternate contraction of its anterior and posterior muscles, because the tergum forms ordinarily a complete dorsal arch over its segment and is relatively immovable. In the Hymenoptera, however, the second valvifer articulates with the first valvifer, which in turn articulates with the ninth tergum, and this interpolation of the first valvifer between the tergum and the second valvifer considerably changes the mechanism; but in the bees a further modification results from the reduction of the ninth tergum to the pair of lateral quadrate plates which are themselves freely movable because of their membranous connections with the surrounding parts. Observations on the freshly extracted sting of a living bee show that the principal activity in the basal apparatus that accompanies the protraction and retraction of the lancets consists of a back-and-forth vibration of the quadrate plates and a quick elevation and depression of the anterior ends of the first valvifers (triangular plates). The second valvifers (oblong plates) remain relatively stationary, but there is sometimes a quivering of the third valvular lobes.

The working of the mechanism that moves the lancets will be readily understood if a cardboard model is cut out representing the skeletal parts of one-half of the sting apparatus (fig. 48). The first valvifer of the model should be attached by pins to the quadrate plate and to the oblong plate, and the lancet must be twisted so that it will slide against the lower edge of the stylet when the two are held together by a wire loop. We have observed on the living bee that the muscles between the quadrate tergal plate (fig. 47 A, *IXT*) and the oblong plate (*2Vlf*) move the quadrate plate and not the oblong plate. This is just the reverse of the usual interaction of the corresponding plates in other insects. If, therefore, the quadrate plate of the model (fig. 48 A, *IXT*) is moved alternately in the direction of its two antagonistic muscles (*17*, *18*), while the oblong plate (*2Vlf*) is held stationary, the effect is a simple back-and-forth movement of the lancet on the lower edge of the stylet. Hence, when the posterior muscle (*18*) contracts, as shown at A, it moves the quadrate plate rearward, and the latter pulls on the dorsal angle (*a*) of the first valvifer (*1Vlf*), with the result that the valvifer is rotated upward on its ventral angle (*b*) and retracts the lancet (*Lct*). On the other hand, when the anterior muscle (*17*) contracts, as at B, the quadrate plate is pulled forward and rotates the valvifer downward, which movement protracts the lancet. It is possible that the slender muscle (*A*, *14*) from the spiracular plate to the posterior end of the first valvifer may be an accessory retractor of the lancet, as supposed by Kraepelin.

Because of the double articulation of the first valvifer on the quadrate plate and the oblong plate (fig. 48 A), and of the difference in length between the two axes (*ab* and *ac*) of the valvifer, a very small movement of the quadrate plate (B, *d*) produces a relatively

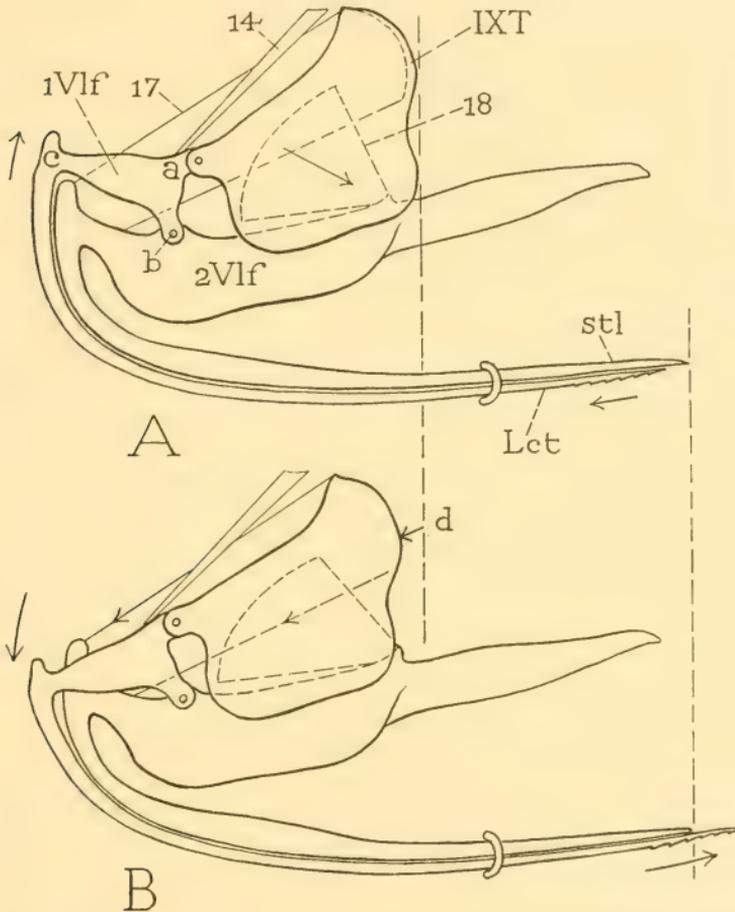


FIG. 48.—Diagrams of a model of the sting of the honey bee to show the mechanism of retraction and protraction of the lancets.

A, the lancet retracted by contraction of ventral muscle (18) of quadrate plate (IXT) attached posteriorly on oblong plate (2Vlf).

B, the lancet protracted by contraction of dorsal muscle (17) of quadrate plate attached anteriorly on oblong plate.

large movement of the lancet. In the living bee the motion of the quadrate plate appears as a quivering or rapid back-and-forth vibration, its actual displacement being scarcely perceptible. When the sting is extracted, however, with the shaft in the wound, the motion of the quadrate plates is greatly increased.

If the oblong plate of the model (fig. 48 A, *zVlf*) is moved simultaneously with the quadrate plate, but in the opposite direction, the effect is to protract and retract the stylet in the same direction as the lancet, but with each stroke the lancet moves faster and farther than the stylet. Observations on the living bee, however, do not show that this movement ordinarily takes place, though it seems entirely possible.

When the tip of the sting of a living bee is examined under the microscope, and is not allowed to touch an object it can penetrate, only one lancet (the left, in the experience of the writer) is seen to move back and forth on the stylet and to be protracted beyond the latter. Hence, it seems probable that as soon as the tip of the shaft is inserted into the skin of the victim by the backward swing of the basal apparatus, the left lancet must be thrust out in advance of the stylet, where it holds its position in the wound by means of its barbs, and that then the right lancet is forced in beyond the left. Successive alternating thrusts of the lancets would then bury the entire sting shaft deeper and deeper in the flesh in the manner commonly observed. The force of the backward pull of the retractor muscles is now expended, not on the retraction of the lancets, but in stretching the protractor muscles, which, when thus restored to a condition of activity, give, each in turn, another thrust to the lancets. The motion of the lancets operates the valves attached to the dorsal margins of the lancets within the cavity of the bulb of the shaft, and the valves drive the poison liquid through the channel of the sting, from which it issues by way of the ventral cleft between the distal ends of the lancets.

#### ABBREVIATIONS USED ON THE FIGURES

|  |  |
|--|--|
| <i>a-a</i> , dorso-pleural line.                           | <i>bv</i> , basivalvula.                             |
| <i>Ac</i> , antecosta.                                     | <i>bw</i> , cut edge of body wall.                   |
| <i>AcGl</i> , accessory gland.                             | <i>Cd</i> , cardo.                                   |
| <i>AcGID</i> , duct of accessory gland.                    | <i>Cdbl</i> , cardioblast.                           |
| <i>AcGIO</i> , opening of accessory gland.                 | <i>Cer</i> , cercus.                                 |
| <i>aiv</i> , anterior intervalvula.                        | <i>cf</i> , caudal filament.                         |
| <i>Am</i> , amnion.  | <i>Coel</i> , coelomic sac.                          |
| <i>An</i> , anus.  | <i>Cx</i> , coxa.                                    |
| <i>Ap</i> , apodeme.                                       | <i>CxC</i> , coxal cavity.                           |
| <i>Apd</i> , appendage                                     | <i>CxP</i> , pleural coxal process.                  |
| <i>b-b</i> , pleuro-ventral line.                          | <i>D</i> , dorsum.                                   |
| <i>bcpx</i> , bursa copulatrix.                            | <i>d<sub>2</sub></i> , dorsal muscles of mesothorax. |
| <i>BGl</i> , "alkaline" gland of bee.                      | <i>d<sub>3</sub></i> , dorsal muscles of metathorax. |
| <i>blb</i> , bulbous basal part of united second valvulae. | <i>dil</i> , lateral internal dorsal muscle.         |
| <i>Bs</i> , basisternum.                                   | <i>dim</i> , median internal dorsal muscle.          |
|  | <i>dls</i> , dilator muscle of spiracle.             |

- Ecd*, ectoderm.  
*EMsd*, somatopleure of mesoderm.  
*Epm*, epimeron.  
*Eppt*, epiproct, eleventh abdominal tergum.  
*Eps*, episternum.  
*ET*, egg tube of ovary.  
  
*Frc*, furcula.  
*Fu*, furca, endosternum.  
  
*GC*, genital chamber (bursa copulatrix).  
*GCl*s, germ cells.  
*Gd*, gonad.  
*gmcl*, muscle of gonapophysis.  
*Gon*, gonapophysis.  
*Gpr*, gonopore, ostium oviductus.  
*Gpr'*, primary median gonopore of female.  
*Grn*, germarium of ovary.  
  
*Ht*, heart.  
  
*I-XI*, abdominal segments.  
*IMsd*, splanchnopleure of mesoderm.  
*IS-XS*, abdominal sterna.  
*IT-XIT*, abdominal terga.  
*IXV*, venter of ninth abdominal segment.  
  
*LB*, limb basis.  
*Lct*, lancet (first valvula).  
*ld*, laterodorsal area.  
*le*, external lateral muscle.  
*li*, internal lateral muscle.  
*Lsp*, lamina spiracularis of eighth tergum.  
  
*Mb*, intersegmental membrane.  
*Mcls*, muscles.  
*Msd*, mesoderm.  
  
*NIR*, neural ridge.  
  
*Od*, oviduct.  
*Odc*, definitive oviductus communis.  
*Odc'*, primary rudiment of median oviduct.  
  
*Odl*, oviductus lateralis.  
*Opr*, oviporus.  
*os*, oclclisor muscle of spiracle.  
*Ovl*, ovariole.  
*Ovp*, shaft of ovipositor.  
  
*P*, pleural, or podial, region of body.  
*Papt*, paraproct.  
*Pcx*, postcoxale.  
*Pdcl*, ovariole pedicel.  
*pv*, posterior intervalvula.  
*Ph*, phragma.  
*pl*, pleurite.  
*Plstn*, pleurosternal plate.  
*PN*, postnotum.  
*pvl*, pons valvularum.  
*Proc*, proctodaeum.  
*PsnSc*, poison sac.  
*pt*, paratergite.  
*Ptgr*, proctiger.  
  
*ra*, ramus of valvula.  
*r1vl*, ramus of first valvula.  
*r1vli*, inner ramus of first valvula.  
*r1vlo*, outer ramus of first valvula.  
*r2vl*, ramus of second valvula.  
*Rect*, rectum.  
  
*S*, definitive sternum.  
*Scx*, subcoxa.  
*smcl*, muscles of stylus.  
*Sp*, spiracle.  
*Spr*, spermathecal pore.  
*Spt*, spermatheca.  
*SptD*, spermathecal duct.  
*St*, stipes.  
*stl*, stylet (slender distal part of united second valvulae).  
*Stn*, primitive sternum.  
*Stng*, sting.  
*Sty*, stylus.  
  
*T*, tergum.  
*td*, dorsal transverse muscle.  
*TF*, terminal filament of ovariole.  
*Tlpd*, telopodite.  
*Tm*, tympanum.  
*tv*, ventral transverse muscle.

|   |   |
|---|---|
| <i>V</i> , venter.  | <i>VI</i> , valvula ( <i>1VI</i> , first valvula; <i>2VI</i> , second valvula; <i>3VI</i> , third valvula). |
| <i>Vag</i> , vagina.  |   |
| <i>VDph</i> , ventral diaphragm.  |   |
| <i>ve</i> , external ventral muscle.  | <i>Vlf</i> , valvifer ( <i>1Vlf</i> , first valvifer; <i>2Vlf</i> , second valvifer).                       |
| <i>vi</i> , internal ventral muscle.  |   |
| <i>VIIIStn</i> , sternum of eighth abdominal segment (not including the first valvifers). | <i>VNC</i> , ventral nerve cord.  |
| <i>VIIIV</i> , venter of eighth abdominal segment.  | <i>Vs</i> , vesicle.  |
| <i>vil</i> , lateral internal ventral muscle.   | <i>Vst</i> , vestibulum.  |
| <i>vin</i> , median internal ventral muscle.  | <i>Vul</i> , vulva, ostium vaginae.   |
|   | <i>W</i> , wing.  |
|   | <i>Y</i> , yolk.  |

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SMITHSONIAN MISCELLANEOUS COLLECTIONS

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NEW ARCTIC FORAMINIFERA COLLECTED BY  
CAPT. R. A. BARTLETT FROM FOX BASIN  
AND OFF THE NORTHEAST COAST  
OF GREENLAND

(WITH TWO PLATES)

BY

JOSEPH A. GUSHMAN



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During the course of his expeditions to the Arctic and sub-Arctic regions in the past seven years, 1925-1932, Capt. Robert A. Bartlett has obtained, in addition to other extensive collections of marine invertebrates, considerable numbers of bottom samples which have been examined for foraminifera. A paper has been completed containing 46 genera and nearly 100 species of foraminifera from the collections from off the northeast coast of Greenland and from Fox Basin, Baffin Land. Ten of these forms that are apparently new are here described and figured so that they may be available while awaiting publication of the larger paper which will carry full station data for these species.

Genus **URNULA** Wiesner, 1931

*Urnula* Wiesner, Deutsche Südpolar Exped., vol. 20, Zool., p. 82, 1931.

*Genotype*.—*Urnula quadrupla* Wiesner.

Test attached, in young stage similar to *Webbinella*, later adding chambers and each becoming polygonal in outline, whole test plano-convex, rounded, base with a thin chitinous layer, dorsal side with a fine arenaceous covering; aperture in adults rounded, one near the middle of each chamber. Recent, Arctic and Antarctic.

This genus has been recently described by Wiesner from material collected in the Antarctic. Another species probably belonging to this genus was also collected in the Antarctic and should be known as *Urnula depressa* (Heron-Allen and Earland). The present new species extends the range of this genus to the Arctic.

**URNULA ARCTICA**, n. sp.

Plate I, figs. 1, 2

Test attached, plano-convex, dorsal side somewhat rounded and convex, ventral side conforming to the surface of attachment; chambers four to eight in number, rather uniformly arranged, those tests having four chambers with the whole test in a circle divided by sutures

nearly at right angles, those with more chambers usually arranged about the central one with the sutures radiating, chambers apparently in communication with one another, distinct, slightly inflated on the dorsal side; sutures distinct, somewhat thickened, depressed on the dorsal side; wall very finely arenaceous, with much yellowish-brown cement, the wall on the attached side very thin and translucent, apparently of chitin and only the bases of the walls between the chambers marked by arenaceous material; apertures indistinct. Diameter, 0.35-0.40 mm; thickness, 0.10 mm.

*Holotype*.—U.S.N.M. No. 26153, from 7 fathoms, Shannon Island, off NE. Greenland.

This peculiar small species has occurred at several stations in the Greenland material and holds its characters very well. It occurs as follows: 10-35 fathoms, Shannon Island, NE. Greenland; 10-35 fathoms, off Clavering Island, NE. Greenland. The specimens apparently may easily become detached, as most of them were found in that condition. This form is distinguished from *Sorosphaera* in its attached form and definitely polygonal chambers.

It is interesting to note that Heron-Allen and Earland have described a very similar species from the Antarctic as *Sorosphaera depressa* Heron-Allen and Earland, which in its characters should belong to this new genus. It may, therefore, be known as *Urnula depressa* (Heron-Allen and Earland). Their species is more irregular in form and has more chambers than the Arctic one, so far as we have seen. It also has accidental openings similar to those shown in our figures.

#### QUINQUELOCULINA FUSCA H. B. Brady var. GROENLANDICA, n. var.

Plate I, fig. 4

Variety differing from the typical in the much smoother test with a much larger proportion of cement of a light gray color, and the test usually more compressed.

*Holotype of variety*.—U.S.N.M. No. 26151, from between Shannon Island and Hochstetter Foreland, NE. Greenland.

When seen with the typical form of the species, this variety is very distinctive.

#### QUINQUELOCULINA ARCTICA, n. sp.

Plate I, figs. 3a-c

Test short and stout, very slightly longer than broad; chambers angled, periphery truncate, sides with definite angles; sutures distinct,

slightly depressed; wall smooth; aperture not projecting above the general outline of the test, large, semicircular, with a very small bifid tooth. Length, 0.50-0.65 mm; breadth, 0.40-0.50 mm; thickness, 0.20-0.30 mm.

*Holotype*.—U.S.N.M. No. 26152, from 10-35 fathoms, off Clavering Island, NE. Greenland.

This species has been found common in the Bartlett collections. It shows some variation in the chambers, and at certain stations the outer angles of the chamber become considerably rounded. It may be that this is the same species as that figured by Parker and Jones in 1865 (pl. 15, figs. 36a-c), and recorded by them as "*Quinqueloculina ferussacii* d'Orbigny." It is, however, very different from d'Orbigny's species. Their specimens were from off Hunde Islands, Davis Strait, 30-70 fathoms. This species occurs at the following localities in the Bartlett material: 7 fathoms, Shannon Island, NE. Greenland; 7 fathoms, fiord between Clavering Island and Homes Foreland, near glacier, NE. Greenland; Labrador; bight of Shannon Island, NE. Greenland; 67 fathoms, off camp, Cape David Gray, Shannon Island, NE. Greenland; 10-35 fathoms, Shannon Island, NE. Greenland; between Shannon Island and Hochstetter Foreland, NE. Greenland; and 50-57 fathoms, off Clavering Island, NE. Greenland.

#### Genus GORDIOSPIRA Heron-Allen and Earland, 1932

*Gordiospira* Heron-Allen and Earland, Journ. Roy. Micr. Soc., vol. 52, p. 254, 1932.

*Genotype*.—*Gordiospira fragilis* Heron-Allen and Earland.

Test free, early coils in varying planes, later planispiral and nearly involute; wall calcareous, imperforate; aperture somewhat triangular, terminal. Recent, Arctic and Antarctic.

This genus has recently been described from the Antarctic *Discovery* material. It is interesting, therefore, to record another species of the genus from the Arctic.

#### GORDIOSPIRA ARCTICA, n. sp.

Plate 1, figs. 5-7

Test planispiral, partially involute, the coils few in number, rounded; suture decidedly depressed; wall calcareous, smooth except for numerous heavy varices of growth which give an irregular appearance to the surface; aperture formed by the open end of the tube.

*Holotype*.—U.S.N.M. No. 26147, from bight of Shannon Island, NE. Greenland.

The thinness of the wall gives a very different appearance from that of the chalky white opaque wall of typical *Cornuspira*. It is found in the Greenland collections at the following localities: NE. Greenland; off camp, Cape David Gray, Shannon Island, NE. Greenland; 67 fathoms, off camp, Cape David Gray, Shannon Island, NE. Greenland; and 10-35 fathoms, off Clavering Island, NE. Greenland.

**ELPHIDIUM GROENLANDICUM, n. sp.**

Plate 1, figs. 10a, b

Test large, close coiled, completely involute, the periphery subacute; chambers numerous, 15 or more in the final coil in the adult, of uniform shape throughout and increasing only slightly in size, the last chambers occasionally very slightly inflated; sutures distinct, very slightly if at all depressed, with a sigmoid curve and numerous retral processes, often 15 or more along a single suture; wall smooth, very finely perforate, polished, the umbilical region often with a clear area; aperture consisting of numerous pores along the base of the apertural face of the last-formed chamber. Diameter, up to 1.00 mm.

*Holotype*.—U.S.N.M. No. 26141, from Bass Rock, NE. Greenland.

This is a large fine species, occurring only in the Bartlett collection from Greenland and not appearing in the collections from Fox Basin. It has occurred at numerous stations and is often common as follows: off Clavering Island, near glacier, NE. Greenland; 7 fathoms, Shannon Island, off NE. Greenland; 7 fathoms, fiord between Clavering Island and Homes Foreland, NE. Greenland; off camp, Cape David Gray, Shannon Island, NE. Greenland; 7 fathoms, near glacier, between Clavering Island and Homes Foreland, NE. Greenland; near Shannon Island, NE. Greenland; 67 fathoms, off camp, Cape David Gray, Shannon Island, NE. Greenland; Koldenian Sound, NE. Greenland; 7 fathoms, off Cape Stosch, Gotthaab Island, Hudson Land, NE. Greenland; and Wollaston Foreland, 5 miles off Cape Borlase Warren, NE. Greenland. It holds its characters very well throughout the different stations. This may possibly be the species referred by authors to "*Polystomella subnodosa*" from Arctic material.

**ELPHIDIUM BARTLETTI, n. sp.**

Plate 1, figs. 9a, b

Test almost completely umbilicate but leaving a slight uncoiled portion at the umbilical area, periphery broadly rounded; chambers dis-

tinct, slightly inflated, especially in the latter half of the last-formed coil, 10 to 12 or more in number; sutures distinct, usually depressed, occasionally with a slightly beaded appearance in the early portion, retral processes numerous and very short, often hardly visible; wall smooth, very finely perforate, polished; aperture formed by numerous small pores along the base of the apertural face of the chamber. Length, 0.90 mm; thickness, 0.35 mm.

*Holotype*.—U.S.N.M. No. 26142, from Labrador.

This species is well developed at several stations as follows: off camp, Cape David Gray, Shannon Island, NE. Greenland; 7 fathoms, near glacier, between Clavering Island and Homes Foreland, NE. Greenland; near Shannon Island, NE. Greenland; 10-35 fathoms, Shannon Island, NE. Greenland; and Fox Basin, latitude  $66^{\circ}43' N.$  It somewhat resembles the young stages of *E. arcticum*, but seems to be distinct from that species. It is named in honor of Capt. Robert A. Bartlett, whose collections have added much to the knowledge of Arctic foraminifera.

#### ELPHIDIUM FRIGIDUM, n. sp.

Plate I, figs. 8a, b

Test usually completely involute, periphery rounded, sides flattened; chambers distinct, slightly inflated, the last ones distinctly so, final chambers often enlarged and projecting beyond the general contour of the test; sutures distinct, depressed, with very numerous short retral processes; wall thin, very distinctly perforate, the last-formed chambers often having distinct elongate markings; aperture consisting of numerous fine pores at the base of the apertural face of the last-formed chamber. Length, 0.90 mm; thickness, 0.25 mm.

*Holotype*.—U.S.N.M. No. 26143, from 25 fathoms, center of Fox Basin.

Except for one station off Greenland, 10-35 fathoms, near Shannon Island, the species has been found only in the stations from Fox Basin as follows: 34-37 fathoms, SE. corner of Fox Basin, latitude  $66^{\circ}46' N.$ , longitude  $69^{\circ}15' W.$ ; and Fox Basin, latitude  $66^{\circ}43' N.$ , longitude  $80^{\circ}7' W.$ , where it is often common. It shows considerable variation in the shape of the last-formed chamber, which is much expanded in the adult and often longer than the others so that it projects beyond the general outline of the test. The apertural face of the chamber often has a peculiar overlapping border at the base extending out somewhat beyond the base of the chamber both along the median line and also toward the umbilical ends. The peculiar arrangement of

the pores in the last-formed chambers gives a striate appearance to the basal portion of those chambers.

**SPIRILLINA ARCTICA, n. sp.**

Plate 2, figs. 1, 2

Test small, forming a low hollow cone, the proloculum very distinct, in the megalospheric form often projecting above the other coils prominently, second undivided, close coiled, overlapping very slightly on the dorsal side leaving a depressed hollow cone as it revolves; suture distinct, very slightly depressed; wall very finely perforate, nearly transparent; aperture formed by the open end of the tube. Diameter, up to 0.50 mm.

*Holotype*.—U.S.N.M. No. 26149, from the Fox Basin, latitude 67° 41' N., longitude 79° 9' W., in 38 fathoms.

This peculiar, small, conical species is fairly abundant in the Fox Basin material, but was not found in any of the collections from off the coast of Greenland. It occurs at the following localities: 25-31 fathoms, Fox Basin; 34-37 fathoms, SE. corner of Fox Basin, latitude 66° 46' N., longitude 69° 15' W.; and Fox Basin, latitude 66° 43' N., longitude 80° 7' W.

Parker and Jones figured a small *Spirillina* from 60-70 fathoms off the Hunde Islands, Davis Strait, but only one view of this is given and it is important to see whether it belongs to this new species. Their short note on it does not reveal its characters. Brady also records the species from the sounding in 72 fathoms at latitude 83° 19' N., from the British North-Polar Expedition. These records of Parker and Jones and of Brady being so near the Fox Basin area, it would seem that they refer to the same species we have here described.

**DISCORBIS BARTLETTI, n. sp.**

Plate 2, figs. 3-6

Test plano-convex, the dorsal side very strongly convex, the ventral side flat, periphery subacute, slightly lobulate; chambers distinct, of rather uniform shape and increasing regularly in size as added, increasing in number until in the adult whorl there are about nine or ten chambers; sutures on the dorsal side distinct, strongly limbate, gently curved, on the ventral side obscured by the peculiar ornamentation of the surface; wall on the dorsal side smooth and polished, very distinctly but finely perforate, ventral side with a very complex secondary growth of shell material forming a vesicular mass over the

entire ventral surface, the outer edge of which extends often slightly beyond the periphery, giving a serrate edge to the test even when viewed from the dorsal side; aperture a low opening between the umbilicus and the periphery at the ventral edge of the last-formed chamber. Diameter, up to nearly 2.00 mm.

*Holotype*.—U.S.N.M. No. 26145, from 34-37 fathoms, SE. corner of Fox Basin, latitude  $66^{\circ}46'$  N., longitude  $69^{\circ}15'$  W.

This is a very finely ornamented species, and has occurred in great abundance in the Fox Basin material, but did not occur in any of the collections from off the NE. coast of Greenland. The ventral side becomes very ornate even in the youngest specimens. Nearly all of our specimens are megalospheric and the proloculum becomes of very large size in comparison to the size of the test. The species is named after Capt. Robert A. Bartlett, collector of this material. It occurs at the following stations in the Fox Basin: 25-31 fathoms, Fox Basin; Fox Basin, latitude  $66^{\circ}43'$  N., longitude  $80^{\circ}7'$  W.; and 25 fathoms, center of Fox Basin.

#### CASSIDULINA NORCROSSI, n. sp.

Plate 2, figs. 7a-c

Test biconvex, periphery subacute or even slightly keeled; chambers distinct, generally triangular in side view, those of each set reaching nearly to the umbilicus on both sides; wall smooth, very finely perforate, clear and almost transparent; aperture elongate, in general in the line of coiling. Diameter, 0.40-0.45 mm; thickness, 0.15-0.18 mm.

*Holotype*.—U.S.N.M. No. 26139, from 7 fathoms, 5 miles off Cape Borlase Warren, NE. Greenland.

This very distinctive species is named for Arthur D. Norcross, of New York City, whose close association and friendly cooperation with Captain Bartlett have enabled him to accomplish so much in the way of Arctic exploration in recent years. It occurs only off the NE. coast of Greenland at but a few stations as follows: 50-57 fathoms, off Clavering Island, NE. Greenland; 7 fathoms, off Cape Stosch, Gott-haab Island, Hudson Land, NE. Greenland; and between Shannon Island and Hochstetter Foreland, NE. Greenland. The chambers at first do not appear to have the usual alternating arrangement, owing to the fact that each one comes nearly to the umbilicus on each side, and the difference in size between the two pairs on the same side is not nearly so well marked as is usual in most species.

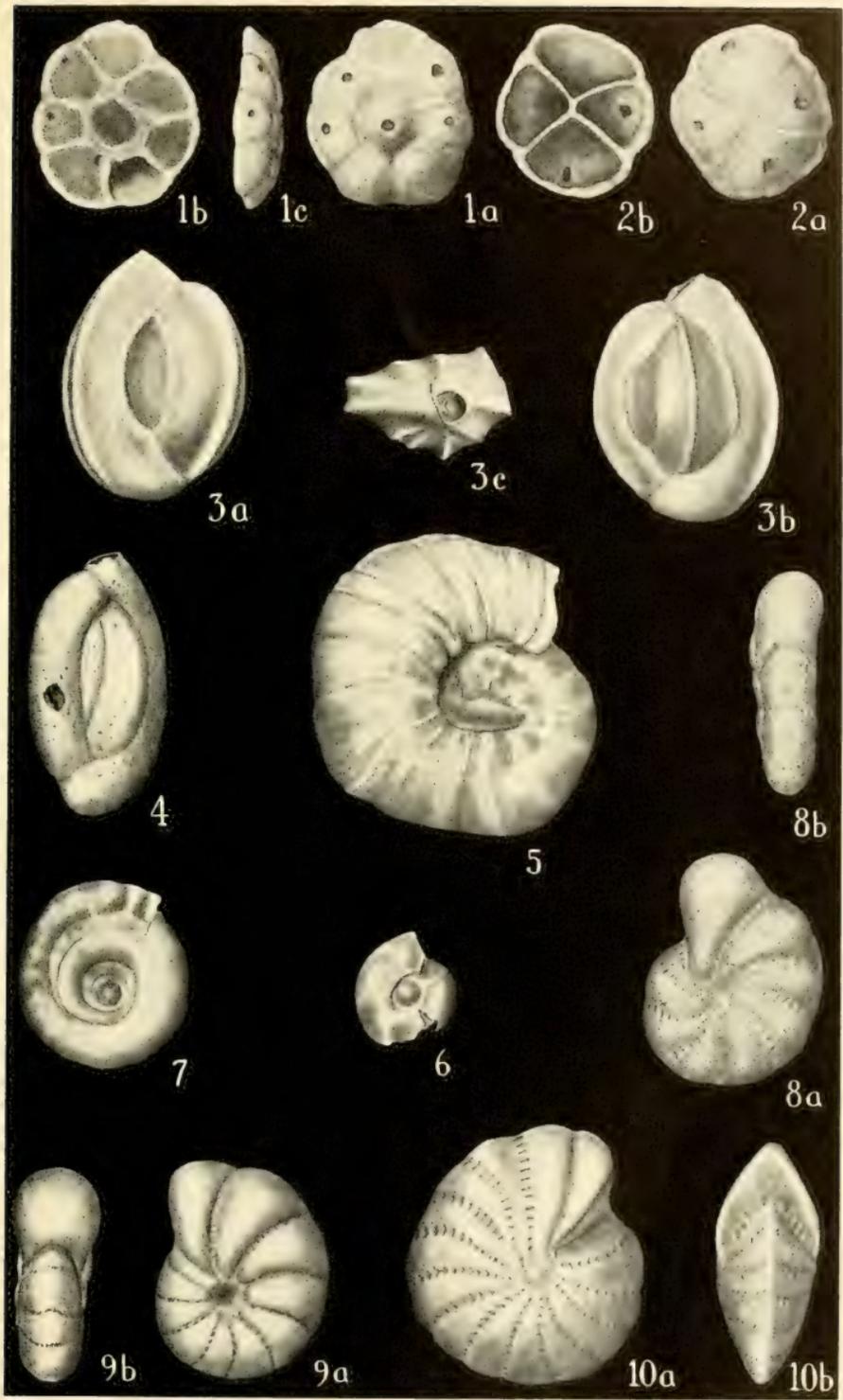
## EXPLANATION OF PLATES

## PLATE I

- FIGS. 1, 2. *Urnula arctica* Cushman, n. sp.  $\times 60$ . Fig. 1, holotype. *a*, dorsal view; *b*, ventral view; *c*, peripheral view. Fig. 2, paratype. *a*, dorsal view; *b*, ventral view.
- 3*a-c*. *Quinqueloculina arctica* Cushman, n. sp.  $\times 50$ . Holotype. *a*, *b*, opposite sides; *c*, apertural view.
4. *Quinqueloculina fusca* H. B. Brady var. *groenlandica* Cushman, n. var.  $\times 60$ .
- 5-7. *Gordiospira arctica* Cushman, n. sp.  $\times 80$ . Fig. 5, holotype. Figs. 6, 7, young stages.
- 8*a, b*. *Elphidium frigidum* Cushman, n. sp.  $\times 35$ . *a*, side view; *b*, peripheral view.
- 9*a, b*. *Elphidium bartletti* Cushman, n. sp.  $\times 35$ . *a*, side view; *b*, peripheral view.
- 10*a, b*. *Elphidium groenlandicum* Cushman, n. sp.  $\times 35$ . *a*, side view; *b*, peripheral view.

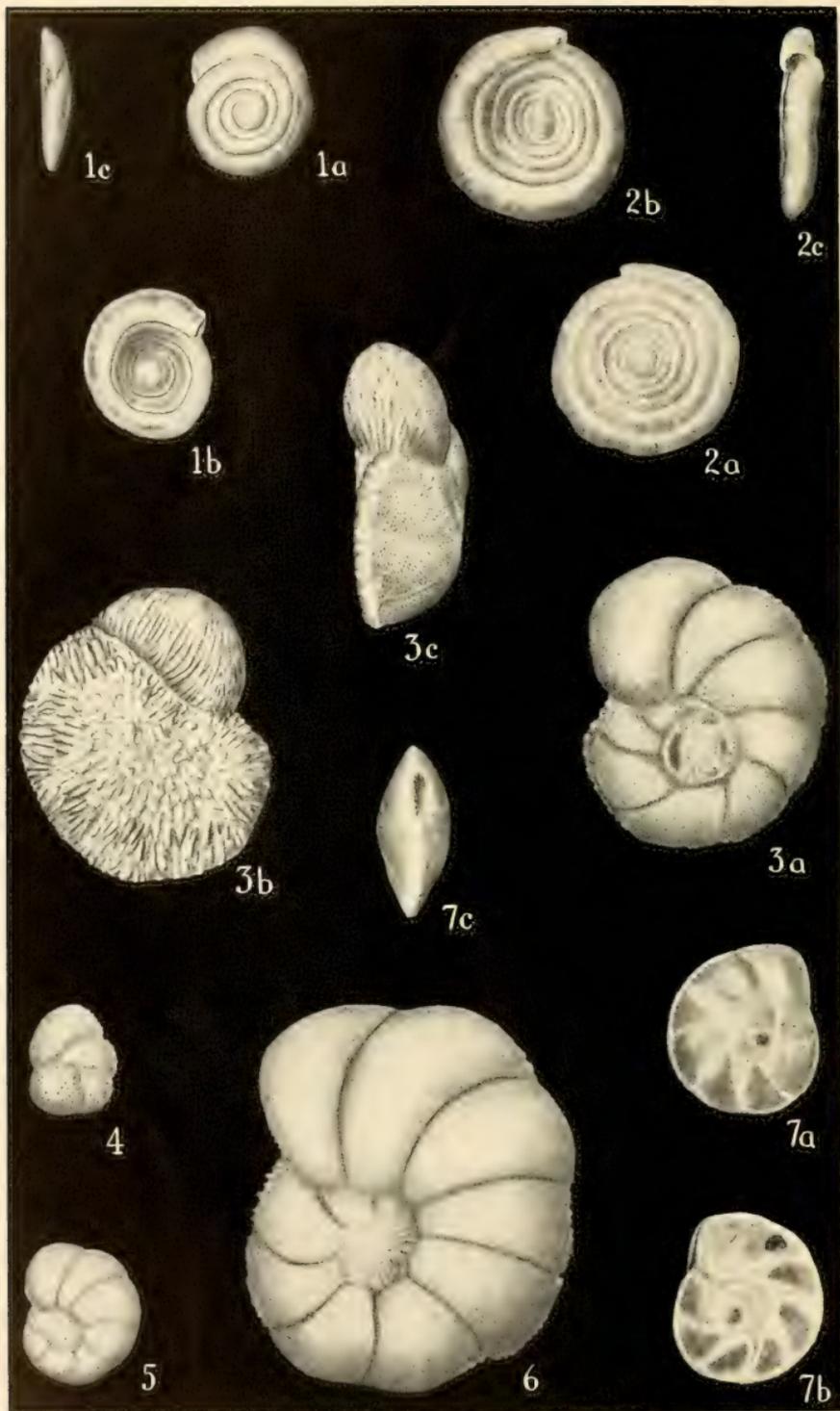
## PLATE 2

- FIGS. 1, 2. *Spirillina arctica* Cushman, n. sp.  $\times 100$ . Fig. 1, holotype. Fig. 2, paratype. *a, a, b, b*, opposite sides; *c, c*, peripheral views.
- 3-6. *Discorbis bartletti* Cushman, n. sp.  $\times 35$ . Fig. 3, holotype. *a*, dorsal view; *b*, ventral view; *c*, peripheral view. Fig. 4, young four-chambered megalospheric form. Fig. 5, later stage. Fig. 6, adult. Figs. 4-6, dorsal views.
- 7*a-c*. *Cassidulina norcrossi* Cushman, n. sp.  $\times 60$ . Holotype. *a, b*, opposite sides; *c*, peripheral view.



ARCTIC FORAMINIFERA

(For explanation, see page 8.)



ARCTIC FORAMINIFERA  
(For explanation, see page 8.)





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STUDIES OF AMERICAN SPECIES OF  
FORAMINIFERA OF THE GENUS  
LEPIDOCYCLINA

(WITH 32 PLATES)

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# STUDIES OF AMERICAN SPECIES OF FORAMINIFERA OF THE GENUS *LEPIDOCYCLINA*

By THOMAS WAYLAND VAUGHAN

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(WITH 32 PLATES)

## INTRODUCTION

The principal purpose of this paper is to complete the description of the species of the foraminiferal genus *Lepidocyclus* that have come into my hands during a number of years and thereby to aid in the solution of problems of geologic correlation in the Mexican Gulf and Caribbean region. Incidentally, it is intended to assist in the identification of some species by publishing additional figures and descriptive notes and also to consider the problems of variation in a few of the species. The accounts here given of the material available to me from Mexico, Cuba, and the Island of Antigua are virtually complete, except that descriptions and figures of a few well-known or recently described species are not included. I still have in hand from the Oligocene of Florida and Mississippi three or four species that probably should be described, and some of the Panama species need more study and comparison with material from other localities, especially Trinidad and Venezuela.

The Mexican material came to me from geologists connected with the Aguila Oil Company of Mexico. The largest collection was made by me personally while working for that company in November and December 1920. Important supplemental collections were made by Messrs. D. R. Semmes, W. S. Adkins, and Ruthven Pike.

The collections from Cuba were obtained by Dr. A. C. Spencer, while engaged in a geologic reconnaissance of Cuba in 1901; by Dr. O. E. Meinzer, while studying for the United States Navy the ground-water problems in the vicinity of Guantánamo in 1915; and by Dr. N. H. Darton, while making geologic investigations in the vicinity of Guantánamo in 1916.

The Antiguan material was obtained first by myself during a reconnaissance of the Island of Antigua in 1914, financed by a grant from the Carnegie Institution of Washington, and after then through the efforts of Mr. W. R. Forrest, an amateur geologist resident in St. John's. Mr. Forrest has collected foraminifera in Antigua for

years and has sent me an extraordinary lot of material. He has added to the number of species that I obtained there in 1914 five new species and a new variety, and the records of the occurrence there of three other species are based on collections made by him. Others who have sent me material from Antigua are Mr. F. W. Penny, the late Prof. A. O. Thomas, and Dr. C. A. Matley.

To all those who have helped in assembling the large collections on which this paper is based, I extend my hearty thanks.

In the final stages of the preparation of the manuscript and plates for this report, I have had the assistance of Dr. W. Storrs Cole of the department of geology of Ohio State University. Dr. Cole is the author of a number of papers on the foraminifera of Mexico and of the Gulf Coastal Plain in Florida and Texas. His scientific knowledge and technical skill have been invaluable, and I am most grateful to him. He has helped with the descriptions of a number of the new species and varieties. The following six new species and two new varieties are published jointly by us:

*Lepidocyclus* *parvula* var. *crassicosta* Vaughan and Cole  
*antiguensis* Vaughan and Cole  
*hodgensis* Vaughan and Cole  
*wetherellensis* Vaughan and Cole  
*tempanii* Vaughan and Cole  
*semmesi* Vaughan and Cole  
var. *granosa* Vaughan and Cole  
*tantoyucensis* Vaughan and Cole

The types of all new species and new varieties are deposited in the United States National Museum.

#### NOTES ON EARLIER LITERATURE

Three attempts have been made to give summary accounts of the American species of *Lepidocyclus*. The first was by Cushman;<sup>1</sup> the second was by H. Douvillé;<sup>2</sup> the third was by myself.<sup>3</sup> Since the publication of these papers many additional articles have been published, and there begins to be need for another monographic summary.

There are in the present paper no descriptions or figures of a few species, the names of which occur in subsequent lists in this paper.

<sup>1</sup> Cushman, J. A., American species of *Orthophragmina* and *Lepidocyclus*. U.S. Geol. Surv. Prof. Pap. 125, pp. 39-105, pls. 7-35, text fig. 3, 1920.

<sup>2</sup> Douvillé, H., Revision des Lépidocyclines. Soc. Géol. France, Mém., n.s., vol. 1, no. 2, pt. 1, pp. 1-49, pls. 1, 2, text figs. 1-48, 1924; pt. 2, pp. 50-115, pls. 3-7, text figs. 49-83, 1925.

<sup>3</sup> Vaughan, T. W., American and European Tertiary larger foraminifera. Bull. Geol. Soc. Amer., vol. 35, pp. 785-822, pls. 30-36, 6 text figs., 1924.

These names are given below. Those included in the three summaries above mentioned are followed by appropriate date references. For those not included in one of the three summaries, there are footnote references. The key locality of each species is also given. The species are as follows:

- Lepidocyclina (Polylepidina) chiapasensis* Vaughan (1924), Isthmus of Tehuantepec  
*adkinsi* Vaughan (1924), Isthmus of Tehuantepec  
*proteiformis* Vaughan (1924), Mecapala Hills, Tantoyuca, Vera Cruz
- (*Pliolepidina*) *duplicata* Cushman (1920) and Vaughan (1924), Rio Vinazco, Chicontepec, Vera Cruz
- (*Lepidocyclina*) *trinitatis* H. Douvillé (1924), Isthmus of Tehuantepec and Rio Vinazco,<sup>1</sup> Chicontepec, Vera Cruz  
*macdonaldi* Cushman (1920), Rio Pantepec, Buena Vista Hacienda, Puebla  
*asterodisca* Nuttall,<sup>2</sup> Alazan shale
- (*Nephrolepidina*) *undosa* Cushman (1920), Meson formation, Vera Cruz  
 var. *tumida* Vaughan,<sup>3</sup> Meson formation, Vera Cruz
- gigas* var. *mexicana* Cushman (1920), Meson formation, Vera Cruz

I have published additional details on *Polylepidina* in the article cited below,<sup>4</sup> and I have discussed the distribution of *L. trinitatis* and *L. macdonaldi* in another article.<sup>5</sup>

H. Douvillé has published a few notes on the Tertiary orbitoids of Mexico, especially on those from the Meson formation,<sup>6</sup> and com-

<sup>1</sup>The specimens from Rio Vinazco identified as *L. trinitatis* are similar to specimens from Venezuela and Trinidad described by Mrs. Helen K. Hodson as *L. hubbardi* (Bull. Amer. Pal., vol. 12, p. 21, pl. 5, figs. 1, 7, 12, 1926). I am inclined to consider this form a variant of *L. trinitatis*, but others may prefer a separate name for it.

<sup>2</sup>Nuttall, W. L. F., Lower Oligocene foraminifera from Mexico. Journ. Pal., vol. 6, p. 34, pl. 7, figs. 5, 8; pl. 9, fig. 10, 1932.

<sup>3</sup>Vaughan, T. W., Species of *Lepidocyclina* and *Carpenteria* from the Cayman Islands. Quart. Journ. Geol. Soc. London, vol. 82, p. 395, pl. 24, figs. 3-5, 1926.

<sup>4</sup>Vaughan, T. W., Studies of orbitoidal foraminifera: the subgenus *Polylepidina* of *Lepidocyclina* and *Orbitocyclina*, a new genus. Proc. Nat. Acad. Sci., vol. 15, pp. 288-295, 1 pl., 1929.

<sup>5</sup>Vaughan, T. W., Species of larger arenaceous and orbitoidal foraminifera from the Tertiary deposits of Jamaica. Journ. Pal., vol. 1, pp. 277-298, pls. 43-50, 1928.

<sup>6</sup>Douvillé, H., Les Orbitoides de la région pétrolifère du Mexique. Soc. Géol. France, C. R. séance, Feb. 21, 1927, pp. 34-35, 1927.

pare the Mexican with European species. W. Staub repeats identification by H. Douvillé in his article on the origin of the Gulf of Mexico.<sup>1</sup> These articles do not affect the present paper, but I wish to say that I sympathize with Douvillé's comparison of American with European species. I feel, however, that the time is not quite ripe for extensive critical comparisons.

## GEOLOGIC DISTRIBUTION OF SPECIES OF LEPIDOCYCLINA IN MEXICO, CUBA, AND ANTIGUA

### MEXICO

#### Eocene

- Lepidocyclina* (*Polylepidina*) *chiapasensis* Vaughan  
*adkinsi* Vaughan  
*proteiformis* Vaughan  
(*Pliolepidina*) *duplicata* Cushman  
(*Lepidocyclina*) *trinitatis* H. Douvillé  
*macdonaldi* Cushman  
(*Nephrolepidina*) *semmesi* Vaughan and Cole  
var. *granosa* Vaughan and  
Cole  
*tantoyucensis* Vaughan and Cole

#### Oligocene

##### Alazan shale

- Lepidocyclina* (*Lepidocyclina*) *supera* (Conrad)  
*asterodisca* Nuttall  
(*Eulepidina*) *favosa* Cushman

##### Meson formation

- Lepidocyclina* (*Lepidocyclina*) *canellei* Lemoine and R. Douvillé  
*waylandvaughani* Cole  
*parvula* Cushman  
var. *crassicosta* Vaughan and  
Cole  
(*Nephrolepidina*) *turnoueri* Lemoine and R. Douvillé  
sp. indet. (previously identified as  
*L. marginata* (Micht))  
*undosa* Cushman  
var. *tumida* Vaughan  
(*Eulepidina*) *favosa* Cushman  
*Lepidocyclina* *gigas* var. *mexicana* Cushman

### CUBA

#### Eocene

- Lepidocyclina* (*Lepidocyclina*) *novitasensis* Vaughan  
*subraulini* Cushman  
*meinzeri* Vaughan  
(*Nephrolepidina*?) *perundosa* Cushman

<sup>1</sup> Staub, W., Zur Entstehungsgeschichte des Golfes von Mexico. *Eclogae Geol. Helvet.*, vol. 24, pp. 61-81, pl. 3, 6 maps, 1931.

Oligocene<sup>1</sup>

- Lepidocyclus* (*Lepidocyclus*) *yurnagunensis* Cushman  
 var. *morganopsis*  
 Vaughan
- (*Nephrolepidina*) *undosa* Cushman  
 sp. cf. *L. verbeeki* Newton and  
 Holland  
*piedrasensis* Vaughan  
*crassimargo* Vaughan  
*dartoni* Vaughan
- (*Eulepidina*) sp. cf. *L. dilatata* (Micht)  
*favosa* Cushman
- Lepidocyclus* *gigas* Cushman  
 sp. indet. *a*  
*b*  
*c*
- Lepidocyclus* (?) *d*

## ANTIGUA

## Antigua formation

- Lepidocyclus* (*Lepidocyclus*) *forresti* Vaughan  
*waylandvaughani* Cole  
*pancanalis* Vaughan and Cole  
*parvula* Cushman  
 var. *crassicosta* Vaughan and  
 Cole  
*wetherellensis* Vaughan and Cole
- (*Nephrolepidina*) *undosa* Cushman  
*tempanii* Vaughan and Cole  
*vaughani* Cushman
- (*Eulepidina*) *favosa* Cushman
- Lepidocyclus* *gigas* Cushman  
*antiguensis* Vaughan and Cole  
*hodgensis* Vaughan and Cole

<sup>1</sup> Under the name *Orbitoides kempfi* (Trans. Amer. Inst. Min. Eng., vol. 51, p. 13, figs. 5, 6, 1916) Dr. Marjorie O'Connell figured specimens from sections cut from a limestone quarry at Arroyo Seboruco, 12 miles from Felton, Cuba. Several sections of Dr. O'Connell's original material have been cut and examined. Figure 5 of Dr. O'Connell's paper represents *Lepidocyclus favosa* Cushman, and figure 6 shows a typical vertical section of *L. yurnagunensis* Cushman. Besides the species figured in Dr. O'Connell's paper, there is also *L. yurnagunensis* var. *morganopsis* Vaughan, n. var. It is apparent that at least two or more species and one variety exist in the material from this locality. As the description of *O. kempfi* is so generalized that no one species can be definitely recognized, and as two different species were figured without the designation of a type, it seems impractical to use the specific name *kempfi*. The horizon of the material is Oligocene.

The zonation of the faunas in the foregoing lists is imperfect. The old problem of where the boundary between the Oligocene and the Miocene should be placed in the American Tertiary sequence still remains unsolved, and zonal studies of the faunas have not yet been made with sufficient refinement in the Tertiary formations of Mexico, Central America, and the West Indies. Whether zones can be recognized in the Mexican Meson and San Rafael is not established, but it is probable that they can be. There may be several horizons in the Cuban Oligocene, and zones may later be recognized in the Antigua formation of Antigua. The zoning of the formations in the Panama Canal Zone is not yet satisfactory. To undertake a detailed discussion of these stratigraphic perplexities, although they are of great importance, is not quite germane to the present paper, but attention should be directed to the facts above stated.

#### VARIATION IN SPECIES OF *LEPIDOCYCLINA*

Variation in several species of *Lepidocyclina* is discussed in some detail on subsequent pages. They are *L. waylandvaughani*, *L. parvula*, *L. yurnagunensis*, and *L. favosa*. The amount of variation in many species of orbitoids is bewildering. Because of such variation and the difficulty of defining certain species, I have for years delayed publication on some of them. It would be expecting too much to hope that all interpretations made in this paper will remain unchallenged or unchanged. A more reasonable hope is that this study may help in a very difficult kind of research.

Normally, in orbitoids there are two kinds of differences that are not due to variation, as follows:

First, the difference due to the alternation of microspheric and megalospheric generations. For each species, before its definition can be completed, the two forms need to be found. For some species there is uncertainty regarding the proper association of the two forms. An example is the *Lepidocyclina gigas*—*L. undosa* couple. The former is probably the microspheric and the latter the megalospheric form of the same species, but as the suggestion of such a relation is still only tentative, I am not calling one form B and the other form A of one species.

Second, the difference due to relative age. Orbitoids grow by the extension of the equatorial layer and by the addition of lateral chambers one above another. Not all features are fully developed in young specimens. There may be marked differences in the ratio,  $\frac{\text{diameter}}{\text{thickness}}$ , in young and old specimens, and pillars, although well developed in old, may be absent in young specimens. Differences of the

kind above indicated must be borne in mind; otherwise grave errors may be committed.

The tests of orbitoids are composed of many elements, every one of which is subject to variation. Unfortunately, it is not always possible to study the range of variation of a species, but sometimes new species are, in my opinion, justifiably based on a single specimen or on only a few specimens. The evaluation of the characters presented by meager material is dependent on the judgment, which is a function of the experience, of the investigator. For many species, however, study of variation is possible.

Some variations seem to be along definite lines and to be parallel in different species. In *L. waylandvaughani*, *L. parvula*, *L. pancanalis*, and *L. yurnagunensis*, the papillae may be scattered but somewhat larger over the center of the test, or they may tend to fuse or increase in size with the production of knobs of variable arrangement, ultimately grading into specimens with large costae on the umbonal part of the test. For the strongly costate variety of *L. parvula* the varietal name *crassicosta* is proposed, and a similar variety of *L. yurnagunensis* is named var. *morganopsis*. Varietal names might also have been proposed for the extreme variants of *L. waylandvaughani* (see pl. 5, fig. 5) and of *L. pancanalis*. For some of the species the material is sufficient for a statistical analysis of the variation. Perhaps a guess may be ventured that strains may be recognized.

The variations presented by some species of *Lepidocyclina* suggest that the phenomena may be fundamentally similar to the variations obtained by Jennings in his experimental study of *Diffugia corona*.<sup>1</sup> This work of Jennings should be studied by everyone who is engaged in taxonomic work on foraminifera. Unfortunately, the difficulties of artificially culturing the sexual, microspheric, generation of foraminifera have not yet been overcome, but of many species the asexual, megalospheric, generation can be raised in numbers. E. H. Myers, working at the Scripps Institution, has produced seven successive generations of asexual reproduction in *Discorbis globularis*.

From the accounts given in this paper of variation in single lots of specimens of species of *Lepidocyclina* and from work such as that of Jennings, it is obvious that to attach a different specific name to every variant in a lot of specimens of *Lepidocyclina* is an absurdity. In a paper on the Tertiary larger foraminifera of Ecuador, recently completed, I have pointed out that very few, if any, of the species of

<sup>1</sup> Jennings, H. S., Heredity, variation, and the results of selection in uniparental reproduction of *Diffugia corona*. *Genetics*, vol. 1, pp. 407-534, 19 figs., 1916.

*Lepidocyclina* named by Willard Berry in his papers on Peruvian species of *Lepidocyclina* are valid.

A brief note will be given on variation in the embryonic chambers of megalospheric forms. The type of embryonic chambers is not absolutely fixed. In some species, such as *L. yurnagunensis*, the chambers may be those of *Lepidocyclina* s.s. or they may verge toward *Nephrolepidina*. In *L. undosa*, the chambers may be nephrolepidine or eulepidine. My surmise is that similar variation may occur in *L. favosa*. Notwithstanding variation, it is my opinion that the embryonic chambers of the megalospheric generation in *Lepidocyclina* furnish convenient and useful features for subdividing the genus into subgenera.

#### DESCRIPTION OF SPECIES

**LEPIDOCYCLINA (LEPIDOCYCLINA) NOVITASENSIS** Vaughan, n. sp.

Plate I, figs. 1-4

1919. *Orthophragmina pustulata* Cushman, Carnegie Inst. Washington Publ. 291, pl. 9, fig. 6 (not pl. 9, fig. 7).

1920. *Orthophragmina sculpturata* Cushman, U.S. Geol. Surv. Prof. Pap. 125, pl. 8, fig. 3 (not pl. 9, figs. 4-7).

The same specimen is referred to in both of the citations given above. The description of the external features of "*Orthophragmina*" *pustulata* is based on this or a similar specimen. It reads as follows:

Test circular, lenticular, thickest in the middle, thence gradually thinning toward the periphery, which is without a carina or thinner portion; thickness about one-fifth the diameter; surface finely pustulose, papillae larger and more numerous near the central region, thence gradually decreasing in size and number toward the periphery.

I picked out of the matrix a number of specimens similar in every respect to the one represented by Cushman's figures cited above and had a horizontal and a vertical section cut. These specimens belong to the genus *Lepidocyclina* and not to *Discocyclina*, as do the other specimens figured by Cushman. Both *Discocyclina* and *Lepidocyclina* occur in the same rock. Cushman made an error in considering a specimen of which he had a surface view as belonging to the same species as specimens of which he examined sections. Fortunately, the type is designated as "section from station 3567, lowermost 100 feet of Tertiary running in above serpentine, northwest of Recreo, Matanzas Province, Cuba" (U.S.N.M. no. 328188). That specimen is *Discocyclina*. The specimens here considered may, therefore, be regarded merely as erroneously identified.

The specimens on which plate 1, figures 1 and 2, are based are designated cotypes. The embryonic chambers are subequal, each of the two chambers being somewhat deformed in the specimen figured. The two diameters of the apparatus are about equal, 0.60 mm.

The equatorial chambers are in general diamond-shaped in horizontal section, but the outer wall tends to be arcuate. The radial and transverse diameters are nearly the same, about 0.10 mm. The height of the chambers increases from the center toward the periphery, being about 0.10 mm at the periphery of the embryonic chambers and about 0.20 mm at the edge of the test 2.5 mm from the embryonic chambers.

The lateral chambers form rather regular tiers, about 10 or 11 layers over the center. Pillars are well developed, attaining a thickness of as much as 0.15 mm on the surface, where they form distinct papillae.

*Localities.*—Cotypes, locality no. 3478, Nuevitas, Cuba, collected by A. C. Spencer; locality no. 7522, Mogote Peak, near Matanzas, collected by O. E. Meinzer.

*Geologic association.*—*L. novitasensis* is associated with *Discocyclina sculpturata* (Cushman), *Lepidocyclina subraulinii* Cushman, *L. perundosa* Cushman, *L. meinzeri* Vaughan, and *Dictyoconus* sp. at locality no. 3478, and with *Discocyclina pustulata* and *Lepidocyclina meinzeri* at locality no. 7522. The horizon is Eocene, probably upper Eocene.

For some time I thought that this form might represent the megalospheric generation of *L. subraulinii* Cushman, which occurs in the same rock with it; however, I could not establish any such relationship and, as will later be shown, it is probable that another form represents the megalospheric generation of *L. subraulinii*.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) SUBRAULINII Cushman

Plate 2, figs. 1-3; probably plate 3, fig. 1

1919. *Lepidocyclina subraulinii* Cushman, Carnegie Inst. Washington Publ. 291, p. 62, pl. 11, figs. 6, 7.

1920. *Lepidocyclina subraulinii* Cushman, U.S. Geol. Surv. Prof. Pap. 125, p. 73, pl. 30, fig. 1.

The figures cited represent the type and a vertical section of a paratype from the same locality as the type. The identification of the other specimens figured by Cushman is doubtful. Cushman's description is as follows:

Test circular, much thickened in the central portion, which occupies about one-third the diameter of the test; peripheral portion much flattened, thin; thick

central portion irregularly papillate, peripheral portion smooth, showing almost no tendency to become saddle-shaped.

Vertical section shows the general thickness, the central lenticular body, and the thin periphery; central portion with very numerous pillars, increasing in diameter toward the surface; lateral chambers crowded between the pillars, very numerous in the vertical columns and much wider than high; equatorial chambers increasing in diameter toward the periphery, the outer margin convex and with a series of fine pores.

Horizontal section shows the equatorial chambers, which are polygonal; the outer margin strongly convex; pillars subpolygonal, with the lateral chambers making irregular polygonal meshes between them, toward the periphery the lateral chambers making up the entire test as the pillars decrease in number.

Diameter up to 24 mm; thickness in center 4.5 mm.

Type specimen (U.S.N.M. no. 328193) from station 3478, Nuevitas, Cuba, collected by A. C. Spencer. Other specimens apparently this species occur at 7666, Sierra Guaso, northeast of Guantánamo, collected by N. H. Darton.

The species was based on microspheric specimens. I have had a vertical and a horizontal section cut of specimens selected from the type material, and they are illustrated by plate 2, figures 1-3. Since the illustrations are clear, it is not necessary to describe the sections in detail. The species is large; the specimen of which the vertical section is figured is about 22.5 mm in diameter, and its thickness through the center is 4.35 mm.

The equatorial chambers are large, spatulate, either short or moderately long. In some chambers the radial diameter, in others the transverse diameter, is the longer. The dimensions of chambers can be measured on the figure, which is enlarged 20 diameters.

The lateral chambers are rather regularly arranged in tiers, with strongly developed pillars over the central part of the test.

*L. subraulinii* in many of its features resembles *L. georgiana* Cushman. The pillars in *L. georgiana* are heavier, thicker, and the lateral chambers are taller and more open.

It was stated in describing *Lepidocyclus novitasensis* that at one time I thought that the specimens now referred to that species might represent the megalospheric generation of *L. subraulinii*, but that I had come to doubt such a relationship. The specimen represented by plate 3, figure 1, is a megalospheric specimen of *Lepidocyclus* s.s., and from a comparison of its structure with that of *L. subraulinii*, it appears to me that it is probably the megalospheric form of *L. subraulinii*, and I am tentatively so identifying it. But there will be doubt regarding the affinities of such specimens until larger collections from the type locality, Nuevitas, Cuba, have been obtained and studied.

## LEPIDOCYCLINA (LEPIDOCYCLINA) MEINZERI Vaughan, n. sp.

Plate 3, figs. 1, 2; plate 4, figs. 1, 2c, 3, 4, 5

Test selliform; because of the downward bending of the margins on four sides a horizontal section through the embryonic chambers has the outline of a four-pointed star (pl. 4, figs. 2c and 3). Diagonal diameter 5.5 mm. On the surface there are a few thick papillae or pustules.

The embryonic apparatus is large; it consists of two chambers, one somewhat larger than the other, separated by a slightly curved wall, but as one chamber does not embrace the other, I am referring the species to *Lepidocyclina* s.s. The greater diameter of the apparatus is about 950  $\mu$ ; lesser diameter about 760  $\mu$ . There is on each side of the larger chamber a long narrow chamber which extends beyond the wall separating the two inner chambers and laps on the sides of the smaller chamber.

The equatorial chambers have curved outer walls and pointed inner ends. They greatly increase in height toward the periphery.

The lateral chambers form six or seven layers on each side of the equatorial layer, but decrease in number toward the periphery. At the actual margin of the test, the equatorial layer appears to be without cover. In some places tiers are definite, but in other places they are indefinite. The walls are rather thick, and in places irregularly distributed thick pillars are developed.

*Localities and geologic horizon.*—The cotypes are the three specimens illustrated on plate 4, figures 1, 2c, 3, and 4. These are from United States Geological Survey locality no. 7522, south side of Mogote Peak, altitude about 375 feet above sea-level, specimens in place and in drift, collected by O. E. Meinzer. In the same thin section there are *Discocyclina pustulata* (Cushman), *Asterocyclina* sp., and *Lepidocyclina novitasensis* Vaughan. *L. meinzeri* was also collected at Nuevitas, Cuba, by A. C. Spencer, where it is associated with *Discocyclina pustulata* (Cushman), *Lepidocyclina novitasensis* Vaughan, *L. subraulinii* Cushman, and *L. perundosa* Cushman. The horizon is clearly Eocene, probably upper Eocene, but the evidence is not conclusive as to horizon within the Eocene.

*Discussion.*—*L. meinzeri* bears some resemblance to *L. perundosa* Cushman, which seems to belong to the subgenus *Nephrolepidina*. A figure of *L. perundosa* is introduced for comparison (pl. 4, fig. 6). In *L. perundosa* the lateral chambers are depressed and the strong pillars of *L. meinzeri* seem to be absent. Furthermore, in *L. meinzeri*

the height of the equatorial chambers increases more rapidly toward the periphery than in *L. perundosa*. The features mentioned above are shown in the illustrations.

**LEPIDOCYCLINA (NEPHROLEPIDINA?) PERUNDOSA** Cushman

Plate 4, fig. 6

1919. *Lepidocyclina perundosa* Cushman, Carnegie Inst. Washington Publ. 291, p. 63, pl. 11, fig. 8.

Cushman's original description is as follows:

Test very much curved in two directions, so that at points 180° from one another the two planes of each set are nearly parallel to one another and nearly at right angles to those of the other set, strongly "saddle-shaped," surface smooth when well preserved, but usually somewhat cancellate, due to erosion.

Vertical section difficult to obtain on account of the very much doubly curved shape of the test, but shows no pillars; the lateral chambers about three times as long as high; central chamber large; equatorial chambers increasing gradually in size toward the periphery; their height and breadth about equal.

Horizontal section, which from the shape of the test can be at best only fragmentary, shows equatorial chambers roughly triangular, with the outer surface convexly curved.

Diameter 8 to 12 mm.

Type specimen, section (U.S.N.M. no. 328194) from station 3478, Nuevitas, Cuba, collected by A. C. Spencer.

An illustration of a vertical section of *L. perundosa* and a copy of Cushman's description of it are introduced for the purpose of comparing it and *L. meinzeri*. Notes on the differences between the two species have been made in discussing *L. meinzeri*.

**LEPIDOCYCLINA (LEPIDOCYCLINA) SUPERA** (Conrad)

Plate 29, figs. 1-3

1865. *Orbitolites supera* Conrad, Proc. Acad. Nat. Sci. Philadelphia, no. 2, p. 74.

1920. *Lepidocyclina supera* Cushman, U.S. Geol. Surv. Prof. Pap. 125, p. 69, pl. 26, figs. 5-7.

1924. *Lepidocyclina (Lepidocyclina) supera* Vaughan, Bull. Geol. Soc. Amer., vol. 35, p. 797, pl. 33, fig. 3.

1927. *Lepidocyclina (Lepidocyclina) supera* Vaughan, Proc. U.S. Nat. Mus., vol. 71, art. 8, p. 4, pl. 3, fig. 3.

In 1920 I collected at the Alazan-Moyutla crossing over Rio Buena Vista, Cantón of Tuxpan, State of Vera Cruz, Mexico, several specimens of a species of *Lepidocyclina (Lepidocyclina)* which I cannot distinguish from *L. supera*. The largest specimen is about 4.5 mm in diameter and has the embryonic chambers of *Lepidocyclina* s.s. External views,  $\times 10$ , of two smaller specimens are figured on plate 29,

figures 1, 2; and an external view, also  $\times 10$ , of a specimen from the Byram marl of Mississippi is illustrated for comparison. The same species is found at the La Ceiba crossing of Rio Buena Vista.

**LEPIDOCYCLINA (LEPIDOCYCLINA) WAYLANDVAUGHANI** Cole

Plate 5, figs. 1-3, 5, 6

1928. *Lepidocyclina (Lepidocyclina) waylandvaughani* Cole, Bull. Amer. Pal., vol. 14, p. 221, pl. 35, figs. 1-10.

Cole's original description of this species is as follows:

Test thin, waferlike without any pronounced umbo; generally flattened, but occasionally slightly sellaeform; surface smooth, occasionally obscurely reticulate, especially toward the margins; entirely without papillae, except a few very small ones which are sometimes present in the umbonal region.

Embryonic chambers nearly equal, separated by a straight wall; outer wall moderately thick, about 0.028 mm; greatest diameter of the embryonic chambers 0.53 mm, the least 0.42 mm.

Equatorial chambers hexagonal, becoming ogival in the outer rings.

In the vertical section, the number of lateral chambers over the center in the megalospheric form, on each side of the equatorial chambers are 5 to 6, which gradually decrease in number toward the periphery. Equatorial chambers very small at the center, gradually increasing in size as they approach the periphery until they occupy the entire thickness of the test. At the periphery, the equatorial chambers are twice as high as broad. The lateral chambers are low, compressed and relatively thick walled; pillars few and weakly developed.

Diameter of the megalospheric form 8 mm; thickness 0.70 to 0.80 mm.

One form of the species develops lobes to such an extent that it almost forms a cross. All graduations between the perfectly round forms and the extreme development of the "cross" form may be found, although the lobate forms are rather scarce.

The illustrations on plate 5 are intended to show the extreme limits of variation of the species. The upper specimen of figure 1 has over the central area papillae so small that they probably will not be visible in the reproduction. In the lower specimen of the same figure the papillae are larger. In the specimen represented by figure 5 there are over the central area five knoblike processes. There appear to be all the intermediate stages between specimens with scattered papillae and specimens in which the papillae are segregated and form knobs. Figure 3 represents a vertical section,  $\times 20$ , of a specimen with scattered papillae; figure 6 illustrates a vertical section,  $\times 20$ , of a specimen with knobs. Figure 2 represents a part of a horizontal section,  $\times 20$ , of a specimen similar to the one represented by figure 3. The hexagonal shape of the equatorial chambers is strikingly regular. *L. waylandvaughani* belongs in the same group of species as do *L. canellei* Lem. and R. Douv., *L. parvula* Cushman, *L. miraflorensis*

Vaughan, and *L. forresti* Vaughan. All five of these species belong to *Lepidocyclus* s.s., which has two equal or subequal embryonic chambers, and all five have hexagonal equatorial chambers.

*Localities and geologic occurrence.*—The type locality of *L. waylandvaughani* is a clayey layer above a massive sandstone in a quarry on the Huasteca Petroleum Company's golf course, opposite Tampico, where it is associated with *L. parvula* Cushman. The species is abundant in the railroad cuttings in the Meson formation from about 5 to 7 km east of Los Naranjos, and at Azteca Incline, about 12.5 km south of Los Naranjos in the State of Vera Cruz, Mexico. It has also been collected at numerous places in the Antigua formation in Antigua; one such locality is Wetherell Cliff. *L. waylandvaughani* is a common species in the middle Oligocene Antigua and Meson formations, and it may range somewhat above that horizon.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) FORRESTI Vaughan

Plate 5, fig. 4

1927. *Lepidocyclus* (*Lepidocyclus*) *forresti* Vaughan, Proc. U.S. Nat. Mus., vol. 71, art. 8, p. 1, pl. 1, figs. 1-4; pl. 2, figs. 1-6.

A single figure of *L. forresti* is given on plate 5, figure 4, to show some of the differences between it and *L. waylandvaughani*. The original illustrations of *L. forresti* should be compared with the illustrations here given and with Cole's original illustrations of *L. waylandvaughani*. The two species belong to the same group within the subgenus *Lepidocyclus* s.s. *L. forresti* lacks the strongly developed papillae of *L. waylandvaughani*, and its lateral chambers are more depressed, in this feature having more resemblance to *L. mantelli* (Morton) and *L. supera* (Conrad).

*Localities and geologic occurrence.*—Island of Antigua, at numerous localities in the Antigua formation; also in Jamaica in deposits of the same stratigraphic position.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) CANELLEI Lemoine and R. Douvillé

Plate 6, figs. 1-5

1904. *Lepidocyclus canellei* Lemoine and R. Douvillé, Soc. Géol. France, Paléont., Mém. 32, p. 20, pl. 1, fig. 1; pl. 3, fig. 5.

1918. *Lepidocyclus canellei* Cushman, U.S. Nat. Mus. Bull., 103, p. 91, pl. 34, figs. 1-6.

1920. *Lepidocyclus canellei* Cushman, U.S. Geol. Surv. Prof. Pap. 125, p. 75, pl. 32, figs. 1-5.

1924. *Lepidocyclus canellei* Vaughan, Bull. Geol. Soc. Amer., vol. 35, pp. 797, 819, pl. 33, fig. 4.

1928. *Lepidocyclus canellei* Vaughan, Journ. Pal., vol. 1, p. 290, pl. 49, figs. 1-5, 7-9.

Excellent descriptions of this species have been published by several authors. Figures are given in this paper in order to facilitate comparison with other species and to show variation from typical specimens. *L. canellei* is closely related to *L. parvula* Cushman, the most important difference being that pillars are absent in *L. canellei*, whereas they are strongly developed in *L. parvula*.

The maximum diameter of megalospheric specimens of *L. canellei* is about 5 mm. The diameter of smaller specimens is as small as 2.5 mm or even less. These notes are on specimens, virtual topotypes, from old Bohio Station on the old Panama Railroad. The locality is now covered by the water of Gatun Lake.

A dwarf variety of *L. canellei* occurs at Arbol Grande station, near Tampico. Specimens from this locality are illustrated by plate 6, figures 4 and 5. The diameter of these specimens is about 1.5 mm.

The treatment that should be accorded these smaller specimens has been perplexing. After considerable thought it has seemed to me that they should be referred to *L. canellei* and designated as a small or dwarf form. Another Canal Zone species, *Lepidocyclina* (*Nephrolepidina*) *vaughani*, is represented in Antigua by specimens smaller than those at the type locality.

*Localities and geologic horizon.*—The localities in the Canal Zone and near Tampico have already been given. The species is widely distributed in the Caribbean region, occurring, for example, in Jamaica and Venezuela. The horizon is in the Oligocene, apparently both middle and upper.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) PANCANALIS Vaughan and Cole

Plate 6, fig. 6

1932. *Lepidocyclina* (*Lepidocyclina*) *pancanalis* Vaughan and Cole, Journ. Washington Acad. Sci., vol. 22, p. 510, figs. 1-9.

This species, which has just been described by Vaughan and Cole from U.S.G.S. locality no. 6025, Bohio Ridge, Panama Canal Zone, has been identified in collections made in Antigua by W. R. Forrest at Coconut Hall, in the upper stratified beds at Half Moon Bay, and at southeast point, Long Island. Commonly associated with *L. pancanalisis* at these localities are specimens of *L. parvula*, *L. undosa*, and *L. vaughani*. The horizon in Antigua is in the Antigua formation, but it may be considerably above the base of the formation.

## LEPIDOCYCLINA (LEPIDOCYCLINA) PARVULA Cushman

Plate 7, figs. 1-5; plate 8, figs. 3-5; plate 9, figs. 1-4; plate 10, figs. 1-6

1919. *Lepidocyclus parvula* Cushman, Carnegie Inst. Washington Publ. 291, p. 58, pl. 3, figs. 4-7.  
1928. *Lepidocyclus* aff. *L. morgani* Cole, Bull. Amer. Pal., vol. 14, p. 222, pl. 4, fig. 9 (not Lemoine and R. Douvillé, 1904).  
1930. *Lepidocyclus parvula* Cole, *ibid.*, vol. 15, p. 125, pl. 18, figs. 4, 5.

Cushman's original description of this species is as follows:

Test lenticular, circular, central region thickened, gradually diminishing in breadth toward the periphery, which has a thin flangelike border, surface fairly smooth.

Vertical section showing the general form of the species; equatorial chambers gradually increasing in size toward the periphery, where they may be 4 to 5 times as high as long; outer surface slightly convex, chambers of the central region in section nearly square; lateral chambers 8 to 10 in a vertical column in the central region, and thence gradually diminishing in number until near the periphery there may be but a single layer of the lateral chambers, central portion with definite pillars, largely confined to this region.

Horizontal section shows the usual form of the equatorial chambers for this genus, the embryonic chambers either subequal or with one slightly larger than the other. In the section illustrated on plate 3, figure 4, a peculiar condition of these chambers is shown, where the two embryonic chambers have a series of chambers apparently coiled about them. This is an unusual character of this genus.

Diameter 5 mm.

Type specimen (U.S.N.M. no. 328191) from U.S.G.S. station 6862, from lower bed at Hodge's Bluff, Antigua, T. W. Vaughan, collector. It is very abundant in material from certain layers at this locality. This species also occurs at station 6854, Rifle Butts, Antigua.

The description quoted above is good, but more detail is needed regarding some features and, as the species is stratigraphically important, it is desirable to have an account of its variation, stratigraphic occurrence, and geographic distribution.

The thickness through the center of two cotypes ranges from a little less to somewhat more than 1 mm, that is, from about one third to one fifth the diameter. The pillars are variable in size on the same specimen, ranging from 0.05 to 0.20 mm thick.

The first variations that will be discussed here are those in size. The cotypes, except one specimen, are megalospheric and, therefore, are small, about 3 mm in diameter; one cotype is probably microspheric, and it is about 5 mm in diameter. Other microspheric specimens from the type locality are between 6 and 7 mm in diameter, and as the edges are broken, the original diameter was probably 8 mm or even somewhat greater. The thickness is a little more than 2 mm.

The variations in the papillae are extraordinary. Plate 9, figures 1, 2, represent external views,  $\times 5$ , of three topotypes from Hodge Bay, Antigua. Originally, I had six specimens photographed, but I am publishing illustrations of only three of them. The progression in size of the papillae from the right hand to the left hand figure is obvious. The series of six microspheric specimens,  $\times 5$ , represented by plate 9, figure 3, are from the same lot of specimens collected along the railroad, 7 km east of Los Naranjos, State of Vera Cruz, Mexico. The range of variation from scattered papillae in the specimen at the lower right-hand corner to large bosses over the central area in the specimen in the upper left-hand corner is shown. Figure 4 illustrates six, probably megalospheric, specimens,  $\times 10$ , selected from the same lot of specimens as those represented by figure 3. As the illustrations speak for themselves, further comment is unnecessary.

Plate 10, figures 1 and 3, represent opposite sides,  $\times 10$ , of the same specimen from Lynch Cliff, Antigua. It will be noticed that on one side some costae extend to the edge of the test, while on the other side there is a rim without costulation. Figure 2 represents a specimen,  $\times 10$ , from Hudson Cove, Antigua. Figures 4 and 5 illustrate two megalospheric specimens from the tilted beds, east of Lynch Cliff, Antigua. Figure 4 is an outside view,  $\times 10$ . Figure 5 represents an equatorial section by reflected light,  $\times 20$ , and shows that the species has the embryonic chambers of *Lepidocyclina*, s.s., and that its equatorial chambers are hexagonal to spatulate near the periphery, but near the center they tend to be lozenge-shaped. This form grades into the variety, *L. parvula* var. *crassicosta*, next to be described. Plate 10, figure 6, illustrates two specimens,  $\times 10$ , from Lynch Path, altitude 150 feet, Antigua. These specimens should be compared with those represented by plate 9, figure 3, especially those in the upper row.

*Localities and geologic horizon.*—The principal localities in Antigua and eastern Mexico have been given above. It also occurs in the Moneague formation of Jamaica. Its geologic horizon is middle Oligocene, Antigua and Meson formations. It is widely distributed geographically in the Caribbean and Gulf of Mexico regions.

**LEPIDOCYCLINA PARVULA** Cushman var. **CRASSICOSTA** Vaughan and Cole, n. var.

Plate 8, figs. 1, 2; plate 10, fig. 7; plate 24, fig. 1

Test small, lenticular, thick through the center, faintly polygonal in outline, usually with an encircling rim. The width of the rim

depends mainly on the state of preservation of the test. The diameter varies from 2 to 5 mm, the thickness from 1 to 2.4 mm. The central inflated part has a diameter ranging from 2 to 3 mm, the rim, when present, a width of 0.3 to 1.0 mm. Surface ornamentation consists of 6 to 8 heavy costae radiating from the center of the test to the inner edge of the rim. These costae are separated from each other by deep grooves about 0.15 mm in width and of about the same depth. The individual costae increase rapidly in width as they approach the rim, and some show a tendency to bifurcate. The apex of the test is variously ornamented. Some specimens have a strong central boss, as much as 0.38 mm in diameter, directly over the center and separated from the radiating costae by a deep groove. In others, there are two much smaller bosses, whereas some specimens have only a depression formed by the intersection of the grooves, separating the individual costae. The entire surface of the test shows rather strong reticulation. The rim, when preserved, is rather sharply demarked from the remainder of the test; flat to slightly undulating, and without ornamentation except the reticulation.

In horizontal sections the equatorial chambers near the center are lozenge-shaped, but near the periphery they become regularly hexagonal. They increase in size as they approach the periphery. Those near the center of the test have a radial diameter of about  $30\ \mu$  and a transverse diameter of about  $50\ \mu$ ; those near the periphery have a radial diameter of  $80\ \mu$  and a transverse diameter of about  $75\ \mu$ . The height of the equatorial layer at the center is  $50\ \mu$ . It increases rather rapidly in height until at the periphery its height is  $275\ \mu$ , measurements including both walls.

In vertical section, the lateral chambers are much restricted and shortened by the very heavy pillars over the center. These pillars vary from 0.3 to 0.55 mm in diameter. There are about 10 lateral chambers on each side of the equatorial layer over the center. The number decreases toward the periphery. On the rim there are no lateral chambers over the equatorial layer. The lateral chambers over the center at the periphery have a length of about  $90\ \mu$ , a height of about  $25\ \mu$ .

The foregoing description is based on sections of microspheric individuals, as the megalospheric form has not been observed.

*Localities and geologic horizon.*—Mercer's Creek, Antigua, collected by W. R. Forrest, Antigua formation, and Arbol Grande near Tampico, Tamaulipas, and Rio Pantépec, just above El Contenido, Cantón of Metlatoyuca, State of Puebla, Mexico, in the Meson formation. The species occurs in the middle Oligocene, and it may range into the upper Oligocene.

This variety differs from typical *L. parvula* in possessing well-developed costae. When viewed in the vertical section, the pillars are much heavier than in *L. parvula*, and the lateral chambers are more crowded and not so well developed. However, this form may be connected with the typical *parvula* through such forms as are illustrated on plate 10, figure 6. These specimens show increase in size of the papillae and, coincidentally, reduction in their number to six radially arranged large papillae or costules. There may or may not be a central papilla or boss.

The next stage apparently is the form that we are describing as the new variety, var. *crassicosta*, illustrated by plate 10, figure 7. This specimen has had its encircling rim broken off, but other specimens in the collection have the rim well developed. Although the series of *L. parvula* is practically unbroken from the forms with many small papillae to the forms with a few large papillae, var. *crassicosta* is so extreme that it is distinguishable from the more usual variants of the species.

LEPIDOCYCLINA ANTIGUENSIS Vaughan and Cole, n. sp.

Plate 10, fig. 8; plate 24, figs. 2, 3

Test small, compressed, lenticular, with a marginal rim about 0.30 mm wide; outline faintly polygonal; diameter 3.0 mm; thickness 1.0 mm. Apical area with a series of large papillae which are about 0.20 mm in diameter. Two or more of the papillae are enclosed by about nine other papillae, which form a circle 0.75 mm in diameter over the central part of the test. From this area the test slopes gradually to the marginal rim. The slope is ornamented by about 11 costae which grade into the papillae at the outer edge of the apical area. Toward the periphery the costae broaden rapidly, but become lower as they approach the rim where they are faint or obsolete. Some costae bifurcate, others remain single. The rim is narrow, flat, and without ornamentation except slight traces of the costae. The entire surface of the test, except on the papillae, shows faint reticulations which become more pronounced on the rim.

In equatorial sections the equatorial chambers near the center are lozenge-shaped; toward the periphery they range in shape from short-spatulate to rudely hexagonal. Chambers near the center have a radial diameter of about 40  $\mu$  and a transverse diameter of about 50  $\mu$ ; those near the periphery have a radial diameter of about 50  $\mu$  and a transverse diameter of about 45  $\mu$ .

In vertical sections the lateral chambers occur in regular tiers between heavy pillars. There are about 10 lateral chambers on each side of the equatorial layer. The chambers over the center and near the periphery are about  $100\ \mu$  in length and  $38\ \mu$  in height. They decrease in number until they are only one layer thick at the periphery. The equatorial layer is  $76\ \mu$  thick at the center of the test. It gradually increases in height toward the periphery, where it is  $200\ \mu$  thick, including both walls. The height of the equatorial chamber cavities at the center is  $40\ \mu$ , at the periphery,  $105\ \mu$ . The pillars have a diameter of  $200\ \mu$ .

*Localities and geologic horizon.*—Ridge southeast of Freetown, Antigua, altitude 200 to 250 feet; Lynch Path, Antigua, altitude, 150 feet; and St. Philip's churchyard, Antigua; all samples collected by W. R. Forrest; middle Oligocene Antigua formation.

The general aspect of *L. antiguensis* is somewhat like that of *L. giraudi* R. Douvillé. The costae in *L. antiguensis*, except at the margin of the apical area, are broad and low and become obsolete at the inner edge of the marginal rim. The costae in *L. giraudi* are more numerous, more trenchantly developed, and extend to the edge of the test. The figures on plate 10 illustrate the differences. Figures 9 and 10 represent topotypes of *L. giraudi*.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) GIRAUDI R. Douvillé

Plate 10, figs. 9, 10; plate 24, fig. 4

1907. *Lepidocyclina giraudi* R. Douvillé, Soc. Géol. France, Bull., ser. 4, vol. 7, p. 307, pl. 10, figs. 9, 10, 15, 16, text figs. 1, 2.  
 1924. *Isolepidina giraudi* H. Douvillé, Soc. Géol. France, Mém., n.s., vol. 1, no. 2, p. 43.

Giraud, just before his death, sent me topotypes from Pointe Macabou, Martinique, and of them the exteriors of two specimens are illustrated on plate 10, figs. 9, 10, and a horizontal section of another on plate 24, figure 4.

The tests are lenticular, small, larger specimens being 3.5 to 4 mm in diameter and about 1.5 mm thick. Over the center of the test there are thick papillae which range in number from a few up to as many as nine. From the outer boundary of the papillate area strong costae extend to the periphery of the test.

The embryonic chambers are subequal. The equatorial chambers are lozenge-shaped near the center, outside this area they become hexagonal, and near the periphery they are short-spatulate, similar to those of *L. parvula*. Since H. Douvillé and I appear to disagree

regarding the equatorial chambers, a photographic illustration of them is given on plate 24, figure 4. *L. giraudi* represents an extreme development of the costulation of the surface. *L. canellei*, without pillars and with very small papillae, stands at one end of the series; *L. parvula* occupies an intermediate position with gradation toward *L. giraudi*, which stands at the other end of the series.

*Locality and geologic horizon.*—The type locality of the species is Pointe Macabou, Martinique, and its immediate vicinity; J. Giraud, collector. H. Douvillé gives the horizon as “couches à *Turritella tornata*, Aquitanien ou Burdigalien.” My inclination is to refer the horizon to the Oligocene, probably upper.

LEPIDOCYCLINA (LEPIDOCYCLINA) YURNAGUNENSIS Cushman

Plate II, figs. 1-4

1919. *Lepidocyclus canellei* var. *yurnagunensis* Cushman, Carnegie Inst. Washington Publ. 291, p. 57, pl. 12, figs. 7-8, text fig. 6.  
 1926. *Lepidocyclus yurnagunensis* Vaughan, Quart. Journ., Geol. Soc. London, vol. 82, p. 391, pl. 25, figs. 2-6 (references and synonymy).

As I gave a detailed description of this species in my paper above referred to, it is necessary here only to make notes on variation and to compare it with other species. In its general external aspect and to some degree in vertical sections, *L. yurnagunensis* resembles *L. canellei*, and it was for these reasons that Cushman considered it a variety of *L. canellei*. There are, however, two important differences. The equatorial chambers in *L. yurnagunensis* are predominantly diamond- or lozenge-shaped, not predominantly neatly hexagonal as in *L. canellei*. In *L. yurnagunensis* there are pillars of varying degrees of development. They may be weakly or strongly developed. Those forms with strongly developed pillars grade directly into the variety *morganopsis*, which will be described below. The largest specimen represented by plate 11, figure 2, a part of Cushman's type material, shows a few pillars.

*Localities and geologic occurrence.*—The type locality is U.S.G.S. locality no. 7548, the west side of Yateras River, about 2½ miles south of Yuraguana, about 2 miles north of El Jique, near Guantánamo, Cuba, collected by O. E. Meinzer. The species is found at numerous localities in the vicinity of Guantánamo, where it is associated with *Lepidocyclus favosa* Cushman, *L. gigas* Cushman var., and other middle Oligocene species. It is found in the limestone on Cayman Brac, Cayman Islands, and in the Moneague formation of Jamaica. It is a rather common, widely distributed species in the Antillean middle Oligocene.

LEPIDOCYCLINA (LEPIDOCYCLINA) YURNAGUNENSIS var.  
MORGANOPSIS Vaughan

Plate 11, figs. 5-9; plate 23, figs. 1-3

1919. *Lepidocyclus morgani* Cushman, Carnegie Inst. Washington Publ. 291, p. 59, pl. 11, figs. 1-3, text fig. 7 (not Lemoine and R. Douvillé).
1920. *Lepidocyclus morgani* Cushman, U.S. Geol. Surv. Prof. Pap. 125, p. 74, pl. 33, figs. 12-14 (not Lemoine and R. Douvillé).
1933. *Lepidocyclus yurnagunensis* var. *morganopsis* Vaughan, Journ. Washington Acad. Sci., vol. 23, p. 354.

Cushman's description of the specimens which he refers to *L. morgani* is as follows:

Test small, discoidal, much thickened in the central portion, from which it tapers rather rapidly to the subacute periphery; central protuberant portion with a series of large pustules ranging from 5 to 12 or more in number, of which one is usually central, surface reticulate between the pustules; the margins stellate; periphery of the test thin and slightly reticulated by the walls of the equatorial chambers.

Vertical sections show the general form and curvature of the surface of the test, the few pillars in the central region rapidly increasing in diameter toward the surface of the test; lateral chambers with the outer wall convex, averaging about three times as wide as high; in the central region with as many as 10 chambers in the vertical columns; equatorial chambers not increasing rapidly in height; height of those at the periphery not more than double that of those near the center.

Horizontal sections show the embryonic chambers, which are unequal, the larger one partially surrounding the smaller, as in the subgenus *Nephrolepidina* of H. Douvillé, and the equatorial chambers more or less diamond-shaped, as in that subgenus. In other specimens the outer wall of the chamber is convex.

Diameter 2 to 5 mm.

*Distribution.*—Specimens seemingly identical with this species were found at the following stations in Cuba: 7513, limestone outcrop where Palmer Trail joins Ocuja Trail; 7516, west end, Los Melones Mountain; 7543, limestone outcrop, east side of Yateras; 7554, south of El Jique, 5 miles above mouth of Yateras River on west side, collected by O. E. Meinzer. Specimens, the sections of which are imperfect, but probably belonging to *L. morgani*, were obtained by O. E. Meinzer at station 7519, limestone from drift near top of landslide next north of Los Melones, and 7522, Mogote Peak. The specimens whose exteriors are figured were obtained by N. H. Darton at station 7664, north slope, La Piedra, northeast of Jamaica, northeast of Guantánamo, Cuba. [The last number is an error. It should be 7554, just south of El Jique, west side, about 6 miles above the mouth of Yateras River, altitude 150 feet above sea-level. O. E. Meinzer, collector.]

A locality at which the form is abundant is U.S.G.S. locality no. 7552, just south of El Jique, about 6 miles above the mouth of Yateras River, altitude about 250 feet, collected by O. E. Meinzer. The specimens of both *L. yurnagunensis* and *L. yurnagunensis* var. *morganopsis* from this locality are very good.

Cushman's figure of the embryonic chambers of a specimen identified by him as *L. morgani* should be compared with his figures (1920, pl. 33, figs. 4-9) of the embryonic chambers of *L. yurnagunensis*. The similarity is obvious. The embryonic chambers of *L. yurnagunensis* vary from *Lepidocyclina* s.s. to *Nephrolepidina*, and some are almost *Pliolepidina*, as Cushman has shown. The embryonic and the equatorial chambers of *L. yurnagunensis* var. *morganopsis* are similar to those of typical *L. yurnagunensis*, from which the variety differs solely by its more greatly developed pillars, which terminate in pustules on the surface.

*Cotypes*.—Locality no. 7543, two thin sections and a few uncut specimens, U.S. National Museum.

**LEPIDOCYCLINA HODGENSIS** Vaughan and Cole, n. sp.

Plate 12, figs. 1-5

Test somewhat compressed lenticular to robustly lenticular, usually bordered by a narrow rim, outline generally irregularly subcircular. Diameter varies from 2.2 to 3.5 mm, thickness from 1 to 2 mm. Surface papillate, the degree of papillation variable. In some specimens very pronounced papillae are developed in the apical region, the remainder of the test being covered with much finer papillae. In other specimens the entire test is covered with fine papillae. On some specimens there are ill-defined radiating costae, which are more conspicuous on the narrow rim and cause in most cases the polygonal outline of the test. Pits occur between the pillars; the entire effect is to give the surface of the test a very rugose appearance.

The following description of the internal features is based on sections of microspheric individuals; the megalospheric form was not discovered in any of the preparations that were made.

The embryonic apparatus of a microspheric individual is composed of about 2 whorls with a diameter of 100  $\mu$ . The outer whorl has 6 chambers. The equatorial chambers vary from those with curved outer and converging inner walls with pointed or slightly truncated inner ends to those of short-spatulate form. They increase gradually in size from the center to the periphery. Those at the center have a radial diameter of 20  $\mu$ ; a transverse diameter of 35  $\mu$ ; those at the periphery have a radial diameter of about 45  $\mu$ , a transverse diameter of 35  $\mu$ . Plate 12, figure 5 shows a section,  $\times 85$ , which indicates the form and size of both the embryonic apparatus and the equatorial chambers.

The lateral chambers are very numerous and are arranged in regular tiers between the rather large pillars. Over the center of the test

there are 22 chambers in each tier on each side of the equatorial layer. The chambers directly over the equatorial layer at the center of the test have a length of  $15\ \mu$  and a height of  $10\ \mu$ ; those in the same tier at the periphery have a length of  $90\ \mu$  and a height of  $30\ \mu$ . The number of chambers decreases regularly toward the periphery. The equatorial layer is  $35\ \mu$  in thickness at the center. It gradually increases in thickness toward the periphery, where it is  $135\ \mu$  thick. Pillars in the thickened central area have a diameter of  $110\ \mu$  at the surface and gradually taper as they approach the equatorial layer.

*Type locality*.—Hodge Hill, uppermost bed, Antigua, collected by W. R. Forrest. The horizon is very high in the Antigua formation and may be upper Oligocene.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) WETHERELLENSIS

Vaughan and Cole, n. sp.

Plate 12, figs. 6, 7; plate 23, figs. 9, 10; plate 24, fig. 5

Test small, stellate, central part inflated, surrounded by a relatively wide, slightly undulating rim. Extending from the central area to the margin of the test, there are about 8 irregularly spreading rays, some of which are more prominent than others. The larger rays generally extend beyond the margin of the test and produce a lobate outline of the test. The surface is entirely covered by papillae which are much larger on the umbo and the rays than in the depressed areas between the rays, where they are rather small. The diameter ranges from 3 to 7 mm; thickness about 1 mm. The amount of the central inflation varies considerably.

The embryonic apparatus consists of two subequal chambers separated by a straight wall. The length of the two chambers is  $220\ \mu$ , the width  $190\ \mu$ . The larger chamber has a length of  $130\ \mu$ ; the chamber wall is thick, about  $22\ \mu$ .

The equatorial chambers have curved outer walls and converging inner walls with pointed inner ends. They gradually increase in size from the center to the periphery, where the radial diameter is about  $60\ \mu$ ; transverse diameter about  $75\ \mu$ . The height of the equatorial chambers at the center of the test is about  $30\ \mu$ ; at the periphery about  $127\ \mu$ .

The lateral chambers are numerous, rather uniform in height, and arranged in regular tiers between well-developed pillars. In the thickened central portion of the test on each side of the equatorial layer there are about 10 chambers to a tier. The number decreases regularly until at the junction of the central area with the flange there

are only three chambers to a tier. At the periphery there are no lateral chambers, the equatorial layer being bare for a considerable distance. Directly over the embryonic apparatus the lateral chambers have a length of about  $50 \mu$  and a height of about  $20 \mu$ . In the same tier at the periphery they have a length of  $110 \mu$  and a height of  $30 \mu$ . The pillars have a diameter of about  $75 \mu$ . In each equatorial chamber there are two stoloniferous apertures about  $10 \mu$  to  $14 \mu$  in diameter.

*Localities and geologic horizon.*—Island of Antigua, at Wetherell Cliff; inland cliff, southward extension of Wetherell Cliff, under oyster beds, 600 feet above sea-level; and lowest tilted bed on beach, Lynch Point, all collected by W. R. Forrest. Horizon, middle Oligocene, Antigua formation. A stellate species of *Lepidocyclina* suggestively like *L. wetherellensis* was collected by O. E. Meinzer at several localities in the vicinity of Guantánamo, Cuba, U.S.G.S. locality no. 7513, about  $\frac{3}{4}$  mile east of Ocuja Spring and about  $4\frac{3}{4}$  miles due east of Monument H6 on the east boundary of the U.S. Naval Reservation. Vertical sections of fragments of two specimens are illustrated by plate 23, figures 9, 10. A stellate species was also collected at Ocuja Spring, U.S.G.S. locality no. 7512.

Recently Nuttall<sup>1</sup> has described a stellate species, *Lepidocyclina* (*Lepidocyclina*) *asterodisca* from the Oligocene Alazan shale of eastern Mexico. Gorter and Van der Vlerk<sup>2</sup> have just described under the name *Lepidocyclina* (*Lepidocyclina*) *senni* from the Eocene "Menegrande series" of Venezuela another stellate species. Later in the present paper still another stellate species, *L. (Nephrolepidina) dartoni* Vaughan is described.

#### LEPIDOCYCLINA (NEPHROLEPIDINA) TOURNOUERI

Lemoine and R. Douvillé

Plate 13, figs. 1, 2

1904. *Lepidocyclina tournoueri* Lemoine and R. Douvillé, Soc. Géol. France, Paléont., Mém. 32, p. 19, pl. 1, fig. 5; pl. 2, figs. 2, 14; pl. 3, fig. 1.  
 1924. *Lepidocyclina tournoueri* H. Douvillé, Soc. Géol. France, Mém., n.s., vol. 2, no. 2, p. 78, pl. 6, figs. 8-12, text figs. 62-68.  
 1924. *Lepidocyclina tournoueri* Vaughan, Bull. Geol. Soc. Amer., vol. 35, p. 798, pl. 33, figs. 6, 7.

<sup>1</sup> Nuttall, W. L. F., Lower Oligocene foraminifera from Mexico. Journ. Pal., vol. 6, p. 34, pl. 7, figs. 5, 8; pl. 9, fig. 10, 1932.

<sup>2</sup> Gorter, Nettie E., and van der Vlerk, I. M., Larger foraminifera from Central Falcón (Venezuela). Leidische Geol. Mededeel., vol. 4, no. 2, p. 105, pl. 11, figs. 4-6, 1932.

A description of the Mexican specimens identified by me as *L. tournoueri* is as follows:

Test small, lenticular, usually bordered by a narrow rim. Surface ornamentation variable, in most specimens a few strong papillae produced by the emergent distal ends of the pillars form an apical crown, in others the pillars are so reduced in size as to be scarcely noticeable. The surface of the test is generally strongly reticulate. The megalospheric form has a diameter of 2 to 4 mm and a thickness of 1 to 1.5 mm.

The embryonic chambers are of nephrolepidine type, a larger chamber partly embracing a somewhat smaller one. Chamber walls relatively thick. The width of the two chambers in an equatorial plane is 0.29 mm. The smaller chamber has a length of 0.19 mm, a width of 0.14 mm; the length of the larger chamber is 0.32 mm. The height of the larger chamber in a vertical section is 0.22 mm. The surrounding wall is 22  $\mu$  in thickness.

The equatorial layer has a thickness at the center of about 80  $\mu$ , at the periphery, about 135  $\mu$ , the measurements including both walls. The equatorial chambers have a radial diameter of about 52  $\mu$ , and a transverse diameter of about 50  $\mu$ , at the center of the test. They increase in size toward the periphery where their radial diameter is 67  $\mu$ , and the transverse diameter 52  $\mu$ . In plan the equatorial chambers vary from short-spatulate at the center to hexagonal and slightly elongate-hexagonal at the periphery.

There are on each side of the equatorial layer about 10 lateral chambers, arranged in regular tiers, at the center. They decrease in number outward until there is but a single layer at the periphery. Directly over the embryonic apparatus the lateral chambers have a length of about 90  $\mu$  and a height of about 30  $\mu$ ; at the periphery in the same tier their length is 225  $\mu$  and their height, 45  $\mu$ . Pillars are rather strong, 75  $\mu$  to 112  $\mu$  in diameter, irregularly spaced in the central area of the test.

*Locality and geologic horizon.*—Near Tampico, Arbol Grande, Tamaulipas, Mexico, collected by D. R. Semmes. The geologic horizon is Oligocene, whether middle or upper is not certain, but upper appears more probable.

**LEPIDOCYCLINA (NEPHROLEPIDINA) TEMPANII** Vaughan and Cole, n. sp.

Plate 13, figs. 3-6

Test small, lenticular, usually with a slight rim. Surface papillate, the degree of papillation variable, papillae much better developed on

the umbo. The diameter of megalospheric individuals ranges from 2.0 mm to 4 mm, the thickness from 1 mm to 1.5 mm.

The embryonic chambers are of nephrolepidine type, a larger chamber partly embracing a somewhat smaller one. They are decidedly large, but have relatively thin walls. The height of the larger chamber in a vertical section is about 0.19 mm, width of the two chambers in the equatorial plane is about 0.45 mm. The smaller chamber has a length of about 0.3 mm and a width of about 0.22 mm. The larger chamber has a length of about 0.46 mm.

In plan the equatorial chambers are elongate-hexagonal, becoming rather large as they approach the periphery. At the center their radial diameter is  $60 \mu$ , transverse diameter,  $40 \mu$ . At the periphery the radial diameter is about  $110 \mu$ , and the transverse diameter about  $75 \mu$ . Near the center the equatorial chambers are about  $40 \mu$  tall and at the periphery, about  $135 \mu$  tall. There are 9 layers of lateral chambers on each side of the equatorial zone in megalospheric forms. Most of the lateral chambers are disposed in regular tiers, but some are interrupted. The chambers directly over the embryonic apparatus have a length of  $40 \mu$  and a height of  $20 \mu$ ; those at the periphery in the same tier have a length of  $187 \mu$  and a height of  $45 \mu$ .

Strong pillars, irregularly spaced, are present; they taper very little, being nearly of the same thickness throughout their length. Their average diameter is about  $75 \mu$ .

*Localities.*—Antigua, Hodge Hill, collected by W. R. Forrest, and U.S.G.S. locality no. 6862, Hodge Point, collected by T. W. Vaughan.

This species is nearly related to the one from Arbol Grande, near Tampico, Mexico, here identified as *L. tournoueri*. The main difference in the two species is readily seen in a comparison of the equatorial section. *L. tempanii* has much more elongate equatorial chambers than *L. tournoueri*.

This species is named for Dr. H. A. Tempany, formerly chemist of the agricultural station in Antigua, and now Director of Agriculture in British Malaya. Dr. Tempany, while resident in Antigua, contributed to the knowledge of local geology as well as to scientific agriculture there.

#### LEPIDOCYCLINA (NEPHROLEPIDINA) FRAGILIS Cushman

Plate 14, figs. 1-4

1920. *Lepidocyclina fragilis* Cushman, U.S. Geol. Surv. Prof. Pap. 125, p. 63, pl. 22, figs. 1, 2.

1924. *Lepidocyclina (Nephrolepidina) fragilis* Vaughan, Bull. Geol. Soc. Amer., vol. 35, p. 798, pl. 33, fig. 5.

Cushman's original description and figures were based on the megalospheric form of the species. His description is as follows:

Test of medium size, 10 to 12 mm in diameter, very thin, flattened or very slightly sellaeform; central portion very slightly thickened but usually forming no definite umbo distinguishable from the remainder of the test; surface very smooth except where eroded and at the periphery, where the walls of the equatorial chambers form a slight reticulation of the surface; whole test thin and fragile; thickness usually about 1 mm or less.

The horizontal section shows the equatorial chambers to be hexagonal and with fairly thick walls. Embryonic chambers not seen.

The vertical section shows the equatorial band of chambers unusually low throughout, increasing very little from center to periphery; the chambers toward the center thin-walled and broader than high; those toward the periphery are thick-walled, slightly higher than wide, and the vertical walls slightly convex and thickened; lateral chambers very low and broad, in central region with not more than six chambers in a vertical column, generally lessening in number toward the periphery, where there may be but one or even none. No pillars apparent.

Type specimens from U.S.G.S. station 7194, Ocala limestone, at mouth of cavern about 200 yards southwest of wagon bridge over Chipola River, east of Marianna, Fla.; bed 4 of section; C. W. Cooke and W. C. Mansfield, collectors.

In 1924 I published an illustration showing that the embryonic chambers were of nephrolepidine type. In the present paper plate 14, figure 1 represents a vertical section of a megalospheric specimen; figures 2 and 3, two parts of one half of a vertical section of a microspheric specimen; and figure 4, the equatorial chambers near the margin of a microspheric specimen. All of the figures are enlarged 20 diameters.

*L. fragilis* is a large species; 30 mm is a common diameter of microspheric specimens and some specimens are almost 40 mm in diameter.

Both the equatorial and lateral chambers are well illustrated in the figures. In general, the lateral chambers are rather low and are long. Pillars are neither so well nor so regularly developed as in *L. georgiana*, and the chamber cavities are not so open. The surface of *L. georgiana* is definitely and rather coarsely papillate, whereas the surface of *L. fragilis* is smooth, flaky, reticulate, nonpapillate. Cushman's enlarged views of the surface features of the two species are good.

Because of similarity in form and size, the microspheric forms of *L. georgiana* and *L. fragilis* look alike, but actually they belong to different subgenera. *L. georgiana* is *Lepidocyclina* s.s., and *L. fragilis* is, as has already been stated, *Nephrolepidina*.

## LEPIDOCYCLINA (NEPHROLEPIDINA) SEMMESI

Vaughan and Cole, n. sp.

Plate 15, figs. 3-5; plate 30, fig. 1; plate 31, figs. 1, 1a; plate 32, figs. 2, 3  
1930. *Lepidocyclus ocalana* Nuttall, Journ. Pal., vol. 4, p. 273 (not Cushman).

Test of medium size, very slightly selliform, a small umbo, more developed on one side than the other. The diameter of the megalospheric individuals ranges from 9 to 14 mm, thickness from 1.4 to 2.5 mm; microspheric individuals attain a diameter of 20 mm or more, with a thickness of about 4.5 mm. The surface is flaky, vermiculate-scribbulate, with numerous small papillae, which are most prominent on the umbo.

The embryonic chambers are of nephrolepidine type, a larger chamber embracing a slightly smaller one. The chamber wall is thick. The width of the two chambers, measured in a slightly oblique section, is approximately 0.69 mm. The smaller chamber has a length of 0.51 mm and a width of 0.38 mm. The chamber wall is 0.06 mm in thickness.

The equatorial chambers are of two types, short-spatulate near the center, grading outward into arcuate chambers. The spatulate chambers commonly are about 100  $\mu$  in radial diameter and about 90  $\mu$  in transverse diameter. The arcuate chambers are about 60  $\mu$  in radial diameter and about 120  $\mu$  in transverse diameter.

The lateral chambers vary in number from about 8 on each side of the equatorial layer at the center in megalospheric individuals to as many as 25 in microspheric individuals. Some of the chambers are arranged in regular tiers, but most are irregularly spaced and overlapping. The chamber floors are much thickened in the layers adjacent to the equatorial layer, the chamber cavities showing only as narrow slits. The peripheral layers have large, open chambers which vary in length from 150 to 275  $\mu$ ; their height being about 45  $\mu$ . The equatorial chambers have a height at the center of about 100  $\mu$ ; at the periphery about 290  $\mu$ .

The pillars are pronounced, but irregularly developed. They commonly do not extend to the surface of the test. Some branch to form two or more pillars that extend separately to the surface. Diameter of the pillars variable, ranging from 75  $\mu$  to as much as 300  $\mu$ ; average about 150  $\mu$ .

*Localities and geologic horizon.*—The cotypes are from locality M106V, 0.6 km southwest of Dos Caminos, near Tantoyuca, State of Vera Cruz, Mexico, collected by T. W. Vaughan and D. R. Semmes; also collected by D. R. Semmes near Tamemas, in the Tantoyuca district at the west end of the second east-west hill north of Peregrino.

Other localities are Chila Cortaza Creek, west side, on road Santa Maria Ixcatapec to Tantoyuca, about 50 feet above the creek bed (M88V), and 4.5 km from Chila Cortaza on road to Tantoyuca (M92V); collections by T. W. Vaughan and D. R. Semmes. The geologic horizon is the upper Eocene Tantoyuca formation.

*Lepidocyclus semmesi* is very nearly related to *L. tantoyucensis*, the species next to be described. *L. semmesi* has more numerous taller, and more open lateral chambers, and better developed pillars than *L. tantoyucensis*.

LEPIDOCYCLINA (NEPHROLEPIDINA) SEMMESI var. GRANOSA

Vaughan and Cole, n. var.

Plate 30, fig. 2

1930. *Lepidocyclus ocalana* var. *subdecorata* Nuttall, Journ. Pal., vol. 4, p. 273 (not Cushman).

This variety differs from typical *L. semmesi* by having a distinctly papillate surface, the papillae being somewhat larger over the center of the test. Plate 30, figure 1, illustrates the surface,  $\times 10$ , of typical *L. semmesi*, and figure 2 of the same plate illustrates the surface, also  $\times 10$ , of var. *granosa*. This variety bears to *L. semmesi* a relation similar to that of *L. ocalana* var. *subdecorata* to *L. ocalana*.

*Localities and geologic horizon.*—Slope east side of Tantoyuca, State of Vera Cruz, Mexico, 50 to 70 feet above the bed of the arroyo (M96V), and 133 to 170 feet above the bed of the arroyo (M99V), collected by T. W. Vaughan and D. R. Semmes.

LEPIDOCYCLINA (NEPHROLEPIDINA) TANTOYUCENSIS

Vaughan and Cole, n. sp.

Plate 15, figs. 1, 2

1930. *Lepidocyclus ocalana* Nuttall, Journ. Pal., vol. 4, p. 273 (not Cushman).

Test thin, thickest at the center, thence thinning regularly to the periphery, slightly selliform, the average diameter of adult megaspheric individuals about 13 mm, thickness about 1.5 mm. Megaspheric individuals range in diameter from 5 to 14 mm; microspheric forms average 18 mm or more in diameter. Surface flaky, reticulate, and scrobiculate from unequal weathering of the outer layers of lateral chambers. Very small, scattered papillae are generally present.

The embryonic chambers are of nephrolepidine type, the large chamber somewhat embracing the smaller. The chamber wall is strikingly thick. The diameter of the embryonic apparatus measured across both chambers in an equatorial section is 1.15 mm; the

diameters of the inner chamber are respectively 0.97 and 0.61 mm. The thickness of the chamber wall is 0.08 mm.

The radial diameter of the equatorial chambers ranges from 75 to 100  $\mu$  and the transverse diameter from 75 to 130  $\mu$ . The transverse usually exceeds the radial diameter in length. The height of the equatorial chamber at the center in a microspheric individual is about 150  $\mu$ , at the periphery about 320  $\mu$ . In plan, they range from short-spatulate to arcuate.

The lateral chambers have thick roofs and floors, and are long, depressed. Although many chambers are disposed in regular tiers, some irregularly overlap the layers above and below. The roofs are often slightly arcuate. The maximum on each side of the equatorial layer at the center is 12. The number decreases regularly as the periphery is approached, until for a distance of about 0.4 mm from the edge the equatorial layer is not covered. The length of the chambers in the center of the test ranges from 110 to as much as 190  $\mu$ . The height of the chamber cavities and the thickness of the roofs and floors are about equal, each ranging from about 20 to 30  $\mu$ .

Pillars are weakly and irregularly developed. Their diameter ranges from 75 to 100  $\mu$ .

*Localities and geologic horizon.*—About 4.5 km from Chila Cortaza on the road to Tantoyuca, about 10 km east of Tantoyuca (M92V), and 0.6 km southwest of Dos Caminos on the road from Dos Caminos to Tierra Colorada, Cantón of Tantoyuca (M106V), State of Vera Cruz, Mexico, collected by T. W. Vaughan and D. R. Semmes. Upper Eocene, Tantoyuca formation.

*Lepidocyclina semmesi* and *L. tantoyucensis* both belong to the subgenus *Nephrolepidina* and are so closely related to *L. (Nephrolepidina) fragilis* Cushman that the senior author has vacillated between referring them to that species and assigning new names to them. By comparing the respective descriptions and illustrations here given, the reasons for specific separation will be obvious. The equatorial chambers of *L. fragilis* are in general hexagonal or spatulate; they are not radially shortened as in *L. semmesi* and *L. tantoyucensis*. The differences from each other of the last two species are brought out by the figures on plate 15.

All three of these species occur in virtually summit beds of the Eocene, *L. fragilis* in the topmost bed of the Ocala limestone, the other two species in the upper Eocene Tantoyuca formation. *Lepidocyclina chaperi* Lemoine and R. Douvillé from the upper Eocene at San Juan de Pequañi, upper Chagres River, Panama, belongs in the same group of species and occupies a very similar, if not identical, stratigraphic position.

## LEPIDOCYCLINA (NEPHROLEPIDINA) VAUGHANI Cushman

Plate 16, figs. 1-5

1918. *Lepidocyclina vaughani* Cushman, U.S. Nat. Mus. Bull. 103, p. 93, pl. 37, fig. 4 (not figs. 1, 2, 3, 5 which represent *L. miraflorensis* Vaughan); pl. 38.
1920. *Lepidocyclina vaughani* Cushman, U.S. Geol. Surv. Prof. Pap. 125, p. 64, pl. 22, fig. 5.
1923. *Lepidocyclina vaughani* Vaughan, Proc. Nat. Acad. Sci., vol. 9, pp. 254, 255, 256.
1924. *Lepidocyclina (Nephrolepidina) vaughani* Vaughan, Bull. Geol. Soc. Amer., vol. 35, p. 798, pl. 33, fig. 9.

Test flattish, center umbonate, periphery thickened; 10 mm or more in diameter.

Cushman's illustrations give a correct idea of the size, of the outline of the test as seen in plan, and of the shape, size, and arrangement of the equatorial chambers, but he did not illustrate the detail of the surface ornamentation, the embryonic chambers, nor a vertical section. In 1923 I stated that embryonic chambers were nephrolepidine, and in 1924 I published an illustration of the embryonic chambers of a specimen from Half Moon Bay, Antigua. In the present paper supplemental illustrations are published, and notes on them are made as follows:

Plate 16, figure 5, shows the nephrolepidine embryonic chambers,  $\times 20$ , and the minute, almost hirsute, angular papillae of the surface just outside the central area. Figure 4 of the same plate is the peripheral part of the same photograph from which figure 5 was made. It illustrates the equatorial chambers near the periphery. They are markedly rhomboid in form. The decrease in the length of the radial diameter at the periphery should also be noted. Figure 1 of plate 16 is a vertical section,  $\times 20$ , of another specimen from the same locality. It shows lateral chambers with open cavities, arranged in regular tiers, separated by rather thin, but distinct, pillars. The number of layers of chambers is considerable, 10 to 13, over the center, but it decreases toward the periphery, where over the expanded edge there are none. At the periphery the equatorial chambers enormously increase in height and become radially crowded. The specimens illustrated by plate 16, figures 1, 4, 5, are topotypes from U.S.G.S. locality no. 6021 (the same locality as no. 6673 in Cushman's papers cited above), limestone along the relocated line of the Panama Railroad, opposite San Pablo, Panama Canal Zone.

The specimens illustrated by plate 16, figures 2, 3, are from Half Moon Bay, Antigua, collected by W. R. Forrest. These specimens are

similar to those from the Canal Zone, except that they are smaller. As the enlargement of all the figures is the same, the relative dimensions are obvious.

*Localities and geologic horizon.*—The two principal localities for *L. vaughani* have been given above. In the Canal Zone it is associated with *L. cancelli*. Therefore, the geologic horizon of the two species is the same. Other associated species at Half Moon Bay, Antigua, are *L. parvula* Cushman and *L. undosa* Cushman. The occurrence is in the Antigua formation, but apparently not in its basal part. The horizon, therefore, is Oligocene, perhaps upper rather than middle.

**LEPIDOCYCLINA (NEPHROLEPIDINA?) CRASSIMARGO** Vaughan, n. sp.

Plate 27, figs. 1, 2, 3

This species is based on a number of fragmentary sections, those represented by plate 27, figures 2 and 3, being selected and designated as cotypes. As the section illustrated by figure 1, on plate 27, seems definitely to represent either a young specimen or the central part of the test of the same species as that represented by figure 2 on the same plate, it will be described first.

Test small, thin, lenticular. Diameter about 3.5 mm, thickness through the center 0.5 mm. Surface smooth or with microscopically minute papillae.

Embryonic chambers unknown.

Equatorial chambers known only in vertical section; height 0.05 to 0.06 mm, increase in height toward the periphery slight; length radially less than the height. The equatorial chambers project beyond the lateral chambers and produce a thin free edge as much as 0.30 mm wide.

Lateral chambers low, longer than tall, rather regular in size and shape; those in the same tier separated by thin walls; between adjacent tiers there are in some places very fine, thin pillars. Six or seven layers over the central part of the test.

The following description is based on the cotypes, illustrated on plate 27, figures 2, 3:

Interior part of test very thin, about 0.25 mm thick; margin expanded to a thickness of 1.0 mm on the edge. The piece here described and figured is 3.5 mm long, the pronounced expansion beginning about 2.5 mm from the periphery.

Equatorial chambers in the central part about 0.06 mm high and 0.10 mm long; at the periphery the vertical distance across the equatorial layer is 1 mm, the chambers may be divided into a few

chamberlets, and the distal wall is outwardly convex. Very near the edge the chamber walls are more or less interrupted. Distance between successive walls from 0.10 to 0.05 mm. Another section, plate 27, figure 3, in an oblique plane shows that the equatorial chambers when cut in the equatorial plane are either rhomboid or have an outer curved wall and an inner pointed end. Communication between adjacent chambers at the inner ends of the walls according to the condition common in *Lepidocyclina* is visible in many parts of the section.

There are three layers of lateral chambers except from the periphery to about 0.5 mm back from it, where there are none. The chambers are low, longer than high, in definite tiers, the tiers separated by thin pillars. Length between 0.05 and 0.10 mm.

*Lepidocyclina crassimargo* appears to represent a species which groups with *Lepidocyclina vaughani* Cushman. Both have thickened margins and diamond-shaped equatorial chambers. *L. vaughani* is a coarser, thicker species, with well-developed pillars. Since it has nephrolepidine embryonic chambers, *L. crassimargo* is tentatively placed in the subgenus *Nephrolepidina*.

*Locality and geologic horizon*.—North slope of La Piedra, north-east of Jamaica, near Guantánamo, Cuba, U.S.G.S. locality no. 7664, collected by N. H. Darton. Oligocene, probably upper.

#### LEPIDOCYCLINA (NEPHROLEPIDINA) PIEDRASENSIS Vaughan, n. sp.

Plate 27, fig. 4

Diameter of test about 10 mm, thickness through the center 1.5 mm. Surface papillate; the papillae rather thick and prominent, 0.20 to 0.25 mm in diameter, represent the emergent ends of pillars; outwardly radiating fibers, which converge at steep angles, distinct. The papillae are more crowded over the central part of the test, separated by interspaces about 0.15 mm wide; they are more distant toward the periphery, interspaces 0.4 mm or more in width.

Since there is only a vertical section the character of the embryonic chambers cannot be fully ascertained. The embryonic apparatus is rather large, composed of two chambers of unequal size separated by a sloping wall. The entire apparatus is about 1 mm in diameter and about half as thick in a vertical plane; the bounding wall rather thick, 0.02 mm or somewhat more.

The equatorial chambers increase in height very gradually and rather slightly as the periphery is approached.

The lateral chambers are low, considerably longer than high, crowded, and irregular in size and outline. There are eight or nine

layers on each side of the center, a little less than half as many at the periphery. Pillars irregular in development; some become very much thickened and form the papillae already mentioned.

*Locality and geologic horizon.*—North slope of La Piedra, northeast of Jamaica, near Guantánamo, Cuba, U.S.G.S. locality no. 7664, collected by N. H. Darton. Oligocene, probably upper.

Although this species is based on a single vertical section, so many features can be made out that, except ascertaining the shape of equatorial chambers in a horizontal section, its specific characterization is virtually complete.

LEPIDOCYCLINA (NEPHROLEPIDINA) sp. cf. *L. VERBEEKI*  
Newton and Holland

Plate 23, fig. 11

1932. *Lepidocyclina verbeeki* Barker, Geol. Mag., vol. 69, p. 278, pl. 16, figs. 1-5.

A Cuban species here figured is very similar to specimens from Ecuador, identified by Barker as *L. verbeeki* Newton and Holland. The specimen figured on plate 23, figure 11, has a half diameter of about 2.2 mm and a full diameter of about 4.5 mm; thickness through the center about 1.3 mm. The figure of the Cuban specimen should be compared with Barker's figures.

*Locality and geologic horizon.*—Just south of El Jique, west side, 6 miles above mouth of Rio Yateras, altitude 150 feet above sea-level, near Guantánamo, Cuba, U.S.G.S. locality no. 7553, O. E. Meinzer, collector. The geologic horizon is middle Oligocene. The Cuban material possesses an especial interest in that it suggests geologic correlation between one horizon of the Ecuadorian Tertiary section and deposits in Cuba.

LEPIDOCYCLINA (NEPHROLEPIDINA) sp.

Plate 21, fig. 2; plate 32, fig. 1

1924. *Lepidocyclina (Nephrolepidina) marginata* Vaughan, Bull. Geol. Soc. Amer., vol. 35, p. 798, pl. 34, fig. 1.

The specimens illustrated by plate 21, figure 2, and plate 32, figure 1, represent forms that have been identified by Cushman and others as *L. marginata*. There are at the Scripps Institution large suites of *L. marginata* from northern Italy, and comparison of them with the American material at my disposal convinces me that I have not seen *L. marginata* in any American collections that I have studied.

The specimens here figured were collected by D. R. Semmes and T. W. Vaughan on Rio Pantepec, 1.5 km south of Buena Vista Hacienda House, Puebla, Mexico, in the Meson middle Oligocene.

## LEPIDOCYCLINA (NEPHROLEPIDINA) DARTONI Vaughan, n. sp.

Plate 25, figs. 1, 2; plate 26, figs. 1, 2, 3

Test stellate, six-rayed; maximum diameter about 8.5 to 9 mm, between the rays much less, probably as little as 4 mm; rather thin. thickness not certainly known, probably about 1.75 mm. Surface reticulate, some rather thin, not very conspicuous, pillars, papillae inconspicuous or absent.

Embryonic chambers nephrolepidine, a smaller chamber partly embraced by a larger one. Dimensions of smaller chamber 0.4 by 0.3 mm; of larger chamber, 0.7 by 0.4 mm. In the type section there are three accessory chambers, one 0.5 mm long by 0.1 mm wide, and two smaller chambers each about 0.1 mm long and about half as wide.

Equatorial chambers spatulate, those on the rays larger than those in the interradial areas. The very variable size is better shown by the illustrations, plate 25, figure 2, than it can be by a description. In one vertical section (pl. 26, fig. 2), they are low, crowded, about 18 in 0.75 mm. The walls between successive layers thin. Between some of the adjacent tiers there are thin pillars.

The following is a description of the vertical section illustrated by plate 26, figure 3:

Test tumid in the central part. Semidiameter 3 mm, total diameter about 6 mm; thickness through the center about 1.7 mm; with a thin edge about 1.5 mm wide, tapering from 0.5 mm thick on the inner side to 0.2 mm thick at the periphery. Outer surface papillate, papillae slightly protuberant, best developed over the center, thickness 0.1 mm or somewhat more, and distant.

Embryonic chambers comprise a central chamber partly embraced by another chamber. Diameter of the apparatus in the equatorial plane 0.5 mm; height, maximum 0.25 mm.

Equatorial chambers low, near the center only 25  $\mu$  high, at the periphery about 50  $\mu$ . Length near the periphery, 100  $\mu$ .

Lateral chambers, height uniform but length very variable; number of layers on each side over the center about 13; the number decreases toward the periphery to only two layers at the outer edge. The walls between successive layers thin and of uniform thickness. Length ranges from 0.1 to 0.3 mm. Pillars not uniformly developed between all tiers of lateral chambers, some well developed, originating at the embryonic or equatorial chambers and increasing in thickness toward the outer surface. Maximum thickness of outer ends, a little more than 0.1 mm.

Comparison of figures 1, 2, and 3 shows that they represent the same species. There is obviously variation in the relative development of pillars and surface papillae.

*Locality and geologic occurrence.*—North slope of La Piedra, northeast of Jamaica, northeast of Guantánamo, Cuba, collected by N. H. Darton. Oligocene.

**LEPIDOCYCLINA (EULEPIDINA) sp. cf. L. DILATATA (Micht) Gumbel**

Plate 26, fig. 4; plate 27, figs. 5, 6; plate 28, figs. 1, 1a

1925. *Eulepidina dilatata* H. Douvillé, Revis. *Lepidocyclus*, p. 71, pl. 4, figs. 1-4; pl. 5, figs. 1-4 (with synonymy).

Since the illustrations here presented show the various features of the specimens here compared with *L. dilatata*, a detailed description seems unnecessary. The test is undulate, at least 16 mm in diameter, slightly umbonate, and as much as 2.7 mm thick through the center. The surface is reticulate-scribbulate with fine papillae, which are particularly well shown on plate 27, figure 5, over the embryonic chambers.

The relative length of the equatorial chambers as compared with their height is striking, the length of many chambers being from 1.5 times to twice the height. Another feature of the equatorial layer is its uniform thickness, there being little or no increase in thickness toward the periphery.

These specimens were identified by Cushman as *L. schlumbergeri* Lemoine and R. Douvillé, which is placed by H. Douvillé in the synonymy of *L. dilatata*. The vertical section of the embryonic chambers resembles the section of *L. clephantina* figured by Lemoine and R. Douvillé, but *L. dilatata* is smaller and it possesses distinct, but small, pillars.

*Locality and geologic horizon.*—North slope of La Piedra, northeast of Jamaica, northeast of Guantánamo, Cuba, U.S.G.S. locality no. 7664, collected by N. H. Darton. Oligocene, probably upper.

**LEPIDOCYCLINA (EULEPIDINA) FAVOSA Cushman**

Plate 17, figs. 1-3; plate 18, figs. 1-4; plate 19, figs. 1-4; plate 20, figs. 1-3; plate 21, figs. 1, 3, 4 (probably); plate 29, fig. 4

1919. *Lepidocyclus favosa* Cushman, Carnegie Inst. Washington Publ. 291, p. 66, pl. 3, figs. 1b, 2; pl. 15, fig. 4.

1919. *Lepidocyclus crassata* Cushman, idem, pp. 61, 62, pl. 11, figs. 4, 5.

1920. *Lepidocyclus chattahoocheensis* Cushman, U.S. Geol. Surv. Prof. Pap. 125, p. 65, pl. 23, figs. 1-4; pl. 24, figs. 1, 2.

1924. *Lepidocyclina* (*Nephrolepidina*) *crassata* Vaughan, Bull. Geol. Soc. Amer., vol. 35, p. 798, pl. 34, figs. 3, 4.
1924. *Lepidocyclina* (*Nephrolepidina*) *chattahoocheensis* Vaughan, idem, p. 798, pl. 34, fig. 2.
1924. *Lepidocyclina* (*Eulepidina*) *favosa* Vaughan, idem, p. 799, pl. 34, fig. 8.
1924. *Lepidocyclina* (*Eulepidina*) *formosa* Vaughan, idem, p. 799 (*not* Schlumberger).
1926. *Lepidocyclina* (*Eulepidina*) *formosa* Vaughan, Quart. Journ. Geol. Soc. London, vol. 82, p. 395 (*not* Schlumberger).

This is an amazingly variable species. Therefore, its discussion will be introduced by quoting the original description of each of three species which are here combined under one specific name.

Cushman's original description of *L. favosa* is as follows:

Test of medium size, compressed, strongly undulate or saddle-shaped, the central portion umbonate, much curved, thick; the remainder of the test thin and flangelike; central umbonate mass with an ornamentation of polygonal areas formed by raised ribs; remainder of test fairly smooth but irregularly eroded in most cases.

Vertical section with numerous distinct pillars in the umbonate region, broad at the exterior and narrowing to a point near the equatorial chambers, flattened peripheral portion with few indistinct pillars.

Diameter 15 to 18 mm for typical specimens.

Type specimens (U.S.N.M. no. 328199) from Antigua, Leeward Islands, U.S.G.S. no. 6881, from bluffs on north side of Willoughby Bay.

Cushman's original description of *L. crassata* is as follows:

Test of medium size, lenticular, comparatively thick in the center, thence tapering toward the sides; central portion convex, changing to a concave curve toward the periphery; surface irregularly pustulate, especially where somewhat weathered.

Vertical section shows the general shape, convex at the center and broadly rounded, thence thinning rapidly toward the periphery, where the surface is concave, to the rather poorly developed peripheral border; height or thickness of the test about one-third the diameter. Embryonic chamber large and very thick-walled, often showing 1 or 2 accessory chambers, also thick-walled and rather conspicuously perforate; young specimens show that for a time the embryonic chamber is the greater part of the test. Equatorial band of chambers rather large, even at the beginning, the outer wall convex and coarsely perforate. Lateral chambers comparatively thick-walled, several times broad as high, somewhat lenticular in section, highest in the middle; thence their height decreases toward the sides. A comparatively small number of pillars in the central part originating in the wall of the embryonic chamber and extending to the periphery.

Horizontal section shows that the equatorial chambers are regularly hexagonal and fairly thick-walled, and that those of successive annuli are of very different sizes.

Diameter up to 9 mm; height up to 3 mm or more.

Type specimen, section (U.S.N.M. no. 328192) from station 7513, orbitoidal limestone, outcrop where Palmer Trail joins Ocuja Trail, Cuba. Specimens are

also numerous in material from 7512, Ocuja; 7519, orbitoidal limestone, from drift near top of landslide next north of Los Melones; 7521, limestone, top of Mogote Peak, Cuba. All the specimens were collected by O. E. Meinzer.

Cushman's original description of *L. chattahoocheensis* is as follows:

Test of medium size, flattened or somewhat undulate; largest specimens measuring 25 mm in diameter, most specimens less, 16 to 22 mm; central region much thickened, prominently umbonate, making up about one-third of the test, nearly 5 mm through in the center of the thickened region in large specimens; the thin flattened peripheral border usually smooth or very finely papillate; the umbonate central region pitted with numerous small depressions.

The horizontal section shows the chambers of the equatorial band either hexagonal or with the peripheral angle an even convex curve; walls rather thin; annuli somewhat irregular in thickness.

In vertical section (pl. xxiii, fig. 4) the equatorial chambers increase in height toward the periphery, where they are at least three times as high as their diameter; lateral chambers compressed, broad and low, somewhat convex in the central region, where there are as many as 40 chambers in the central columns, diminishing in number toward the periphery, where in the flattened flangelike portion there are from 3 to 5 chambers superimposed, not together equaling the height of the equatorial chambers at the periphery. Pillars in the umbonal region strongly developed, wedge-shaped in section, the distal ends broadest and projecting beyond the lateral columns of chambers, giving the characteristic pitting of the surface.

Type specimen a vertical section from U.S.G.S. collection 3392, from the Chattahoochee formation at Glenns Well, 5 miles southeast of Bainbridge, Ga., collected by T. W. Vaughan.

In some of its characters this species resembles *L. favosa* Cushman, from Antigua, but it is less undulate, and its umbonal region is not so prominent nor so distinctly reticulate as in *L. favosa*. *L. favosa* does not attain so large a size as *L. chattahoocheensis*. The number of lateral chambers in the central columns in the species here described is unusually large.

In my 1926 paper cited above I briefly discussed some of the variations of *L. favosa* in considering *L. undosa* and its variants.

For this paper I have prepared, arranged, and had photographed a series of specimens to illustrate the features that I wish to emphasize. All of the specimens represented on plate 17 were collected by W. S. Adkins in the village of Espinal, State of Vera Cruz, Mexico, and all are from one lot from the base of what Adkins called the upper horizon. The six microspheric specimens illustrated by figure 1,  $\times 2$ , range from almost globose to compressed-undulate. The diameters can be measured on the figure. The thicknesses, measured from left to right, are as follows: First row, 6 mm, 8.5 mm, 6 mm; second row, 7.5 mm, 5.5 mm, 5 mm.

The specimen 8.5 mm thick has a diameter smaller than that of either of the specimens at the right-hand end of the rows, and their

thickness is respectively 6 and 5 mm. Figure 2 of plate 17 represents two megalospheric specimens,  $\times 5$ . The upper specimen has a nearly flat rim surrounding the inflated central part; while the lower specimen is distinctly saddle-shaped. Plate 17, figure 3, represents a megalospheric specimen,  $\times 10$ , to show the detail of the surface ornamentation. Every intermediate between the extremes of the variations is represented in the same lot of specimens.

Plate 18, figure 1, illustrates the type specimen of *L. chattahoocheensis* Cushman,  $\times 10$ . The type specimen is a vertical section caused by breaking. Figures 2, 3, 4 are illustrations of polished sections, each  $\times 10$ , of three specimens from the lowest bed exposed at Espinal. Comparison of figures 1 and 2 shows that they represent the same species. The other figures show variation.

Plate 19, figure 1, represents a vertical section,  $\times 20$ , of a topotype of *L. favosa*, while figures 2, 3, 4 illustrate topotypes of *L. chattahoocheensis*,  $\times 20$ . *L. favosa* varies in the thickness of its pillars and in the length of its lateral chambers. Specimens from Antigua completely overlap those from Espinal, Vera Cruz.

Plate 20, figures 1 and 2, are respectively a vertical and an equatorial section,  $\times 20$ , of megalospheric specimens from Espinal. Figure 3 represents the type specimen of Cushman's *L. crassata* from Cuba. Figures 1 and 2 obviously represent the same species.

Plate 21, figure 1, is a vertical section,  $\times 20$ , of a less inflated specimen collected by D. R. Semmes and myself at El Contento, Rio Pantepec, State of Puebla. A horizontal section, not illustrated, shows eulepidine embryonic chambers. Figures 3 and 4 represent vertical sections,  $\times 20$ , of specimens respectively from U.S.G.S. locality nos. 7518 and 7512, near Guantánamo, Cuba. These specimens have been identified as *L. sp. cf. L. marginata*. I am convinced that they do not belong to *L. marginata*. It is my opinion that figure 3 represents *L. favosa* and that figure 4 probably does. Figure 2 of the same plate illustrates an oblique equatorial section of a specimen collected by D. R. Semmes and myself near Buena Vista Hacienda House, Rio Pantepec, State of Puebla, not far from El Contento on the same river. This specimen is a *Nephrolepidina*, but I suspect that it may be a variant of *L. favosa*. Unfortunately, not enough specimens were obtained to study its variations.

*Localities and geologic occurrence.*—A number of specific localities have been given in quoting the original descriptions and in the discussion of the variation of the species. *L. favosa* is a common species in the middle Oligocene Glendon formation in Georgia, Florida, and Alabama; in the middle Oligocene Meson formation and the Oligocene

Alazan shale of Mexico; at many places in the Oligocene of eastern Cuba; in the middle Oligocene Antigua formation; and in Venezuela.

The specimen illustrated by plate 29, figure 4, deserves a note. It was collected by me in the Alazan shale at the crossing of the Alazan-Moyutta road over Rio Buena Vista, in association with *L. supera*. The specimen was hardened with shellac, removed from the shale in which it was embedded, and the side opposite the one photographed was ground down to the embryonic chambers. The species is a *Eulepidina* and differs from typical *L. favosa* only by the somewhat smaller pitting of the central inflated part of the test: if the Alazan is lower Oligocene, then both *L. supera* and *L. chattahoocheensis* range as low as lower Oligocene.

### LEPIDOCYCLINA GIGAS Cushman

Plate 22, figs. 1-4

1919. *Lepidocyclina gigas* Cushman, Carnegie Inst. Washington Publ. 291, p. 64, pl. 1, figs. 3-5; pl. 5, fig. 4.  
 1919. *Lepidocyclina undulata* Cushman, idem, p. 65, pl. 3, figs. 1a, 2, 8, 9; pl. 15, fig. 5.  
 1920. *Lepidocyclina undulata* Cushman, U.S. Geol. Surv. Prof. Pap. 125, p. 60, pl. 15, figs. 2-5.  
 1920. *Lepidocyclina gigas* Cushman, idem, p. 63, pl. 19, figs. 1-3 (not fig. 4).  
 1924. *Lepidocyclina gigas* and *Lepidocyclina undulata* Vaughan, Bull. Geol. Soc. Amer., vol. 35, p. 799.  
 1926. *Lepidocyclina gigas* Vaughan, Quart. Journ. Geol. Soc. London, vol. 82, p. 396, pl. 25, figs. 1a and 1b.

Cushman has given good descriptions and figures of the external features of *L. gigas* and its undulate variety, to which he applied the name *L. undulata*. In my 1924 and 1926 papers I discussed both *L. gigas* and *L. undulata* and their relation to *L. undosa*. In the collection of the Scripps Institution there is of *L. gigas* a topotype which is 85 mm in diameter. Originally, this specimen must have been fully 100 mm in diameter. A specimen of the *undulata* variety, although broken on the edges, is 80 mm in diameter. This species is probably not exceeded in size by any other species.

Plate 22, figure 1 is intended to illustrate the equatorial chambers,  $\times 20$ , near the periphery of a test, the upper edge of the figure being toward the periphery. Figures 2, 3, and 4 of the same plate illustrate a vertical section,  $\times 20$ , of the equatorial chambers and the lateral chambers on one side of the equatorial layer of less than one half of a specimen from the type locality in Antigua, lower bed at Hodges Bluff. Pillars are poorly developed, showing only occasionally in the

part of the specimen illustrated. As the number, arrangement, and other features can be seen in the figures, further description seems unnecessary. It will be remarked, however, that stoloniferous apertures can be seen in a few chambers near the peripheral end of figure 4.

*Localities and geologic horizon.*—*Lepidocyclina gigas* is one of the most conspicuous and widely distributed species in the middle Oligocene of the Caribbean and Gulf regions. The types were obtained by me at Hodges Bluff in the Island of Antigua, where it is an abundant species at many localities. It has been found in its typical or some varietal form in Cuba, southern Georgia and Alabama, Florida, eastern Mexico (where Cushman's var. *mexicana* is characteristic of the Meson formation), Jamaica, and elsewhere.

LEPIDOCYCLINA sp. indet. a

Plate 26, fig. 5

Test strongly inflated in the central portion; diameter, about 8 mm; thickness through the center, 4 mm; narrow, thin margin, about 1 mm wide and 0.4 mm thick around the edges; surface finely but strongly papillate, papillae, 0.10 to 0.15 mm thick and about the same distance apart, project very slightly above the outer surface.

Embryonic chambers unknown.

Equatorial chambers increase in height from the center toward the periphery, about 0.05 mm high at the center and 0.20 mm high at the periphery 4 mm from the center; the increase in length (radially) much less, about 0.05 mm near the center and between 0.075 and 0.10 mm at the periphery.

Lateral chambers strikingly regular in size and arrangement. Number of layers over the center about 35; the number decreases toward the periphery to only 3 or 4 at the margin of the test. The walls between successive layers are uniform in thickness, considerably thicker at the junction of adjacent tiers. The length of the chambers is also irregular, increasing somewhat toward the outer surface; a common length is about 0.15 mm. Pillars are well developed and are long; they increase slightly in thickness toward the outer surface where the emergent distal ends produce the papillae above described.

*Locality and geologic horizon.*—North slope of La Piedra, north-east of Jamaica, northeast of Guantánamo, Cuba, U.S.G.S. locality no. 7664, collected by N. H. Darton. Oligocene.

**LEPIDOCYCLINA** sp. indet. *b*

Plate 23, figs. 4, 5

The following notes are based on the examination of two vertical sections. Without additional material, it would not be advisable to name this form specifically, although it probably represents a new species.

Test lenticular, with a wide, sharply demarked, very thin marginal rim, which in one specimen attains a width of 0.63 mm. The more complete specimen has a diameter of 2.09 mm and a thickness of 0.57 mm. The other, in which the marginal rim is missing on one side, has a diameter of 1.52 mm and a thickness of 0.65 mm.

Embryonic chambers unknown.

The lateral chambers form regular tiers, each with 5 or 6 chambers, on each side of the equatorial layer. Their number decreases to the inner edge of the marginal rim, which is entirely composed of equatorial chambers. The lateral chambers at the periphery of the umbonate area have a length of 80  $\mu$  and a height of about 40  $\mu$  in one specimen, a length of 70  $\mu$  and a height of about 30  $\mu$  in the other. The floors are moderately thick and noticeably arched. The equatorial layer is about 40  $\mu$  thick at the center, increasing to 75  $\mu$  at the outer edge of the rim. The equatorial chambers have a radial diameter of about 30  $\mu$  at the center and of about 70  $\mu$  at the periphery.

Pillars are well developed in the umbonate portion of the test and have a diameter ranging from 60 to 90  $\mu$ . These would form a group of rather pronounced papillae on the surface of the test.

*Locality and geologic horizon.*—About  $\frac{3}{4}$  mile east of Ocuja Spring, and about  $4\frac{3}{4}$  miles due east of Monument H6 on the east boundary of the U.S. Naval Reservation at Guantánamo, U.S.G.S. locality, no. 7513, O. E. Meinzer, collector. Middle Oligocene.

**LEPIDOCYCLINA** sp. indet. *c*

Plate 23, figs. 6-8

Three vertical sections form the basis of the following notes. The material, however, is not sufficient for an adequate specific characterization.

Test compressed lenticular, with a narrow marginal rim. The diameter ranges from 3 mm to 5.5 mm and the thickness from 0.80 mm to 1.5 mm.

Embryonic chambers unknown.

There are about 10 lateral chambers on each side of the equatorial layer at the middle of the test. Although some of these are arranged in regular tiers, many are irregular and overlapping. The most marked irregularity occurs in the layers just over the equatorial layer. They regularly decrease in number toward the periphery, stopping at the marginal rim, which is composed of uncovered equatorial chambers. The chambers at the surface over the middle of the test have a length of about  $130\ \mu$  and a height of about  $40\ \mu$ . The roofs are thick and arched, particularly in those chambers nearest the equatorial layer. The equatorial layer is about  $120\ \mu$  thick in the middle of the test, increasing to about  $190\ \mu$  at the periphery. The equatorial chambers have a radial diameter of  $75\ \mu$  at the middle of the test. Those near the periphery have a radial diameter of about  $60\ \mu$ .

Pillars are irregularly developed. They range in surface diameter from  $75\ \mu$  to as much as  $120\ \mu$ .

*Localities and geologic horizon.*—Top of Mogote Peak,  $\frac{1}{2}$  mile east of east boundary of U.S. Naval Reservation and  $\frac{1}{4}$  mile south of Monument H4, U.S.G.S. locality no. 7521; O. E. Meinzer, collector. The geologic horizon is doubtful. The most abundant species is the one described. There is also an indeterminable small species of *Lepidocyclina* and a specimen of a species of *Carpenteria* identified by Cushman as *C. americana*, an Oligocene species. Until a larger fauna is known or *Lepidocyclina* sp. *c* indet. is found in association with other species, the geologic horizon will remain problematic.

#### LEPIDOCYCLINA? sp. indet. *d*

Plate 25, fig. 3

This is a small species, about 2 mm in diameter and 0.7 mm thick through the center. The section on which this note is based is oblique and unsatisfactory.

Embryonic chambers unknown.

Equatorial chambers project very slightly beyond the lateral. In the central part of the test they seem to form an irregular double series; series single toward the periphery. Height at the periphery 0.1 mm.

Lateral chambers form 3 layers over the center; the successive layers separated by thin walls; tiers of lateral chambers very indistinctly or not at all differentiated, there being long undivided spaces between the inner and outer walls of a layer.

This species may not belong to *Lepidocyclina*.

*Locality and geologic horizon.*—North slope of La Piedra, northeast of Jamaica, northeast of Guantánamo, Cuba, U.S.G.S. locality no. 7664, collected by N. H. Darton. Oligocene, probably upper.

## EXPLANATION OF PLATES

## PLATE 1

*Lepidocyclina (Lepidocyclina) novitasensis* Vaughan, n. sp.

FIGS. 1, 2. Cotypes from U.S.G.S. locality no. 3478, Nuevitas, Cuba, collected by A. C. Spencer. Fig. 1, horizontal section,  $\times 20$ , embryonic and equatorial chambers. Fig. 2, vertical section,  $\times 20$ .

FIG. 3. Vertical section,  $\times 20$ , of another specimen from U.S.G.S. locality no. 3478, Nuevitas, Cuba, collected by A. C. Spencer.

FIG. 4. Vertical section,  $\times 17$ , from locality no. 7522, Mogote Peak, near Guantánamo, Cuba, collected by O. E. Meinzer.

## PLATE 2

*Lepidocyclina (Lepidocyclina) subraulinii* Cushman. Microspheric form.

Topotypes from U.S.G.S. locality no. 3478, Nuevitas, Cuba, collected by A. C. Spencer.

FIGS. 1, 2. Vertical sections,  $\times 20$ , of the same specimen. Fig. 2 fits on the lower end of fig. 1.

FIG. 3. Equatorial chambers,  $\times 20$ , near the periphery, of another specimen.

## PLATE 3

FIG. 1. *Lepidocyclina (Lepidocyclina)* sp., probably *L. subraulinii* Cushman. Megalospheric form from U.S.G.S. locality no. 3478, Nuevitas, Cuba, collected by A. C. Spencer. Oblique section,  $\times 20$ , showing embryonic, lateral, and a few equatorial chambers.

FIGS. 2, 3. *Lepidocyclina (Lepidocyclina) meinzeri* Vaughan, n. sp. Oblique sections,  $\times 20$ , of two specimens from U.S.G.S. locality no. 3478, Nuevitas, Cuba, collected by A. C. Spencer.

## PLATE 4

FIG. 1. *Lepidocyclina (Lepidocyclina) meinzeri* Vaughan, n. sp. Section,  $\times 5$ , showing two specimens. Cotypes from U.S.G.S. locality no. 7522, south side of Mogote Peak, altitude about 375 feet above sea-level, collected by O. E. Meinzer.

FIG. 2. Another section,  $\times 5$ , U.S.G.S. locality no. 7522, showing (a) *Lepidocyclina (Lepidocyclina) novitasensis* Vaughan, n. sp. (see pl. 1, fig. 4, for enlarged view of this same specimen), (b) *Discocyclina (Discocyclina) pustulata* Cushman, (c) *Lepidocyclina (Lepidocyclina) meinzeri* Vaughan, n. sp. Cotype.

FIG. 3. *Lepidocyclina (Lepidocyclina) meinzeri* Vaughan, n. sp. Enlarged view,  $\times 17$ , of specimen represented by 2c.

FIG. 4. *Lepidocyclina (Lepidocyclina) meinzeri* Vaughan, n. sp. view,  $\times 17$ , of upper specimen in figure 1.

FIG. 5. *Lepidocyclina (Lepidocyclina) meinzeri* Vaughan, n. sp., peripheral part of a specimen,  $\times 17$ , from U.S.G.S. locality no. 7522.

FIG. 6. *Lepidocyclina (Nephrolepidina) perundosa* Cushman. Vertical section,  $\times 20$ . Type from U.S.G.S. locality no. 3478, Nuevitas, Cuba,

collected by A. C. Spencer, to show the very low lateral chambers and to bring out the difference between the lateral chambers of *Lepidocyclus meinzneri* and *L. perundosa*. *L. perundosa* lacks the strong pillars that are so well developed in *L. meinzneri*.

## PLATE 5

- FIGS. 1-3. *Lepidocyclus (Lepidocyclus) waylandvaughani* Cole. Fig. 1, surface views,  $\times 5$ , of two specimens. Topotypes. Locality, quarry on the Huasteca Petroleum Company's golf course, opposite Tampico, Tamaulipas, Mexico, collected by W. S. Cole. Figs. 2 and 3, *Lepidocyclus (Lepidocyclus) waylandvaughani* Cole from locality M29V, east of Los Naranjos, Vera Cruz, Mexico, collected by T. W. Vaughan and D. R. Semmes. Fig. 2, horizontal section,  $\times 20$ , to show equatorial chambers. Fig. 3, vertical section,  $\times 20$ .
- FIG. 4. *Lepidocyclus (Lepidocyclus) forresti* Vaughan. Vertical section,  $\times 20$ , of a cotype from Antigua.
- FIGS. 5, 6. *Lepidocyclus waylandvaughani* Cole from locality M38V, Huasteca Incline, Vera Cruz, Mexico, collected by T. W. Vaughan and D. R. Semmes. Fig. 5, surface view,  $\times 5$ , of a specimen to show extreme development of papillae. Fig. 6, vertical section,  $\times 20$ , of another specimen similar to foregoing specimen, also showing relatively large papillae.

## PLATE 6

- FIGS. 1-5. *Lepidocyclus (Lepidocyclus) canellei* Lemoine and R. Douvillé. Fig. 1, surface views of six specimens,  $\times 5$ , topotypes, from U.S.G.S. locality no. 6027, Bohio, Panama Canal Zone (locality now covered by the water of Gatun Lake), collected by T. W. Vaughan and D. F. MacDonald. Fig. 2, vertical section,  $\times 20$ , topotype. Fig. 3, horizontal section,  $\times 20$ , topotype. Fig. 4, surface views of four specimens, a dwarf variety,  $\times 10$ , from locality M12V, Arbol Grande, near Tampico, Tamaulipas, Mexico, collected by D. R. Semmes. Fig. 5, horizontal section,  $\times 20$ , of one of the specimens represented by fig. 4.
- FIG. 6. *Lepidocyclus (Lepidocyclus) pancanalis* Vaughan and Cole, surface views of six specimens,  $\times 10$ . Coconut Hill, Antigua.

## PLATE 7

*Lepidocyclus (Lepidocyclus) parvula* Cushman.

- FIGS. 1-3. Sections,  $\times 20$ , of three cotypes from U.S.G.S. locality no. 6862, lower bed at Hodges Bluff, Antigua, collected by T. W. Vaughan.
- FIGS. 4, 5. Two microspheric specimens from High Point, Antigua, collected by W. R. Forrest. Fig. 4, horizontal section,  $\times 20$ . Fig. 5, vertical section,  $\times 20$ .

## PLATE 8

- FIGS. 1, 2. *Lepidocyclus (Lepidocyclus) parvula* Cushman, var. *crassata* Vaughan and Cole, n. var., from locality M12V, Arbol Grande,

near Tampico, Tamaulipas, Mexico, collected by T. W. Vaughan. Fig. 1, vertical section,  $\times 20$ , showing the heavy pillars and restricted lateral chambers. Fig. 2, horizontal section,  $\times 20$ .

- FIGS. 3-5. *Lepidocyclina parvula* Cushman. Three specimens from locality M30V, Transcontinental Railroad, 5 km east of Los Naranjos, Cantón of Tuxpan, Vera Cruz, Mexico, collected by T. W. Vaughan and D. R. Semmes. Fig. 3, vertical section,  $\times 20$ , of a microspheric specimen. Fig. 4, section of pillars,  $\times 20$ . Fig. 5, horizontal section,  $\times 20$ , cutting a part of the equatorial plane of a probably microspheric specimen.

## PLATE 9

*Lepidocyclina (Lepidocyclina) parvula* Cushman.

- FIGS. 1, 2. Surface views,  $\times 5$ , of three specimens. Topotypes from U.S.G.S. locality no. 6862, lower bed at Hodges Bluff, Antigua, collected by W. R. Forrest.
- FIG. 3. Six specimens,  $\times 5$ , from 7 km east of Los Naranjos, Vera Cruz, Mexico.
- FIG. 4. Six specimens,  $\times 10$ , from 7 km east of Los Naranjos, collected by D. R. Semmes.

## PLATE 10

- FIGS. 1-6. *Lepidocyclina (Lepidocyclina) parvula* Cushman, collected by W. R. Forrest. Fig. 1, surface view,  $\times 10$ , from altitude 100 feet, Lynch Cliff, Antigua. Fig. 2,  $\times 10$ , Hudson Cove, Antigua. Fig. 3,  $\times 10$ , the other side of the specimen represented by fig. 1. Fig. 4, surface view,  $\times 10$ , from tilted beds east of Lynch's, Antigua. Fig. 5, horizontal sections,  $\times 20$ , of a specimen similar to the one represented by fig. 4, from tilted beds east of Lynch's, Antigua. Fig. 6, surface views of two specimens,  $\times 6$ , from Lynch Path, altitude 150 feet, Antigua.
- FIG. 7. *Lepidocyclina (Lepidocyclina) parvula* Cushman, var. *crassicosta* Vaughan and Cole, n. var., surface view,  $\times 10$ , of the type from Mercer's Creek, Antigua, collected by W. R. Forrest. This specimen has a central knob from which six arms radiate. It is an extreme form, but it should be compared with the upper of the two specimens illustrated in fig. 6 and with other specimens referred to *L. parvula*.
- FIG. 8. *Lepidocyclina antiguensis* Vaughan and Cole, n. sp., surface view,  $\times 10$ , of the type from ridge southeast of Freetown, altitude 200-250 feet, Antigua, collected by W. R. Forrest.
- FIGS. 9, 10. *Lepidocyclina (Lepidocyclina) giraudi* R. Douvillé. Surface views,  $\times 10$ , of two topotypes from Martinique Island, French West Indies, collected by J. Giraud.

## PLATE 11

- FIGS. 1-3. *Lepidocyclina (Lepidocyclina) yurnagunensis* Cushman from U.S. G.S. locality no. 7548, west side of Yateras River, about  $2\frac{1}{2}$  miles south of Yuraguana, Cuba, collected by O. E. Meinzer. Fig. 1,

surface views,  $\times 10$ , of two topotypes. Fig. 2, vertical sections,  $\times 20$ , of original cotypes. Fig. 3, horizontal section,  $\times 20$ , of topotype.

FIG. 4. *Lepidocyclus* (*Lepidocyclus*) *yurnagunensis* Cushman, horizontal section,  $\times 27$ , of a specimen from U.S.G.S. locality no. 7516, west end of Los Melones Mountain, Cuba, collected by O. E. Meinzer.

FIGS. 5-9. *Lepidocyclus* (*Lepidocyclus*) *yurnagunensis* Cushman var. *morgani* Vaughan. Figs. 5, 6, vertical sections,  $\times 21$ , from U.S.G.S. locality no. 7513, outcrop where Palmer Trail joins Ocuja Trail, Cuba, collected by O. E. Meinzer, identified by Cushman as *L. morgani*. Fig. 7, vertical section,  $\times 20$ , specimen from U.S.G.S. locality no. 7554, south of El Jique, 5 miles above the mouth of Yateras River on west side, Cuba, collected by O. E. Meinzer, identified by Cushman as *L. morgani*. Figs. 8, 9, vertical sections of cotypes,  $\times 21$ , from U.S.G.S. locality no. 7543, limestone outcrop east of Yateras, Cuba, collected by O. E. Meinzer, showing the same features as specimens identified by Cushman as *L. morgani*.

#### PLATE 12

- FIGS. 1-5. *Lepidocyclus* *hodgensis* Vaughan and Cole, n. sp. Locality, Hodge's Hill, uppermost bed, Antigua, collected by W. R. Forrest. Figs. 1, 2, surface views,  $\times 10$ , of four specimens. Fig. 3, vertical section,  $\times 20$ . Fig. 4, horizontal section of a microspheric individual,  $\times 20$ . Fig. 5, enlarged portion,  $\times 85$ , of same section illustrated in fig. 4, showing initial embryonic coil of the microspheric form.
- FIGS. 6, 7. *Lepidocyclus* (*Lepidocyclus*) *wetherellensis* Vaughan and Cole, n. sp. Locality, Wetherell Cliff, Antigua, collected by W. R. Forrest. Fig. 6, surface view,  $\times 10$ , of the type. Fig. 7, horizontal section,  $\times 7$ , showing embryonic chambers.

#### PLATE 13

- FIGS. 1, 2. *Lepidocyclus* (*Nephrolepidina*) *tournoyeri* Lemoine and R. Douvillé from locality M12V, Arbol Grande near Tampico, Tamaulipas, Mexico, collected by T. W. Vaughan. Fig. 1, vertical section of a megalospheric individual,  $\times 20$ . Fig. 2, horizontal section,  $\times 20$ , showing the embryonic and equatorial chambers.
- FIGS. 3-6. *Lepidocyclus* (*Nephrolepidina*) *tempanii* Vaughan and Cole, n. sp. Fig. 3, vertical section,  $\times 21$ , of specimen from near top of Hodge Hill, Antigua, collected by W. R. Forrest. Fig. 4, horizontal section,  $\times 21$ , of a megalospheric individual from the same locality as fig. 3. Fig. 5, same section as that represented by fig. 4, but  $\times 43$ . Fig. 6, horizontal section,  $\times 20$ , of a specimen from U.S.G.S. locality no. 6862, Hodge Point, collected by T. W. Vaughan.

#### PLATE 14

*Lepidocyclus* (*Nephrolepidina*) *fragilis* Cushman from U.S.G.S. locality no. 7194, Ocala limestone at the mouth of cavern about 200 yards southwest of wagon bridge over Chipola River, east of Marianna, Florida.

FIG. 1. Vertical section,  $\times 20$ , megalospheric form.

FIGS. 2, 3. Vertical section,  $\times 20$ , microspheric form; fig. 3 fits on the upper end of fig. 2.

FIG. 4. Part of a horizontal section,  $\times 20$ , near the periphery, showing the equatorial chambers.

## PLATE 15

FIGS. 1, 2. *Lepidocyclina (Nephrolepidina) tantoyucensis* Vaughan and Cole, n. sp., from locality M92V, about 4.5 km from Chila Cortaza, on the road to Tantoyuca, about 10 km east of Tantoyuca, Mexico, collected by T. W. Vaughan and D. R. Semmes. Fig. 1, vertical section,  $\times 20$ , of a microspheric individual. Fig. 2, horizontal section,  $\times 20$ , of a megalospheric individual.

FIGS. 3-5. *Lepidocyclina (Nephrolepidina) semmesi* Vaughan and Cole, n. sp. from locality D.R.S. 26 near Tamemas, in the Tantoyuca district, at the west end of the second east-west hill north of Peregrino, Mexico, collected by D. R. Semmes. Figs. 3, 4, oblique section,  $\times 20$ , of a specimen showing embryonic chambers. Fig. 5, vertical section,  $\times 20$ , of another specimen, probably a megalospheric individual.

## PLATE 16

*Lepidocyclina (Nephrolepidina) vaughani* Cushman.

FIG. 1. Vertical section,  $\times 20$ , of a topotype from U.S.G.S. locality no. 6021, limestone along the relocated line of the Panama Railroad, opposite San Pablo, Panama Canal Zone, collected by T. W. Vaughan and D. F. MacDonald.

FIG. 2. Vertical section,  $\times 20$ , from Half Moon Bay, Antigua, collected by W. R. Forrest.

FIG. 3. Horizontal section,  $\times 20$ , of specimen from Half Moon Bay, Antigua, collected by W. R. Forrest.

FIGS. 4, 5. Parts of same specimen,  $\times 20$ , topotype, U.S.G.S. locality no. 6021, Panama Canal Zone. Fig. 4, section,  $\times 20$ , near the periphery to show the lozenge-shaped equatorial chambers. Fig. 5 shows the embryonic chambers,  $\times 20$ , and the fine papillae on the surface near the center of the test.

## PLATE 17

*Lepidocyclina (Eulepidina) favosa* Cushman. All specimens from Espinal, Vera Cruz, Mexico, collected by W. S. Adkins.

FIG. 1. Surface view,  $\times 2$ , of six microspheric specimens.

FIG. 2. Surface view,  $\times 5$ , of two megalospheric specimens.

FIG. 3. Surface view,  $\times 10$ , of a megalospheric specimen.

## PLATE 18

*Lepidocyclina (Eulepidina) favosa* Cushman.

FIG. 1. Type specimen,  $\times 10$ , of *L. chatahoocheensis* Cushman from U.S.G.S locality no. 3392, at Glens Well, 5 miles south of Bainbridge, Ga., collected by T. W. Vaughan.

FIGS. 2, 3, 4. Vertical sections,  $\times 10$ , of three specimens, all from Espinal, Mexico, for comparison with the type of *L. chatahoocheensis*.

## PLATE 19

*Lepidocyclina (Eulepidina) favosa* Cushman.

FIG. 1. Vertical section,  $\times 20$ , of a topotype from U.S.G.S. locality no. 6881, from bluffs on north side of Willoughby Bay, Antigua.

FIG. 2. Embryonic chambers,  $\times 20$ , of a topotype of *Lepidocyclina chatahoocheensis* Cushman.

FIG. 3. Vertical section,  $\times 20$ , of a topotype of *L. chatahoocheensis* Cushman.

FIG. 4. Vertical section,  $\times 20$ , of a topotype, *L. chatahoocheensis* Cushman.

## PLATE 20

*Lepidocyclina (Eulepidina) favosa* Cushman.

FIG. 1. Vertical section,  $\times 20$ , of a megalospheric specimen from Espinal, Vera Cruz, Mexico.

FIG. 2. Horizontal section,  $\times 20$ , of a megalospheric specimen from Espinal, Vera Cruz, Mexico.

FIG. 3. *Lepidocyclina crassata* Cushman, holotype,  $\times 20$ , U.S.G.S. locality no. 7513, outcrop where Palmer Trail joins Ocuja Trail, Cuba, collected by O. E. Meinzer.

## PLATE 21

FIGS. 1, 3, 4. *Lepidocyclina (Eulepidina) favosa* Cushman. Fig. 1, vertical section,  $\times 20$ , of a less inflated specimen from locality M70V, at El Contento, Rio Pantepec, State of Puebla, Mexico, collected by T. W. Vaughan and D. R. Semmes. Fig. 3, vertical section,  $\times 20$ , from U.S.G.S. locality no. 7518, south side of Los Melones Mountain near west end, Cuba. Fig. 4, vertical section,  $\times 20$ , from U.S.G.S. locality no. 7512, Ocuja, Cuba.

FIG. 2. *Lepidocyclina (Nephrolepidina)* sp. Horizontal section,  $\times 20$ , of a form which has been identified as *L. marginata* by Cushman and others, from Rio Pantepec, 1.5 km south of Buena Vista Hacienda House, Puebla, Mexico. (See also pl. 32, fig. 1.)

## PLATE 22

*Lepidocyclina gigas* Cushman. Topotypes from U.S.G.S. locality no. 6862, lower bed at Hodges Bluff, Antigua, collected by T. W. Vaughan.

FIG. 1. Equatorial chambers,  $\times 20$ , near the periphery.

FIGS. 2-4. Vertical section,  $\times 20$ . These three figures fit together and make one continuous section.

## PLATE 23

- FIGS. 1-3. *Lepidocyclina yurnagumensis* var. *morganopsis* Vaughan. Figs. 1, 3, vertical sections,  $\times 27$ , of specimens from U.S.G.S. locality no. 7516, west end of Los Melones Mountain, Cuba, collected by O. E. Meinzer. Fig. 2, oblique section,  $\times 29$ , of a specimen from U.S.G.S. locality no. 7548, west side of Yateras River, about  $2\frac{1}{2}$  miles south of Yuraguana, Cuba.
- FIGS. 4, 5. *Lepidocyclina* sp. indet. *b*. Vertical section,  $\times 21$ , of specimens from U.S.G.S. locality no. 7513, outcrop where Palmer Trail joins Ocuja Trail, Cuba, collected by O. E. Meinzer.
- FIGS. 6-8. *Lepidocyclina* sp. indet. *c*. Three vertical sections of specimens from U.S.G.S. locality no. 7321, top of Mogote Peak, Cuba, collected by O. E. Meinzer.
- FIGS. 9, 10. *Lepidocyclina* sp. cf. *L. wetherellensis* Vaughan and Cole, n. sp. Vertical sections of specimens from U.S.G.S. locality no. 7513, outcrop where Palmer Trail joins Ocuja Trail, Cuba, collected by O. E. Meinzer.
- FIG. 11. *Lepidocyclina* (*Nephrolepidina*) sp. cf. *L. verbeeki* Newton and Holland. Vertical section,  $\times 29$ , of specimen from U.S.G.S. locality no. 7553, south of El Jique, west side, 6 miles above mouth of Rio Yateras, near Guantánamo, Cuba, collected by O. E. Meinzer.

## PLATE 24

- FIG. 1. *Lepidocyclina parvula* Cushman var. *crassicosta* Vaughan and Cole, n. var. Surface view,  $\times 10$ , of two specimens from locality M70V, El Contento on Rio Pantepec, State of Puebla, Mexico, collected by T. W. Vaughan and D. R. Semmes.
- FIGS. 2, 3. *Lepidocyclina* (*Lepidocyclina*) *antiguensis* Vaughan and Cole, n. sp., from Lynch Path, Antigua, altitude 150 feet, collected by W. R. Forrest. Fig. 2, horizontal section,  $\times 28$ , of a microspheric individual to show equatorial chambers. Fig. 3, vertical section,  $\times 28$ , of another specimen.
- FIG. 4. *Lepidocyclina* (*Lepidocyclina*) *giraudi* R. Douvillé. Horizontal section,  $\times 28$ , of a microspheric individual to show the initial coil and the size and shape of the equatorial chambers. Topotype from Pointe Macabou, Martinique, collected by J. Giraud.
- FIG. 5. *Lepidocyclina wetherellensis* Vaughan and Cole, n. sp. Vertical section,  $\times 28$ , cotype from Wetherell Cliff, south end, Antigua, collected by W. R. Forrest.

## PLATE 25

- FIGS. 1, 2. *Lepidocyclina* (*Nephrolepidina*) *dartoni* Vaughan, n. sp. from U.S. G.S. locality no. 7664, north slope of La Piedra, northeast of Jamaica, northeast of Guantánamo, Cuba, collected by N. H. Darton. Fig. 1, surface view,  $\times 5$ , to show the stellate form of the test. Fig. 2, horizontal section,  $\times 20$ , to show the character of the embryonic apparatus and the variable size and shape of the equatorial chambers, particularly along the rays.

- FIG. 3. *Lepidocyclina?* sp. indet. *d*, also from locality no. 7664. Vertical section,  $\times 55$ , to show the peculiar arrangement of equatorial and lateral chambers.

## PLATE 26

- FIGS. 1-3. *Lepidocyclina* (*Nephrolepidina*) *dartoni* Vaughan, n. sp., from U.S. G.S. locality no. 7664, north slope of La Piedra, northeast of Jamaica, northeast of Guantánamo, Cuba, collected by N. H. Darton. Fig. 1, oblique section,  $\times 20$ , showing some of the equatorial chambers. Figs. 2, 3, vertical sections,  $\times 20$ , of megalospheric individuals.
- FIG. 4. *Lepidocyclina* (*Eulepidina*) sp. cf. *L. dilatata* (Micht) Gümbel, also from U.S.G.S. locality no. 7664. Surface view,  $\times 2$ , to show the small umbo and characteristic appearance of the surface.
- FIG. 5. *Lepidocyclina* sp. indet. *a* from U.S.G.S. locality no. 7664. Vertical section,  $\times 20$ , showing the inflated test and the striking regular tiers of lateral chambers.

## PLATE 27

- FIGS. 1-3. *Lepidocyclina* (*Nephrolepidina?*) *crassimargo* Vaughan n. sp., from U.S.G.S. locality no. 7664, north slope of La Piedra, northeast of Jamaica, near Guantánamo, Cuba, collected by N. H. Darton. Fig. 1, vertical section,  $\times 20$ . Fig. 2, cotype,  $\times 20$ , shows the expanded marginal portion as seen in a fragmentary vertical section. Fig. 3, cotype,  $\times 20$ , represents the type of equatorial chambers observed in a slightly oblique section.
- FIG. 4. *Lepidocyclina* (*Nephrolepidina*) *piedrasensis* Vaughan, n. sp., from U.S. G.S. locality no. 7664. Vertical section,  $\times 20$ , of a megalospheric individual.
- FIGS. 5, 6. *Lepidocyclina* (*Eulepidina*) sp. cf. *L. dilatata* (Micht) Gümbel from U.S.G.S. locality no. 7664. Fig. 6,  $\times 20$ , represents a continuation of the same vertical section as seen in fig. 5. The eulepidine embryonic chambers and the elongate, compressed equatorial chambers are well illustrated in these figures.

## PLATE 28

*Lepidocyclina* (*Eulepidina*) sp. cf. *L. dilatata* (Micht) Gümbel from U.S.G.S. locality no. 7664, north slope of La Piedra, northeast of Jamaica, northeast of Guantánamo, Cuba. All figures represent portions of the same vertical section,  $\times 20$ . The undulate character of the test as well as the internal details can be observed in this section.

## PLATE 29

- FIGS. 1-3. *Lepidocyclina* (*Lepidocyclina*) *supera* (Conrad). Figs. 1, 2, are external views,  $\times 10$ , of two specimens from the Alazan-Moyutla crossing over the Rio Buena Vista, Cantón of Tuxpan, State of Vera Cruz, Mexico, collected by T. W. Vaughan and D. R.

Semmes. Fig. 3 is an external view of a specimen,  $\times 10$ , from the Byram marl of Mississippi, introduced for comparison with the Mexican specimens.

- FIG. 4. *Lepidocyclina favosa* Cushman. External view,  $\times 10$ , of a specimen from the Alazan-Moyutla crossing over the Río Buena Vista, Cantón of Tuxpan, State of Vera Cruz, Mexico, collected by T. W. Vaughan and D. R. Semmes. This figure should be compared with the figures of *L. favosa* on preceding plates.

## PLATE 30

- FIG. 1. *Lepidocyclina (Nephrolepidina) semmesi* Vaughan and Cole, n. sp. Surface view,  $\times 10$ , of a specimen from 0.6 km southwest of Dos Caminos (M106V), near Tantoyuca, Mexico. Compare with plate 32, fig. 3.
- FIG. 2. *Lepidocyclina (Nephrolepidina) semmesi* var. *granosa* Vaughan and Cole, n. var. Surface,  $\times 10$ , of a specimen from east side of Tantoyuca, 50 to 70 feet above bed of arroyo (M96V).

## PLATE 31

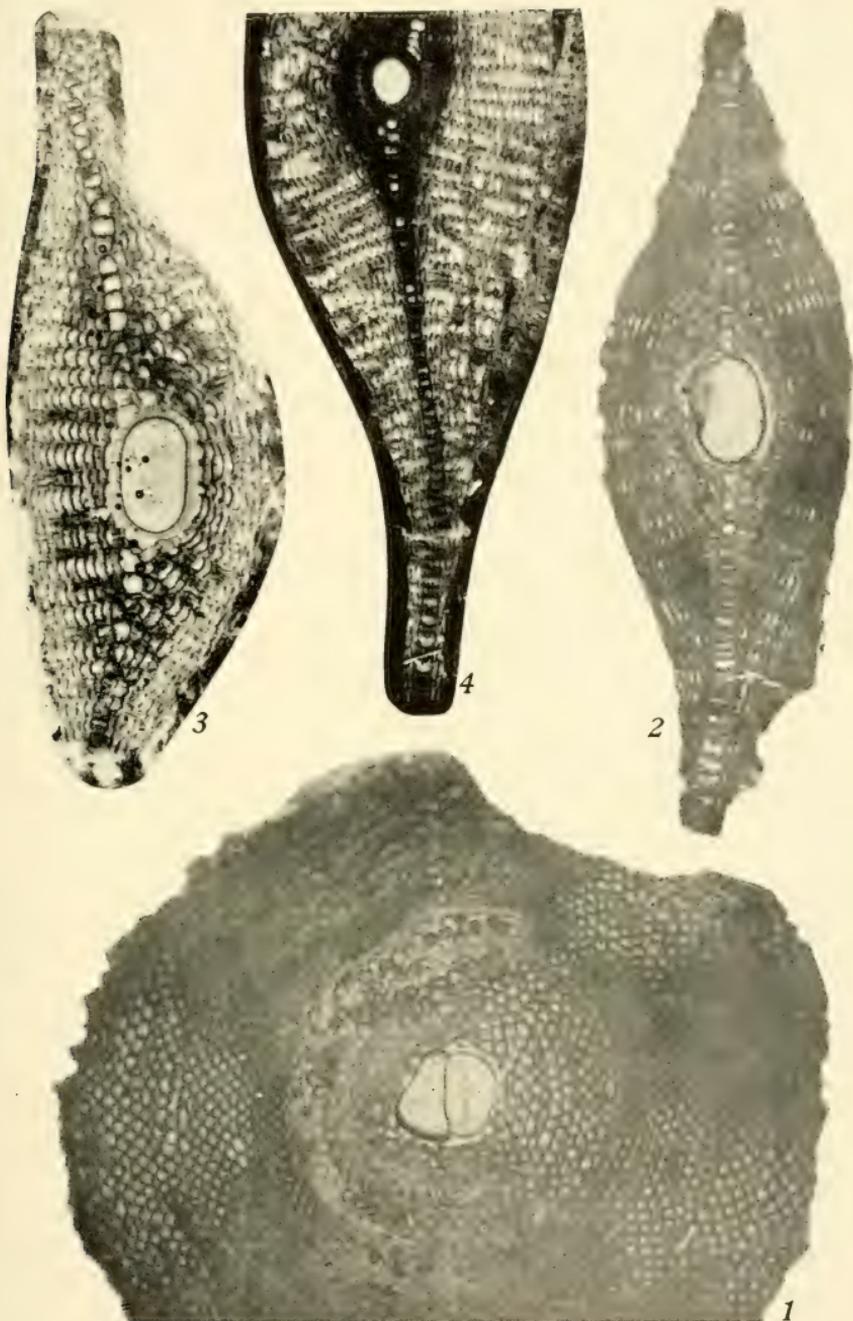
*Lepidocyclina (Nephrolepidina) semmesi* Vaughan and Cole, n. sp.

- FIGS. 1, 1a. Vertical section,  $\times 20$ , of a large, microspheric specimen from west side of the creek at Chila Cortaza (M88V). Compare this section with plate 32, fig. 3, a specimen from 0.6 km southwest of Dos Caminos.

## PLATE 32

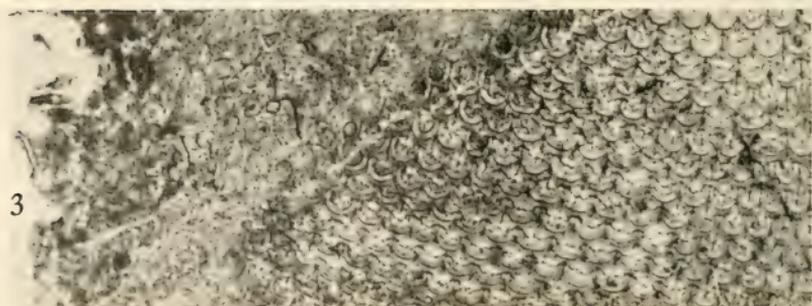
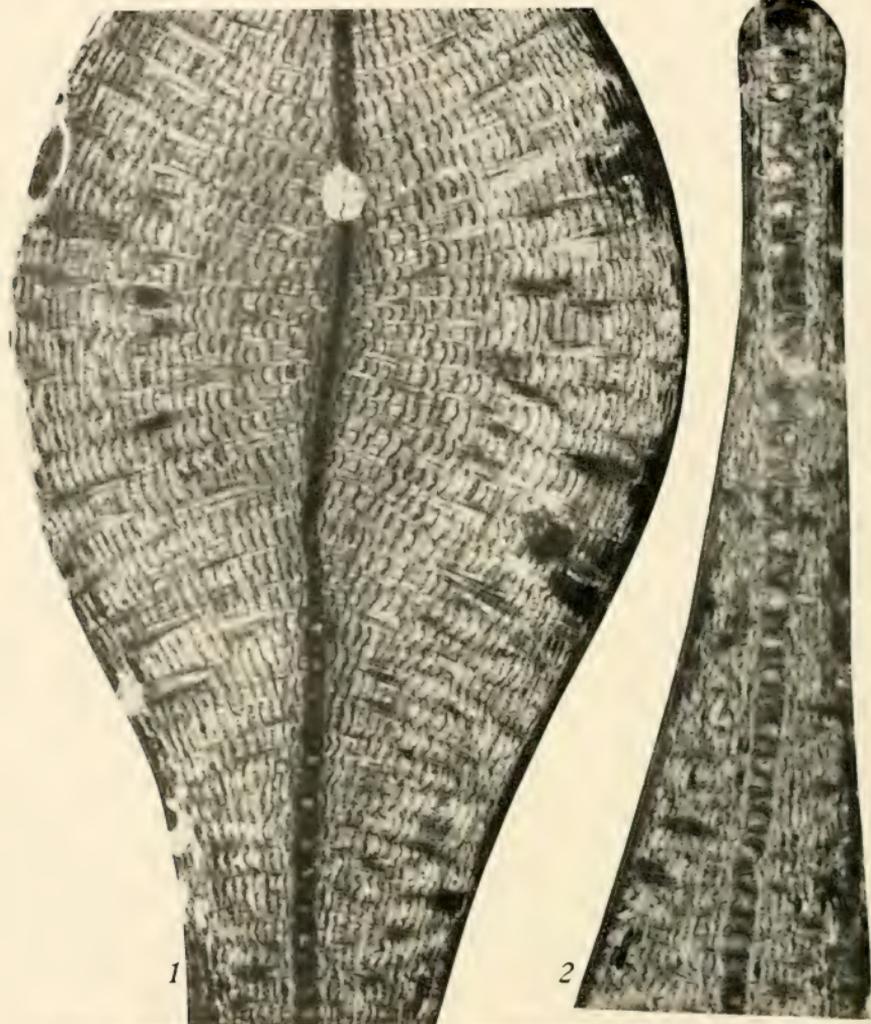
- FIG. 1. *Lepidocyclina (Nephrolepidina)* sp. Surface view of a specimen,  $\times 10$ , from El Contento, Río Pantepec, State of Puebla, Mexico. This specimen shows blisters over what appear as pits in weathered specimens. This is the same species as that represented by plate 21, fig. 2, and has been identified as *L. marginata* (Micht).
- FIGS. 2, 3. *Lepidocyclina (Nephrolepidina) semmesi* Vaughan and Cole, n. sp. Fig. 2, vertical section,  $\times 20$ , of a small, probably megalospheric specimen, from west side of Chila Cortaza Creek (M88V). Compare with plate 15, figs. 3-5. Fig. 3, vertical section,  $\times 15$ , of a specimen from 0.6 km southwest of Dos Caminos. This specimen is one of the same lot and similar in every respect to the specimen figured on plate 30, fig. 1. Compare it also with the specimen figured on plate 31. Their similarity is obvious.





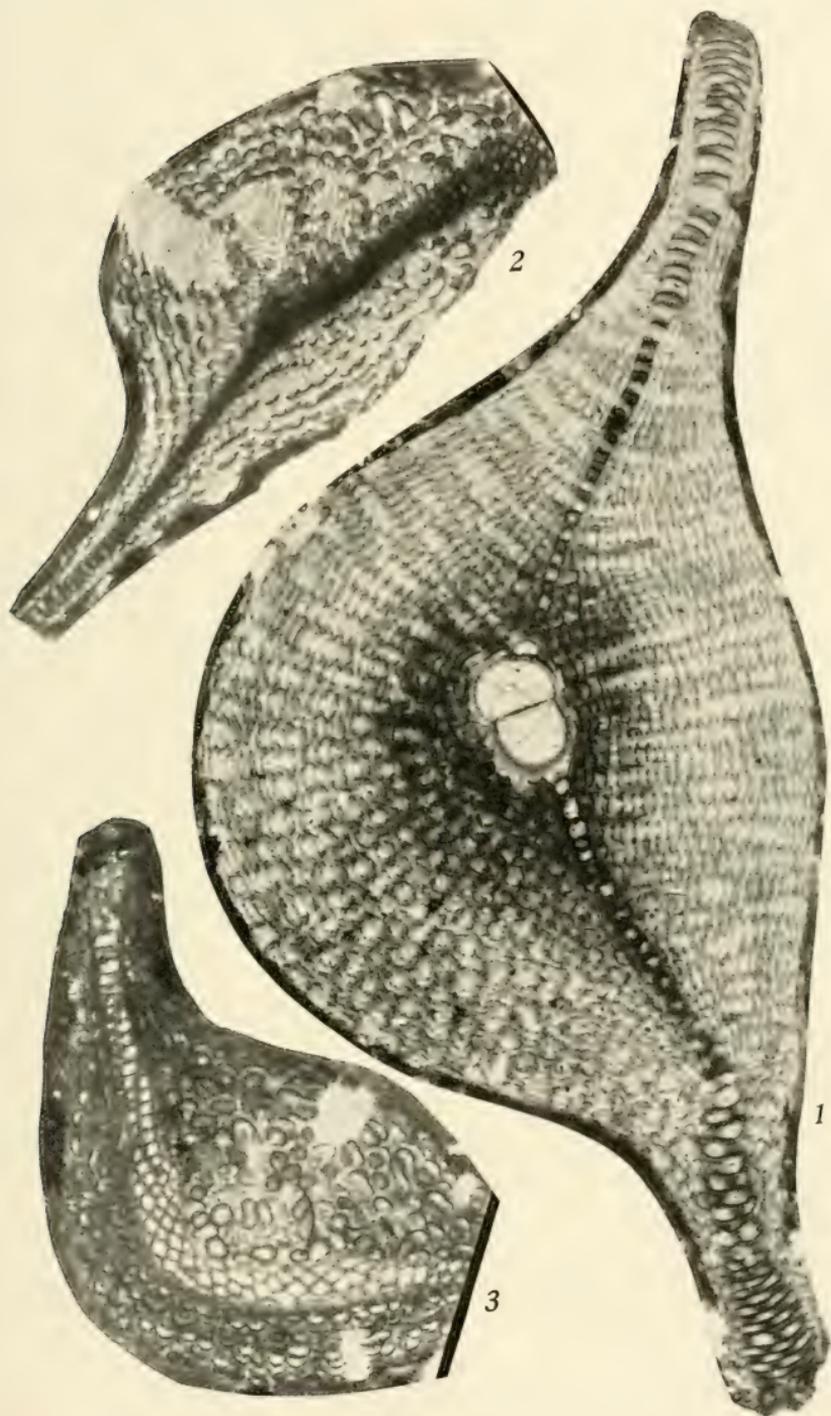
AMERICAN SPECIES OF *LEPIDOCYCLINA*

(For explanation, see page 45.)



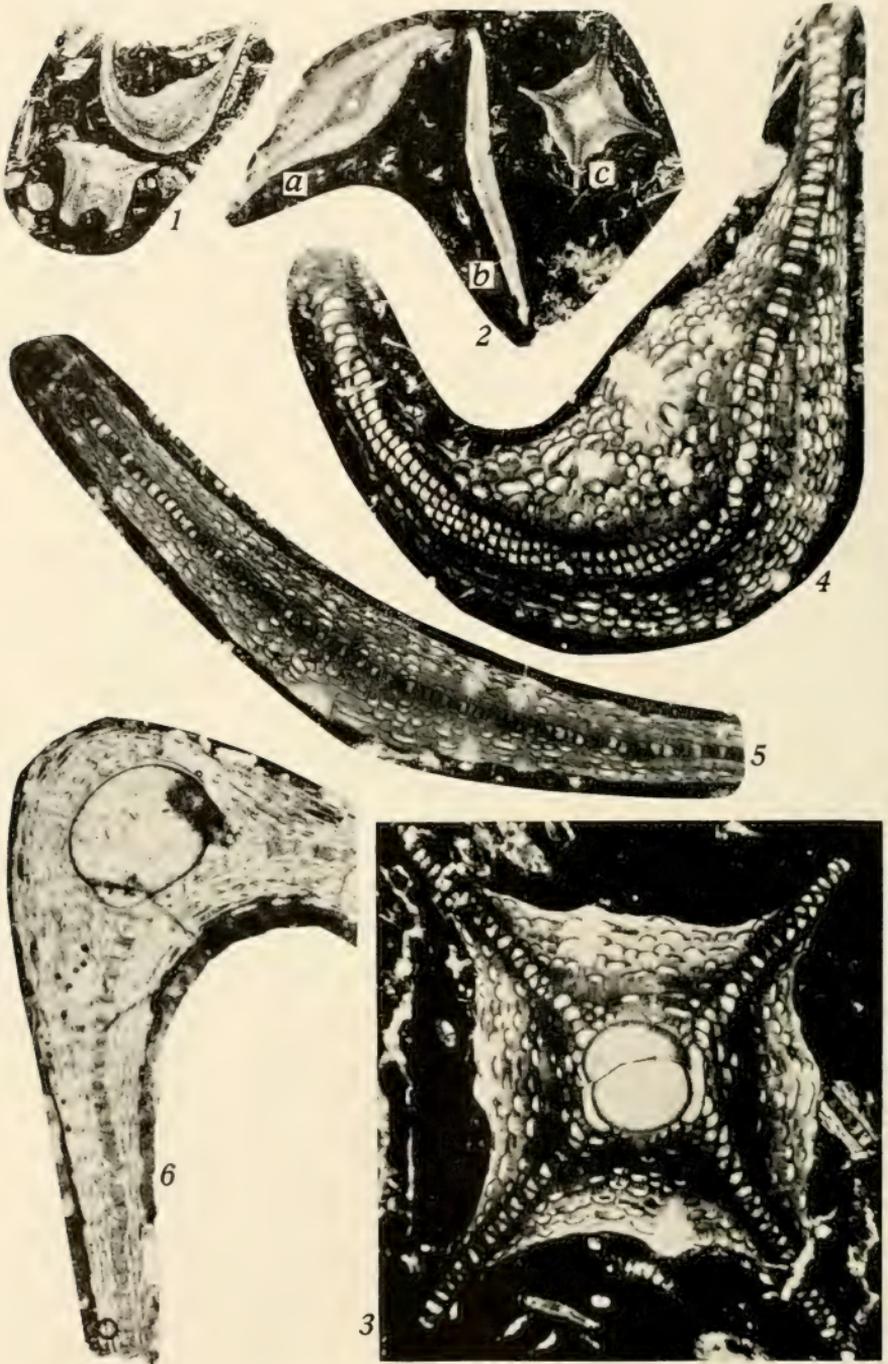
AMERICAN SPECIES OF LEPIDOCYCLINA

(For explanation, see page 45.)

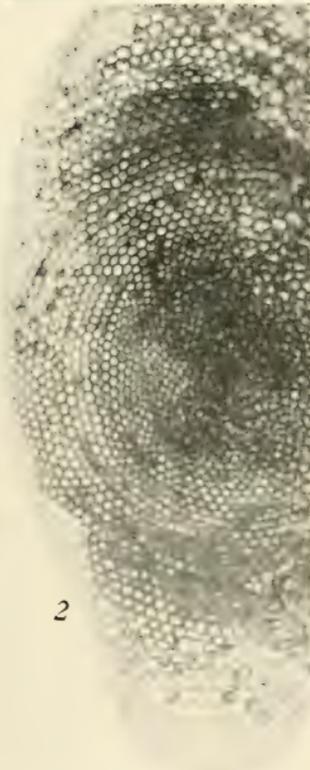
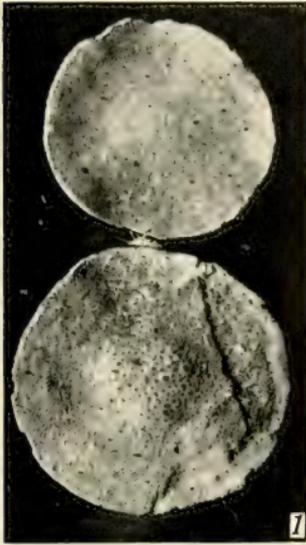


AMERICAN SPECIES OF LEPIDOCYCLINA

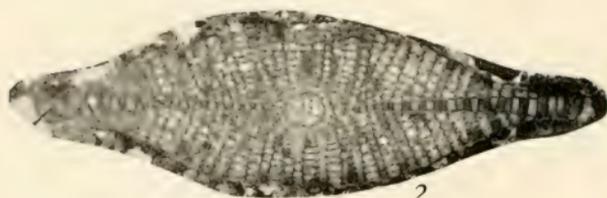
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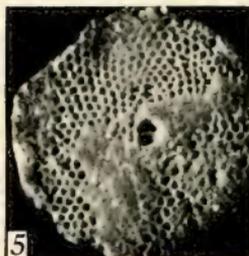
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(For explanation, see page 45.)



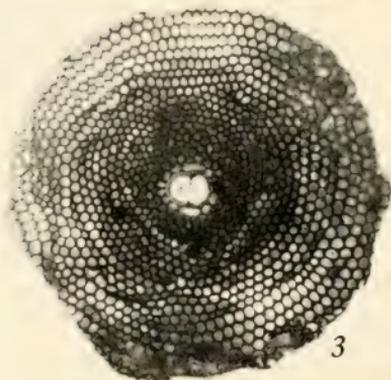
AMERICAN SPECIES OF *LEPIDOCYCLINA*  
(For explanation, see page 46.)



2



5



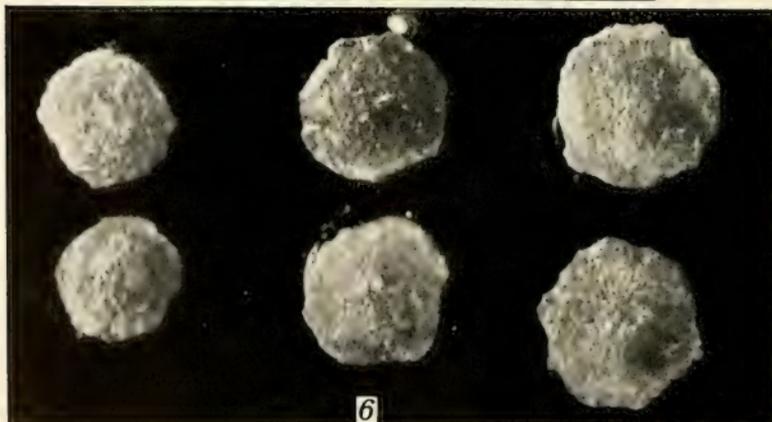
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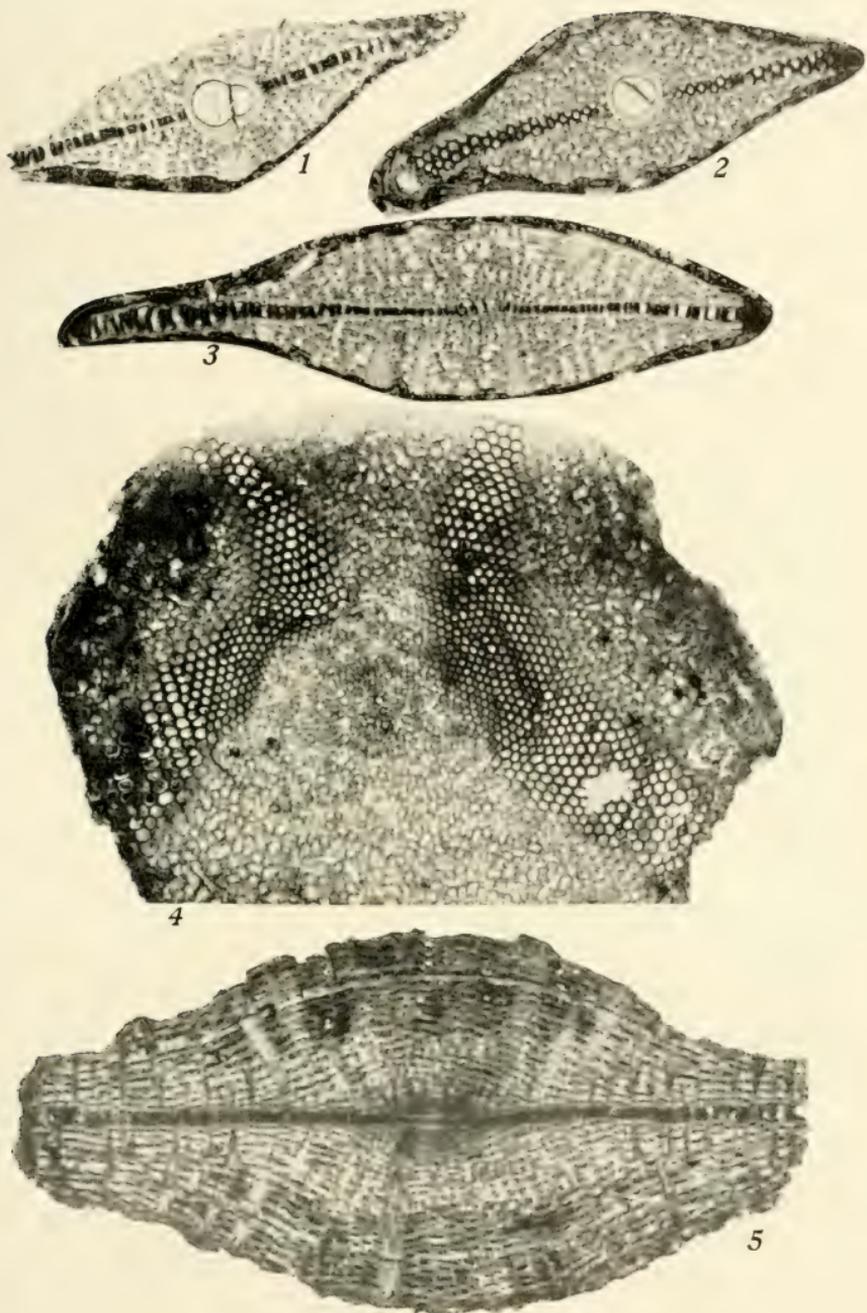


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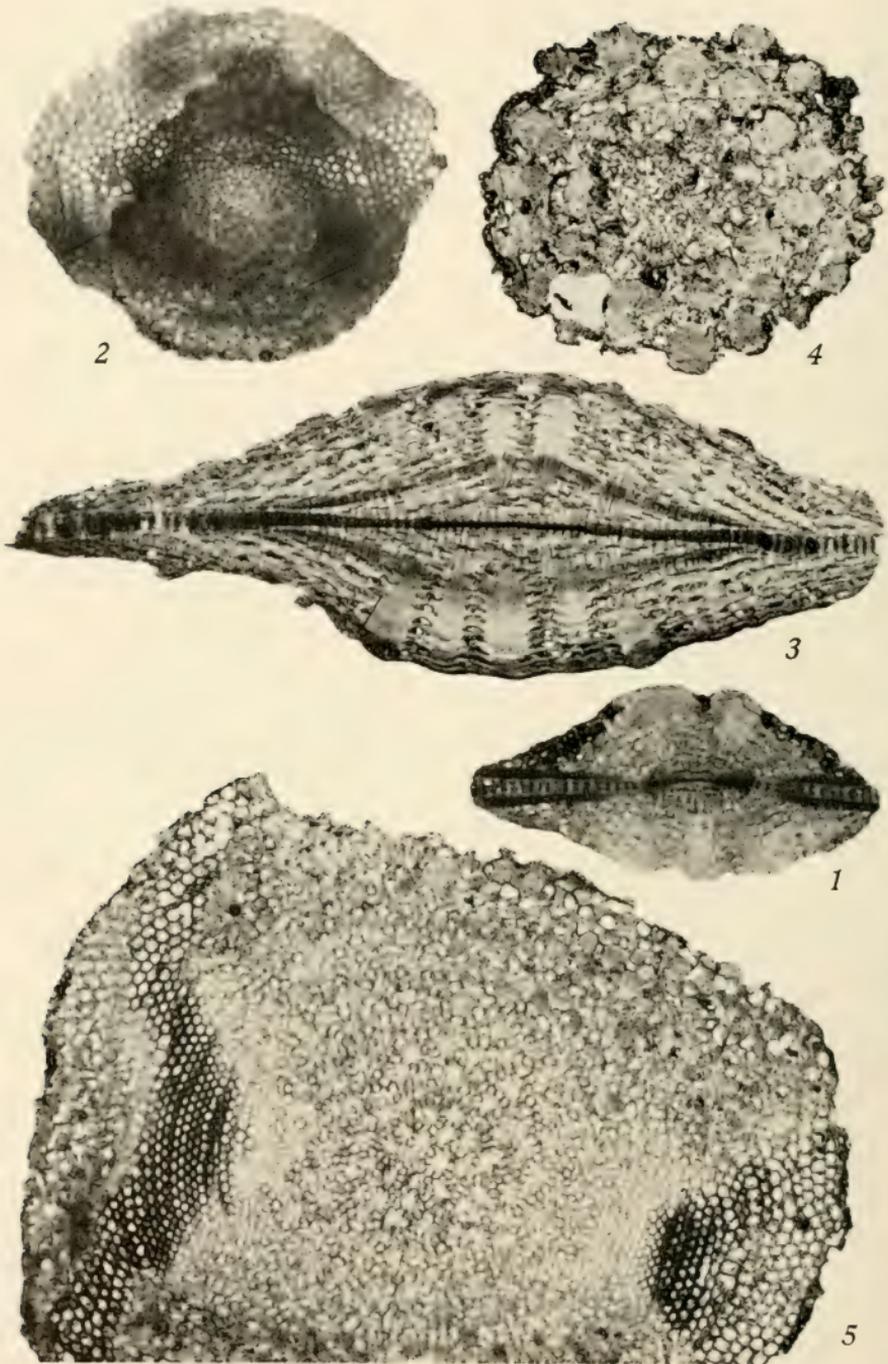


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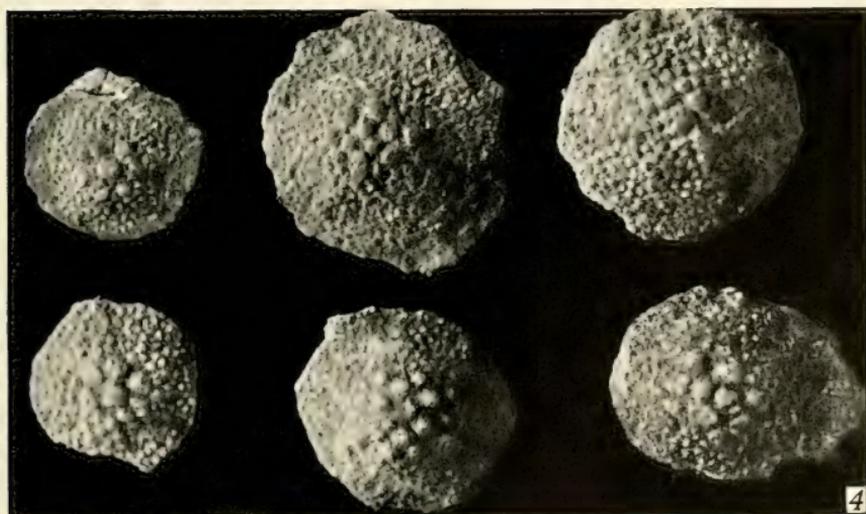
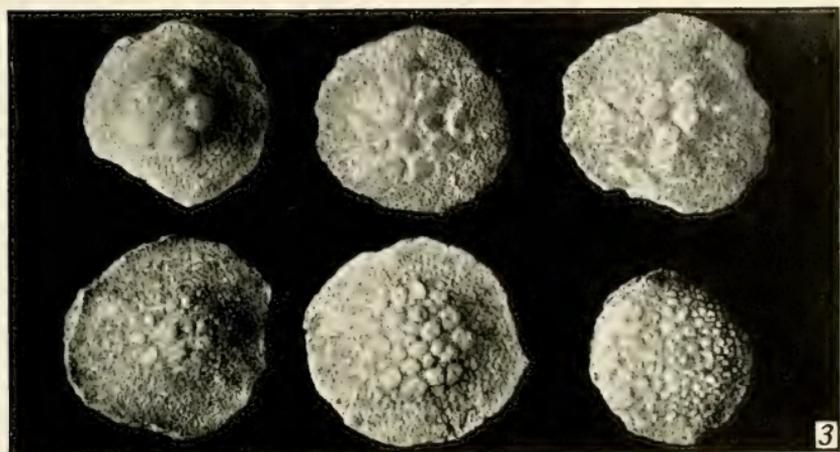
AMERICAN SPECIES OF LEPIDOCYCLINA  
(For explanation, see page 46.)



AMERICAN SPECIES OF *LEPIDOCYCLINA*  
(For explanation, see page 46.)



AMERICAN SPECIES OF *LEPIDOCYCLINA*  
(For explanation, see page 46.)

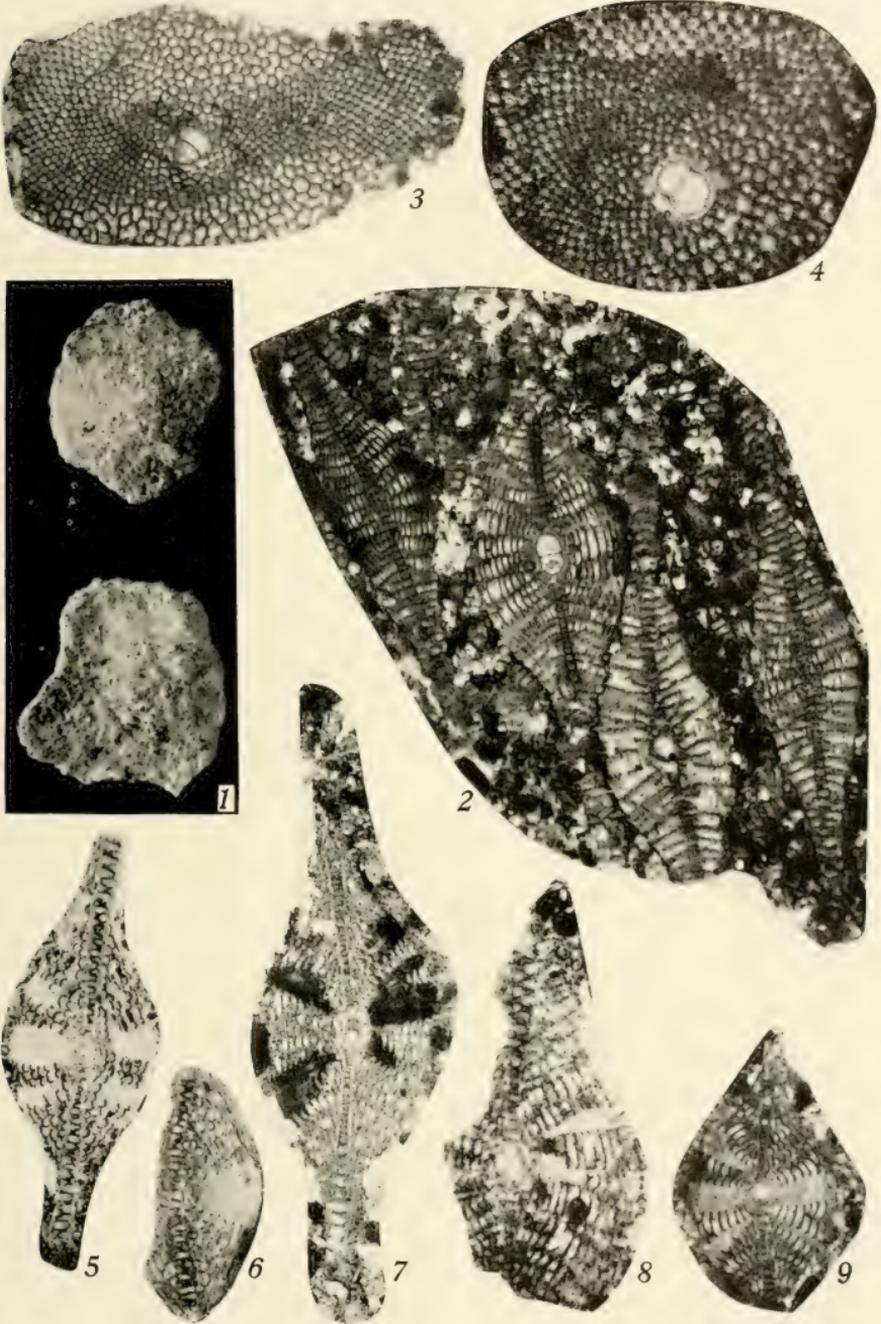


AMERICAN SPECIES OF LEPIDOCYCLINA

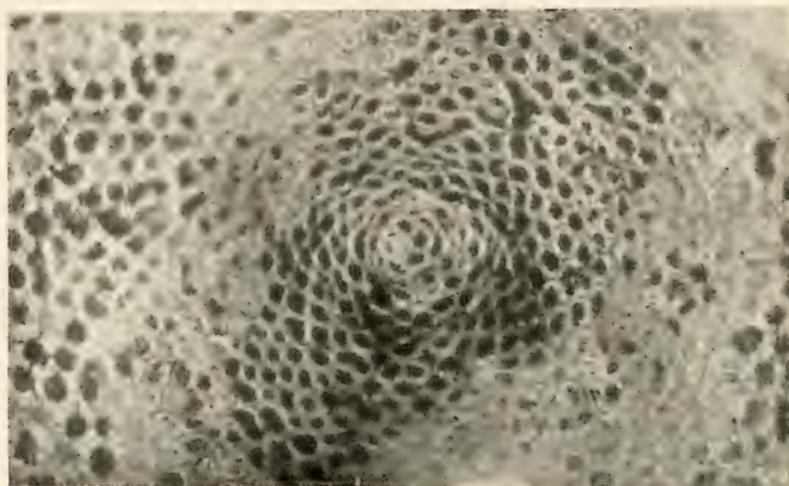
(For explanation, see page 47.)



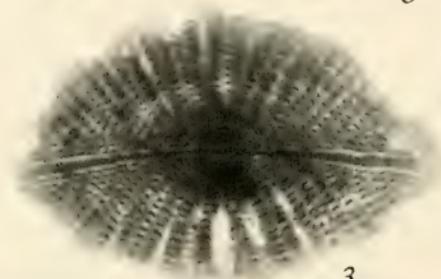
AMERICAN SPECIES OF *LEPIDOCYCLINA*  
(For explanation, see page 47.)



AMERICAN SPECIES OF LEPIDOCYCLINA  
(For explanation, see page 47.)



5



3



4



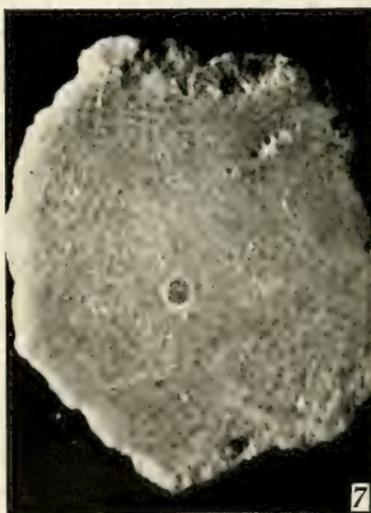
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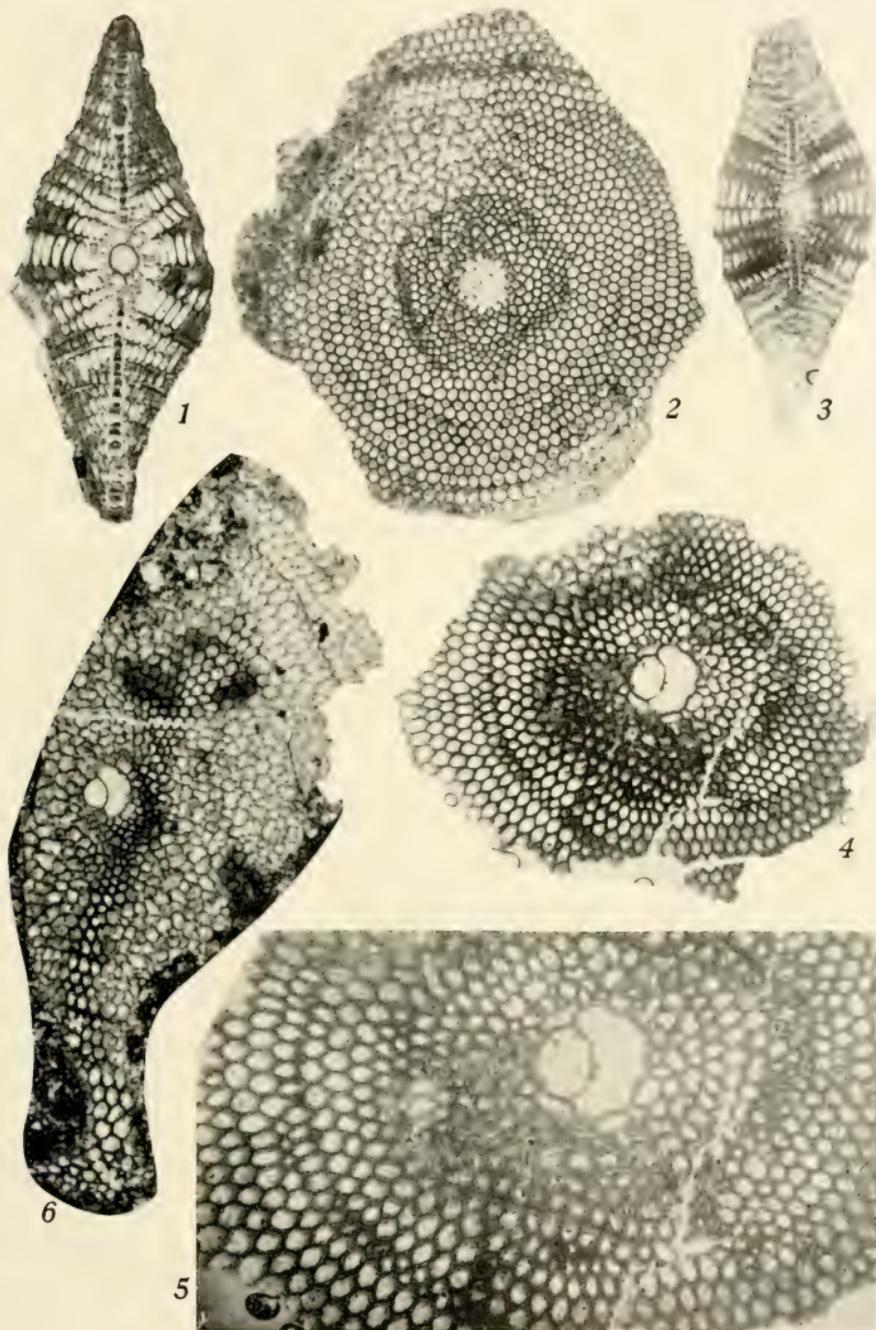
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7

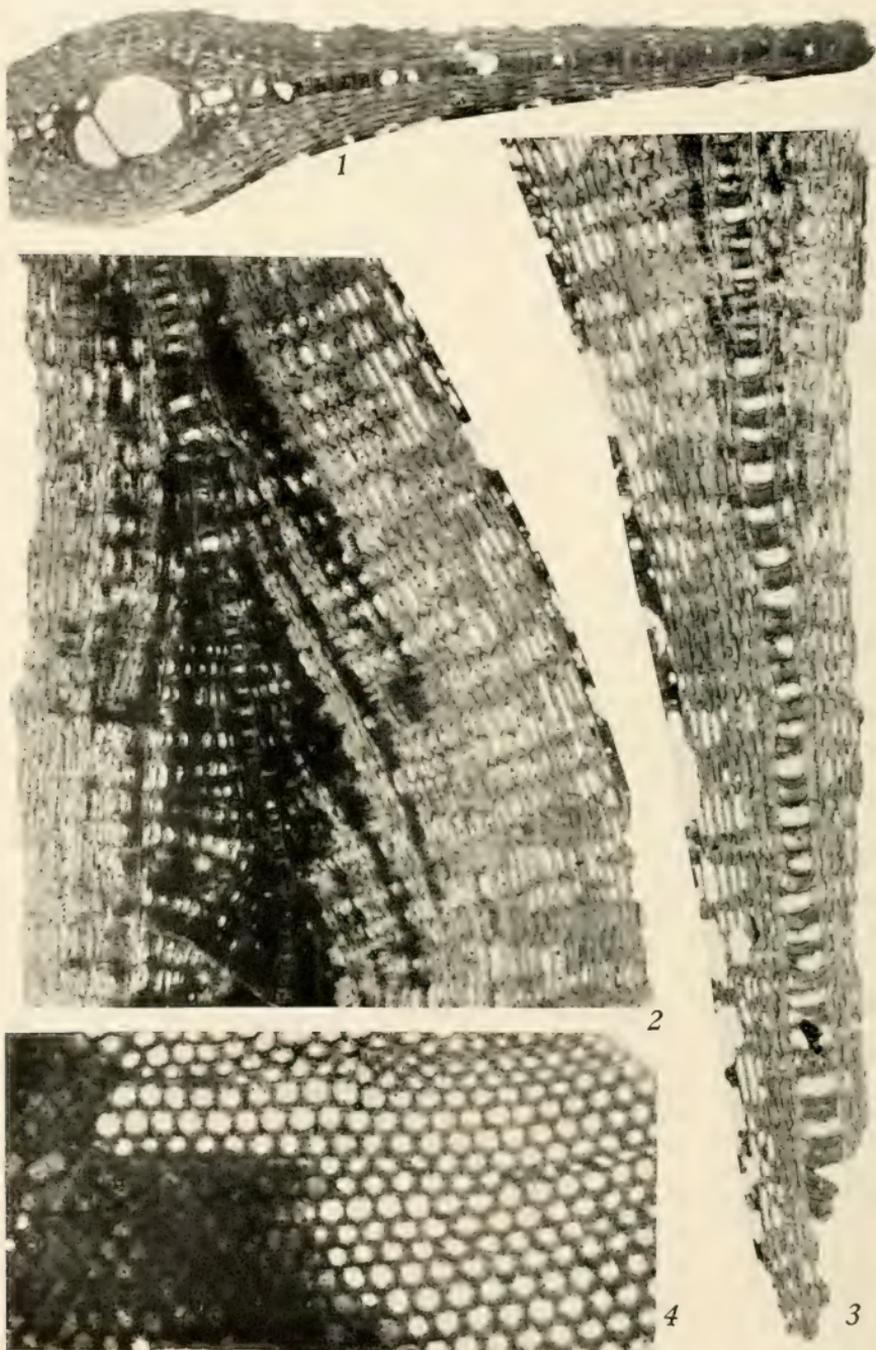
AMERICAN SPECIES OF *LEPIDOCYCLINA*

(For explanation, see page 48.)



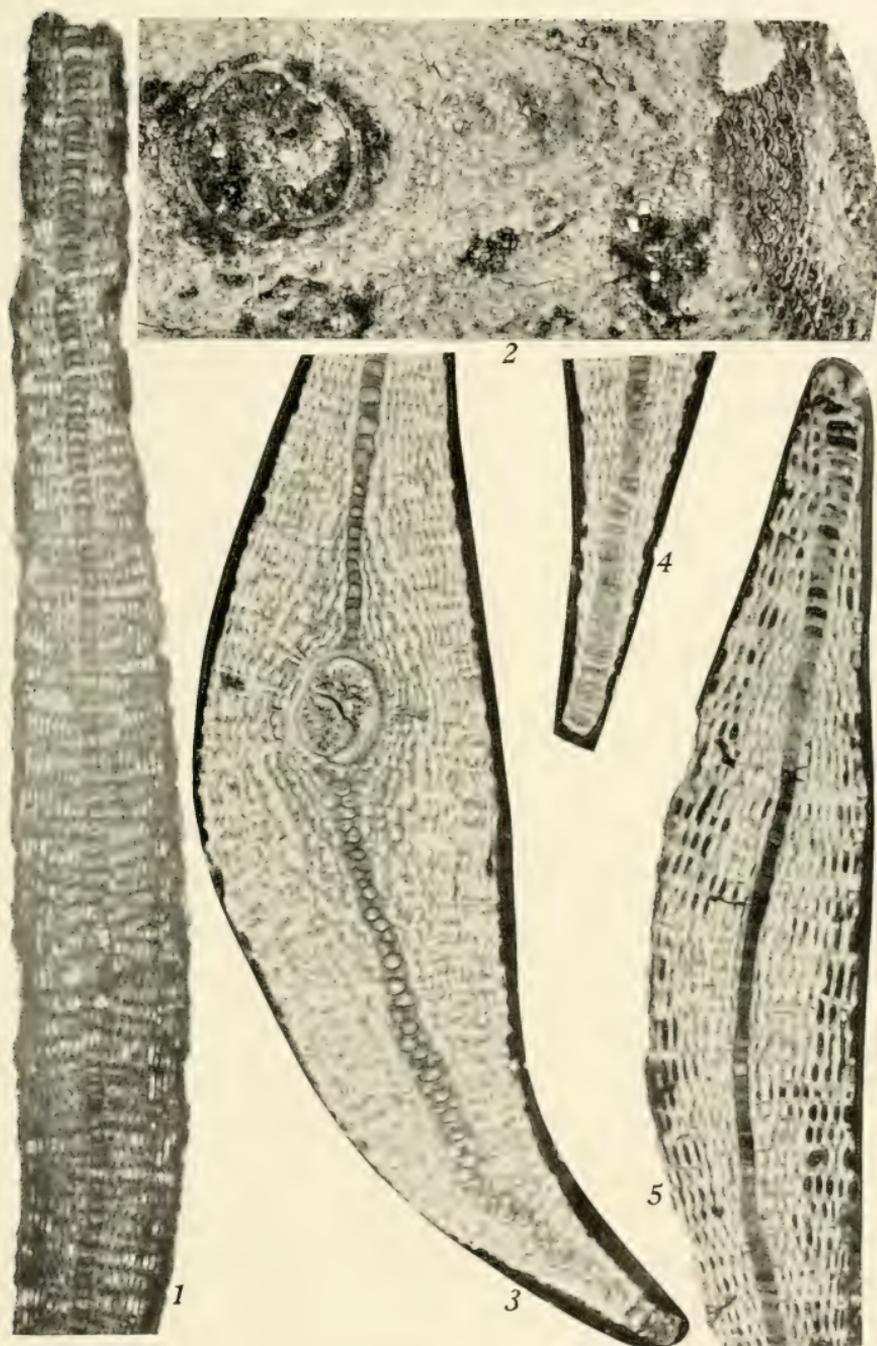
AMERICAN SPECIES OF *LEPIDOCYCLUS*

(For explanation, see page 48.)



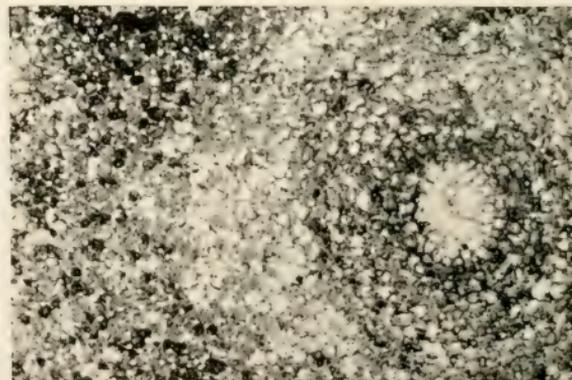
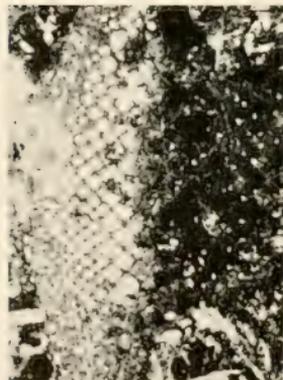
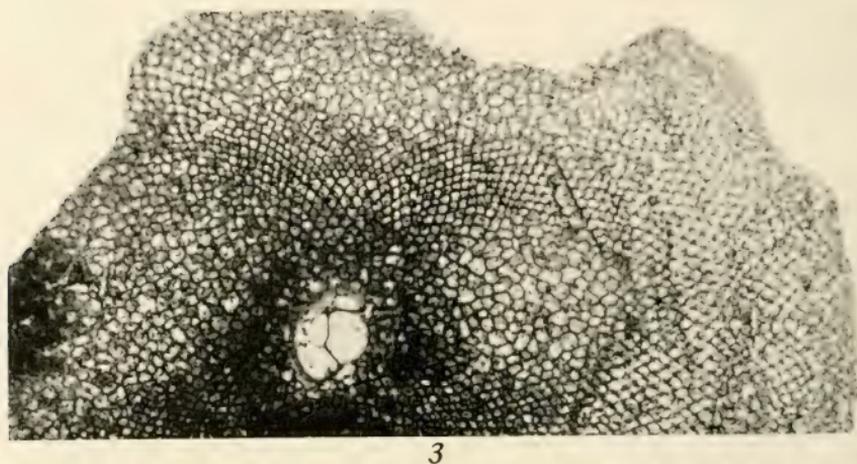
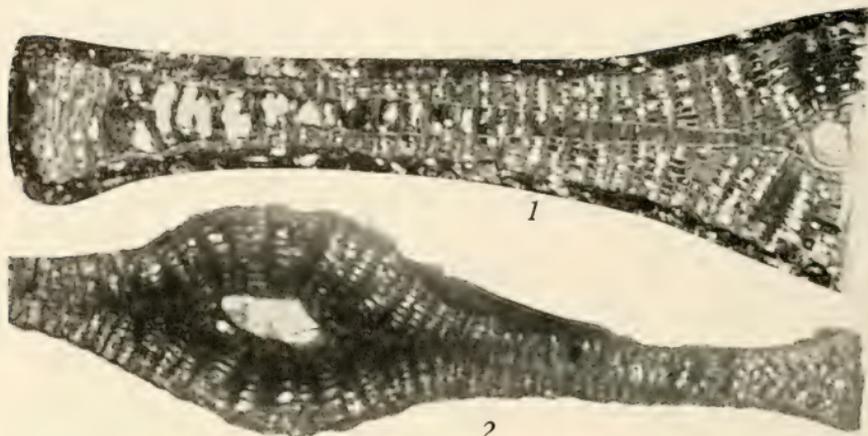
AMERICAN SPECIES OF *LEPIDOCYCLINA*

(For explanation, see page 48.)



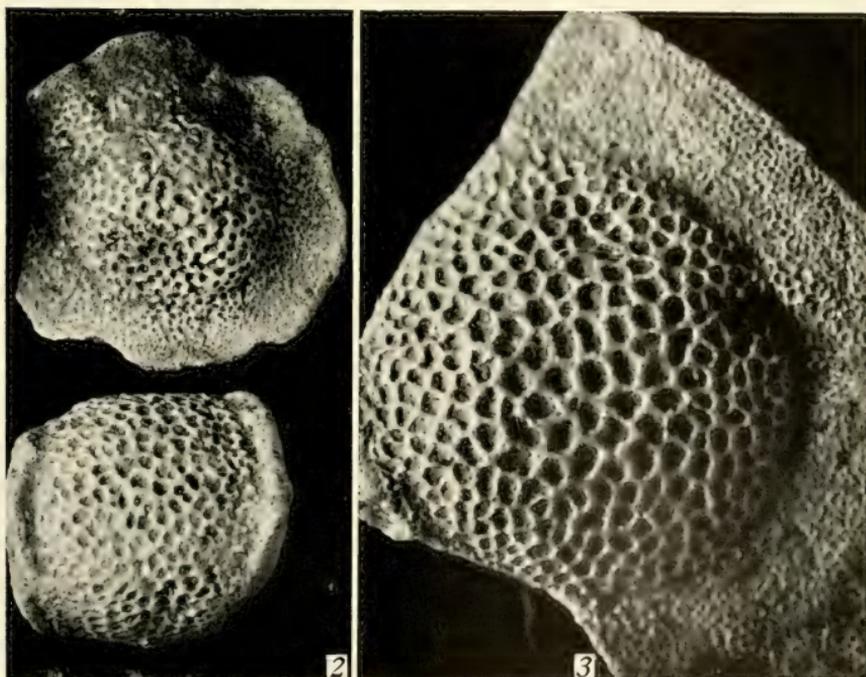
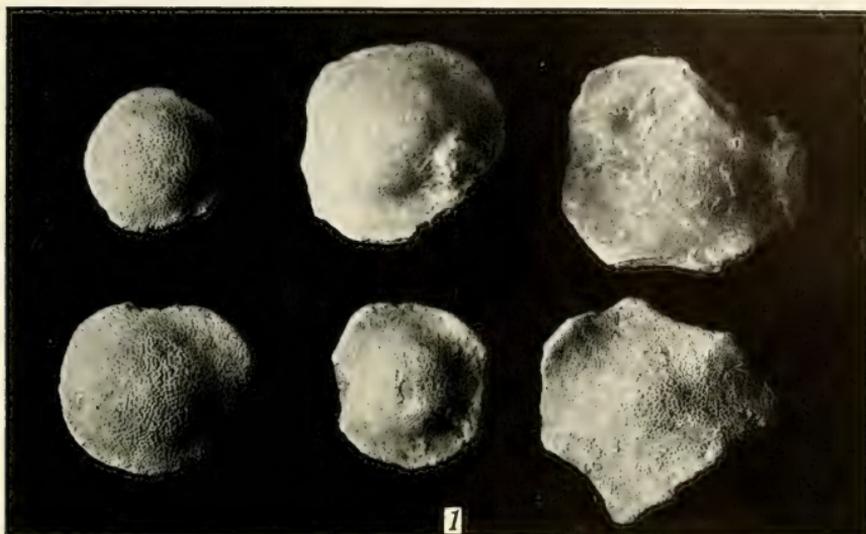
AMERICAN SPECIES OF *LEPIDOCYCLUS*

(For explanation, see page 49.)



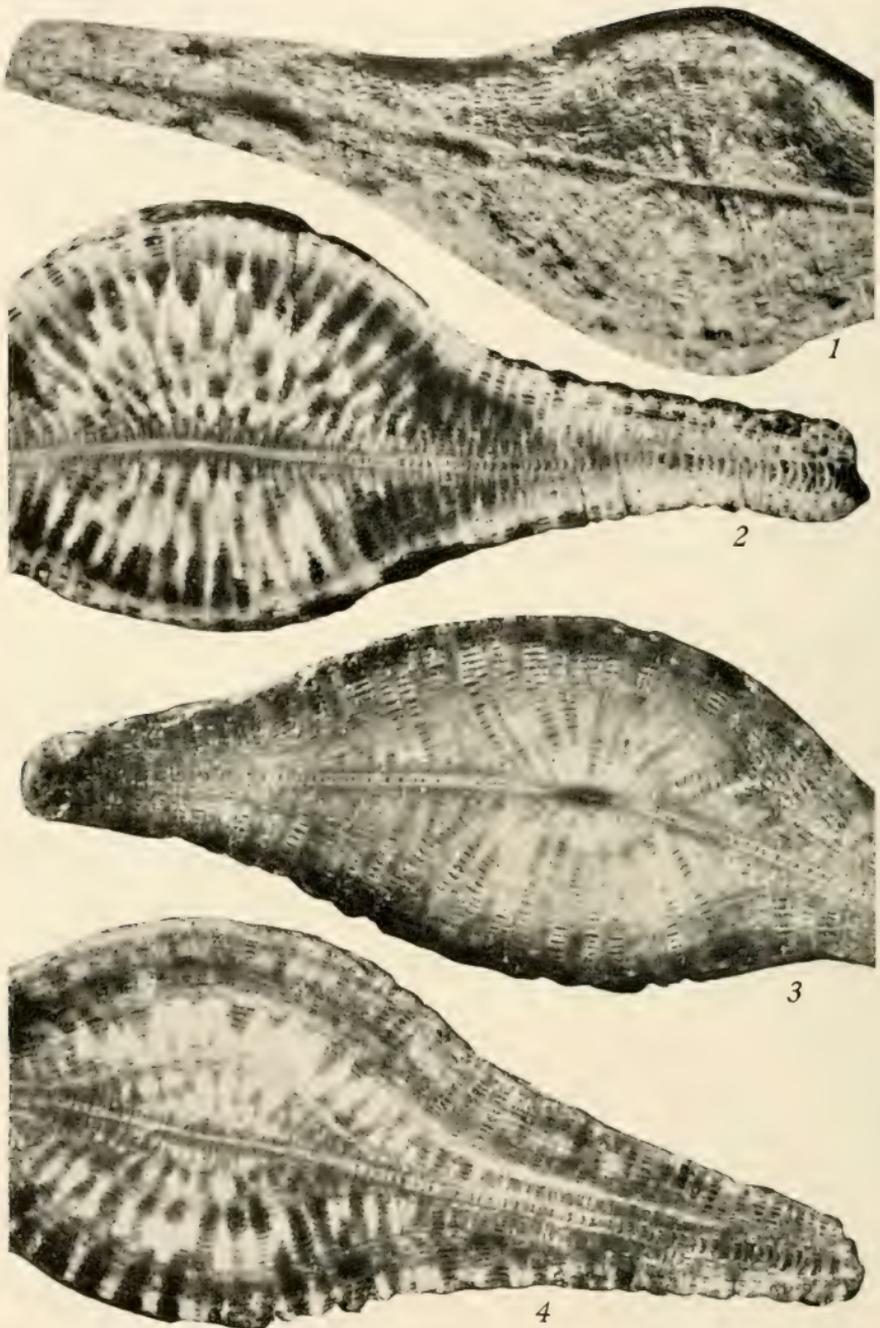
AMERICAN SPECIES OF LEPIDOCYCLINA

(For explanation, see page 49.)



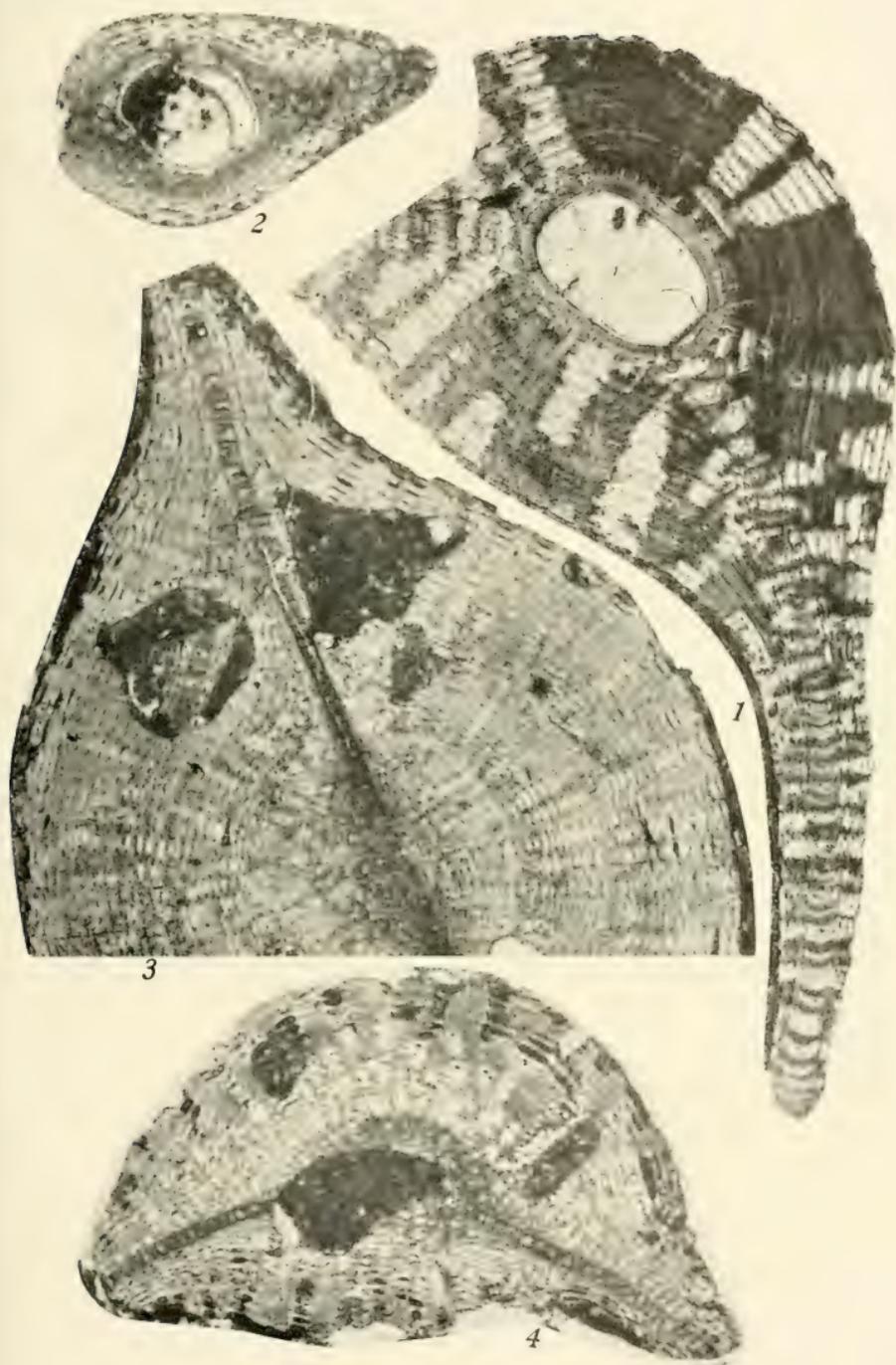
AMERICAN SPECIES OF *LEPIDOCYCLINA*

(For explanation, see page 49.)



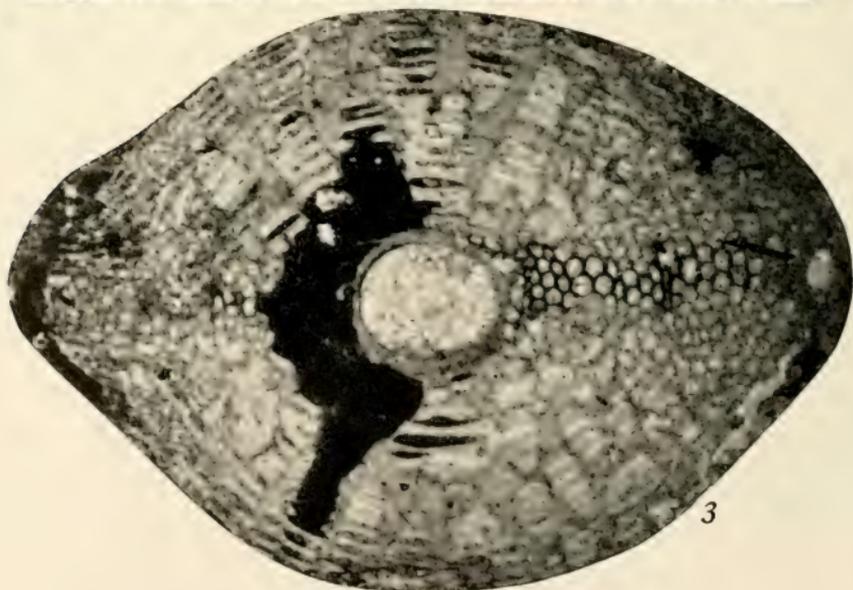
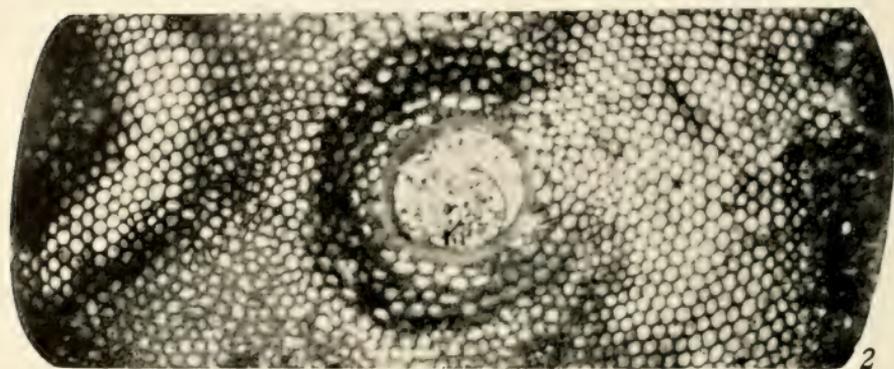
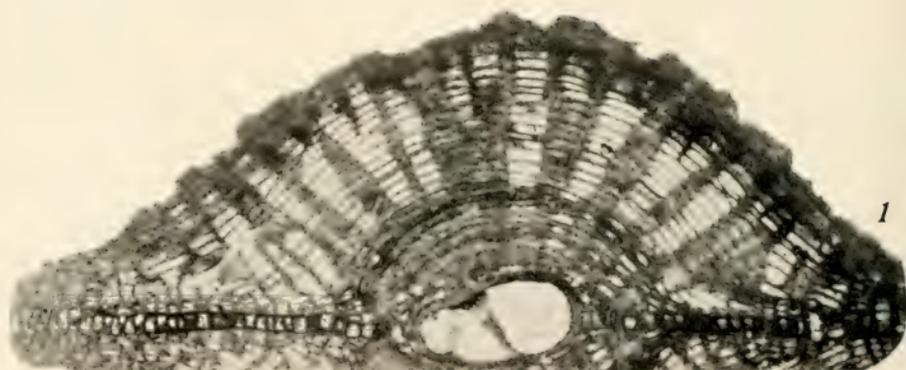
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(For explanation, see page 50.)



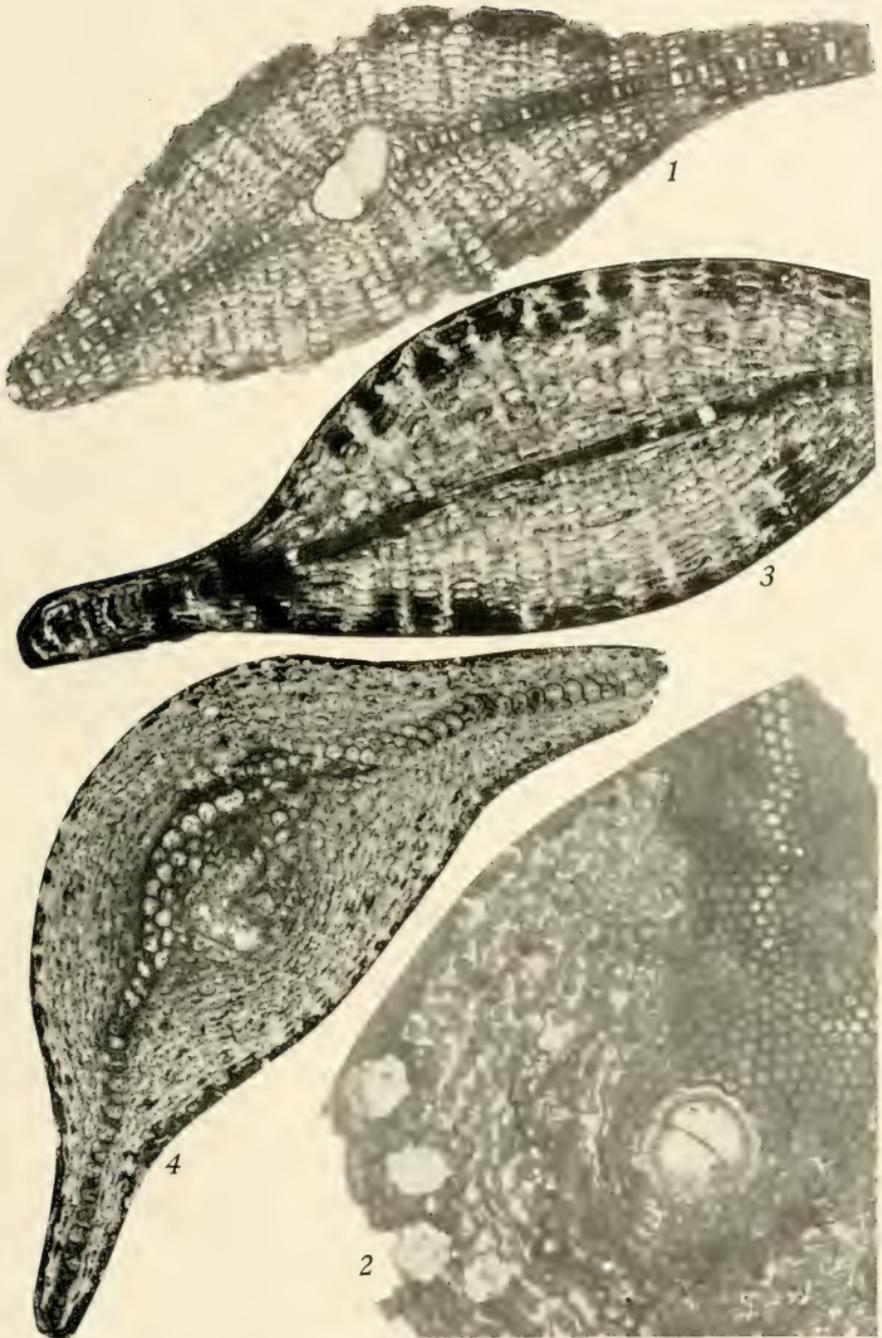
AMERICAN SPECIES OF *LEPIDOCYCLUS*

(For explanation, see page 50.)



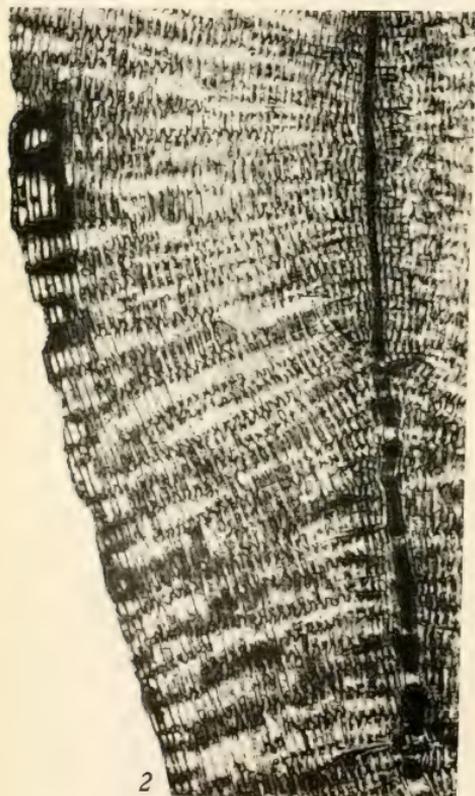
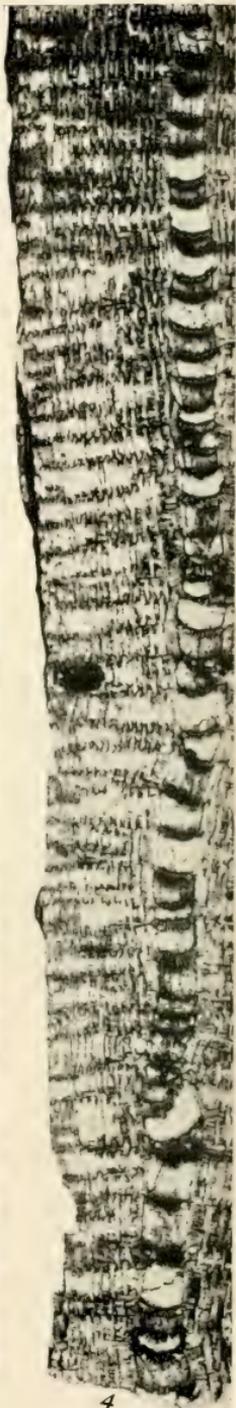
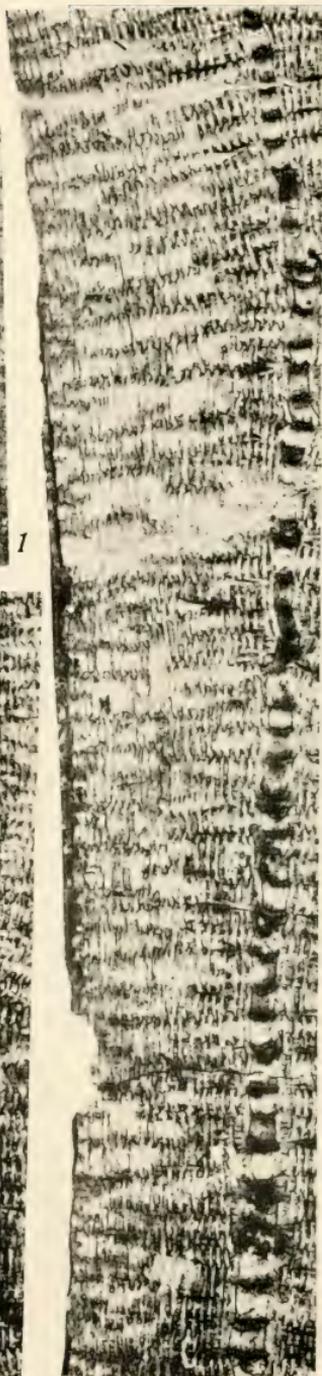
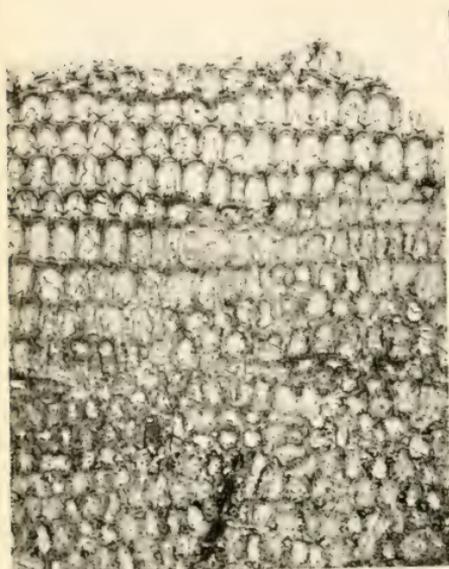
AMERICAN SPECIES OF *LEPIDOCYCLINA*

(For explanation, see page 50.)



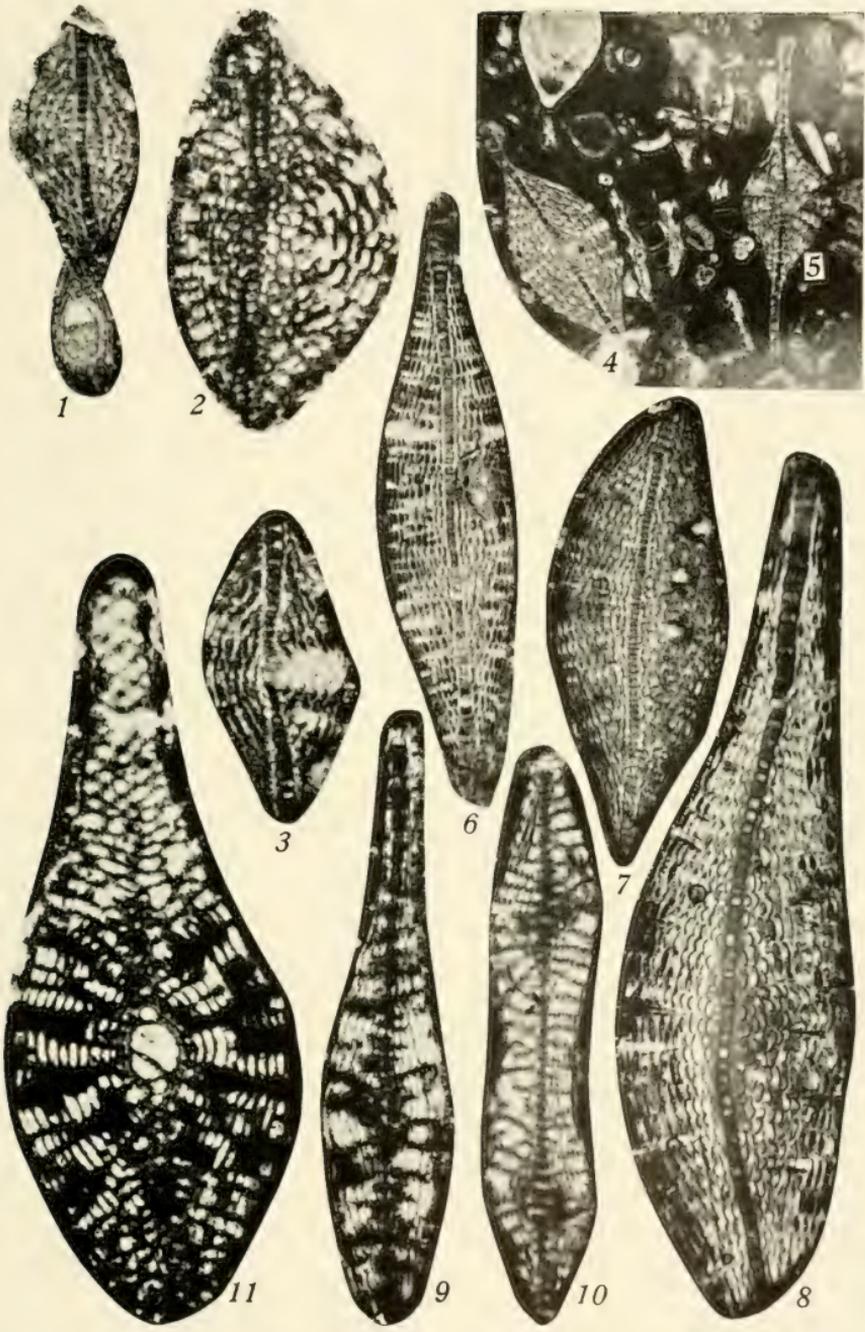
AMERICAN SPECIES OF LEPIDOCYCLUS

(For explanation, see page 50.)

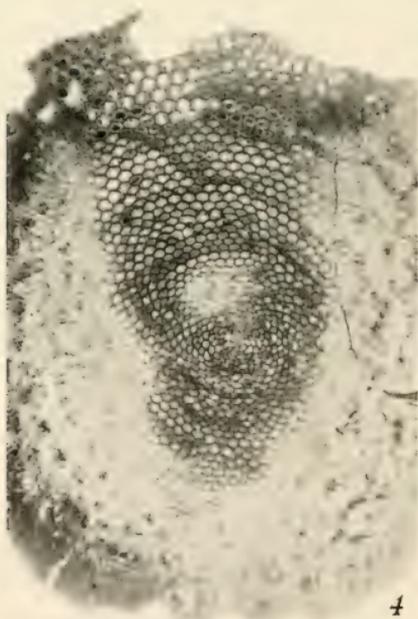
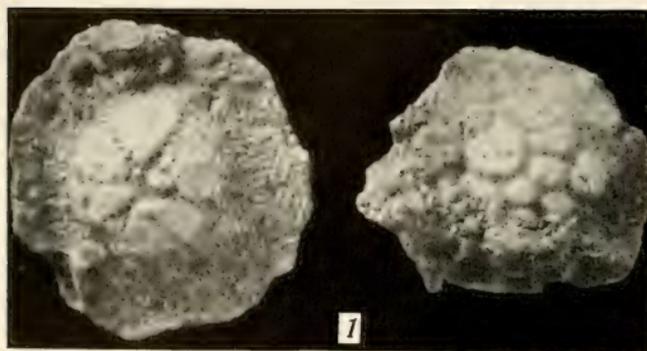


AMERICAN SPECIES OF *LEPIDOCYCLINA*

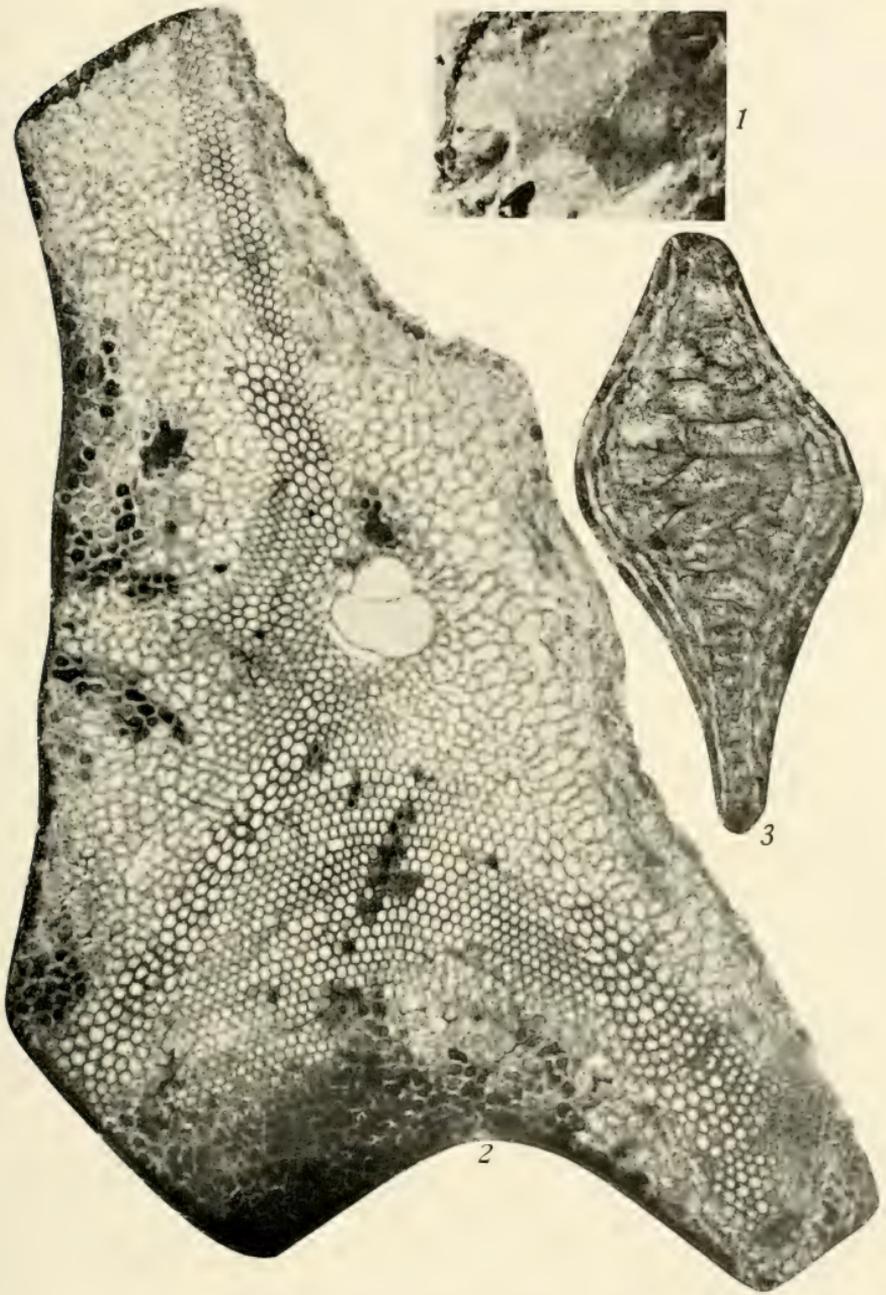
(For explanation, see page 50.)



AMERICAN SPECIES OF LEPIDOCYCLUS  
(For explanation, see page 51.)

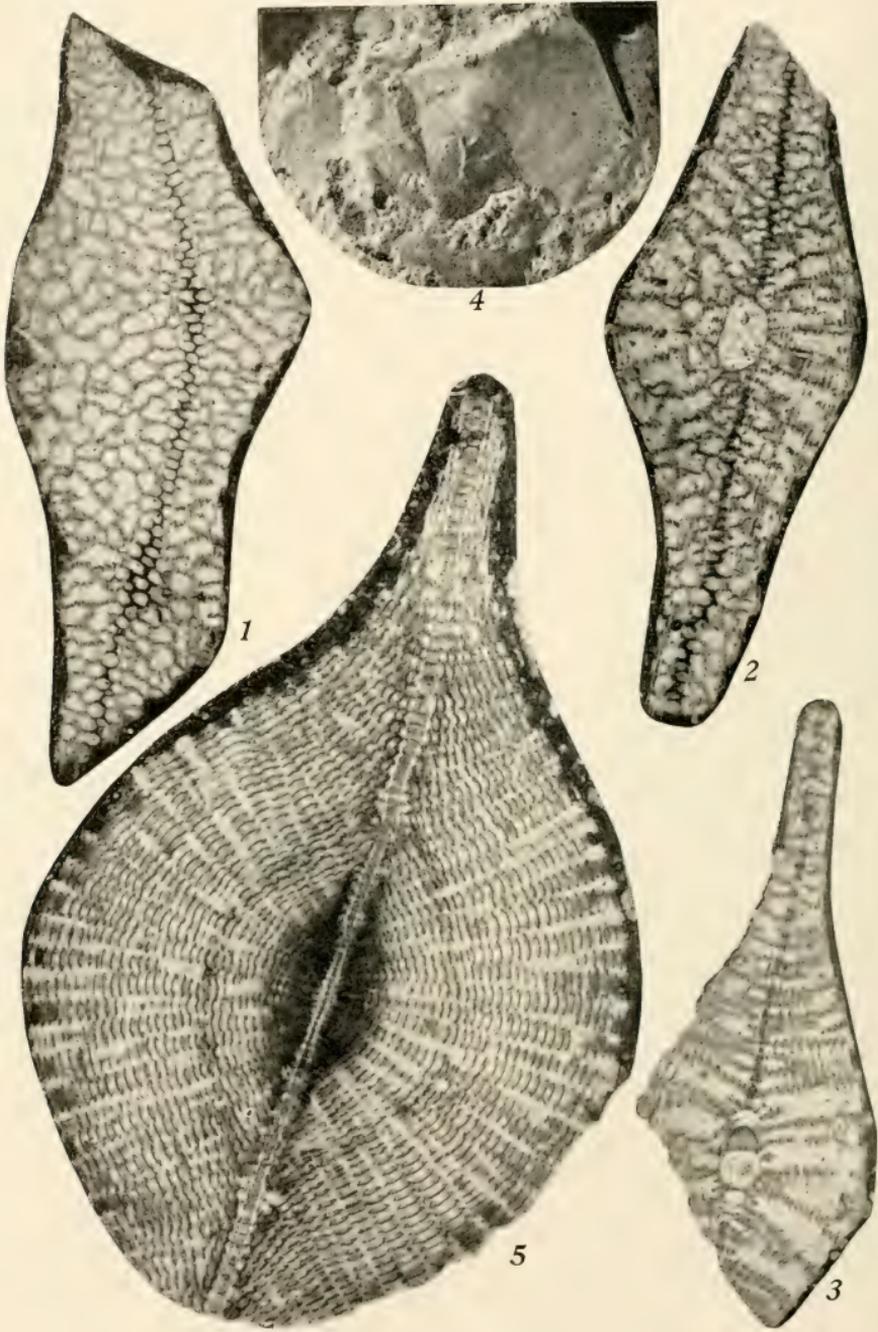


AMERICAN SPECIES OF LEPIDOCYCLINA  
(For explanation, see page 51.)

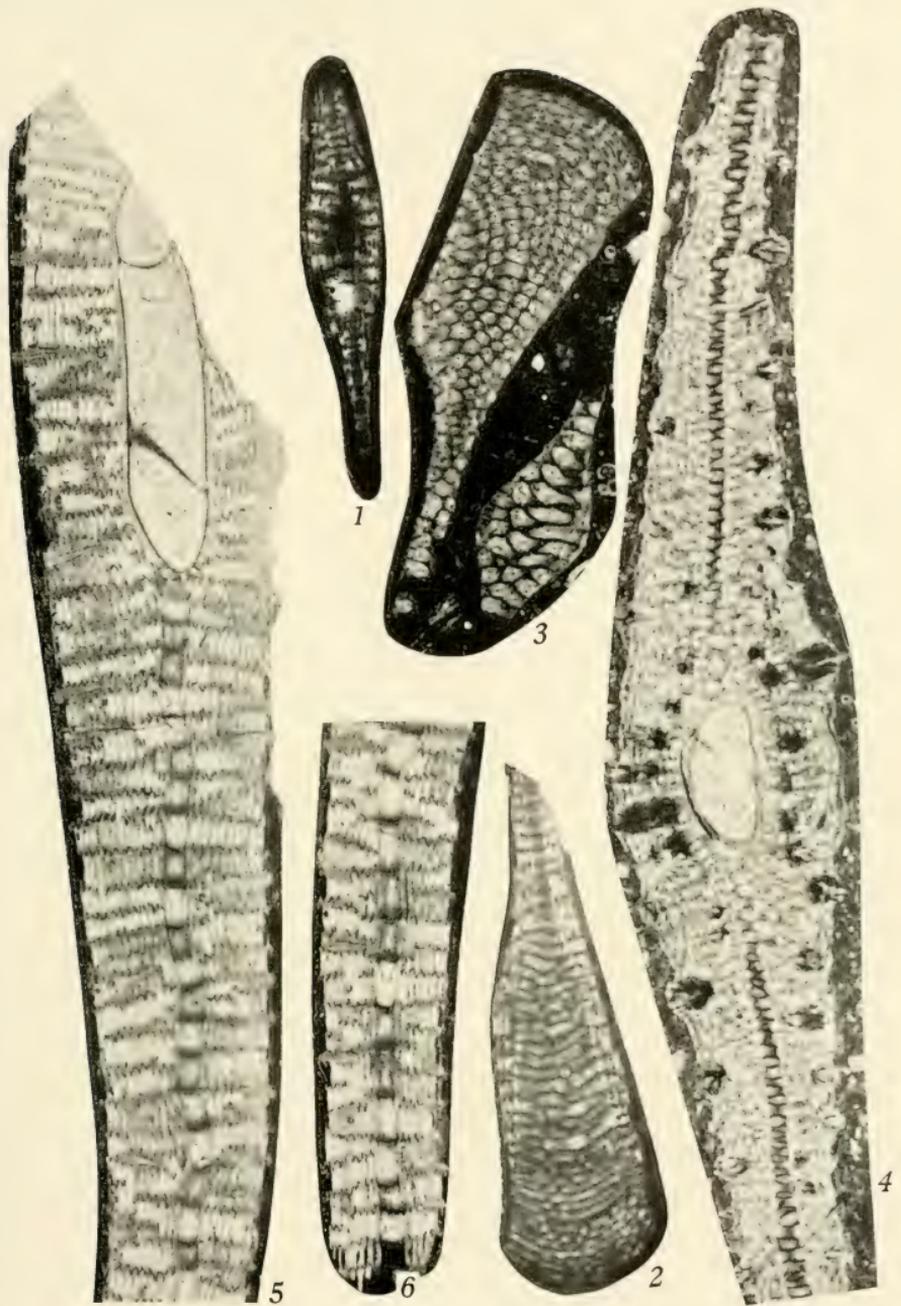


AMERICAN SPECIES OF *LEPIDOCYCLINA*

(For explanation, see page 51.)

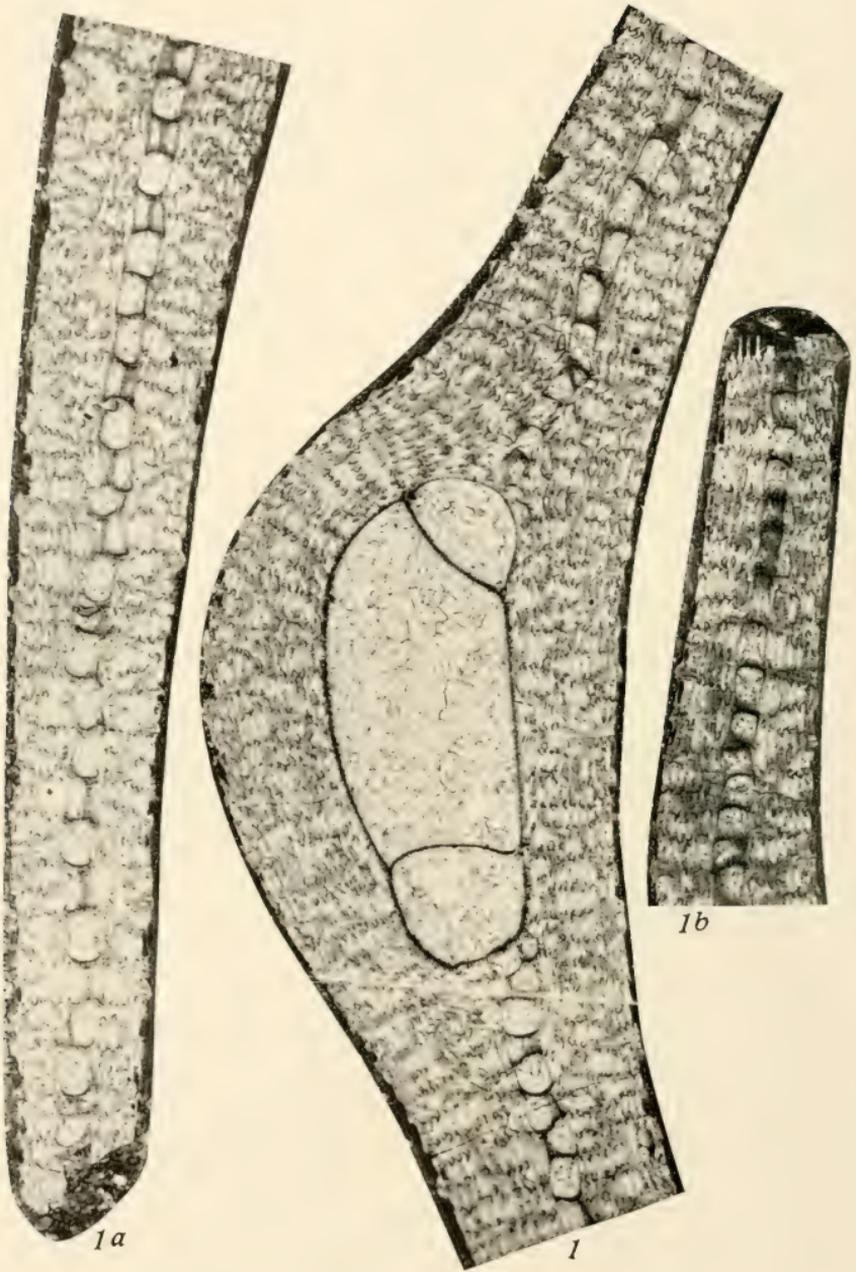


AMERICAN SPECIES OF LEPIDOCYCLINA  
(For explanation, see page 52.)

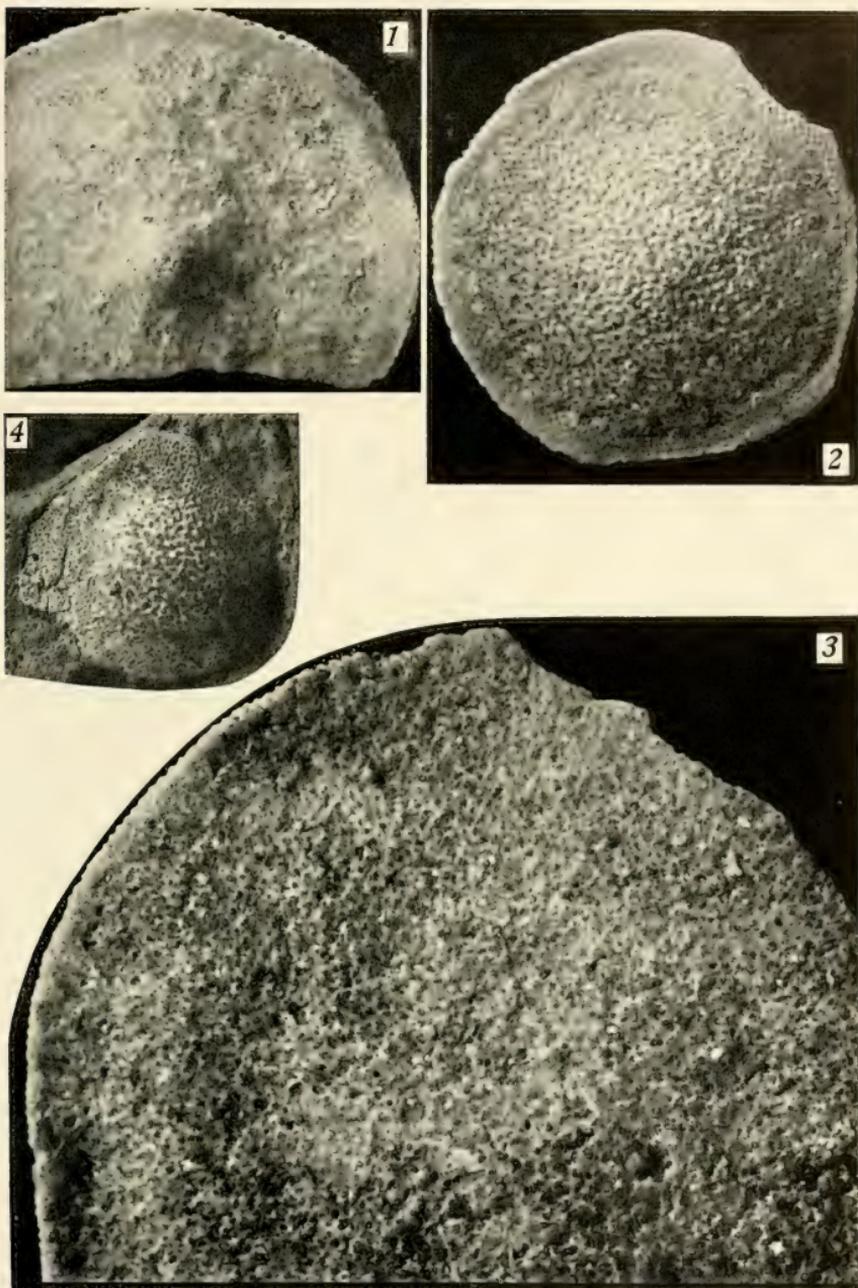


AMERICAN SPECIES OF LEPIDOCYCLINA

(For explanation, see page 52.)

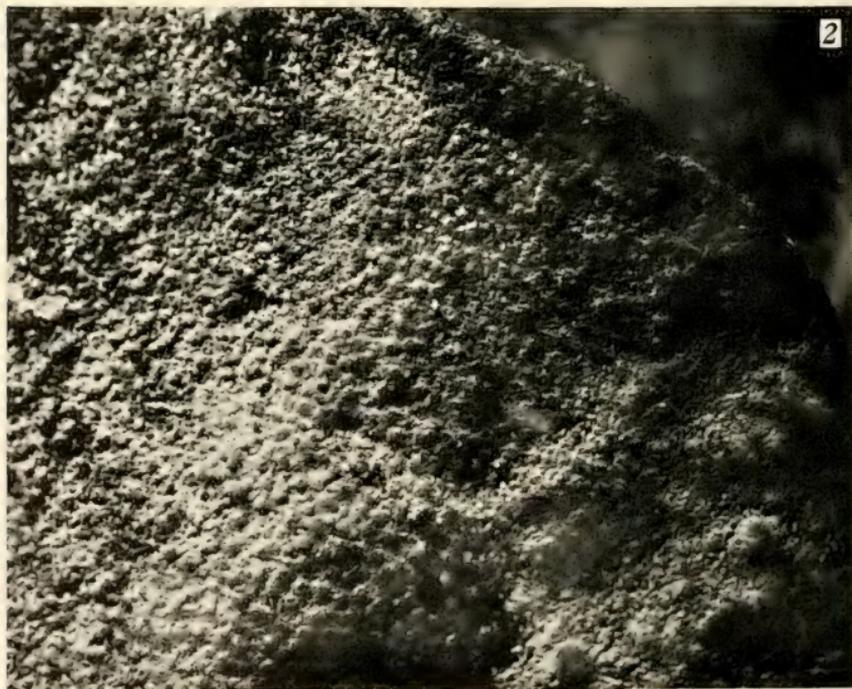
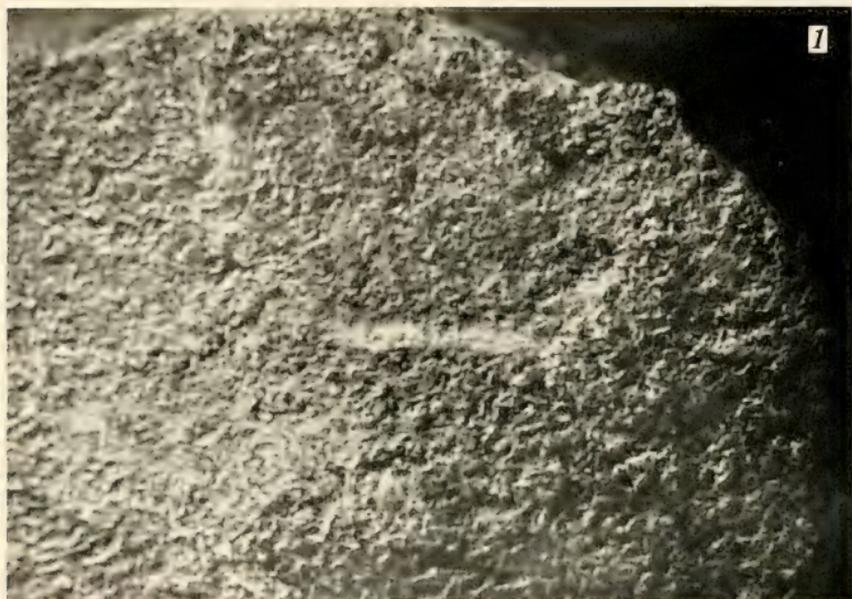


AMERICAN SPECIES OF LEPIDOCYCLINA  
(For explanation, see page 52.)

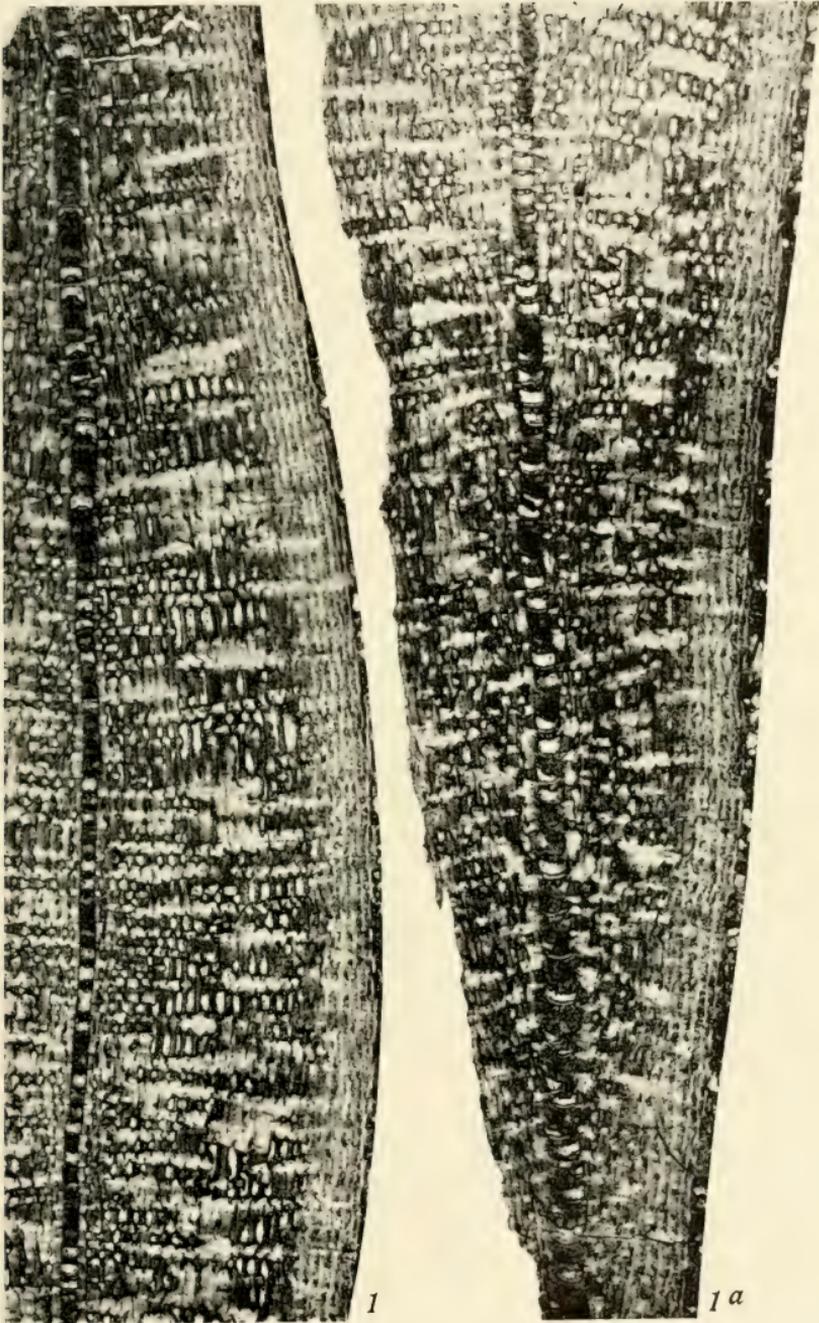


AMERICAN SPECIES OF LEPIDOCYCLINA

(For explanation, see page 52.)

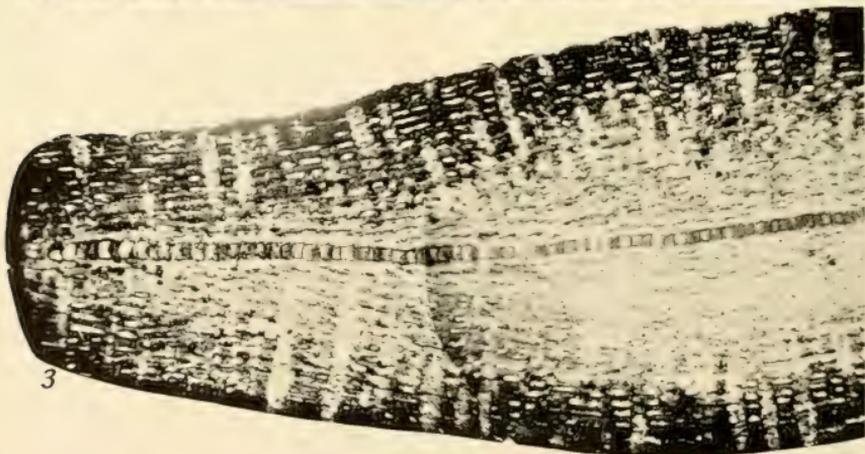
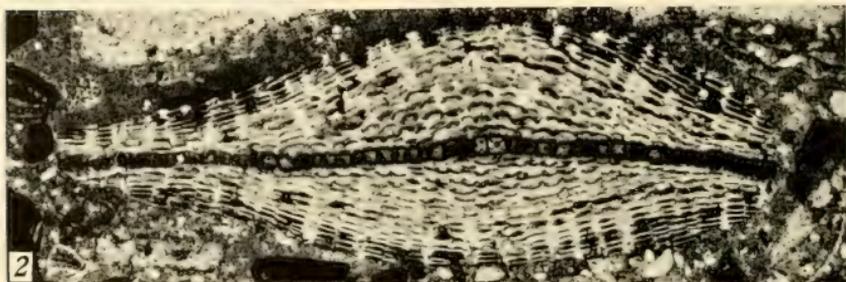
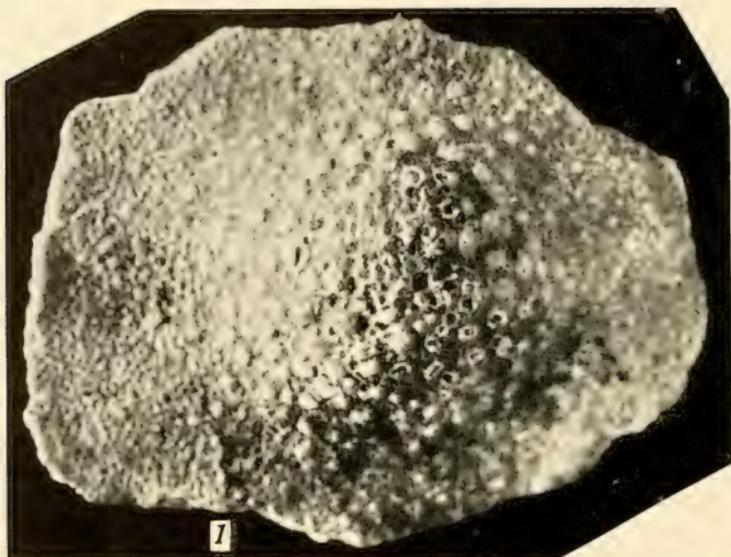


AMERICAN SPECIES OF LEPIDOCYCLINA  
(For explanation, see page 53.)



AMERICAN SPECIES OF LEPIDOCYCLINA

(For explanation, see page 53.)



AMERICAN SPECIES OF LEPIDOCYCLINA  
(For explanation, see page 53.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 89, NUMBER 11

TERTIARY LARGER FORAMINIFERA  
OF VENEZUELA

(WITH SIX PLATES)

BY

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Gulf Production Co., Houston, Texas



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# TERTIARY LARGER FORAMINIFERA OF VENEZUELA

BY DONALD WINCHESTER GRAVELL

*Gulf Production Co., Houston, Texas*

(WITH SIX PLATES)

## INTRODUCTION

This paper presents the results of a study of larger Tertiary foraminifera of Venezuela, collected in 1925-26 by Dr. H. G. Kugler and Dr. L. Vonderschmitt; in 1927 by Drs. P. Leuzinger, P. A. Messmann, and A. Senn; and in 1928 by Mr. M. N. Bramlette. These were sent to Dr. T. Wayland Vaughan, Director of Scripps Institution of Oceanography, University of California, La Jolla, California, who permitted me to study the material.

The great portion of the material in these collections is indurated, and therefore the specimens had to be studied mostly in thin sections, of which I prepared nearly 300. For these reasons specific determinations of many specimens have not been made. It is possible that additional material from other localities may yield specimens which may be separated from the matrix, and the study of them in thin sections may make possible the determination of part of the specimens in this collection. Among the genera recognized were *Acerculina*, *Archaias*, *Carpenteria*, *Camerina*, *Heterostegina*, *Operculina*, and certain species of *Discocyclina* and *Lepidocyclina*. Some specimens of the last two genera were free from the matrix.

While at Scripps Institution of Oceanography, I was able to compare this Venezuelan collection with the valuable collection belonging to that Institution, and also with a part of the United States National Museum collection which Dr. Vaughan was using at the time. These collections contain authentically identified specimens of most of the described American species of larger foraminifera.

Types of the new species and a complete set of the other material will be deposited in the United States National Museum; and paratypes together with other material will be divided between the Naturhistorisches Museum in Basel, Switzerland, and the Scripps Institution of Oceanography.

The work on this paper was done under the supervision of Dr. T. Wayland Vaughan, to whom I am greatly indebted for many helpful



- D. (Asterocyclus) asterisca* (Guppy)  
     *venezuelana* (H. K. Hodson)  
     *zuliana* (H. K. Hodson)  
     *pariana* (H. K. Hodson)  
     *trinidadensis* (H. K. Hodson)  
     *weeksii* (H. K. Hodson)  
         *maracaibensis* (H. K. Hodson)  
     *parva* (H. K. Hodson)  
     *aurarensis* (H. K. Hodson)

Unfortunately, the localities from which the above were obtained were referred to only by numbers, no description being given of them other than the states in which they occur.

As the material from Venezuela that I have studied consists almost entirely of indurated rock, I have not been able to recognize Mrs. Hodson's variants.

The following species of *Lepidocyclus* are reported by Mrs. Hodson from the Eocene of Venezuela:

- L. (Lepidocyclus) trinitatis* H. Douvillé  
     *carribbeanensis* H. K. Hodson  
     *venezuelana* H. K. Hodson  
     *hubbardi* H. K. Hodson  
     *bolivarensis* H. K. Hodson  
     *aurarensis* H. K. Hodson  
     *weeksii* H. K. Hodson

In regard to the above reputed species and subspecies, although I have not been able to study the types of them, it appears that they are all variants of *L. (Lepidocyclus) trinitatis* H. Douvillé. A large suite of material from locality 163 contained abundant specimens of *L. trinitatis*. These specimens were free from the matrix. All of the above reputed species and subspecies of Mrs. Hodson were represented by specimens in this collection. However, these forms intergrade so gradually that it is impossible to draw any distinct lines between the various forms. For this reason I believe that the reputed species and subspecies listed above are all variants of *L. trinitatis* H. Douvillé.

The following species are also described in the same paper:

- L. (Lepidocyclus) maracaibensis* H. K. Hodson  
     (*Nephrolepidina*) *kochi* H. K. Hodson  
     (*Polylepidina*) *zuliana* H. K. Hodson  
         *mirandana* H. K. Hodson  
     (*Polylepidina?*) *churugaritana* H. K. Hodson  
         *sp.* H. K. Hodson

Also two new species of *Miogypsina* from Oligocene-Miocene:

- Miogypsina hawkinsi* H. K. Hodson  
     *venezuelana* H. K. Hodson

In 1928 Liddle (31, pp. 1-552) made a few references to certain larger foraminifera occurring in Venezuela, namely *Amphistegina* sp. (p. 295) in the Damsite formation, middle Miocene; *Lepidocyclina* sp. associated with *Orthaulax* (p. 265) in the Agua Clara shale, upper Oligocene; “. . . bluish gray limestone, which contains two predominant species of *Lepidocyclina*, one a large species which is common in the San Luis formation elsewhere.” It is possible that the large species referred to by Liddle is *Lepidocyclina undosa* Cushman, which is abundant in parts of the San Luis formation.

Liddle also reports (p. 258) the occurrence of *Lepidocyclina duplicata* Cushman, *L.* cf. *panamensis* Cushman, *L.* cf. *antillea* Cushman, and specimens called *Orthophragmina hayesi* (Cushman). The latter form is not a *Discocyclina* (*Orthophragmina*), but a *Lepidocyclina*. On the basis of the above reported fauna Liddle erroneously called the material Oligocene, although he stated that it suggested upper Eocene. If the foraminifera were correctly identified, the formation is upper Eocene rather than Oligocene.

In 1927 Woodring (71, pp. 992-996) described an Eocene fauna from material collected by Dr. N. H. Darton from the Eastern slope of the Venezuelan Andes. “The material was collected half a mile southeast of the village of Masparito, or about 12 miles east of Calderas, in the State of Zamora (U.S. Geol. Survey locality 1/1189).” The fauna contains a “*Nummulites*”, a stellate (“*Orthophragmina*”), and a *Lepidocyclina*. “The megalospheric form of the *Lepidocyclina* belongs to the subgenus *Pliolepidina* and represents *L. panamensis* Cushman or a very similar species.” Woodring (71, pp. 995-996) considers this fauna to be upper Eocene in age.

The most recent publication on the larger foraminifera of Venezuela is by Gorter and Van der Vlerk (25, pp. 94-122). They report the occurrence of the following species in Central Falcón, Venezuela:

- L. (Lepidocyclina) r. douvillei* Lisson
- falconensis* Gorter and Van der Vlerk
- kugleri* Gorter and Van der Vlerk
- pustulosa* Gorter and Van der Vlerk
- trinitatis* H. Douvillé
- sp. indet.
- L. (Polylepidina) adkinsi* Vaughan
- L. (Nephrolepidina) marginata* Michelotti
- L. (Eulepidina) senni* Gorter and Van der Vlerk
- undosa* Cushman
- L. (Helicolepidina) spiralis* Tobler
- D. (Discocyclina) blumenthali* Gorter and Van der Vlerk
- flintensis* Cushman

*D. (Asterocyclina) georgiana* Cushman  
*maracaibensis* Gorter and Van der Vlerk  
*vaughani* Cushman

*Discocyclina* sp.  
? *Pellatispira* sp.  
*Heterostegina* sp.  
*Operculinella* sp.  
*Operculina* sp.  
*Camerina* sp.  
*Amphistegina* sp.  
*Carpenteria* sp.  
*Gypsina* sp.

It is most unfortunate that the localities from which the types of the above new species were obtained were not specified.

As parts of the above paper and of the present paper are based upon the same collection, a brief discussion of the major differences in the results is given.

Figures of surface views and thin sections and the description published by Gorter and Van der Vlerk (25, p. 105, pl. 11, fig. 3) are not *L. (Lepidocyclina) r. douvillei* Lisson, as these specimens have an embryonic apparatus at least twice the size of topotypes of *L. (Lepidocyclina) r. douvillei* Lisson that are in the collection of the Scripps Institution of Oceanography. The figures appear to be *L. (Lepidocyclina) trinitatis* H. Douvillé.

The name *L. (Lepidocyclina) kugleri* Gorter and Van der Vlerk appears to have been applied to specimens of *L. trinitatis* that have a well-developed flange. A study of a large number of specimens of *L. trinitatis* from locality 163 Venezuela, Soldado Rock, and Bella Vista, San Fernando, Trinidad, shows the presence of a complete series of forms of *L. trinitatis* ranging from flat, lenticular forms with a narrow flange to highly inflated umbonate types with a wide flange. There appear to be no structural characteristics upon which this series may be divided into two or more recognizable species. *L. (Lepidocyclina) kugleri* Gorter and Van der Vlerk, like *L. trinitatis* Douvillé var. *caribbeanensis* Hodson, *L. trinitatis* var. *venezuelana* Hodson, *L. (Lepidocyclina) hubbardi* Hodson, *L. hubbardi* var. *bolivarensis* Hodson, *L. hubbardi* var. *aurarensis* Hodson, and *L. (Lepidocyclina) weeksi* Hodson, seem to be based upon individual variations of *L. (Lepidocyclina) trinitatis* H. Douvillé.

Gorter and Van der Vlerk (25, p. 99) report the presence of *L. (Polylepidina) adkinsi* Vaughan in material from localities 1149 and 1152. Thin sections of our material from these localities contain no sections which are *L. (Polylepidina) adkinsi* Vaughan.

Gorter and Van der Vlerk (25, p. 104) identify specimens of *Lepidocyclina* occurring in material 1116 and 1120 as *L. (Nephrolepidina) marginata* Michelotti. These specimens are not *L. (Nephrolepidina) marginata* but are *L. (Lepidocyclina) sanluisensis*, n. sp. As is stated in the discussion of *L. sanluisensis*, n. sp., this species closely resembles *L. (Nephrolepidina) marginata* in form and surface ornamentation, but differs in the character of the embryonic apparatus, belonging to *Lepidocyclina* s.s., whereas *L. marginata* is distinctly a *Nephrolepidina*. It is very probable that Gorter and Van der Vlerk may have based their determination upon a specimen with a deformed embryonic apparatus, because one of our specimens from locality 1120 showed an embryonic apparatus which was so deformed as to have a nephrolepidine form. The other sectioned specimens have the true *Lepidocyclina* s.s. type of embryonic apparatus and are identical with the cotypes of *L. (Lepidocyclina) sanluisensis*, n. sp.

*Helicolepidina spiralis* Tobler is reported by Gorter and Van der Vlerk (25, p. 97) as occurring at locality 163. This species may be present, but it was not recognized in our material.

*L. (Lepidocyclina) pustulosa* H. Douvillé was reported by Gorter and Van der Vlerk (25, pp. 96-97) as occurring at localities 163 and 165. Their illustrations seem to be closer to *L. (Lepidocyclina) trinitatis* H. Douvillé than to *L. pustulosa*, especially plate 12, figure 8.

*Lepidocyclina* occurring at localities 469 and 476, reported by Gorter and Van der Vlerk (25, p. 101) as "*Lepidocyclina* sp. (small specimens)", are *L. (Lepidocyclina) canellei* Lemoine and R. Douvillé.

The several species of *Asterocyclina* specifically identified by Gorter and Van der Vlerk are from localities not represented in our collections.

#### STRATIGRAPHY OF THE TERTIARY FORMATIONS OF VENEZUELA

The following is the stratigraphic column of the Tertiary formations occurring in the State of Falcón, Venezuela, according to Drs. H. G. Kugler and V. A. Senn:

- Pliocene
  - Cadore series
- Upper Miocene
  - La Vela series
- Middle Miocene
  - Damsite series
- Lower Miocene
  - Socorro series
  - Querales series

Aquitanian<sup>2</sup>

Cerro Pelado series

## Upper Oligocene

Agua Clara series

## Middle Oligocene

San Luis series

## Lower Oligocene

Churuguara series

## Upper Eocene

Guayaval series (Cerro Campaña limestone)

? Pauji shales? (occurrence not definitely proved)

## ? Middle Eocene ?

Paraíso series (probably also upper Eocene)

STRATIGRAPHIC DISTRIBUTION OF THE LARGER  
FORAMINIFERA

The following is a list of the species according to their apparent stratigraphic positions:

## PLIOCENE

## Cadore series

*Amphistegina lessonii* d'Orbigny

## UPPER MIOCENE

## La Vela series

No material from this series.

## MIDDLE MIOCENE

## Damsite series

*Amphistegina lessonii* d'Orbigny

## LOWER MIOCENE

## Socorro-Querales series

*Amphistegina lessonii* d'Orbigny

## AQUITANIAN

## Cerro Pelado series

No material from this series.

## UPPER OLIGOCENE

## Agua Clara series

*Amphistegina lessonii* d'Orbigny*Amphisorus?* sp.*L. (Lepidocyclina)* sp. indet. *a* (possibly from the San Luis series)

<sup>2</sup> The Cerro Pelado series, which is considered by Kugler to be Aquitanian, is placed by Liddle (31, composite geologic column for Venezuela) in the lower Miocene. Vaughan (48, p. 704) states: ". . . and there has been difference of opinion as to whether the Aquitanian should be classified as Oligocene or Miocene."

## MIDDLE OLIGOCENE

## San Luis series

- Amphistegina lessonii* d'Orbigny  
*Archaias* sp.  
*Camerina* sp. indet.  
*Carpenteria* sp.  
*Heterostegina panamensis* Gravell, n. sp.  
*L. (Lepidocyclina) canellei* Lemoine and R. Douvillé  
*L. (Lepidocyclina) forresti* Vaughan  
*L. (Lepidocyclina) sanluisensis* Gravell, n. sp.  
*Lepidocyclina gigas* Cushman  
*Lepidocyclina* sp. indet. b  
*L. (Nephrolepidina) undosa* Cushman  
*L. (Nephrolepidina)* sp.  
*L. (Eulepidina) favosa* Cushman  
*Miogypsina bramlettei* Gravell, n. sp.  
*Miogypsina hawkinsi* Hodson

## LOWER OLIGOCENE

## Churuguara series

- Amphistegina lessonii* d'Orbigny  
*Camerina* sp. a  
*Heterostegina* sp. cf. *H. antillea* Cushman

## UPPER EOCENE

## Guayaval series (Cerro Campaña limestone)

- Camerina* sp. cf. *C. parvula* (Cushman)  
*Carpenteria* sp.  
*D. (Asterocyclina) asterisca* (Guppy)  
*D. (Asterocyclina) kugleri* Gravell, n. sp.  
*Gypsina vesicularis* (Parker and Jones)  
*Operculina* sp. cf. *O. cookei* Cushman  
*L. (Lepidocyclina) trinitatis* H. Douvillé  
*L. (Lepidocyclina) macdonaldi* Cushman

## ? MIDDLE EOCENE ?

## Paraíso series

- Discocyclina* sp. indet. (probably *Discocyclina flintensis* (Cushman))

## DISCUSSION

No larger foraminifera were observed in the Pliocene and Miocene sediments, with the exception of *Amphistegina lessonii*, which has no value for interregional correlation.

The upper Oligocene Agua Clara series is represented by material from only four localities, and of these, three contain large foraminifera. Sections of material from locality 204 contain specimens of *Amphistegina lessonii* d'Orbigny, and a few fragments of a small

*Lepidocyclina* which may be *L. (Lepidocyclina) canellei* Lemoine and R. Douvillé. Sections of indurated yellowish limestone from locality 443 consist largely of shell fragments and contain a few sections of a small indeterminate *Lepidocyclina (Lepidocyclina)* sp. indet. *a*. Kugler considers it possible that material from locality 443 may be from the San Luis series. The few specimens of indeterminate *Lepidocyclina* do not present sufficient paleontologic evidence to determine definitely the stratigraphic age of the material.

The material from locality 468 is dense algal limestone. Sections of this limestone contain a few poor specimens of an indeterminate species of large foraminifera, which Dr. H. G. Kugler by personal communication informed Dr. T. Wayland Vaughan had been identified by G. D. Hawkins as *Orbitolites sanluisensis* Hodson. A survey of the literature has thus far failed to reveal any description or mention of any such species. The large foraminifera occurring in this material do not belong to the genus *Orbitolites*, but appear to be *Amphisorus*.

The San Luis series is represented by material from numerous localities. This formation contains *Amphistegina lessonii* d'Orbigny, *Archaias* sp., *Camerina* sp. indet., *Carpenteria* sp., *Heterostegina panamensis* Gravel, n. sp.

*Gypsina globulus* (Reuss), *L. (Lepidocyclina) canellei* Lemoine and R. Douvillé, *L. (Lepidocyclina) forresti* Vaughan, *L. (Lepidocyclina) sanluisensis* Gravel, n. sp., *L. (Nephrolepidina) undosa* Cushman, *L. (Nephrolepidina)* sp., *Lepidocyclina gigas* Cushman, *L. (Eulepidina) favosa* Cushman, *Lepidocyclina* sp. indet. *b*, *Miogypsina hawkinsi* Hodson, and *Miogypsina bramlettei* Gravel, n. sp. The stratigraphic occurrence of the latter is somewhat uncertain, although the specimens are probably from the San Luis series.

The San Luis series is most probably susceptible of division into zones on the basis of the larger foraminiferal fauna. This would require the collection of material at frequent intervals across as many sections of the formation as possible, in order that geologic succession, range, and the lateral distribution and persistence of the faunal units could be accurately determined.

It appears that the San Luis series may safely be correlated with at least the lower part of the Antigua formation of the Island of Antigua, West Indies, which contains a similar fauna. The following species are reported by Cushman (14, p. 24) from Antigua: *L. (Eulepidina) favosa* Cushman, *L. (Nephrolepidina) undosa* Cushman, *Lepidocyclina gigas* Cushman, *Lepidocyclina undulata* Cushman. In addition to the above species of Cushman, Vaughan (55, pp. 1, 2) described *L. (Lepidocyclina) forresti* from the Oligocene of Antigua.

The Antiguan Oligocene and the San Luis series contain the following species in common: *L. (Nephrolepidina) undosa* Cushman, *L. (Eulepidina) favosa* Cushman, *Lepidocyclina gigas* Cushman, and *L. (Lepidocyclina) forresti* Vaughan.

The San Luis series may also be correlated with the Oligocene of Panama.

The following species have been reported from the Oligocene of Panama by Cushman (12, pp. 94-97): *L. (Lepidocyclina) canellei* Lemoine and R. Douvillé, specimens which Cushman referred to as *Lepidocyclina chaperi* Lemoine and R. Douvillé (Vaughan, 47, p. 798, states that the *Lepidocyclina chaperi* of Cushman from the Panama Canal zone is not *L. chaperi* Lemoine and R. Douvillé); *L. (Nephrolepidina) vaughani* Cushman; and *Miogypsina panamensis* (Cushman). In the same paper Cushman also described *L. (Lepidocyclina) macdonaldi* Cushman, and *L. (Pliolepidina) duplicata* Cushman from strata in Panama which were at that time considered Oligocene, and tentatively placed *L. (Pliolepidina) panamensis* Cushman in the Oligocene. Vaughan (47, pp. 796-797) places *L. macdonaldi* and *L. duplicata* in the Eocene. He also tentatively placed *L. panamensis* in the Oligocene. Vaughan has reported and described the following species from Panama (47, p. 813, pl. 36, figs. 4-6): *Miogypsina cushmani* Vaughan from the upper part of the Culebra formation, an undescribed species of *Heterostegina* (47, p. 789) from the Culebra formation at Bohio Ridge Switch, and *L. (Lepidocyclina) miraflorensis* Vaughan (55, p. 4, figs. 3-5), "The horizon is supposed to be the lower Miocene, Emperador limestone, but the stratigraphic position is not definitely known."

The following species are common to the San Luis series of Venezuela and the Oligocene of Panama: *L. canellei* and the undescribed species of *Heterostegina* reported from Panama by Vaughan, which is described in this paper as *Heterostegina panamensis* Gravell, n. sp.

As the stratigraphic relations of the lower Tertiary formations of Panama are still somewhat uncertain, only the general relationships of the San Luis series of Venezuela to the Oligocene of Panama are indicated.

The San Luis series may also be correlated with the Oligocene of Jamaica, which is represented by the Moneague formation and at least part of the Montpelier white limestone. Vaughan (57, p. 280) lists their faunas as follows:

Moneague formation: *L. (Lepidocyclina) canellei* Lemoine and R. Douvillé, *L. (Lepidocyclina) yurnagunensis* Cushman, *L. (Lepidocyclina) miraflorensis* Vaughan, *L. (Lepidocyclina) forresti*

Vaughan, *L. (Lepidocyclus) parvula* Cushman, *L. (Lepidocyclus) matleyi* Vaughan, *L. (Nephrolepidina) undosa* Cushman, *Lepidocyclus gigas* Cushman var., *L. (Nephrolepidina) crassata* Cushman.

Montpelier white limestone: *Miogypsina bracuensis* Vaughan, *L. (Lepidocyclus) canellei* Lemoine and R. Douvillé, *L. (Nephrolepidina) undosa* Cushman, *L. (Nephrolepidina) crassata* Cushman.

Vaughan (57, p. 279) quotes Dr. C. A. Matley as follows: "The flint-bearing, chalky, and globigerinal 'Montpelier formation' of Hill lies below the *Lepidocyclus undosa* zone, but its type of sedimentation is missing from the succession in many parts of the island and it seems to be a deep-water facies of the White Limestone that passes laterally into shallower-water mollusca-bearing beds. Hill's 'Moneague formation' certainly includes the *L. undosa* zone but its upper limit was not defined by the writer."

Vaughan (57, p. 280), in summarizing the stratigraphic distribution of the larger foraminifera of Montpelier white limestone and the Moneague formation shows that the larger foraminiferal fauna supports Dr. Matley's conclusions regarding the relations of these formations.

The Oligocene of Jamaica and the San Luis series contain the following species in common: *Lepidocyclus canellei*, *L. forresti*, *L. undosa*, *L. gigas*. They also contain species of the genus *Miogypsina*.

Rocks of Oligocene age, which for the present may be considered equivalent to the San Luis series of Venezuela, occur on the island of Trinidad, although a description of their Oligocene fauna has not, to my knowledge, yet been published. Oligocene material from Trinidad, containing *L. (Nephrolepidina) undosa* Cushman, *L. (Lepidocyclus) canellei* Lemoine and R. Douvillé, *L. (Lepidocyclus) yurnagunensis* Cushman, *L. (Eulepidina) favosa* Cushman, and other Oligocene forms, is in the collection of the Scripps Institution of Oceanography.

The San Luis series of Venezuela may be correlated with the Meson, from which Vaughan (48, p. 732) reports the occurrence of abundant *Lepidocyclus gigas* var. *mexicana* Cushman and *L. (Nephrolepidina) undosa* Cushman, and states: "The formation is approximately the equivalent of the Glendon formation of Alabama, Florida, and Georgia, and of at least the lower part of the Antigua formation of Antigua."

Collections from Mexico, at the Scripps Institution of Oceanography, also contain other middle Oligocene large foraminifera. Some of these species are *L. (Eulepidina) favosa* Cushman, *L. (Nephrolepidina) crassata* Cushman, *L. (Nephrolepidina) tournoueri* Lemoine and R. Douvillé, and *L. (Nephrolepidina) chattahoocheensis* Cushman.

Cole (8a, pp. 3-5, pl. 1) lists the following species from the Meson formation of Mexico: *L. (Lepidocyclina) parvula* Cushman, *L. (Nephrolepidina) undosa* Cushman, *L. undosa* var. *tumida* Vaughan, *Lepidocyclina gigas* Cushman, *Lepidocyclina gigas* var. *mexicana* Cushman, *L. (Nephrolepidina) crassata* Cushman, *Lepidocyclina* sp., and *Heterostegina antillea* Cushman.

The San Luis series and the middle Oligocene of Mexico are known to contain the following large foraminifera in common: *L. undosa*, *L. gigas*, *L. (Eulepidina) favosa*, and possibly *Heterostegina antillea*.

A section through the anticline of Buena Vista at the town of Buena Vista, State of Lara (personal communication of Dr. H. G. Kugler to Dr. T. Wayland Vaughan), shows a thick series of variegated shales referred to as the lower part of the lower Oligocene, resting with apparent conformity upon a series of upper Eocene conglomerates and orbitoidal limestones.

The collection that I have studied contained material from only one locality in the variegated shale series. No larger foraminifera were observed in this material.

Along the section through the Buena Vista anticline, a thick series of nummulitic limestone occurs directly above the variegated glauconitic shales. This nummulitic limestone series is placed by Kugler as upper to lower Oligocene. The larger foraminiferal fauna of this series consists of abundant specimens of *Amphistegina lessonii* d'Orbigny, *Camerina* sp. a, and *Heterostegina* cf. *H. antillea* Cushman. The above fauna sheds but little light upon the stratigraphic position of this nummulitic limestone.

Material from sediments of upper Eocene age were collected from Guacharaca out of the Guayaval series (Cerro Campaña limestone), District of Acosta, East Falcón, and also from the Buena Vista anticline at Buena Vista, State of Lara. The fauna contains *D. (Asterocyclina) asterisca* (Guppy), *D. (Asterocyclina) kugleri* Gravell, n. sp., *L. (Lepidocyclina) trinitatis* H. Douvillé, *L. (Lepidocyclina) macdonaldi* Cushman, *Camerina* sp. cf. *C. parvula* (Cushman), *Operculina* sp. cf. *O. cookei* Cushman, and *Gypsina vesicularis* (Parker and Jones). The fauna is distinctly of an upper Eocene type.

The Guayaval series (Cerro Campaña limestone) is evidently of the same age as the formation from Panama from which Cushman (12, pp. 90-91) described the following species: *L. (Lepidocyclina) macdonaldi* Cushman, *L. duplicata* Cushman, *L. (Pliolepidina) panamensis* Cushman, and *Discocyclina minima* (Cushman). Cushman questionably referred these species to the Oligocene. Vaughan (47,

pp. 796-797) places all of the above in the Eocene. *Lepidocyclina macdonaldi* is common to both the Guayaval series (Cerro Campaña limestone) and the upper Eocene of Panama.

The upper Eocene of Jamaica, Vaughan (57, p. 279), contains *Dictyoconus codon* Woodring, *D. fontabellensis* (Vaughan), *Discocyclina crassa* (Cushman), *Discocyclina* sp. aff., *Discocyclina pustulata* (Cushman), *Discocyclina perkinsi* Vaughan, *D. (Asterocyclina) georgiana* (Cushman), *D. (Asterocyclina)* sp. indet., *L. (Pliolepidina) kinlossensis* Vaughan, *L. (Lepidocyclina) macdonaldi* Cushman, *L. (Lepidocyclina) trinitatis* H. Douvillé, *L. (Lepidocyclina) sherrwoodensis* Vaughan, *L. (Nephrolepidina) haddingtonensis* Vaughan, *L.* sp. cf. (*Nephrolepidina*) *perundosa* Cushman.

*L. (Lepidocyclina) trinitatis* H. Douvillé, *L. (Lepidocyclina) macdonaldi* Cushman, and species of the genus *Asterocyclina* are common to both the upper Eocene of Jamaica and the Guayaval (Cerro Campaña limestone) of Venezuela.

The upper Eocene of Trinidad contains several species which also occur in the upper Eocene deposits of Venezuela. These species are *L. (Lepidocyclina) trinitatis* H. Douvillé, and *D. (Asterocyclina) asterisca* (Guppy).

It appears that the Guayaval series (Cerro Campaña limestone) may be safely considered approximately the equivalent of the Ocala limestone of Florida, Georgia, and Alabama; with at least part of the Lobitos shales of northwestern Peru; and with a formation exposed on sea cliffs near Ancón, province of Guayas, Ecuador.

Several papers have been published on the larger foraminifera of the upper Eocene Cerro di Cueba limestone of the island of Curaçao by Koch (28, 1926), L. Rutten (39, 1928), and Rutten and Vermunt (41, 1932). Koch considered the limestone to be lower Oligocene in age. L. Rutten recognized the fauna to be Eocene. M. G. Rutten and Vermunt (41, p. 7) regard the Cerro di Cueba limestone as upper Eocene.

The Guayaval series (Cerro Campaña limestone) of Venezuela may be approximately equivalent in age to the Cerro di Cueba, since both formations contain *L. trinitatis* H. Douvillé and *L. macdonaldi* Cushman, also specimens of *Operculina* and *Camerina* ("Nummulites"). The chief difference in faunas is that in Cerro di Cueba *Discocyclina* and *Asterocyclina* are absent, these subgenera not having yet been reported in the literature on Curaçao.

The Pauji shale is represented by a collection from only one locality. The material contains no large foraminifera.

The Paraíso series is placed by Kugler in the middle Eocene. Only two localities in Venezuela are represented by the material that I have studied. Of these only one contains larger foraminifera, an indeterminate species of *Discocyclina* which closely resembles *D. flintensis* (Cushman), in material from locality 1142. On the basis of this species of *Discocyclina* it is concluded that the geologic age is Eocene. Gorter and Van der Vlerk (25, p. 111) identify this species as *Discocyclina flintensis* (Cushman), which would suggest that at least part of the Paraíso series of Venezuela and the Brito formation of Nicaragua are of the same age.

#### DESCRIPTION OF SPECIES

##### Family CAMERINIDAE

##### Genus CAMERINA Brugière

##### CAMERINA sp. cf. *C. PARVULA* (Cushman)

##### Plate 1, fig. 6

*Nummulites parvula* Cushman (14, p. 51, pl. 4, figs. 3-6).

Poorly preserved specimens which appear to belong to this species occur in Orbitoidal limestone from several upper Eocene localities in Venezuela.

Test small, robustly lenticular; umbo composed of light-colored shell material, surface rather poorly preserved, shows only traces of slightly raised gently curved septal markings.

Both the microspheric and megalospheric forms were found. They have the same exterior form, but differ in size and number of whorls. The microspheric form has a diameter of about 3.5 mm and a thickness of about 2.0 mm, composed of about four closely coiled whorls, having about 32 chambers in the last whorl.

The megalospheric form is only about half as large, diameter about 2.0 mm; thickness about 1.2 mm. Test composed of about three whorls, there being about 24 chambers in the last whorl; septal walls gently curved. The marginal chord of both forms is thick.

The poor preservation and occurrence in hard limestone, which made the extraction of specimens from the matrix impractical, renders the identification of these specimens as *Camerina parvula* (Cushman) a little uncertain.

These specimens also resemble *C. matleyi* Vaughan (63, p. 376, pl. 39, figs. 2-7) from the middle Eocene "Yellow limestone" of Jamaica.

*Localities and geologic horizon.*—Fairly abundant in material from locality 163. Rock sections of material from localities 148, 149, 165, 1149, 1152, and 1162 contain a few poor sections of this species. That the above localities are upper Eocene is shown by the association of *D. (Asterocyclina) asterisca* (Guppy), *D. (Asterocyclina) kugleri* Gravell, n. sp., *L. (Lepidocyclina) macdonaldi* Cushman, *L. (Lepidocyclina) trinitatis* H. Douvillé, and other species.

#### CAMERINA sp. a

Plate I, figs. 1-5

Test small, compressed, lenticular; outer surface without surface ornamentation except the slightly raised narrow septal markings. Diameter about 1.5 to 2.5 mm; thickness about 0.5 to 0.75 mm. The thickness is about one third the diameter.

Test composed of four to five whorls, the fourth having about 26 chambers and the fifth about 32.

The specimens sectioned are all of the megalospheric form. The initial chamber has a diameter of about 70  $\mu$ .

*Localities and geologic horizon.*—This species occurs in the Oligocene at localities 480, 481, 482, 496, 497, 1147, 1166, 1186, 1222, and possibly 514. Associated with *Heterostegina* sp. cf. *H. antillea* Cushman.

*Camerina* sp. a is probably closely related to *C. panamensis* (Cushman) (12, p. 98, pl. 43, figs. 9-10), from the Culebra formation of Panama, as that species has approximately the same size, shape, and number of whorls, but it differs in the width of its whorls, which are not so wide as those of *C. panamensis*.

This species and *Heterostegina* sp. cf. *antillea* compose the bulk of the limestone from several localities. Unfortunately, good specimens cannot be separated from the matrix, owing to poor preservation of the specimens or to hardness of the matrix. Although this is probably a new species, it is not named because the material is too poor for adequate specific characterization.

#### CAMERINA sp. indet.

Sections of hard middle Oligocene San Luis limestone from localities 498, 959, 1121,, 1123, 1209, and 1221 contain a few random sections of a small indeterminate species of *Camerina*.

Test small, lenticular, thickest in center, gradually sloping to the periphery, which is broadly rounded; diameter about 2.0 mm; thickness about 0.8 mm. Test composed of four to five whorls.

These specimens are less compressed and have thicker chamber roofs than those of *Camerina* sp. *a* and *C. panamensis* (Cushman) (12, p. 98, pl. 43, figs. 9, 10).

Genus OPERCULINA d'Orbigny

OPERCULINA sp. cf. *O. COOKEI* Cushman

Plate 1, figs. 7-9

*Operculina cookei* Cushman (16, pp. 127, 128, pl. 18, figs. 1, 2).

These specimens differ somewhat from the typical *Operculina cookei*.

Test small, with a large excentrically placed thick swelling occupying about one half the test, surrounded by a thin flange. The diameter of the test measured from the periphery of the apertural face across the center is about 2.75 mm; thickness through center about 0.8 mm; outside the central area about 0.2 mm. Test composed of three and one half whorls, which widen rapidly; septa gently curved to near the periphery, where they turn backward abruptly. Chambers numerous, 30 to 34 in last whorl.

The center of the thickened part of the test is composed of an umbo of light-colored shell material and is about 0.5 mm in diameter. The sutures are but slightly raised; surface slightly depressed between the sutures.

These specimens differ from *O. cookei* as described by Cushman from the Ocala Limestone (upper Eocene), United States Geological Survey Station 7116, near Oakfield, Ga., in that they are only about half as large, and the width of the whorls does not increase quite so rapidly as does that of the whorls of typical *O. cookei*.

*Localities and geologic horizon.*—Fairly abundant at locality 163. Thin sections of material from localities 148, 1149, and 1162 contain a few poor sections of an *Operculina* which appear to be *Operculina* sp. cf. *O. cookei*.

That the above localities are upper Eocene is shown by the association of *Discocyclina* (*Asterocyclina*) *asterisca* (Guppy), *D. (Asterocyclina) kugleri* Gravell n. sp., *L. (Lepidocyclina) trinitatis* H. Douvillé, and *L. (Lepidocyclina) macdonaldi* Cushman.

Genus **HETEROSTEGINA** d'Orbigny**HETEROSTEGINA** sp. cf. **H. ANTILLEA** Cushman

Plate 1, fig. 12

*Heterostegina antillea* Cushman (14, p. 49, pl. 2, fig. 1; pl. 5, figs. 1-2).*Heterostegina antillea* Cushman (16, p. 131, pl. 20, figs. 13, 14).

Test medium-sized, thin; diameter up to about 8.0 mm; thickness through umbo up to about 0.7 mm, generally about 0.5 mm. The umbonate area low and gently curved; excentrically located, about 1.5 mm from the margin of the test, surrounded by a wide, thin flange; thickness of flange at junction of umbonate area about 0.35 mm, decreasing gradually to about 0.17 mm at the periphery of the test. The test is composed of about two and one half whorls, which rapidly increase in width.

*Localities and geologic horizons.*—*Heterostegina* sp. cf. *H. antillea* and *Camerina* sp. *a* compose a large part of the material from localities 482, 497, 1147, 1157, 1166, and 1222. A few sections of *Heterostegina* which may be *H.* sp. cf. *H. antillea* occur in thin sections of material from localities 496, 1210, 1221. All of the above listed localities are in the Nummulitic Limestone series, upper to lower Oligocene.

In thin sections *Heterostegina* sp. cf. *H. antillea* closely resembles *Heterostegina antillea* Cushman. No positive identification could be made, because the surface ornamentation could not be studied, owing to the impracticability of separating the fragile specimens from their indurated matrix.

**HETEROSTEGINA PANAMENSIS** Gravell, n. sp.

Plate 1, figs. 10, 11

*Heterostegina* sp. Vaughan (47, p. 789).

Test of the megalospheric form small; diameter up to about 3.0 mm; thickness up to about 0.75 mm; test composed of a rounded thickened area occupying about one half of the diameter, surrounded by a thin flange, which increases in breadth, giving the thickened area an excentric position. In the center of this thickened area is a small umbo of light-colored shell material. Periphery of the test broadly rounded; central portion ornamented by irregular, radial, slightly raised costae, which meet the chamberlets near the base of the thickened area. Test composed of about three and one half whorls, which gradually increase in breadth.

The embryonic apparatus of the megalospheric form (pl. 1, fig. 10) consists of a globular chamber about  $140\ \mu$  in diameter, followed by a crescent-shaped chamber about 70 to  $140\ \mu$  in diameter. The division of the chambers into chamberlets begins in the fourth chamber.

The microspheric form resembles very closely the megalospheric form, having the same number of whorls and the same surface ornamentation; however, its thickness through the center is as much as 1.25 mm. A horizontal section (pl. 1, fig. 11) shows the embryonic apparatus to be of the same type as the megalospheric form, though only about half as large. The first chamber has a diameter of about  $75\ \mu$ ; the second about 40 by  $90\ \mu$ , followed by four unsubdivided chambers; the chambers following are subdivided.

*Localities and geologic horizon.*—Locality 4. This species is associated with *L. (Lepidocyclina) canellei* Douvillé, *L. (Nephrolepidina) undosa* Cushman, *Miogypsina hawkinsi* Hodson, and *Amphistegina lessonii* d'Orbigny in the San Luis limestone, middle Oligocene.

These specimens differ in no significant characteristics from specimens of *Heterostegina* collected by Vaughan and McDonald from the "Culebra" formation, U.S.G.S. station 6025, south end of Bohio Ridge switch, Panama Railroad, Panama, and mentioned by Vaughan (46, p. 789).

## Family PENEROPLIDAE

### Genus ARCHAIAS Montfort

#### ARCHAIAS sp.

Plate 2, fig. 1

A few specimens of this genus were found in thin sections of limestone from localities 1123, and 1206, middle Oligocene, collected by H. G. Kugler. They appear to be very close to, if not identical with, the recent specimens of *Archaias aduncus* (Fichtel and Moll). Plate 2, figure 1, is a horizontal section of a specimen having a diameter of about 1.4 mm.

These specimens are associated with *Gypsina globulus* Reuss, *Camerina* sp. indet., and *Miogypsina hawkinsi* Hodson.

### Genus AMPHISORUS Ehrenberg

#### Amphisorus? sp.

Test thin, disklike; diameter up to about 8 mm. Horizontal sections show the median chambers to be almost circular, about  $40\ \mu$  in

diameter, arranged in annular rings. The annular and radial walls are about  $20 \mu$  thick. The specimens were too poorly preserved to permit determination of the type of communication between the median chambers.

The specimens occur in limestone. As it was impossible to remove them from the matrix, the margins of the test could not be examined. Several thin sections were made, but these did not yield sections from which the species or even the genus might safely be determined. However, these specimens appear to be much closer to *Amphisorus* than to *Orbitolites*.

*Locality and geologic horizon.*—From locality 468 in limestone lenses in the Agua Clara shales, which are believed to be upper Oligocene.

Dr. H. G. Kugler has informed Dr. T. Wayland Vaughan that these specimens have been identified as *Orbitolites sanluisensis* Hodson. I have thus far been unable to find any description or mention of this species in the literature.

#### Family AMPHISTEGINIDAE

##### Genus AMPHISTEGINA d'Orbigny

##### AMPHISTEGINA LESSONII d'Orbigny

Plate 2, fig. 2

*Amphistegina lessonii* d'Orbigny (35, p. 304, pl. 17, figs. 1-4).

*Amphistegina lessonii* Brady (6, p. 740, pl. III, figs. 1-7).

*Amphistegina lessonii* Cushman (10, p. 35, pl. 19, fig. 2. 12, p. 77. 13, p. 20, pl. 4, fig. 3; p. 70, pl. 26, fig. 5; pl. 27, fig. 3; pl. 28, fig. 1. 14, p. 50, pl. 7).

This species occurs in material from localities 204, 228, 322, 404, 468, 476, 477, 478, 494, 496, 510, 556, 843, 957, 960, 962, 1042, 1043, 1119, 1121, 1127, 1208, 1223, and Cerro Gauche.

In this collection the geologic range of this species is from middle Oligocene to Recent. This species also occurs at numerous places in Trinidad, Dominican Republic, Panama, Mexico, southern United States, Europe, and the West Indies.

#### Family PLANORBULINIDAE

##### Genus GYPSINA Carter

##### GYPSINA GLOBULUS (Reuss) Carter

Plate 2, fig. 3

*Cerriopora globulus* Reuss (37, p. 33, pl. 5, fig. 7).

*Gypsina globulus* Brady (6, p. 717, pl. 101, fig. 8).

*Gypsina globulus* Cushman (14, p. 44, pl. 4, fig. 7).

Test small, globular; diameter up to about 1.4 mm; surface marked by an irregular network of raised chamber walls.

A horizontal section through the medium plane of a specimen having a diameter of 1.4 mm (pl. 2, fig. 3) shows that the chambers in the test are irregularly polygonal in shape, having a diameter of from 40 to 60  $\mu$ . At a point about 240  $\mu$  from the center, the chambers become regular in shape and are arranged in definite radial rows, the chambers being short rectangular, the tangential diameter exceeding the radial diameter. The dimensions of the chambers increase toward the periphery of the test; at a point about 240  $\mu$  from the center, radial diameter about 40  $\mu$ ; tangential diameter about 50  $\mu$ ; at a point 700  $\mu$  from the center, radial diameter about 45  $\mu$ ; tangential diameter about 60  $\mu$ . Chamber walls are about 18  $\mu$  thick; roofs and floors of chambers perforated by cribriform perforations having a diameter of about 4  $\mu$ .

*Localities and geologic horizon.*—Thin sections of material from localities 4, 469, 960, 1117, 1123, 1208, and 1209 contain a few specimens that resemble this species too closely to be referred to any other.

All the localities listed are in the San Luis series, which is considered middle Oligocene.

#### GYPSINA VESICULARIS (Parker and Jones)

Plate 2, figs. 4, 5

*Orbitolina vesicularis* Parker and Jones (36, p. 31, no. 5).

*Tinoporos vesicularis* Brady (6, p. 718, pl. 101, figs. 9-12).

*Gypsina vesicularis* Cushman (14, p. 43).

A few specimens apparently belonging to this species were found in material from localities 149 and 163.

Diameter of test 1 to 3 mm; thickness from about 0.3 to 0.7 mm; smaller specimens disk-shaped; larger ones curved and wavy, attached side concave. Surface entirely covered by areolae, which have a fairly constant size, about 39 to 50  $\mu$ , but are very irregular in form. Vertical section of a specimen from locality 149 (pl. 2, fig. 4) has a diameter of about 2 mm, thickness about 0.5 mm.

This species is associated with *D. (Asterocyclina) asterisca* (Guppy), *D. (Asterocyclina) kugleri* Gravell, n. sp., *L. (Lepidocyclina) trinitatis* H. Douvillé, and *L. (Lepidocyclina) macdonaldi* Cushman.

Although this species has no stratigraphic value, the associated species indicate that the horizon is upper Eocene.

## Family RUPERTIIDAE

## Genus CARPENTERIA Gray

## CARPENTERIA sp.

Plate 2, figs. 6, 7

Thin sections of both Eocene and Oligocene limestone contain a few sections of *Carpenteria*. Owing to the impracticability of removing them from the indurated matrix, it was not possible to study their surface or to obtain complete information regarding their form.

In view of the reasons stated above it would be very hazardous to attempt specific determination of these specimens. It is possible that they represent two or more species.

A horizontal section from locality 12 is shown on plate 2, figure 7. A vertical section of a specimen from locality 1206 is figured on plate 2, figure 6.

*Localities and geologic horizon.*—Localities 12, 148, 163, 469, 957, 960, 970, 1043, 1206, and 1223. Localities 12, 148, and 163 are from the upper Eocene. The remaining localities are from the middle Oligocene.

## Family ORBITOIDIDAE

## Genus DISCOCYCLINA Gumbel

## DISCOCYCLINA sp. indet.

Plate 2, figs. 8, 9

Test flat to slightly undulate, very thin, only slightly increasing in thickness toward the center; no distinct umbo. All the specimens examined were broken, the thinness of the test making preservation of unbroken specimens difficult. Diameter at least 5.5 mm, possibly as much as 8 mm; thickness through center about 0.4 mm, decreasing very gradually to the periphery, which is about 30  $\mu$  thick; surface of test apparently covered by very small concentrically arranged papillae, about 30  $\mu$  in diameter.

The embryonic apparatus is composed of two chambers, the initial chamber being spherical, about 90  $\mu$  in diameter, and the second being crescent-shaped, half surrounding the initial chamber. The dimensions of the second chamber are about 80 by 110  $\mu$ .

Equatorial chambers rectangular, elongated radially, and in definite annuli; near center chambers have a radial length of 40  $\mu$ ; width about 25  $\mu$ ; toward periphery radial length from 40 to 100  $\mu$ , average length being about 80  $\mu$ ; average width about 30  $\mu$ .

The equatorial layer is very thin, nearly uniform in thickness, about 30 to 40  $\mu$ ; chamber cavities are elliptical, about 24  $\mu$  high and about 26  $\mu$  long; thickness of roofs and floors about 8 to 10  $\mu$ .

Lateral chambers in vertical section are small and have arched roofs. There are about seven to eight layers of lateral chambers on each side of the equatorial layer over the center, and these are not arranged in definite tiers. The number of tiers decreases toward the periphery, which is not covered by lateral chambers. This uncovered portion of the equatorial layer has a width of about 1.5 mm, and a thickness of about 30  $\mu$ . Height of chamber cavities varies from 8 to 10  $\mu$ ; length varies from 20 to 30  $\mu$ ; roofs and floors about 6  $\mu$  thick.

*Locality and geologic horizon.*—Locality 1142, Paraíso series, middle Eocene. This species is fairly abundant and is associated with a few poorly preserved specimens of an indeterminable species of *Camerina*.

These specimens resemble *Discocyclus flintensis* (15, p. 44, pl. 9, figs. 3-6) from the Brito formation of Nicaragua (U.S.G.S. station 6408). Their poor preservation makes specific determination impossible. Better material may show this to be a new species.

Gorter and Van der Vlerk (25, p. 111, pl. 16, figs. 5-6) identify what are probably better-preserved specimens from locality 1142 as *Discocyclus flintensis* Cushman.

#### Subgenus ASTEROCYCLINA Gumbel

#### DISCOCYCLINA (ASTEROCYCLINA) ASTERISCA (Guppy) Vaughan

*Cisseis asteriscus* Guppy (26, p. 584, pl. 25, figs. 19a-b).

*Cisseis asteriscus* Guppy, Hodson (27, pp. 11-13, pl. 2, figs. 1, 2, 10).

*Discocyclus (Asterocyclina) asterisca* (Guppy) Vaughan (62, p. 3).

Material collected by H. G. Kugler and L. Vonderschmitt from locality 163, Venezuela, contained four broken specimens of this species. Rock sections of material from localities 12, 148, 163, 1149, and 1162 contain sections of this species. Fragments of *Asterocyclina* occur at locality 1152. These may possibly be *D. (Asterocyclina) asterisca* (Guppy).

This species is associated with *L. (Lepidocyclina) trinitatis* H. Douvillé, *Camerina* sp. cf. *C. parvula* (Cushman), *D. (Asterocyclina) kugleri*, Gravell, n. sp., *Operculina* sp. cf. *O. cookei* Cushman, *Gypsina vesicularis* (Parker and Jones), and *Carpenteria* sp.

**DISCOCYCLINA (ASTEROCYCLINA) KUGLERI** Gravel, n. sp.

Plate 3, figs. 1, 2, 3, 4, 5

Test small, swollen, lenticular, with five to six short arms that start near the periphery of the test; surface densely papillate. Only megalospheric individuals were found. Diameter of test 2.0 to 4.0 mm; thickness, 1.0 to 1.7 mm, being about one half the diameter. The central portion of the test is thick, double-domed, its sides sloping gradually to a distance of about three fourths the radial distance from the center and from there less steeply to the periphery. There is a narrow, slightly undulating rim around the periphery, and it is extended into five or six short rounded arms which are usually broken off. Surface ornamented by small hexagonal papillae. The diameter of those near the center is about 80  $\mu$ . They decrease in size toward the edge, until the diameter is about 30  $\mu$  at the periphery. The distance between papillae is approximately equal to their diameters.

The embryonic apparatus is composed of two chambers. The initial chamber is subglobular about 114 by 134  $\mu$ , partly embraced by a crescent-shaped chamber whose dimensions are about 110 by 220  $\mu$ ; the walls are about 30  $\mu$  thick.

Equatorial chambers are rectangular, arranged in annuli of varying width. This irregularity of the width of the annuli makes the raylike *Asterocyclina*-pattern of the equatorial chambers a little indefinite. The equatorial chambers of the rays are radially elongate, radial diameter about 50 to 60  $\mu$ ; transverse diameter, 25 to 35  $\mu$ . The chambers between the rays vary in length, ranging from square, about 30  $\mu$  on a side, to radially elongate forms about 30 by 60  $\mu$ . The radial walls of adjacent annuli alternate in alignment and have a thickness of about 6  $\mu$ . The equatorial layer is about 20  $\mu$  high near center and 80  $\mu$  high at a point 1.5 mm from the center; the length of equatorial chambers is about 20  $\mu$  near the center and about 100  $\mu$  at a point 1.5 mm from the center.

The lateral chambers are very numerous, regular in size and form, arranged in tiers. The number of layers in the thick umbonate region is as many as 40 on each side of the equatorial layer, decreasing gradually to one or two at the periphery. The length of the lateral chambers varies from 60 to 80  $\mu$ ; roofs and floors are about 6  $\mu$  thick. There are no real pillars, although the overlapping ends of the lateral chambers, which are arranged in very regular tiers, give the appearance of pillars.

*Localities and geologic horizons.*—Cotypes from locality 163. This species also occurs at locality 149, associated with *L. macdonaldi*

Cushman, *L. trinitatis* Douvillé, *D. (Asterocyclina) asterisca* (Guppy). It is evidently upper Eocene.

Wiedenmayer (68) stated that the genus *Discocyclina* did not occur in the Cerro Campana limestone and placed the latter in the Oligocene.

This species appears to be rather closely related to a form which was obtained near Calita Sal, Department of Piura, Peru, and was described by Berry (2, pp. 405-407, pl. 1), as *D. (Asterodiscocyclina) stewardi*, new genus and new species, but it differs from the latter species in important respects. It has distinct *Asterocyclina* arms, although they are small and often broken off, and its test is thicker than that of *D. (Asterodiscocyclina) stewardi* Berry.

#### Genus LEPIDOCYCLINA Gumbel

#### LEPIDOCYCLINA (LEPIDOCYCLINA) CANELLEI Lemoine and R. Douvillé

Plate 5, figs. 4, 5, 6, 7, 8

*Lepidocyclina canellei* Lemoine and R. Douvillé (30, p. 20, pl. 1, fig. 1; pl. 3, fig. 5).

*Lepidocyclina canellei* Cushman (15, p. 75, pl. 32, figs. 1-5).

*Lepidocyclina (Lepidocyclina) canellei* Vaughan (47, p. 797, pl. 33, fig. 4, 57, pp. 290-291, pl. 49, figs. 1-5, 7-9).

Test small, discoid; diameter about 2.8 mm; thickness about 0.75 mm, or approximately one fourth the diameter. Test composed of a large, low, evenly curved swelling, surrounded by a thin, narrow collar, increasing in thickness toward the periphery; surface of test evenly covered by very small papillae. Only the megalospheric form was observed.

Embryonic apparatus composed of two small equal chambers, divided by a straight wall; diameter of embryonic apparatus in a horizontal plane about 220 by 260  $\mu$ ; peripheral wall about 14  $\mu$  thick. Embryonic apparatus in vertical section about 240  $\mu$  high and about 260  $\mu$  long.

Equatorial chambers in horizontal section are distinctly hexagonal, slightly increasing in size from center toward the periphery; near the center radial diameter about 55  $\mu$ ; tangential diameter about 40  $\mu$ ; near the periphery radial diameter about 80  $\mu$ ; tangential diameter about 60  $\mu$ . The chamber walls are relatively thin, measuring about 5  $\mu$ . Roofs and floors perforated by cribriform perforations about 1.0  $\mu$  in diameter. Equatorial chambers in vertical section are rectangular; height of chambers near center about 50  $\mu$ ; radial diameter about 35  $\mu$ ; height at periphery about 100  $\mu$ ; radial diameter about 75  $\mu$ .

Lateral chambers regular in size and distribution, in center of test about 10 layers in a tier on each side of the equatorial layer; length of tier about 400  $\mu$ , therefore about one chamber to 40  $\mu$ ; length of chambers about 50 to 80  $\mu$ . Some of the specimens have small pillars in the central part of the test.

*Localities and geologic horizon.*—*L. (Lepidocyclina) canellei* Lemoine and R. Douvillé occurs in material from localities 4, 469, 476, 957, 960, 1042, 1043, 1206, Cerro Gauche, and possibly 204, San Luis series, middle Oligocene. (See check list for associated foraminifera.)

*L. (Lepidocyclina) canellei* also occurs at many places in Panama, Jamaica, and Mexico.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) FORRESTI Vaughan

Plate 3, fig. 6

*Lepidocyclina (Lepidocyclina) forresti* Vaughan (55, p. 3, pl. 1, figs. 1-4; pl. 2, figs. 1-6).

*Lepidocyclina (Lepidocyclina) forresti* Vaughan (57, p. 291).

Specimens which differ in no significant characteristics from the cotypes of *Lepidocyclina (Lepidocyclina) forresti* Vaughan (from east of Lynch Point, Willoughby Bay, Antigua, West Indies) were collected by H. G. Kugler from the San Luis series, middle Oligocene, at locality 1206 near Agua Clara, District of Democracia, Falcón, Venezuela.

They are associated with *L. (Lepidocyclina) canellei* Lemoine and R. Douvillé.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) MACDONALDI Cushman

Plate 5, figs. 1, 2, 3

*Lepidocyclina macdonaldi* Cushman (12, pp. 94, pl. 40, figs. 1-6).

*Lepidocyclina macdonaldi* Cushman (15, p. 77, pl. 34, figs. 1-3).

*Lepidocyclina (Lepidocyclina) macdonaldi* Vaughan (47, p. 797).

*Lepidocyclina (Lepidocyclina) macdonaldi* Vaughan (57, p. 288).

*Lepidocyclina (Lepidocyclina) macdonaldi* M. Rutten and Vermunt (41, p. 9, pl. 1, fig. 13).

H. G. Kugler and L. Vonderschmitt collected limestone containing this species from the following localities in the upper Eocene of the State of Falcón, Venezuela: 12, 16, 148, and 149, from Guacharaca, Guayaval series; 163 and 165, from Cerro Campaña, Cerro Campaña limestone, also out of the Guayaval series.

This species is abundant. It is associated with *D. (Asterocyclina) kugleri* n.sp., *D. (Asterocyclina) asterisca* (Guppy), *L. (Lepidocyclina) trinitatis* H. Douvillé, and *Carpenteria* sp.

The indicated horizon is upper Eocene. *L. (Lepidocyclina) macdonaldi* also occurs in Panama and Jamaica.

**LEPIDOCYCLINA (LEPIDOCYCLINA) TRINITATIS H. Douvillé**

Plate 3, figs. 7, 8

*Isolepidina pustulosa* H. Douvillé (21, p. 844, fig. 3, not fig. 4).

*Isolepidina trinitatis* H. Douvillé (22, p. 34, pl. 1, text figs. 7-9).

*Lepidocyclina (Lepidocyclina) trinitatis* Hodson (27, p. 19, pl. 4, fig. 10).

*Lepidocyclina (Lepidocyclina) trinitatis* Vaughan (47, p. 797. 57, p. 289, pl. 49, figs. 10-13).

*Lepidocyclina (Lepidocyclina) trinitatis* Gorter and Van der Vlerk (25, pp. 107-108).

Test small; shape variable, globular to umbonate. In the umbonate forms the flange ranges in development from a mere vestige to a rim occupying over one half the diameter of the test. The central thickened area is covered with pustules which decrease in size toward the flange, absent on the outer margin of flange. Diameter of test about 1 to 5 mm; thickness about 1 to 2 mm.

Embryonic apparatus composed of two equal to subequal chambers, whose greater diameter is about 480 to 540  $\mu$  and lesser diameter about 350 to 420  $\mu$ . On each side of the junction of the embryonic chambers there is in many specimens a crescent-shaped chamber which is larger than the succeeding equatorial chambers. Vertical section shows the embryonic apparatus to be about 480 to 540  $\mu$  long and about 320  $\mu$  high; walls about 20  $\mu$  thick.

Equatorial chambers have rounded outer walls and pointed inner ends, largest at the center, with a radial diameter of about 100  $\mu$ ; tangential diameter about 80  $\mu$ . Equatorial chambers decrease in size toward the periphery, where the radial diameter is about 64  $\mu$  and the tangential 50  $\mu$ ; walls about 20  $\mu$  thick; roofs and floors perforated by evenly distributed pores with a diameter of about 2  $\mu$ . Height of equatorial layer near center about 120  $\mu$ ; height at a point 1.5 mm from the center about 240  $\mu$ ; thickness of the roofs and floors about 25  $\mu$ .

Lateral chambers arranged in tiers of 5 to 12 layers over the center on each side of the equatorial layer, decreasing in number toward the periphery where the equatorial layer is not covered by lateral chambers. The length of the lateral chambers ranges from 80 to 200  $\mu$ , longest over embryonic apparatus near the surface of test;

height fairly constant, about  $60\ \mu$ ; roofs about  $16\ \mu$  thick. Pillars cone-shaped in vertical section, regularly distributed in central part of the test. They are largest over the center, where they have a diameter of about  $180\ \mu$ , decreasing in size toward the flange.

*Localities and geologic horizon.*—Fairly abundant at localities 12, 16, 148, 149, 163, 165, and 1149. The material from localities 1152 and 1162 contains abundant fragments of *Lepidocyclina* and *Asterocyclina*. Some of the specimens of *Lepidocyclina* appear to be *L. (Lepidocyclina) trinitatis* H. Douvillé.

Associated with *D. (Asterocyclina) asterisca* (Guppy), *D. (Asterocyclina) kugleri* Gravell, n. sp., and *L. (Lepidocyclina) macdonaldi* Cushman.

The indicated geologic horizon is upper Eocene. *L. (Lepidocyclina) trinitatis* also occurs in the upper Eocene of Trinidad and Jamaica.

A single section (pl. 3, fig. 8) of a specimen of *Lepidocyclina* which in many features resembles *L. (Lepidocyclina) trinitatis* H. Douvillé was observed in rock sections of material from locality 165. This specimen differs from *L. trinitatis* in that its embryonic apparatus is double, composed of two pairs of subequal embryonic chambers. This specimen has the type of embryonic apparatus exhibited by *L. (Polylepidina) vanslobbeni* M. G. Rutten and Vermunt (41, p. 13, pl. 1, fig. 11; pl. 2, fig. 9; pl. 3, figs. 3, 4). *Lepidocyclina vanslobbeni* does not belong to the subgenus *Polylepidina*, as its embryonic apparatus is not polyepidine, but is a double or twinned *Lepidocyclina* s.s. type of embryonic chambers.

This twinning of the embryonic apparatus also occurs in the genus *Discocyclina*. Vaughan (62, pp. 14-16, pl. 5, figs. 1-6) described *Discocyclina cloptoni* Vaughan, some specimens of which species contain the normal type of embryonic apparatus, and others two, three, and even four sets of embryonic chambers.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) SANLUISENSIS Gravell n. sp.

Plate 4, figs. 1, 2, 3, 4

Only the megalospheric form of this species was observed.

Test medium size, lenticular, rather thick, with a narrow, stout projecting rim; diameter ranges from about 3 to 8 mm; thickness from about 2 to 2.7 mm; rim varies from a well-developed conspicuous collar about  $200\ \mu$  wide to a mere vestige. The margin of the largest specimen is broken; diameter of this specimen about 8 mm; rim projects about 2 mm on each side; thickness about 2.75 mm. Large polygonal papillae about  $250\ \mu$  in diameter cover the central part of

the test, decreasing to about  $90\ \mu$  near the rim. The papillae are separated by a distance approximately equal to their diameter.

The embryonic apparatus is composed of two subequal chambers, initial chamber subspherical, about  $210$  by  $280\ \mu$  in diameter; second chamber nearly hemispherical,  $170$  by  $320\ \mu$ ; the wall between chambers slightly curved toward the second chamber. On each side of the junction of embryonic chambers is a chamber about  $100\ \mu$  long and  $50\ \mu$  wide.

The equatorial chambers in horizontal section have curved outer walls and pointed inner ends, the radial diameter only slightly greater than the transverse diameter; dimensions near the embryonic apparatus about  $50\ \mu$ ; near periphery about  $60\ \mu$ . In vertical section equatorial chambers are about  $30\ \mu$  wide and  $60\ \mu$  high near the embryonic apparatus; at the periphery about  $40\ \mu$  wide and  $140\ \mu$  high; roofs and floors about  $10$  to  $16\ \mu$  thick, perforated by pores from  $2$  to  $3\ \mu$  in diameter.

The lateral chambers in vertical section  $20$  to  $40\ \mu$  high;  $40$  to  $200\ \mu$  long. The smaller chambers are next to the equatorial layer and increase in size toward the surface of the test; as many as  $16$  layers over the center of the test in a tier  $0.9$  mm high, decreasing in number toward the periphery. Large, cone-shaped pillars, irregular in width interrupt the development of the lateral chambers. The pillars are largest over the center of the test, where they attain a thickness of more than  $300\ \mu$ .

*Localities and geologic horizon.*—Cotypes from locality 168 of M. N. Bramlette's collection. Other localities at which this species occurs are 960, 970, 1042, 1116, and 1120, San Luis limestone, middle Oligocene. This species appears to be restricted to the San Luis limestone.

*L. (Lepidocyclus) sanluisensis* resembles *L. (Nephrolepidina) marginata* (Michelotti) in form and surface ornamentation, but differs in the character of the embryonic apparatus. The species is named after the San Luis limestone of Venezuela.

Gorter and Van der Vlerk (25, p. 104) identified specimens of *L. (Lepidocyclus) sanluisensis*, n. sp., from localities 1116 and 1120, as *L. (Nephrolepidina) marginata*. The embryonic apparatus, however, is not that of a *Nephrolepidina*, but is that of *Lepidocyclus* s.s.

#### LEPIDOCYCLINA (LEPIDOCYCLINA) sp. indet. (a)

Thin sections of a limestone largely composed of mollusk fragments contain a few rather unsatisfactory sections of a small *Lepidocyclus*.

Test small, lenticular; diameter 1.60 to 2.5 mm; thickness through center 0.6 to 0.7 mm, decreasing gradually to the periphery. Two subequal embryonic chambers; initial chamber globular, about 100  $\mu$  in diameter and about 100  $\mu$  high, followed by a subglobular chamber, length about 100  $\mu$ ; width about 50  $\mu$ ; walls of embryonic chambers about 15  $\mu$  thick.

Equatorial chambers open arcuate in form, increasing in size toward the periphery; tangential diameter 70 to 100  $\mu$ ; radial diameter 40 to 60  $\mu$ ; roofs and floors perforated by cribriform pores having a diameter of about 2  $\mu$ . Equatorial layer about 50  $\mu$  high near embryonic apparatus, increasing to about 160  $\mu$  high at a point approximately 0.6 mm from the center; roofs and floors about 15  $\mu$  thick.

Lateral chambers rather uniform in size; length about 80 to 100  $\mu$ ; height about 20 to 30  $\mu$ ; roofs and floors about 15  $\mu$  thick, perforated by minute pores. There are about six to seven tiers of lateral chambers on each side of the equatorial layer over the center of the test, the number decreasing toward the periphery, where the equatorial layer is covered by only one layer of chambers.

Pillars small, formed by the overlapping of ends of the lateral chambers. These pillars obtain a maximum diameter of about 30  $\mu$  at their distal ends over the center of the test.

*Locality and geologic horizon.*—From locality 443, lower part of producing zone, British Controlled Oil Fields Ltd., Buchivacoa, Falcón. This locality is believed to be in the Agua Clara or even the San Luis series.

#### LEPIDOCYCLINA sp. indet. (b)

Test small, with a large, thick central area, surrounded in some specimens by a narrow collar. Diameter up to 3 mm; thickness up to about 1.24 mm.

As specimens were rare and in a rock matrix, it was impossible to obtain sections that showed the character of the embryonic apparatus; therefore no specific determination has been attempted.

Although no good horizontal sections were obtained, the equatorial chambers appear to be spatulate to hexagonal. Several good vertical sections were obtained, showing the equatorial chambers to be square to rectangular, in vertical section; at center about 30  $\mu$  high; radial diameter about 60  $\mu$ ; roofs and floors about 20  $\mu$  thick.

Lateral chambers in vertical section resemble flat convex lenses and are in regular tiers, as many as 11 chambers over the center in a tier 450  $\mu$  high, or about one chamber to every 40  $\mu$ . They decrease in number toward the periphery, ending at the collar, which is not

covered by lateral chambers. The chambers increase slightly in size toward the surface of the test. Near the equatorial layer, height about  $18\ \mu$ ; length about  $130\ \mu$ ; roofs and floors about  $18\ \mu$  thick. A few large cone-shaped pillars over center of test originate at point a little above the equatorial layer and rapidly increase in thickness, attaining a diameter of as much as  $240\ \mu$  at the surface. A section parallel to the equatorial layer shows 11 large polygonal pillars in center of test, one occupying a central position; they are surrounded by a polygonal mesh formed by the walls of the lateral chambers.

*Locality and geologic horizon.*—Locality 1043, San Luis series, middle Oligocene. Associated with *Lepidocyclus canellei* Lemoine and R. Douvillé and *Amphistegina lessonii* d'Orbigny.

#### LEPIDOCYCLINA GIGAS Cushman

*Lepidocyclus gigas* Cushman (15, p. 63, pl. 19, figs. 1, 2, 3, not fig. 4).

*Lepidocyclus gigas* Vaughan (47, p. 799. 51, p. 295).

This species is associated with *L. (Nephrolepidina) undosa* Cushman at localities 477, 478, and in transported blocks at locality 1223 from the San Luis series, which is considered to be middle Oligocene.

*Lepidocyclus (Lepidocyclus) gigas*, according to Vaughan (42, p. 799), appears to be the microspheric form of *L. (Nephrolepidina) undosa* Cushman, as it invariably occurs with *L. (Lepidocyclus) undosa* and also has the same type of equatorial chambers.

*Lepidocyclus gigas* is a very common and widely distributed middle Oligocene species. Besides occurring in Venezuela, it has been found at numerous localities in Antigua, Mexico, Jamaica, and Trinidad.

#### Subgenus NEPHROLEPIDINA H. Douvillé

#### LEPIDOCYCLINA (NEPHROLEPIDINA) UNDOSA Cushman

Plate 6, fig. 4

*Lepidocyclus undosa* Cushman (15, p. 68, pl. 25, fig. 3).

*Lepidocyclus (Nephrolepidina) undosa* Vaughan (57, p. 294, pl. 48, fig. 3).

*Lepidocyclus (Eulepidina) undosa* Gorter and Van der Vlerk (25, p. 110, pl. 15, figs. 1-4).

This species is very abundant in parts of the San Luis limestone of Venezuela. It occurs in material from localities 4, 477, 478, 959, 960, 968, Cerro Gauche, and in transported blocks at localities 1219, 1221, and 1223, and possibly as fragments in a limestone at locality 236, which is composed of unweathered fragments of *Heterostegina* sp., *L. (Lepidocyclus)* sp., and *Amphistegina lessonii* d'Orbigny, cemented with calcite. The foraminifera appear to be primary, as they are unweathered.

*Lepidocyclina (Nephrolepidina) undosa* is a very common and widely distributed middle Oligocene species. Besides Venezuela, it occurs at numerous localities in Mexico, Antigua, Jamaica, and Trinidad. Gorter and Van der Vlerk (25, p. 110) place *L. undosa* in the subgenus *Nephrolepidina*. A large number of sections of this species show the embryonic apparatus varying from the nephrolepidine to eulepidine type, making the assignment of this species to either subgenus virtually optional.

#### LEPIDOCYCLINA (NEPHROLEPIDINA) sp.

Plate 5, figs. 9, 10; plate 6, fig. 1

Thin sections of hard San Luis limestone from locality 1209 contain a few rather poorly preserved specimens of *Nephrolepidina*, associated with a few specimens of *Gypsina globulus* (Reuss), a few specimens of a small indeterminate species of *Camerina*, several genera of small foraminifera, and calcareous algae.

Test variable in shape; some specimens have a large centrally thickened area, well demarked from a surrounding rim, in others the thickness of the test decreases gradually from the center to the periphery. Some of the specimens are strongly curved, whereas others show little or no curvature.

A megalospheric specimen, which has its edges broken, is 12 mm in diameter. It is possible that the megalospheric form attains a diameter of 20 mm; thickness through center up to about 2 mm.

Embryonic apparatus of *Nephrolepidina* type, composed of an initial ovate chamber about 360  $\mu$  long and about 260  $\mu$  wide, half surrounded by a crescent-shaped chamber about 200 by 530  $\mu$ . Both chambers are enveloped in a common wall about 50  $\mu$  thick; height about 500  $\mu$ .

Equatorial chambers hexagonal in horizontal section; radial and tangential diameters about 70  $\mu$ . The equatorial layer increases but slowly in height toward the periphery; height about 80  $\mu$  near the embryonic apparatus; about 120  $\mu$  high at a distance of 1.6 mm from the embryonic apparatus; roofs about 15  $\mu$  thick.

Lateral chambers low and flat, about 15 layers over the center of the test in a tier 660  $\mu$  high, or about one chamber to 44  $\mu$ ; chamber spaces about 30  $\mu$  high; roofs about 15  $\mu$  thick; length increases from about 60  $\mu$  at the equatorial layer to about 200  $\mu$  at the surface of the test. The number of layers of lateral chambers decreases from 15 over the center to one or two layers at the periphery. The pillars are small, regular in distribution, originating at the equatorial layer

and attaining a maximum thickness of about  $70\ \mu$  at their outer ends, about  $45\ \mu$  being more common.

The hardness of the matrix made it impractical to separate the specimens from the matrix. Although the specimens appear to belong to a single species, better material may show the arched and unarched forms to constitute two distinct species.

Subgenus **EULEPIDINA** H. Douvillé

**LEPIDOCYCLINA (EULEPIDINA) FAVOSA** Cushman

Plate 5, fig. 11; plate 6, fig. 2

*Lepidocyclus favosa* Cushman (14, p. 66, pl. 3, figs. 1, 2b; pl. 15, fig. 4. 15, p. 66, pl. 15, fig. 5(B)).

*Lepidocyclus (Eulepidina) favosa* Vaughan (47, p. 799, pl. 34, fig. 8).

*Lepidocyclus* sp. Gorter and Van der Vlerk (25, p. 103).

Specimens of *L. (Eulepidina) favosa* were found in limestone from localities 498 and 967.

The indicated geologic horizon is middle Oligocene. *Lepidocyclus (Eulepidina) favosa* was described by Cushman from the Antigua formation, middle Oligocene. The type locality is U.S.G.S. station 688r, Antigua, Leeward Islands, bluffs on north side of Willoughby Bay.

Subfamily **MIOGYPSININAE**

Genus **MIOGYPSINA** Sacco

**MIOGYPSINA BRAMLETTEI** Gravell, n. sp.

Plate 6, figs. 5-10

Both megalospheric and microspheric forms of this species were found. The microspheric form (pl. 6, fig. 5) is flat disk-shaped; diameter as much as 4 mm; thickness about 0.75 mm; entirely covered by glassy pustules from 50 to 80  $\mu$  in diameter, separated by a distance of about twice their diameter. The surface of the test is marked by a mesh work formed by the lateral chamber walls.

Test of the megalospheric form is smaller and wedge-shaped (pl. 6, figs. 8, 10). The dimensions of one specimen are 2.6 mm long, 2.4 mm wide, and about 0.4 mm thick in the thickest portion, which is near the apex of the test. The thickness decreases gradually toward the periphery, which is rounded. The surface is covered with pustules as in the microspheric form, though they are somewhat smaller, having a diameter of about 39 to 70  $\mu$ , being largest over the thickest portion of the test.

The embryonic apparatus of a specimen 2.1 mm in length and 1.8 mm wide (pl. 6, fig. 9) peripherally located at the apex of the test, consists of an initial globular chamber about 140  $\mu$  in diameter, followed by two globular chambers about 120  $\mu$  in diameter. The initial chambers are followed by four or five slightly smaller chambers which are intermediate in character between the first two embryonic chambers and the equatorial chambers and are cyclically arranged around the inner side of the first three initial chambers; walls of embryonic chambers about 30  $\mu$  thick.

The equatorial chambers are diamond-shaped and vary in size, the radial diameter almost always being the greater. The average size is about 140 by 160  $\mu$ , though chambers half this size are found. The walls are about 20  $\mu$  thick; roofs and floors of the equatorial chambers are pierced by numerous cribriform perforations, having a diameter of about 3  $\mu$ .

The equatorial chambers of the microspheric form near the embryonic chambers are arcuate in form; diameter about 40  $\mu$ ; at a distance of about 0.8 mm from the apex they become diamond-shaped; radial diameter about 160  $\mu$ ; tangential diameter about 140  $\mu$ ; at a distance of about 2 mm from the apex, radial diameter about 200  $\mu$ ; transverse diameter about 130  $\mu$ ; chamber walls about 20  $\mu$  thick; roofs and floors perforated by numerous cribriform perforations about 3  $\mu$  in diameter.

In a vertical section of a broken specimen having a diameter of 1.52 mm and a thickness of 0.48 mm, the equatorial layer is 120 to 160  $\mu$  high; chamber spaces elliptical, from 60 to 100  $\mu$  high; length near embryonic apparatus about 40  $\mu$ ; at a point about 1.5 mm from the embryonic apparatus, length about 180  $\mu$ . The roofs and floors of the equatorial layer are about 20  $\mu$  thick.

There are about four layers of lateral chambers on each side of the equatorial layer, irregular in arrangement and size, not arranged in tiers. Dimensions of chamber spaces: Height, about 30 to 40  $\mu$ ; length, about 40 to 200  $\mu$ ; roofs and floors slightly arched, thickness about 20  $\mu$ , perforated by numerous cribriform perforations. This species has no pillars.

*Locality and geologic horizon.*—These specimens were obtained by M. N. Bramlette from well Rodriguez No. 23 from a depth of 2,482 feet, Ambrosia Field, District of Bolivar, Venezuela.

The geologic horizon from which these specimens were obtained is not definitely known, though it is probably middle or upper Oligocene.

This species differs from other described species of American *Miogypsina* in its lack of definite pillars. It is also thinner. Mature megalospheric specimens have a thickness of only 0.4 mm. This species has the peripherally located type of embryonic apparatus which is possessed by *M. cushmani* Vaughan, *M. hawkinsi* Hodson, *M. bracuensis* Vaughan, and *M. venezuelana* Hodson. It differs from the first three in being only about half as thick, and from the latter by its much smaller size.

This species is named in honor of Mr. M. N. Bramlette.

#### MIOGYPSINA HAWKINSI Hodson

Plate 6, figs. 11, 12, 13, 14\*

*Miogypsina hawkinsi* Hodson (27, pp. 28-29, pl. 7, fig. 9; pl. 8, figs. 1-2).

Specimens of this species occur in material from the San Luis series, middle Oligocene, at the following localities: 4, 8, 168, 960, 1042, 1123, 1127, and possibly at localities 500, 843, 1119, and 1120. Some of the associated species are *L. (Lepidocyclina) canellei* Lemoine and R. Douvillé, *L. (Lepidocyclina) sanluisensis*, n. sp., *L. (Nephrolepidina) undosa* Cushman, *Camerina* sp. indet., and *Heterostegina* sp.

#### DESCRIPTION OF LOCALITIES

All the following localities are in the States of Falcón, East Falcón, or Lara, Venezuela.

Cerro Gauche. Three kilometers south of San Luis, District of Bolivar, Falcón. Collected by M. N. Bramlette.

Rodriguez No. 23. From well Rodriguez No. 23, 2,482 feet, Ambrosia Field, District of Bolivar, Falcón. Collected by M. N. Bramlette.

4. About 1 kilometer northeast of Pecaya, District of Democracia. Collected by M. N. Bramlette.

8. District of Buchivacoa, Falcón. Collected by M. N. Bramlette.

12. From Guacharaca, out of Guayaval series, District of Acosta, East Falcón. Collected by H. G. Kugler and L. Vonderschmitt.

16. From Guacharaca, out of Guayaval series, District of Acosta, East Falcón. Collected by H. G. Kugler and L. Vonderschmitt.

148. From Guacharaca, out of Guayaval series, District of Acosta, East Falcón. Collected by H. G. Kugler and L. Vonderschmitt.

149. Same locality as 148.

163. From Cerro Campana, out of Guayaval series (Cerro Campana limestone), District of Acosta, East Falcón. Collected by H. G. Kugler and L. Vonderschmitt.

165. From Cerro Campana, out of Guayaval series (Cerro Campana limestone), District of Acosta, East Falcón. Collected by H. G. Kugler and L. Vonderschmitt.



168. District of Democracia, Falcón. Collected by M. N. Bramlette.
204. El Mene del Salto from base of El Mene beds, Agua Clara series, District of Acosta, East Falcón. Collected by H. G. Kugler and L. Vonderschmitt.
228. Quebreda Juso near El Pozon, District of Acosta, East Falcón. Collected by L. Vonderschmitt.
233. From alluvial drift block on west side of Rio Ricoa nearly opposite town of Moturo, District of Zamora, East Falcón. Collected by H. G. Kugler and L. Vonderschmitt.
236. Outcrop on road from Carorita to Agua Linda, District of Acosta, East Falcón. Collected by H. G. Kugler and L. Vonderschmitt.
322. Caparare limestone between La Caridad and Mirimiri. Collected by H. G. Kugler and L. Vonderschmitt.
404. Near Curamichate. Loose blocks? Collected by L. Vonderschmitt.
443. From lower part of producing zone, British Controlled Oil Fields, Ltd., District of Buchivacoa, Falcón. Collected by H. G. Kugler.
468. From Guarabal, District of Mirandana, State of Falcón. Collected by H. G. Kugler.
469. San Luis limestone about 3 miles south of Cabure, on Cabure-Churuguara Road, District of Petit. Collected by H. G. Kugler.
476. Cabure-Churuguara Road, about 1 mile north of Juan Diaz, District of Federación, Falcón. Collected by H. G. Kugler.
477. Cabure-Churuguara Road, District of Federación, Falcón. Collected by H. G. Kugler.
478. San Luis limestone, between Parucia and Churuguara, District of Federación, Falcón. Collected by H. G. Kugler.
480. Churuguara beds just south of Churuguara, District of Federación, Falcón. Collected by H. G. Kugler.
481. Churuguara beds just south of Churuguara, District of Federación, Falcón. Collected by H. G. Kugler.
482. Churuguara beds just south of Churuguara, District of Federación, Falcón. Collected by H. G. Kugler.
494. Just north of town of Aguada Grande, State of Lara. Collected by H. G. Kugler.
496. Between El Tupi and Campo Alegre, District of Federación, State of Falcón. Collected by H. G. Kugler.
497. Between El Tupi and Campo Alegre, District of Federación, Falcón. Collected by H. G. Kugler.
498. On road between Guarabal and Pecaya between La Puerta and Porvenir, District of Bolivar, San Luis limestone. Collected by H. G. Kugler.
500. About 2 miles south of Agua Clara, District of Miranda, Falcón. Collected by H. G. Kugler.
510. About 2 miles east of Sabanas Altas, District of Zamora, East Falcón. Collected by H. G. Kugler.
514. About 2 miles south of Guarabal, District of Miranda, Falcón. Collected by H. G. Kugler.
556. Ojo de Agua beds at Repelón, near El Mene, District of Acosta, East Falcón. Collected by L. Vonderschmitt.
843. La Penita, Guayaval. Collected by L. Vonderschmitt.

957. Facies of San Luis limestone, Macoruca, District of Colina, Falcón. Collected by L. Vonderschmitt.
959. Marly limestone underlying the main San Luis limestone layer, El Cumbre, District of Colina, Falcón. Collected by H. G. Kugler and L. Vonderschmitt.
960. Main San Luis limestone. El Cumbre, District of Colina. Collected by H. G. Kugler and L. Vonderschmitt.
962. Marly limestone overlying the San Luis beds separated from them by a thick shale formation. At El Solito, District of Colina, Falcón. Collected by H. G. Kugler.
967. Bluish limestone. At La Guyia, District of Colina, Falcón. Collected by L. Vonderschmitt.
968. Orbitoidal marl at La Guyia, just south of locality 967, District of Colina, Falcón. Collected by L. Vonderschmitt.
970. Acurigua, District of Colina, Falcón. San Luis limestone. Collected by L. Vonderschmitt.
1042. Acurigua, District of Colina, Falcón. San Luis limestone. Collected by L. Vonderschmitt.
1043. El Cumbre (Orbitoidal marl underlying locality 959), District of Colina, Falcón. Collected by H. G. Kugler and L. Vonderschmitt.

Material from the following localities were collected by Drs. P. Leuzinger, P. A. Messmann, and A. Senn, and sent to Scripps Institution of Oceanography by Dr. H. G. Kugler.

1116. Pedregosa, District of Democracia, Falcón. Fine conglomerate cemented with lime.
1117. La Caca, District of Bolivar, Falcón. Stratigraphically about 150 feet above 1209.
1119. Guasiqui, District of Bolivar, Falcón.
1120. Pedregosa, District of Democracia, Falcón. Stratigraphically about 300 feet above locality 1116.
1121. Along the "Carretera de Falcón" on the summit of the Cordillera de Agua Negra, South of Tupí, District of Federación, Falcón.
1123. Pedregosa, District of Democracia, Falcón. About 130 feet above locality 1116.
1127. Pedregosa, District of Democracia, Falcón. Stratigraphically about 170 feet above 1116.
1142. Buena Vista, State of Lara.
1147. About half way between El Paujicito and El Vadillal, and stratigraphically about 2,300 feet above 1149.
1149. Between El Vadillal and El Oso, about 700 feet north of El Vadillal, State of Lara.
1152. Between El Oso and El Vadillal, State of Lara. About 80 feet north and stratigraphically about 60 feet below locality 1149.
1157. Paso Grande, District of Democracia, Falcón.
1162. Between El Oso and El Vadillal, about 1,000 feet north of El Vadillal, and stratigraphically about 200 feet below locality 1149.
1166. Paso Grande, District of Democracia, Falcón.

1186. About half way between El Vadillal and El Paujicito, State of Lara, stratigraphically about 200 feet above locality 1149.
1194. A short distance north of El Oso, State of Lara.
1206. East side of Baño Gorge, Los Baños, District of Democracia, Falcón.
1208. West side of Baño Gorge. Stratigraphically about 750 feet above locality 1210, District of Democracia, Falcón.
1209. La Caca, District of Bolivar, Falcón.
1210. Los Baños, west side of Baño Gorge, District of Democracia, Falcón.
1219. Transported blocks from El Yavito, District of Democracia, Falcón.
1221. Transported blocks from La Idea, State of Lara.
1222. El Vadillal, State of Lara.
1223. Transported blocks from El Mamonsito, State of Lara.

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## EXPLANATION OF PLATES

The locality numbers are explained under "Description of Localities."

## PLATE I

- FIGS. 1-5. *Camerina* sp. a. Figs. 1, 2, exterior views of three specimens,  $\times 13$ , from locality 497; fig. 3, horizontal section,  $\times 20$ , from locality 482; fig. 4, vertical section,  $\times 20$ , from locality 497; fig. 5, horizontal section,  $\times 20$ , from locality 496.
- FIG. 6. *Camerina* sp. cf. *C. parvula* Cushman, vertical section,  $\times 20$ , from locality 163.
- FIGS. 7-9. *Operculina* sp. cf. *O. cookei* Cushman. Fig. 7, exterior view a specimen,  $\times 13$ ; fig. 8, vertical section,  $\times 42$ ; fig. 9, horizontal section,  $\times 20$ . All specimens are from locality 163.
- FIGS. 10, 11. *Heterostegina panamensis* Gravell, n. sp. Fig. 10, horizontal section of a megalospheric specimen,  $\times 20$ ; fig. 11, horizontal section of a microspheric specimen,  $\times 19$ . Both specimens are from locality 4.
- FIG. 12. *Heterostegina* sp. cf. *H. antillea* Cushman, vertical section,  $\times 20$ , from locality 482.

## PLATE 2

- FIG. 1. *Archaias* sp., horizontal section,  $\times 20$ , from locality 1123.
- FIG. 2. *Amphistegina lessonii* d'Orbigny, vertical section,  $\times 50$ , from locality 228.
- FIG. 3. *Gypsina globulus* (Reuss), horizontal section,  $\times 36$ , from locality 1208.

- FIGS. 4, 5. *Gypsina vesicularis* (Parker and Jones.) Fig. 4, vertical section,  $\times 20$ , from locality 149; fig. 5, vertical section,  $\times 34$ , from locality 163. (*Lepidocyclina trinitatis* H. Douvillé at the right margin of the fig. 4.)
- FIGS. 6, 7. *Carpenteria* sp. Fig. 6, vertical section,  $\times 21$ , from locality 1206; fig. 7, horizontal section,  $\times 21$ , from locality 12.
- FIGS. 8, 9. *Discocyclina* sp. indet. Fig. 8, portion of horizontal section,  $\times 86$ , from locality 1142; fig. 9, portion of vertical section,  $\times 86$ , from locality 1142.

## PLATE 3

- FIGS. 1-5. *Discocyclina* (*Asterocyclina*) *kugleri* Gravel, n. sp. Figs. 1, 2, surface views of cotypes,  $\times 12$ ; fig. 3, surface view of a cotype,  $\times 5$ ; fig. 4, vertical section of a cotype (fig. 4,  $\times 21$ ); fig. 5, horizontal section of a cotype,  $\times 20$ . All specimens are from locality 163.
- FIG. 6. *L. (Lepidocyclina) forresti* Vaughan, portion of horizontal section,  $\times 25$ , from locality 1206.
- FIG. 7. *L. (Lepidocyclina) trinitatis* H. Douvillé, vertical section,  $\times 21$ , from locality 149.
- FIG. 8. *L. (Lepidocyclina) trinitatis*, vertical section of a specimen that has a twin embryonic apparatus,  $\times 20$ , from locality 165.

## PLATE 4

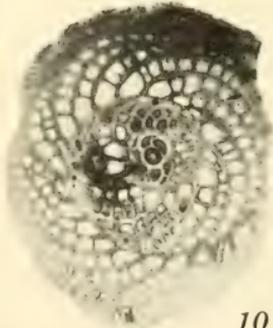
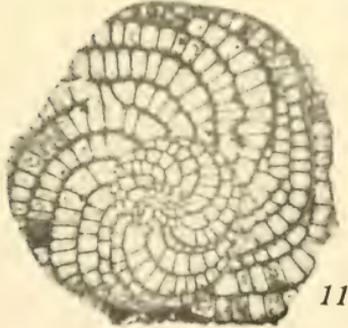
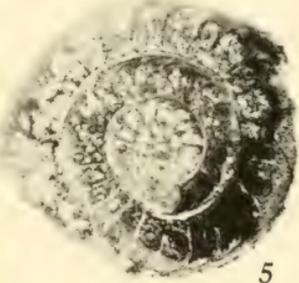
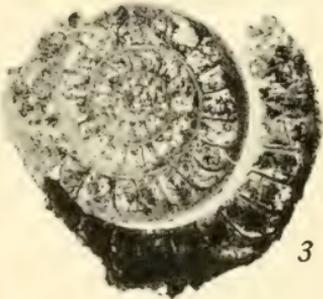
- FIGS. 1-4. *Lepidocyclina (Lepidocyclina) sanluisensis* Gravel, n. sp. Fig. 1, surface view of a cotype,  $\times 13$ ; fig. 2, horizontal section of a cotype,  $\times 18$ ; fig. 3, vertical section of a cotype,  $\times 16$ ; fig. 4, portion of horizontal section of a cotype,  $\times 40$ . All specimens are from locality 168.

## PLATE 5

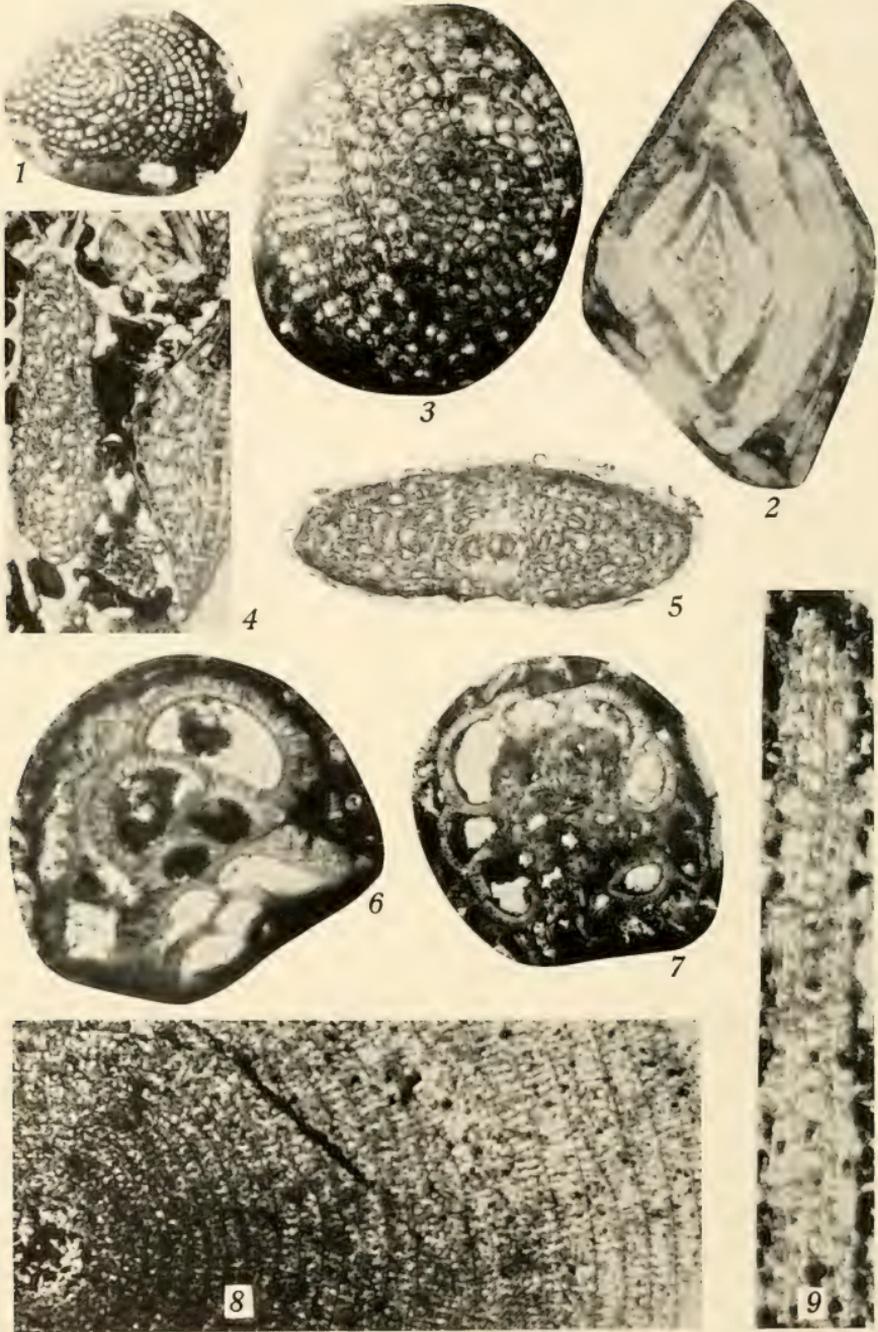
- FIGS. 1-3. *Lepidocyclina (Lepidocyclina) macdonaldi* Cushman. Fig. 1, vertical section,  $\times 46$ , from locality 149; fig. 2, horizontal section,  $\times 13$ , from locality 163; fig. 3, horizontal section,  $\times 20$ , from locality 12.
- FIGS. 4-8. *Lepidocyclina (Lepidocyclina) canellei* Lemoine and R. Douvillé. Fig. 4, surface view,  $\times 10$ , from locality 4; fig. 5, vertical section,  $\times 20$ , from locality 469; fig. 6, horizontal section,  $\times 20$ , from locality 469; fig. 7, vertical section of two specimens,  $\times 20$ , from locality 469; fig. 8, portion of horizontal section,  $\times 40$ , from locality 4.
- FIGS. 9, 10. *Lepidocyclina (Nephrolepidina)* sp. Fig. 9, vertical section,  $\times 12$ ; fig. 10, vertical section,  $\times 20$ . Both specimens are from locality 1209. (See pl. 6, fig. 1.)
- FIG. 11. *Lepidocyclina (Eulepidina) favosa* Cushman, vertical section,  $\times 19$ , from locality 498.

## PLATE 6

- FIG. 1. *Lepidocyclina* (*Nephrolepidina*) sp., horizontal section,  $\times 11$ , from locality 1209. (See pl. 5, figs. 9, 10.)
- FIG. 2. *Lepidocyclina* (*Eulepidina*) *favosa* Cushman, vertical section,  $\times 21$ , from locality 967.
- FIG. 3. *Lepidocyclina* sp. indet. (*b*), vertical section,  $\times 20$ , from locality 1043.
- FIG. 4. *Lepidocyclina* (*Nephrolepidina*) *undosa* Cushman, vertical section,  $\times 20$ , from locality 1223.
- FIGS. 5-10. *Miogypsina bramlettei* Gravell, n. sp. Figs. 5-7, surface views; fig. 5, microspheric specimen,  $\times 18$ ; figs. 6, 7, megalospheric specimens (fig. 6  $\times 23$ , fig. 7,  $\times 13$ ); fig. 8, horizontal section,  $\times 20$ ; fig. 9, horizontal section of another specimen,  $\times 20$ ; fig. 10, vertical section of microspheric specimen,  $\times 36$ . The above specimens are all from well Rodriguez 23.
- FIGS. 11, 12, 13, 14. *Miogypsina hawkinsi* Hodson. Fig. 11, horizontal section,  $\times 20$ , locality 9; figs. 12-14, surface view of three specimens,  $\times 13$ , from locality 8.



TERTIARY FORAMINIFERA OF VENEZUELA  
 (For explanation, see page 42.)



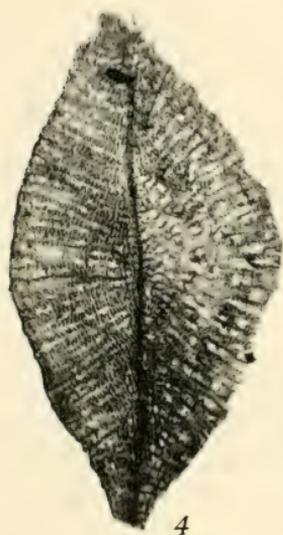
TERTIARY FORAMINIFERA OF VENEZUELA  
(For explanation, see page 42.)



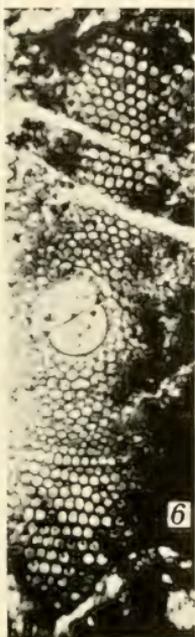
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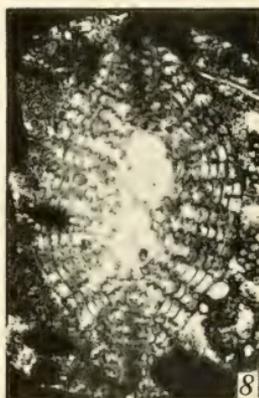
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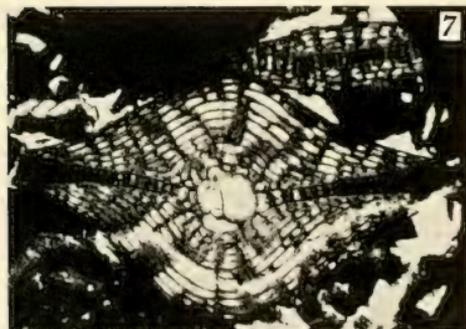
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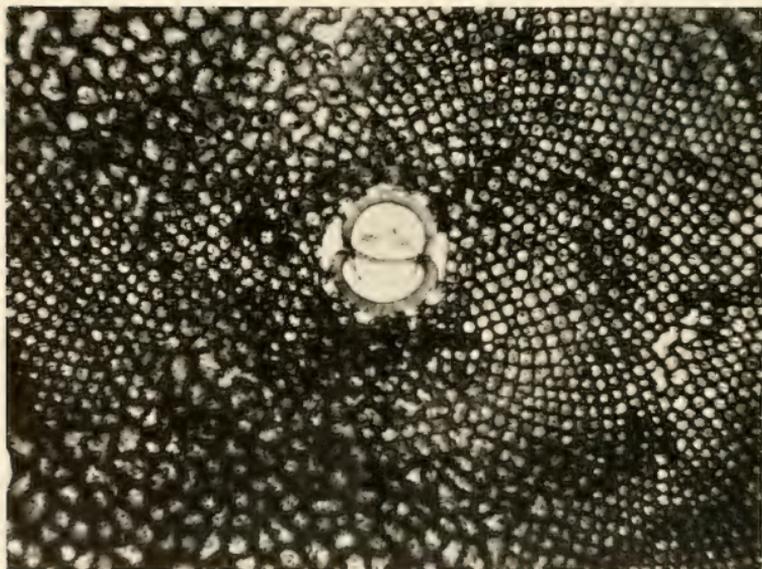
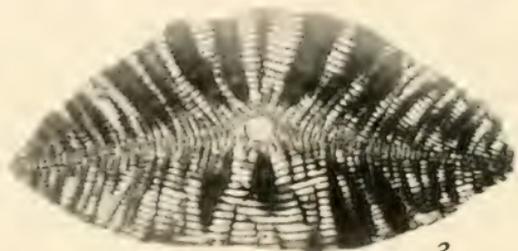
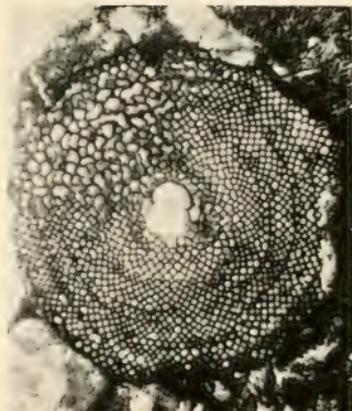
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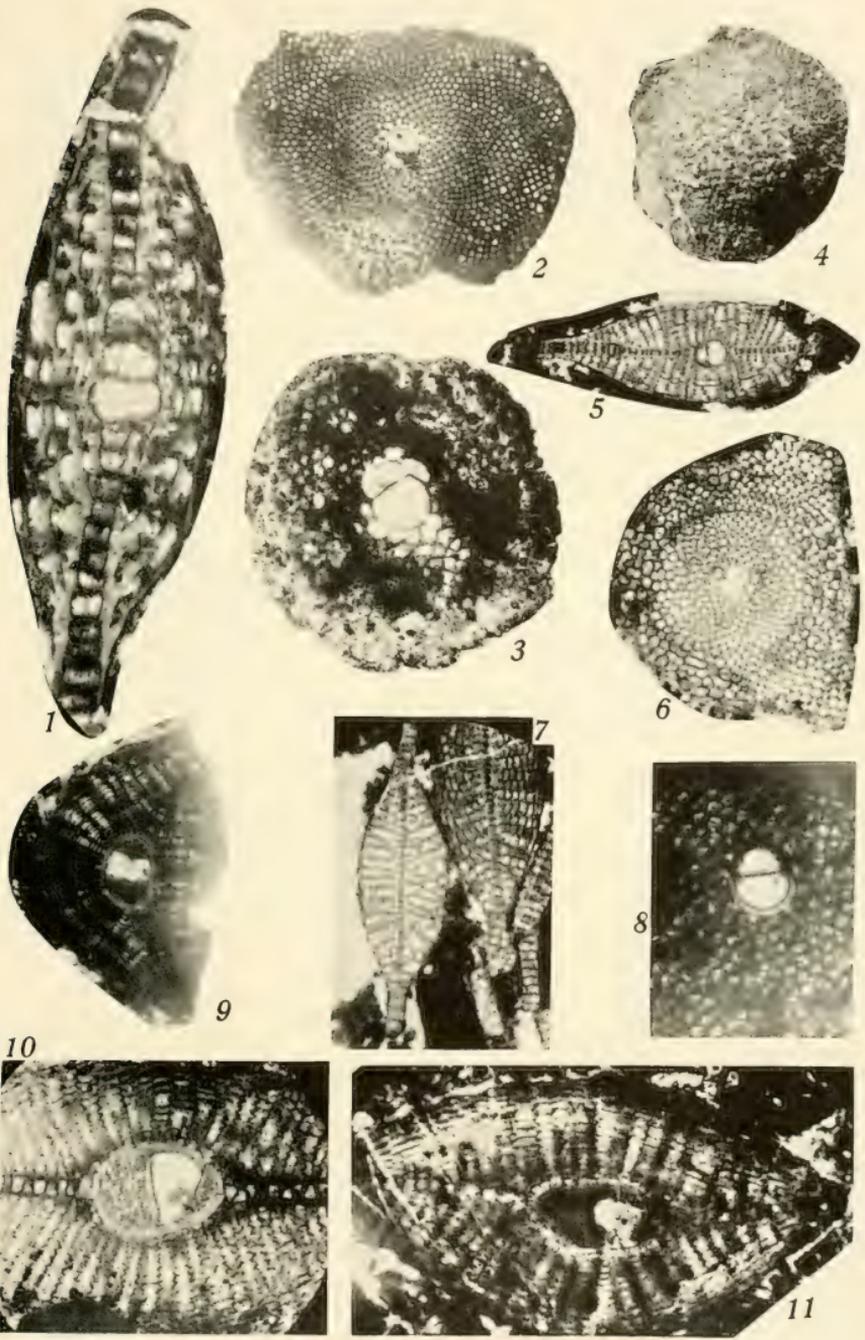
TERTIARY FORAMINIFERA OF VENEZUELA

(For explanation, see page 43.)

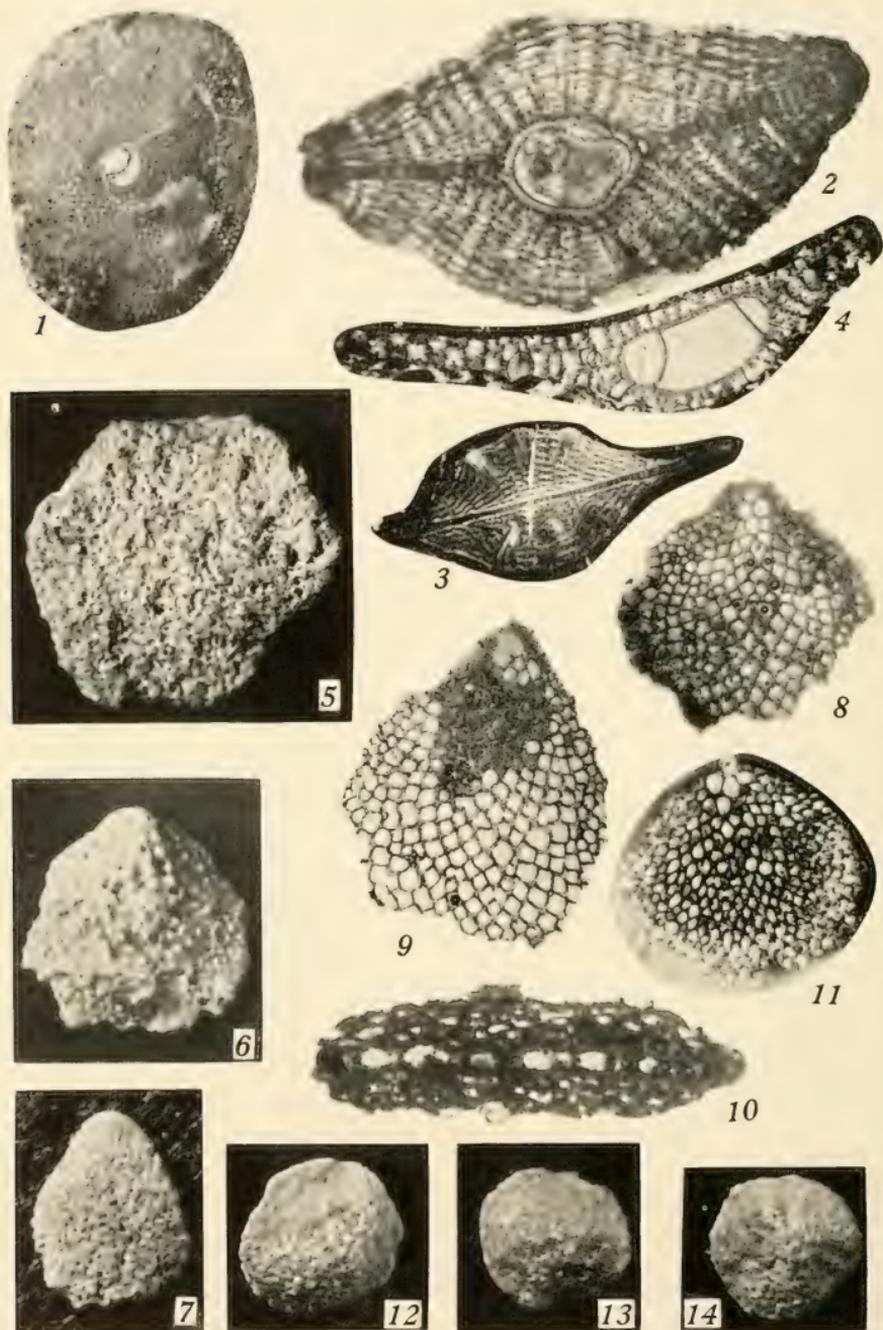


TERTIARY FORAMINIFERA OF VENEZUELA

(For explanation, see page 43.)



TERTIARY FORAMINIFERA OF VENEZUELA  
(For explanation, see page 43.)



TERTIARY FORAMINIFERA OF VENEZUELA

(For explanation, see page 44.)





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TRIBAL MIGRATIONS EAST OF  
THE MISSISSIPPI

(WITH FOUR MAPS)

BY

DAVID I. BUSHNELL, JR.



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# TRIBAL MIGRATIONS EAST OF THE MISSISSIPPI

By DAVID I. BUSHNELL, JR.

(WITH FOUR MAPS)

## INTRODUCTION

The map entitled "Linguistic Families of American Indians North of Mexico", by J. W. Powell, issued by the Bureau of American Ethnology, Smithsonian Institution, some years ago and several times revised and reprinted, indicates the position of the various groups of tribes when they first became known to Europeans. The map, as its title implies, includes the entire North American continent north of Mexico, but in the present paper, only that portion bordering on the lower Mississippi, and eastward to the Atlantic coast, will be considered.

The principal stocks indicated on the map as having been encountered within this region during historic times, those with whom the early Spanish and French explorers came in contact during the sixteenth and seventeenth centuries, as well as others who entered the country or subsequently changed their position, are the Caddoan, Siouan, and Algonquian, west of the Mississippi, and the Muskhogean, Algonquian, Iroquoian, Timuquanan, and Siouan, together with a small group of Uchean, east of the river.

Although some of the native tribes may have been long established in the localities in which they were discovered, it is evident that movements of various separated groups had taken place during the generations immediately preceding their first contact with Europeans. It is likewise believed that sufficient evidence is now available, as a result of the investigation of many ancient sites, and a comparative study of the languages, customs, and traditions of the scattered tribes, to make it possible to trace, with a degree of certainty, the routes followed by the tribes during their migrations, and to discover some of the causes that may have impelled their removal into the regions which they continued to occupy in historic times.

Four maps have been prepared to indicate the country occupied or traversed by the several groups during their migrations. The maps are presented not only in the endeavor to trace the possible routes followed by the tribes, but also in the attempt to ascertain the prob-

able points of contact of the various groups and to reveal how the movement of one must necessarily have affected the position of others.

In tracing the movements of the native peoples away from their earlier habitat, and later after they had become more widely dispersed, the linguistic families have been treated as units, with few specific references to any of the numerous tribes, often detached, of which each group was composed.

In determining the section of country claimed or occupied by the groups centuries ago, the conclusions have been reached by tracing back from the present to the distant past, but in presenting the evidence, the opposite method has been adopted, and consequently the first map shows the probable position of the tribes during the earliest period now being considered. No attempt has been made to indicate, nor will it ever be possible to determine, the exact bounds of the regions dominated by the groups at a given time. The areas as shown on the maps are only approximated and consequently must not be considered as definite or positive, although their relative positions, based on such information as is now available, are assumed to be very nearly correct.

The migratory movements of the tribes resulted in the crossing and recrossing of some parts of the country by peoples who differed greatly in manners and customs, whose characteristic forms of burial, varied types of pottery vessels, and stone implements and weapons are now discovered intermingled on the same sites. However, tribes belonging to the same group often differed as greatly from one another as they did from tribes of other stocks. Thus, the material recovered from the numerous sites is often difficult or impossible to identify, but in the future, when additional mounds, burial places, and camp sites have been examined and the objects discovered have been studied and compared, new light will be shed on the early movements of the tribes, which will result in either the verification or refutation of certain theories about to be presented.

Obviously, many of the conclusions expressed in this brief sketch are hypothetical, but nevertheless it is believed that they are based on sufficient evidence to justify their presentation in this form in order to provide a basis for future research in the endeavor to determine, more clearly, the tribal movements east of the Mississippi in prehistoric times.

#### EARLY TRIBES EAST OF THE MISSISSIPPI

The Algonquian tribes are believed to have come from the far northwest and to have skirted the shores of the Great Lakes before reaching the country farther south. At their first coming, long before

the Iroquoian peoples had arrived in the regions south of the St. Lawrence, some tribes of the Algonquian stock appear to have penetrated far south along the mountains into Tennessee or beyond, while others pushed onward into the piedmont sections of the present Virginia and of the Carolinas. Certain stone implements or weapons found in these regions reveal great age and are readily distinguished from others that were undoubtedly made and used by the later historic tribes of the same regions. These older specimens were evidently made during the early period of occupancy, during which time the numerous soapstone quarries were probably opened and worked.

The explorations conducted by M. R. Harrington in Loudon County, Tenn., during the summer and autumn of 1919, resulted in the discovery of evidence of very early tribes in the upper valley of the Tennessee. Traces of three distinct periods of occupancy were recognized. The earliest was termed that of the "Round Grave people" by reason of the characteristic form of burial encountered. The objects of stone and types of pottery vessels attributed to this early period resemble similar material found from New England southward to Virginia. The extensive use of soapstone in the same localities is another important similarity. "It thus seems logical to state that our 'Round Grave people' were either Algonkians closely related to those of the Middle Atlantic slope, or had at least been profoundly influenced by them."<sup>1</sup> Possibly one or more of the proto-Muskogean tribes followed the "Round Grave people", and these in turn may have been succeeded by the Cherokee, who continued to occupy the region in historic times.

The earlier wave of Algonquian tribes into the south probably receded before the approach of the Siouan and other peoples coming from the west or southwest. The connection between these early tribes and the inhabitants of tidewater Virginia at the beginning of the seventeenth century may have been very slight.

Although the Algonquian tribes came from the northwest, all other native peoples encountered east of the Mississippi are generally thought to have migrated from the west or southwest. These coming from their earlier habitat arrived on the right bank of the Mississippi, probably southward from the vicinity of the mouth of the Arkansas River; thence, having crossed to the eastern side, they became widely dispersed throughout the river valleys, pinelands, and mountain ranges.

The first movements of the native peoples into the country eastward from the Mississippi, those from whom some of the historic

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<sup>1</sup>Harrington, M. R., Cherokee and earlier remains on Upper Tennessee River, p. 167. Museum of the American Indian, New York, 1922.

tribes have descended, probably occurred at an earlier time than has been usually conceded. They may have been the true aborigines of the southeastern country, for as yet no indisputable evidence of Pleistocene man has been discovered in any locality between the Mississippi River and the Atlantic coast.

The languages of all the peoples of the southeastern section, with the exception of the Iroquoian and the smaller Algonquian groups, show structural similarities that suggest a very early contact or association of the various tribes, obviously in a region west of the Mississippi before their removal eastward. The numerous tribes appear to have entered the trans-Mississippi country in successive waves, the movements continuing through centuries.

The Uchean and Siouan groups were probably among the earliest to arrive on the left bank of the Mississippi and, belonging to the same early period, may have been the ancestors of the Natchez, who did not move far eastward, and also of the Timucua tribes and of the little known Calusa, who at the beginning of the historic era occupied many villages on the peninsula of Florida. Undoubtedly, others joined in the early movements, but their identity will never be revealed. The various tribes just mentioned will be considered and referred to in this sketch as the proto-Muskhogeian groups; however, the Uchean and Siouan peoples will be traced separately on the maps.

It is evident that the Siouan tribes, and others who may have been allied with them, after crossing to the left bank of the Mississippi, continued their advance into the valley of the Ohio. The majority are believed to have settled north of the river and to have developed the remarkable cultures that have been revealed in recent years. All did not cross the Ohio; some remained south of the stream and continued eastward into the mountainous country, and these probably constituted the southeastern group of Swanton's classification, as mentioned later in this article.

The Uchean<sup>2</sup> peoples, centuries ago, were probably a numerous, powerful group, some of whom, together with other proto-Muskhogeian tribes, are believed by the writer to have extended northward to the vicinity of the junction of the Missouri and Mississippi Rivers. It is likewise believed that during this early period of occupancy the great earthworks of southern Ohio were erected by the Siouan peoples, and that the massive mounds of the Cahokia and related groups not far from the mouth of the Missouri, and others as far distant as

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<sup>2</sup>Historical references to the Yuchi and related tribes have been brought together by Swanton in his work: *Early history of the Creek Indians and their neighbors*. Bull. 73, Bur. Amer. Ethnol., 1922.

Etowah in Georgia, were raised by the proto-Muskhogeian tribes. Some of the ancient mounds, especially the larger ones, reveal evidence of having been enlarged at a subsequent time. This may represent the work of later Muskhogeian tribes, or possibly in some instances that of the Cherokee (Iroquoian).

#### DESCRIPTION OF MAPS

##### MAP I

The first map is intended to visualize the position of the linguistic groups after the proto-Muskhogeian tribes, including the Uchean and Siouan, had crossed the Mississippi, and while the Iroquoian and Muskhogeian peoples were still on the right bank of the river with the Caddoan adjoining them to the westward.

The reasons for so placing the Iroquoian group may be briefly stated: First, the languages of the Iroquois and Pawnee (Caddoan) show certain similarities that suggest the possibility of early contact of the two groups; second, a strong resemblance between early historic Pawnee (Caddoan) archeological remains in Nebraska and those of the Iroquois in New York is indicated by the recent discoveries made by W. R. Wedel, whose account of the work in Nebraska is awaiting publication by the Bureau of American Ethnology; third, the Ozark region, extending eastward from the country occupied by Caddoan tribes when they first appeared in history, reveals evidence of a very early and extensive occupancy during a long period, preceding the coming of the Siouan peoples from the valley of the Ohio, after which time the Osages dominated a large part of the country of hills and valleys.

Algonquian tribes may, at that time, have extended much farther south in the region east of the mountains, in the present States of Maryland, Virginia, and West Virginia, than is indicated on the map, but others of the same stock had evidently already abandoned the country westward from the mountains.

##### MAP 2

The fertile valleys of Tennessee and Kentucky present more convincing evidence of having been occupied by a great number of tribes, at different times, than does any other section of the southeastern United States. Many of the tribes differed in manners and customs, as indicated by the great variety of archeological material recovered from the innumerable sites.

During the migratory movements, as theoretically expressed on the maps, the present States of Tennessee and Kentucky were crossed and recrossed by many tribes, representing the historic Siouan, Uchean, Iroquoian, and Muskogean stocks, while probably at an early time, and certainly at a later day, Algonquian tribes frequented the same region. The archeologist of the future may be able to differentiate the material recovered from the scattered sites, and thereby determine the sequence of the tribal movements.

If the theory that the Iroquoian tribes formerly occupied the Ozark region and later crossed to the left bank of the Mississippi is accepted, it is assumed that some traversed the western and central portions of the present State of Tennessee before pushing northward. By so doing they would have displaced the earlier inhabitants of the country, undoubtedly proto-Muskogean tribes.

Many Muskogean migration legends refer to the coming of the people from the west, and it is possible that the removal of some of the tribes into the trans-Mississippi region was contemporaneous with the movement of the Iroquoian peoples into the same country farther north, nearer the Ohio. Possibly some of the earlier tribes became absorbed by the Muskogean peoples, while others moved eastward to the mountains or beyond. The Timucua group, preceded by the Calusa, of whom so little is known, may at this time have reached the peninsula of Florida. The last two are now considered with the proto-Muskogean peoples.

#### MAP 3

Fortified camp or village sites have been traced northward from central Tennessee and Kentucky and across the Ohio in the eastern counties of Indiana to the northern part of the State, thence eastward through the ancient home of the Eries to the historic sites of the Iroquois. The embankments differ in form and style of construction, a condition influenced by the nature of the locality in which they occur.

Many of the protected sites may have been constructed and occupied by the Iroquoian tribes during the movement northward, and consequently a comparative study of the archeological material recovered from them should prove to be of the greatest interest. If this hypothesis is correct, it is probable that before the Iroquoian tribes had reached the left bank of the Ohio the Siouan peoples were living in security in the upper valley of the stream. The great majority were north of the river, but others, including the Catawba, may have been south of the Ohio in the mountains to the eastward. The region

northward from the Siouan territories, extending to the shores of the Great Lakes, was probably at that time occupied by Algonquian tribes.

The relative position of the Siouan tribes when they occupied the Ohio valley, claiming the southern section of the present State of Ohio, has been suggested by Swanton,<sup>3</sup> who wrote in conclusion: "The occupancy of the territory of our Middle West between the Great Lakes and the Ohio by Siouan tribes seems therefore to rest on grounds almost historical. With the strong indications now at hand there seems to be reason to think that a close comparative study of the Siouan dialects would enable us to reconstruct the general outlines of their ancient geographical positions with considerable accuracy. If present indications are not deceptive, when that is done we shall find that they fell into four major linguistic groups; a northeastern, consisting of the ancestors of the later Siouan tribes of Virginia, the Hidatsa, Dakota, Biloxi, and Ofo; a southeastern, including most of the later Siouan peoples of the two Carolinas; a southwestern composed of the five tribes of Dorsey's Dhegiha group; and a northwestern, Dorsey's Tciwere.

"Admittedly there is much of speculation in all this, but I have considered that the facts are of sufficient importance to both the ethnologist and the archaeologist of the Ohio region to present them in usable form."

The five tribes included in Dorsey's Dhegiha group are the Omaha, Ponca, Quapaw, Osage, and Kansa. The Tciwere group consists of the Iowa, Oto, and Missouri.

There is historical proof that one or more Siouan villages remained in southern Ohio until late in the seventeenth century, and tribal traditions place the ancient settlements of the Quapaw and Osage near the junction of the Ohio and Wabash Rivers.

The line of contact between the Algonquian and Siouan tribes appears to have been to the north and east of the area occupied by the latter peoples.

Michelson<sup>4</sup> in a recent article discussed certain phases of the Algonquian languages, and in closing wrote: "Summing up, we may say that Powhatan clearly belongs with the Cree group of Central Algonquian languages, that it is closer to Cree than to any other member of that group, but that it can not be classified as a Cree dialect. A prehistoric migration is thereby shown." "Powhatan" in this

<sup>3</sup> Swanton, John R., New light on the early history of the Siouan peoples. Journ. Washington Acad. Sci., vol. 13, no. 3, Feb. 4, 1923.

<sup>4</sup> Michelson, Truman, The linguistic classification of Powhatan. Amer. Anthropol., vol. 35, no. 3, July-Sept., 1933.

quotation refers to the language spoken by the Algonquian tribes of tidewater Virginia in the early seventeenth century.

From the two quotations just made it is evident that some centuries ago the Siouan tribes who later reached the mountainous country of Virginia were living in close contact with others who moved westward beyond the Mississippi; also that the Algonquian tribes encountered in Virginia by the first colonists had been separated from some related tribes with whom they had formerly been closely associated.

The northern thrust of the Iroquoian peoples, when they crossed the Ohio from the south, is now suggested as the cause of the separation of tribes that belonged to the Siouan and Algonquian groups, some going eastward and south, others seeking new homes toward the west.

Where the Iroquoian tribes may have crossed the Ohio is not known; however, if the line of fortified camps, already mentioned, prove to have been associated with the movement of the tribes, the approximate locality of their crossing will be suggested. But it is not within reason to suppose that all reached the right bank of the Ohio at the same time or at the same place, and some may have followed up the valley of the stream from its mouth.

The Cherokee were at that time a part of the Iroquoian group and as such would have participated in the movement from west of the Mississippi; however, they may have continued eastward to the mountains without having crossed the Ohio, thus approaching the country where they were first encountered by Europeans. Probably the Catawba and other Siouan tribes who occupied parts of Carolina in historic times then moved away from the Ohio valley and advanced farther southward into the mountains.

#### MAP 4

The groups of tribes continued to move, and by the beginning of the sixteenth century they were located approximately as indicated on the last map.

The Iroquoian tribes had moved far eastward, and some occupied the country south of the St. Lawrence. The Hurons had settled north of Niagara, and the Eries remained south of the lake that bears their name. The Cherokee had become established far south in the Alleghenies, with Uchean tribes to the west of them.

The Siouan peoples had scattered far from their ancient homes in the valley of the Ohio. Some had traversed the mountainous sections

of Virginia and Carolina and reached the coast ; others moving more slowly, and undoubtedly reluctant to abandon the rich hunting grounds west of the Wabash, had probably arrived on the banks of the Mississippi and the shores of Lake Michigan. The Algonquian tribes had likewise moved farther away from their earlier habitat and some had already pushed southward on the Atlantic coast.

Muskogean tribes occupied the greater part of the southeastern United States, and some of their villages, already old when visited by the Spanish invaders in 1540, may have been the sites of much earlier proto-Muskogean settlements. The villages of the Calusa and Timucua tribes dominated the peninsula of Florida.

This was the distribution of the linguistic groups at the beginning of the historic era, when Europeans were soon to enter and traverse the vast, unknown region that lay between the Atlantic coast and the Mississippi.

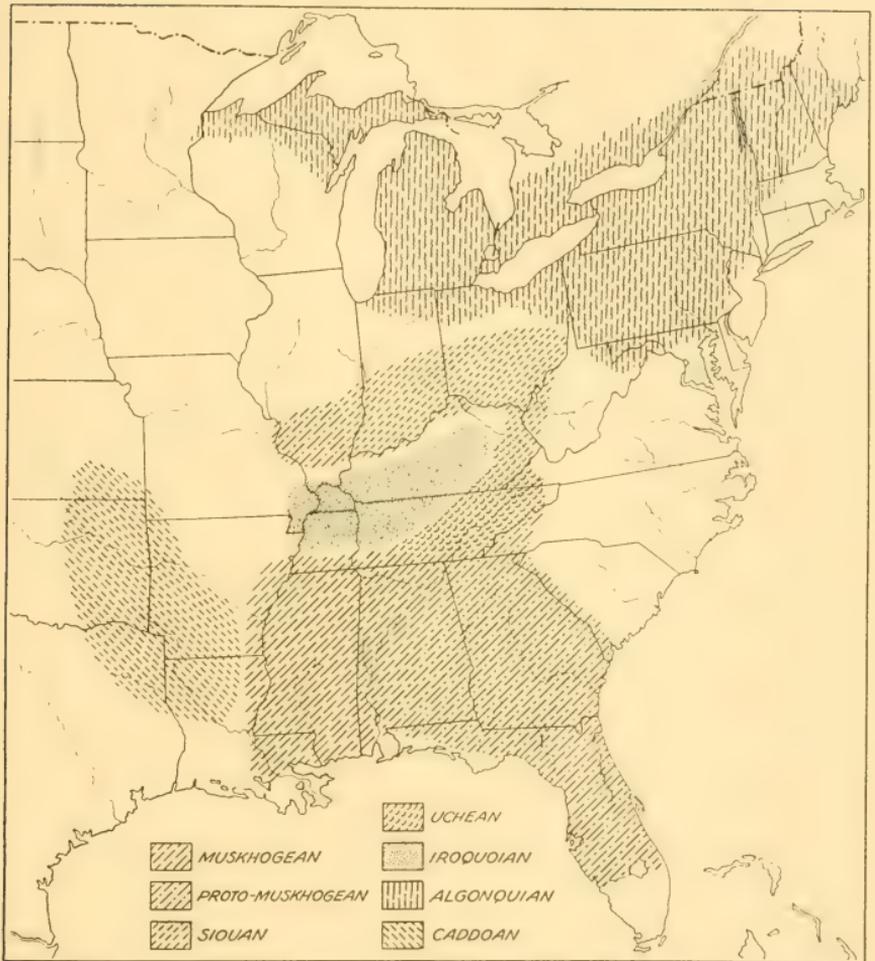




MAP INTENDED TO VISUALIZE THE POSITION OF THE SEVERAL LINGUISTIC STOCKS DURING THE EARLIEST PERIOD CONSIDERED IN THIS PAPER

(For explanation, see p. 5.)

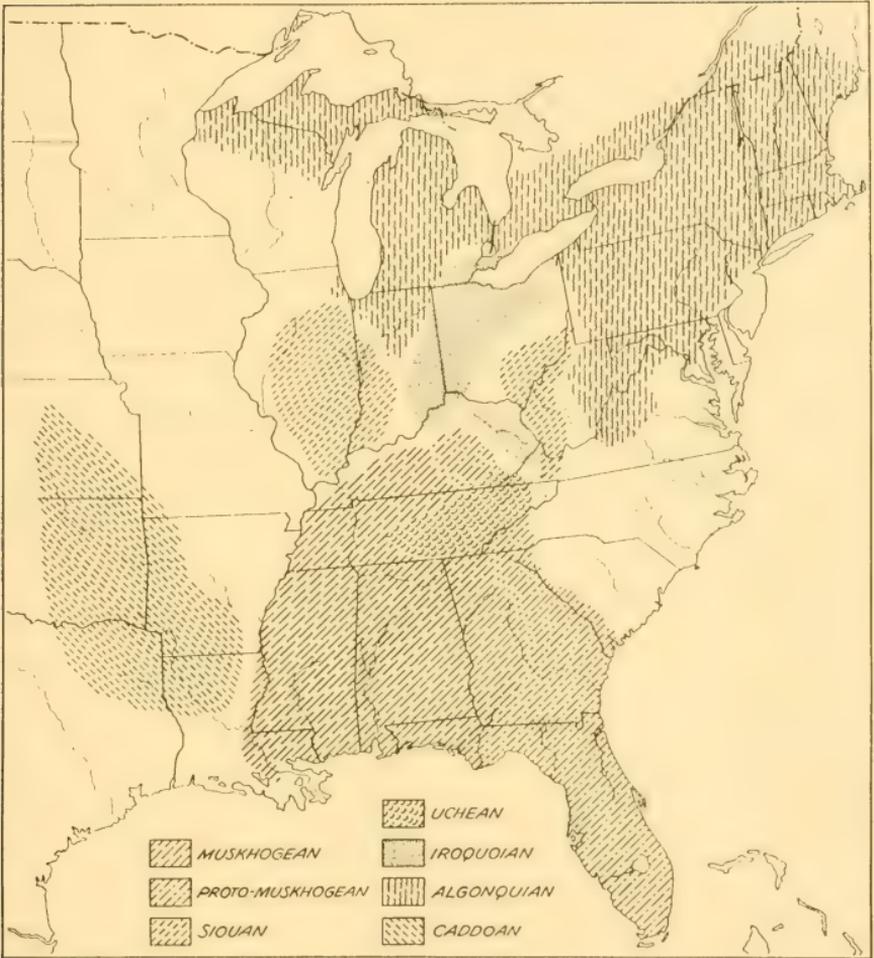




AFTER THE IROQUOIAN AND MUSKOGEAN TRIBES HAD ARRIVED EAST OF THE MISSISSIPPI

(For explanation, see p. 5.)





THE NORTHERN THRUST OF THE IROQUOIAN PEOPLES RESULTED IN THE SEPARATION OF THE SIOUAN AND ALGONQUIAN TRIBES  
 (For explanation, see p. 6.)





THE RELATIVE POSITION OF THE LINGUISTIC GROUPS AT THE BEGINNING OF THE SIXTEENTH CENTURY

(For explanation, see p. 8.)



SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 89, NUMBER 13

A SYSTEMATIC CLASSIFICATION FOR THE BIRDS  
OF THE WORLD, REVISED AND AMENDED

BY

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# A SYSTEMATIC CLASSIFICATION FOR THE BIRDS OF THE WORLD, REVISED AND AMENDED

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The present classification is offered as the result of further study, since publication of a previous paper on the same subject in 1930,<sup>1</sup> of the intricate relationships of our forms of birds, including the fossil species, as far as at present known. As in the previous list, only such changes from the current order have been accepted as seem to be definitely settled and established, leaving various other proposals still in abeyance until they have been developed by further research.

The major changes from the previous list have been the segregation of the penguins in a distinct superorder, Impennes, in accordance with Lowe's investigations,<sup>2</sup> and a revision of the fossil families, following the appearance of Lambrecht's *Handbuch der Palaeornithologie* and as the result of certain studies by the writer. Lambrecht's proposal to place the Hesperornithidae near the grebes and loons, and the Ichthyornithidae near the Diatrymiformes and the pigeons, to me does not seem justified. The resemblances in form that Lambrecht cites as basis for his action, while pertaining to two different schemes of life (one natant and the other volant), include limiting factors that have confined the evolution of birds as a whole within narrow lines, compared, for example, to what has taken place in reptiles and mammals. In view of this, the possession of teeth and other peculiarities assume greater importance in weighing probable evolutionary origins and trends. It seems probable that teeth were a characteristic of Cretaceous birds that disappeared with advance into the Tertiary period.

Under the Galliformes the quails (formerly the family *Perdidae*) have been united with the Phasianidae, as there appear to be no trenchant characters to separate the two. Under the Charadriiformes

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<sup>1</sup> A systematic classification for the birds of the world. *Proc. U.S. Nat. Mus.*, vol. 76, art. 27, Jan. 8, 1930, pp. 1-8.

<sup>2</sup> See *Proc. Zool. Soc. London*, 1933, pt. 2, pp. 483-538.

the peculiar painted snipe are recognized as a distinct family, Rostratulidae, from anatomical peculiarities.<sup>3</sup> The Psittaciformes and Cuculiformes have been transposed in order to allow the parrots to stand nearer the pigeons.

The number of families and their arrangement in the great order Passeriformes is far from satisfactory. The bower birds (formerly Ptilinorhynchidae) are united with the Paradiseidae, as here again alleged characters overlap. The curious parrot-bills and their allies merit recognition as a distinct family Paradoxornithidae to stand near the Paridae. Mayr has shown that *Paramythia* (formerly *Paramythiidae*) of New Guinea belongs in the Dicaeidae. The fork-tails (formerly *Enicuridae*) do not seem separable from the Turdidae, *Aërocharis* (formerly *Aërocharidae*), the curious helmet-bird of Madagascar, is placed in the Vangidae, and the glossy starlings (formerly *Graçulidae*) are united with the Sturnidae, as no definite lines of difference appear to separate them.

Arrangement of the various passeriform families in linear sequence, particularly in the suborder Passeres, or song birds, is a matter of difficulty, since the problem is one of three-dimensional relationship that must be represented in a single column. Obviously, the treatment in some instances must be arbitrary and subject therefore to individual opinion. Without going too deeply into the matter, it has been suggested that such specialized families of the fringilline series as the Coerebidae and Icteridae should come at the end of the list in place of the Fringillidae. In considering the evolution of this assemblage, it appears to me that the more specialized families have been derived by modification from the Fringillidae, while the latter family has retained and carried along more general characters from which further specialization may take place, if with civilized man's disturbance of natural conditions on our Earth continuation of evolution among birds is possible. The Coerebidae and Icteridae, to take these as examples, are specialized branches that are assumed now to be more or less static and fixed and therefore should stand at the side. The Fringillidae, representing the central group through which further progress may be expected, should be placed as the terminus of the central stem at the end.

One change in terminology incorporated in the present list has been the use of the suffix -oidea to designate superfamily names. In the preparation of the classification for the official Checklist of the

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<sup>3</sup> See Lowe, P. R., *Ibis*, 1931, pp. 503, 507-531.

American Ornithologists' Union the form -oidea was used in the original scheme but was disapproved by the committee in charge of that work as a whole. To be consistent, therefore, in the complete classification issued at that time, I used the Latin plurals, recommended then for the A.O.U. list, for the names in question. Subsequently, the committee reversed its decision, and the suffix -oidea was used in the fourth edition of the A.O.U. Checklist published in 1931. The same usage is here incorporated in the complete classification.

Class Aves, Birds.

Subclass Archaeornithes, Ancestral Birds.

Order Archaeopterygiformes, *Archaeopteryx*, *Archaeornis*.

Family Archaeopterygidae, *Archaeopteryx*, *Archaeornis* (fossil).

Subclass Neornithes, True Birds.

Superorder Odontognathae, New World Toothed Birds.

Order Hesperornithiformes, Hesperornithes.

Family Hesperornithidae, *Hesperornis*, *Hargeria* (fossil).

Enaliornithidae,<sup>4</sup> *Enaliornis*, *Baptornis* (fossil).

Order Ichthyornithiformes, Ichthyornithes.

Family Ichthyornithidae,<sup>5</sup> *Ichthyornis* (fossil).

Superorder Palaeognathae, Struthious Birds and Allies.

Order Struthioniformes, Ostriches.

Family Struthionidae, Ostriches.

Order Rheiformes, Rheas.

Family Rheidae, Rheas.

Order Casuariiformes, Cassowaries, Emus.

Family Casuariidae, Cassowaries.

Dromiceidae, Emus.

Dromornithidae, *Dromornis* (fossil).

Order Dinornithiformes, Moas.

Family Dinornithidae, Moas (fossil and extinct).

Anomalopterygidae, *Anomalopteryx*, *Emeus*,  
and Allies (fossil and extinct).

<sup>4</sup> Position provisional. Lambrecht, Handbuch der Palaeornithologie, 1933, pp. 255-261, unites the formerly recognized Baptornithidae with this group, which he considers closely related to the loons and grebes.

<sup>5</sup> Lambrecht, Handbuch der Palaeornithologie, 1933, p. 585, has separated *Apatornis* in the family Apatornithidae. This genus is here left in the Ichthyornithidae pending further consideration.

- Order Aepyornithiformes, Elephant-birds.  
 Family Aepyornithidae, *Aepyornis* (fossil and extinct).
- Order Apterygiformes, Kiwis.  
 Family Apterygidae, Kiwis.
- Order Tinamiformes, Tinamous.  
 Family Tinamidae, Tinamous.
- Superorder Impennes, Penguins.  
 Order Sphenisciformes, Penguins.  
 Family Spheniscidae, Penguins.  
 Cladornithidae, *Cladornis* (fossil).
- Superorder Neognathae, Typical Birds.  
 Order Gaviiformes, Loons.  
 Family Gaviidae, Loons.
- Order Colymbiformes, Grebes.  
 Family Colymbidae, Grebes.
- Order Procellariiformes, Albatrosses, Shearwaters, Petrels,  
 and Allies.  
 Family Diomedeidae, Albatrosses.  
 Procellariidae, Shearwaters, Fulmars.  
 Hydrobatidae, Storm Petrels.  
 Pelecanoididae, Diving Petrels.
- Order Pelecaniformes, Tropic-birds, Pelicans, Frigate-birds,  
 and Allies.  
 Suborder Phaëthontes, Tropic-birds.  
 Family Phaëthontidae, Tropic-birds.
- Suborder Pelecani, Pelicans, Boobies, Cormorants, Snake-  
 birds.  
 Superfamily Pelecanoidea, Pelicans and Allies.  
 Family Pelecanidae, Pelicans.  
 Cyphornithidae, *Cyphornis*, *Palaeochenöides*  
 (fossil).
- Superfamily Suloidea, Boobies, Cormorants, and Allies.  
 Family Pelagornithidae, *Pelagornis* (fossil).  
 Sulidae, Boobies, Gannets.  
 Elopterygidae, *Elopteryx*, *Eostega*, *Actiornis*  
 (fossil).  
 Phalacrocoracidae, Cormorants.  
 Anhingidae, Snake-birds.
- Suborder Fregatae, Frigate-birds.  
 Family Fregatidae, Frigate-birds.

Suborder Odontopteryges, *Odontopteryx*, *Pseudodontornis*  
(fossil).

Family Odontopterygidae, *Odontopteryx* (fossil).

Pseudodontornithidae,<sup>6</sup> *Pseudodontornis* (fossil).

Order Ciconiiformes, Herons, Storks, and Allies.

Suborder Ardeae, Herons, Bitterns.

Family Ardeidae, Herons, Bitterns.

Cochleariidae, Boat-billed Herons.

Suborder Balaenicipites, Whale-headed Storks.

Family Balaenicipitidae, Whale-headed Storks.

Suborder Ciconiae, Storks, Ibises, Spoonbills.

Superfamily Scopoidea, Hammerheads.

Family Scopidae, Hammerheads.

Superfamily Ciconioidea, Storks.

Family Ciconiidae, Storks, Jabirus.

Superfamily Threskiornithoidea, Ibises.

Family Threskiornithidae, Ibises, Spoonbills.

Suborder Phoenicopter, Flamingos.

Family Agnopterygidae, *Agnopteryx* (fossil).

Scaniornithidae, *Scaniornis*, *Parascaniornis*  
(fossil).

Phoenicopteridae, Flamingos.

Order Anseriformes, Screamers, Ducks, Geese, Swans.

Suborder Anhimae, Screamers.

Family Anhimidae, Screamers.

Suborder Anseres, Ducks, Geese, Swans.

Family Anatidae, Ducks, Geese, Swans.

Order Falconiformes, Vultures, Hawks, Falcons.

Suborder Cathartae, New World Vultures.

Family Cathartidae, New World Vultures.

Teratornithidae, *Teratornis* (fossil).

Suborder Falcones, Secretary-birds, Hawks, Falcons.

Superfamily Sagittarioidea, Secretary-birds.

Family Sagittariidae, Secretary-birds.

Superfamily Falconoidea, Hawks, Falcons, and Allies.

Family Accipitridae, Hawks, Old World Vultures,  
Harriers, Ospreys.

Falconidae, Falcons, Caracaras.

<sup>6</sup> Position not certain; see Lambrecht, *Handbuch der Palaeornithologie*, 1933, pp. 305-308.

- Order Galliformes, Megapodes, Curassows, Pheasants, Hoatzins.
- Suborder Galli, Megapodes, Curassows, Grouse, Pheasants.
- Superfamily Cracoidea, Megapodes, Curassows.
- Family Megapodiidae, Megapodes.
- Gallinuloididae, *Gallinuloides* (fossil).
- Cracidae, Curassows, Guans, Chachalacas.
- Superfamily Phasianoidea, Grouse, Pheasants, Turkeys.
- Family Tetraonidae, Grouse.
- Phasianidae,<sup>7</sup> Quails, Pheasants, Peacocks.
- Numididae, Guinea-fowl.
- Meleagrididae, Turkeys.
- Suborder Opisthocomi, Hoatzins.
- Family Opisthocomidae, Hoatzins.
- Order Gruiformes, Cranes, Rails, and Allies.
- Suborder Mesoenatides, Roatelos, Monias.
- Family Mesoenatidae, Roatelos, Monias.
- Suborder Turnices, Bustard-quails, Hemipodes.
- Family Turnicidae, Bustard-quails.
- Pedionomidae, Collared Hemipodes.
- Suborder Grues, Cranes, Limpkins, Trumpeters, Rails.
- Superfamily Gruoidea, Cranes, Limpkins, Trumpeters.
- Family Geranoididae, *Geranoides* (fossil).
- Eogruidae, *Eogrus* (fossil).
- Gruidae, Cranes.
- Aramidae, Limpkins.
- Psophiidae, Trumpeters.
- Superfamily Ralloidea, Rails.
- Family Orthocnemidae,<sup>8</sup> *Orthocnemus*, *Elaphrocnemus* (fossil).
- Rallidae, Rails, Coots, Gallinules.
- Suborder Heliornithes, Sun-grebes.
- Family Heliornithidae, Sun-grebes.
- Suborder Rhynocheti, Kagus.
- Family Rhynochetidae, Kagus.
- Suborder Eurypygae, Sun-bitterns.
- Family Eurypygidae, Sun-bitterns.

<sup>7</sup> Includes the quails, formerly recognized as the family Perdidae.

<sup>8</sup> Position provisional. See Lambrecht, *Handbuch der Palaeornithologie*, 1933, pp. 490-493.

- Suborder Phororhaci, *Phororhacos* and Allies.  
 Family Phororhacidae, *Phororhacos*, *Pelecyornis* and Allies (fossil).  
 Brontornithidae, *Brontornis*, *Liornis* and Allies (fossil).  
 Opisthodactylidae, *Opisthodactylus* (fossil).
- Suborder Cariamae, Cariamas and Allies.  
 Family Bathornithidae, *Bathornis* (fossil).  
 Hermosiornithidae, *Hermosiornis*, *Procariama* (fossil).  
 Cariamidae, Cariamas.
- Suborder Otides, Bustards.  
 Family Otididae, Bustards.
- Order Diatrymiformes, *Diatryma*, *Omorhamphus* and Allies.  
 Family Diatrymidae, *Diatryma* (fossil).  
 Gastornithidae, *Gastornis*, *Remiornis* (fossil).
- Order Charadriiformes, Shore-birds, Gulls, Auks.  
 Suborder Charadrii, Shore-birds.  
 Superfamily Jacanoidea, Jacanas.  
 Family Jacanidae, Jacanas.  
 Superfamily Charadrioidae, Plovers, Sandpipers, and Allies.  
 Family Rostratulidae, Painted Snipe.  
 Haematopodidae, Oyster-catchers.  
 Charadriidae, Plovers, Turnstones, Surf-birds.  
 Scolopacidae, Snipe, Woodcock, Sandpipers.  
 Recurvirostridae, Avocets, Stilts.  
 Presbyornithidae, *Presbyornis* (fossil).  
 Phalaropodidae, Phalaropes.
- Superfamily Dromadoidea, Crab-plovers.  
 Family Dromadidae, Crab-plovers.
- Superfamily Burhinoidea, Thick-knees.  
 Family Burhinidae,<sup>9</sup> Thick-knees.
- Superfamily Glareoloidea, Pratincoles, Coursers.  
 Family Glareolidae, Pratincoles, Coursers.
- Superfamily Thinocoroidea, Seed-snipe.  
 Family Thinocoridae, Seed-snipe.
- Superfamily Chionoidea, Sheath-bills.  
 Family Chionidae, Sheath-bills.

<sup>9</sup> Replaces Oedicnemidae as a family name for this group.

- Suborder Lari, Gulls, Terns, Skimmers.
  - Family Stercorariidae, Skuas, Jaegers.
  - Laridae, Gulls, Terns.
  - Rynchopidae, Skimmers.
- Suborder Alcae, Auks.
  - Family Alcidae, Auks, Auklets, Murres.
- Order Columbiformes, Sand-grouse, Pigeons, Doves.
  - Suborder Pterocletes, Sand-grouse.
    - Family Pteroclididae, Sand-grouse.
  - Suborder Columbæ, Pigeons and Doves.
    - Family Raphidae, Dodos, Solitaires.
    - Columbidae, Pigeons, Doves.
- Order Psittaciformes, Lories, Parrots, Macaws.
  - Family Loriidae, Lories.
  - Psittacidae, Parrots, Macaws.
- Order Cuculiformes, Plantain-eaters, Cuckoos.
  - Suborder Musophagi, Plantain-eaters.
    - Family Musophagidae, Plantain-eaters.
  - Suborder Cuculi, Cuckoos, Roadrunners, Anis.
    - Family Cuculidae, Cuckoos, Roadrunners, Anis.
- Order Strigiformes, Owls.
  - Family Protostrigidae, *Protostrix* (fossil).
  - Tytonidae, Barn-owls.
  - Strigidae, Owls.
- Order Caprimulgiformes, Oil-birds, Goatsuckers.
  - Suborder Steatornithes, Oil-birds.
    - Family Steatornithidae, Oil-birds.
  - Suborder Caprimulgi, Frogmouths, Goatsuckers.
    - Family Podargidae, Frogmouths.
    - Nyctibiidae, Potoos.
    - Aegothelidae, Owlet-frogmouths.
    - Caprimulgidae, Goatsuckers.
- Order Micropodiformes, Swifts, Hummingbirds.
  - Suborder Micropodi, Swifts.
    - Family Aegialornithidae,<sup>10</sup> *Aegialornis* (fossil).
    - Micropodidae, Swifts.
    - Hemiprocnidae, Crested Swifts.
  - Suborder Trochili, Hummingbirds.
    - Family Trochilidae, Hummingbirds.

<sup>10</sup> Placed here provisionally. See Lambrecht, *Handbuch der Palaeornithologie*, 1933, pp. 623-624.

- Order Coliiformes, Colies.
  - Family Coliidae, Colies.
- Order Trogoniformes, Trogons.
  - Family Trogonidae, Trogons.
- Order Coraciiformes, Kingfishers, Bee-eaters, Rollers, Hornbills.
  - Suborder Alcedines, Kingfishers, Todies, Motmots.
    - Superfamily Alcedinoidea, Kingfishers.
      - Family Alcedinidae, Kingfishers.
    - Superfamily Todoidea, Todies.
      - Family Todidae, Todies.
    - Superfamily Momotoidea, Motmots.
      - Family Momotidae, Motmots.
  - Suborder Meropes, Bee-eaters.
    - Family Meropidae, Bee-eaters.
  - Suborder Coracii, Rollers, Hoopoes.
    - Family Coraciidae, Rollers.
      - Leptosomatidae, Cuckoo-rollers and Ground-rollers.
      - Upupidae, Hoopoes.
      - Phoeniculidae, Wood-hoopoes.
  - Suborder Bucerotes, Hornbills.
    - Family Bucerotidae, Hornbills.
- Order Piciformes, Jacamars, Barbets, Toucans, Woodpeckers.
  - Suborder Galbulae, Jacamars, Barbets, Toucans.
    - Superfamily Galbuloidea, Jacamars, Puff-birds.
      - Family Galbulidae, Jacamars.
      - Bucconidae, Puff-birds.
    - Superfamily Capitonoidea, Barbets, Honey-guides.
      - Family Capitonidae, Barbets.
      - Indicatoridae, Honey-guides.
    - Superfamily Ramphastoidea, Toucans.
      - Family Ramphastidae, Toucans.
  - Suborder Pici, Woodpeckers.
    - Family Picidae, Woodpeckers, Piculets.
- Order Passeriformes, Perching Birds.
  - Suborder Eurylaimi, Broadbills.
    - Family Eurylaimidae, Broadbills.
  - Suborder Tyranni, Ovenbirds, Tyrant Flycatchers, and Allies.

Superfamily Furnarioidea, Ovenbirds, Wood-hewers, and Allies.

- Family Dendrocolaptidae, Wood-hewers.  
 Furnariidae, Ovenbirds.  
 Formicariidae, Ant-thrushes.  
 Conopophagidae, Ant-pipits.  
 Rhinocryptidae, Tapaculos.

Superfamily Tyrannoidea, Tyrant Flycatchers, Pittas, and Allies.

- Family Cotingidae, Cotingas.  
 Pipridae, Manakins.  
 Tyrannidae, Tyrant Flycatchers.  
 Oxyruncidae, Sharp-bills.  
 Phytotomidae, Plant-cutters.  
 Pittidae, Pittas.  
 Xenicidae, New Zealand Wrens.  
 Philepittidae, Asities.

Suborder Menurae, Lyre-birds.

- Family Menuridae, Lyre-birds.  
 Atrichornithidae,<sup>11</sup> Scrub-birds.

Suborder Passeres, Song Birds.

- Family Alaudidae, Larks.  
 Palaeospizidae, *Palaeospiza* (fossil).  
 Hirundinidae, Swallows.  
 Campephagidae, Cuckoo-shrikes.  
 Dicruridae, Drongos.  
 Oriolidae, Old World Orioles.  
 Corvidae, Crows, Magpies, Jays.  
 Paradiseidae,<sup>12</sup> Birds of Paradise.  
 Paradoxornithidae, Parrot-bills, Suthoras.  
 Paridae, Titmice.  
 Sittidae, Nuthatches.  
 Hyposittidae, Coral-billed Nuthatches.  
 Certhiidae, Creepers.  
 Chamaeidae, Wren-tits.  
 Timeliidae, Babbling Thrushes.  
 Pycnonotidae, Bulbuls.  
 Cinclidae, Dippers.

<sup>11</sup> Position not fully established.

<sup>12</sup> Includes the bower-birds, sometimes recognized as the family Ptilinorhynchidae.

- Family Troglodytidae, Wrens.
- Mimidae, Thrashers, Mockingbirds.
  - Turdidae,<sup>13</sup> Thrushes.
  - Zeledoniidae, Wren-thrushes.
  - Sylviidae, Old World Warblers.
  - Regulidae, Kinglets.
  - Muscicapidae, Old World Flycatchers.
  - Prunellidae, Accentors, Hedge Sparrows.
  - Motacillidae, Wagtails, Pipits.
  - Bombycillidae, Waxwings.
  - Ptilonotidae, Silky Flycatchers.
  - Dulidae, Palm-chats.
  - Artamidae, Wood-swallows.
  - Vangidae,<sup>14</sup> Vanga Shrikes.
  - Laniidae, Shrikes.
  - Prionopidae, Wood-shrikes.
  - Cyclarhidae, Pepper-shrikes.
  - Vireolaniidae, Shrike-vireos.
  - Sturnidae,<sup>15</sup> Starlings.
  - Melithreptidae, Honey-eaters.
  - Nectariniidae, Sun-birds.
  - Dicaeidae,<sup>16</sup> Flower-peckers.
  - Zosteropidae, White-eyes.
  - Vireonidae, Vireos.
  - Coerebidae, Honey-creepers.
  - Drepanididae, Hawaiian Honey-creepers.
  - Compsothlypidae, Wood Warblers.
  - Ploceidae, Weaver-finches.
  - Icteridae, Blackbirds, Troupials.
  - Procnatiidae, Swallow-tanagers.
  - Thraupidae, Tanagers.
  - Catamblyrhynchidae, Plush-capped Finches.
  - Fringillidae, Grosbeaks, Finches, Buntings.

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<sup>13</sup> Includes the group of fork-tails placed by some in the family Enicuridae.

<sup>14</sup> Includes the genus *Aërocharis* that has been separated by some as the family Aërocharidae.

<sup>15</sup> Includes the glossy starlings or Graculidae of various authors.

<sup>16</sup> According to E. Mayr, Orn. Monatsb., vol. XLI, 1933, pp. 112-113, *Paramythia*, formerly separated in a distinct family, Paramythiidae, is an aberrant member of the Dicaeidae.







SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 89, NUMBER 14

MILLIPEDS OF THE WEST INDIES AND GUIANA  
COLLECTED BY THE ALLISON V. ARMOUR  
EXPEDITION IN 1932

(WITH FOUR PLATES)

BY

H. F. LOOMIS

Bureau of Plant Industry,  
U.S. Department of Agriculture



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INTRODUCTION

During the first three months of 1932 the writer visited many of the Bahama and West Indian islands, and British and Dutch Guiana, while a member of the Allison V. Armour Expedition engaged in collection of seeds and plants for introduction into the United States. In the course of the expedition 30 islands were touched, many of which have been little explored by naturalists, the information on their flora and fauna being exceedingly fragmentary or entirely lacking. Although the time allotted to any of the islands or countries was very limited and was devoted principally to making general surveys and gathering material of the outstanding plants, it usually was found possible to spare a few moments to search for members of the humus fauna, particularly the millipeds, at each stop. In spite of the incidental opportunities for such collecting the final results were very satisfactory. New localities for many previously known millipeds were recorded, over two dozen undescribed species were discovered,<sup>1</sup> and interesting observations on environmental conditions and general distribution were made at first hand.

In the Bahamas the islands of New Providence, Cat, Conception, Mariguana, Great Inagua, and Rum Cay were visited, and the humus fauna was found to be very sparse, probably from a number of contributing causes. Most of the islands of the Bahamas are low and of limestone formation which drains rapidly, and the vegetation is seldom dense enough to provide material for large accumulations of humus. Rains are strictly seasonal, and long periods of drought are experi-

<sup>1</sup> Several of these forms had previously been found in Haiti, and descriptions were prepared for a paper on Haitian millipeds. These descriptions are included in this paper, but when the specimens collected by the Armour Expedition came from some other island, the Haitian type locality has been allowed to remain.

enced, when the earth surface dries to considerable depths, except in well-protected locations. The constant sea breezes cause rapid surface evaporation, and in general the islands are so arid that many of the plants are decidedly xerophytic in character. During the hurricanes, which are a menace throughout much of the year, many of the smaller islands are more or less inundated by sea water or drenched by spray for periods long enough to have a serious effect on many small creatures living in the soil. When it is understood that the delicate humus animals, like most millipeds, require an environment with an unbroken supply of food and moisture, and protection from the sun and flooding, it will be realized that such animals have lived in these islands under great difficulties. In the face of these difficulties it is astonishing that these creatures have managed to maintain the unbroken continuity through past ages that accounts for their presence on some of the islands today.

Unsatisfactory environmental conditions were found on many of the small West Indian islands where collecting was done, such as Beata and Saona Islands off the south coast of Haiti; Barbuda, Anguilla, and Saba in the northern Lesser Antilles; and Bequia, Cannouan, and Mayero in the Grenadines to the south. None of these islands has high elevations where rain forest conditions are approached, with the possible exception of Saba. The single day spent on that island did not allow a visit to the highest part, which is frequently cloud-covered and is said to have considerable rainfall. At the time of our visit Saba was rather dry, and few humus insects and no millipeds were found during the walk from the sea up through the town of Bottom to the still higher town of Windward at an elevation of 2,500 feet.

In the larger and more fertile West Indian islands, agricultural activities, which include cutting down the forests, burning of brush and grass lands, cultivation of various crops, pasturing of cattle, and general denuding of the land by other means, have undoubtedly contributed very greatly toward reducing the humus population. A striking example of these effects was found in St. Vincent, the most intensively and generally cultivated island seen by the expedition. In a trip over about half of the island few places were found where humus insects might exist continuously, and no millipeds were seen, although seven species have been reported, and one of these might be expected to be rather abundant, as in other places where it is known. There is little doubt that satisfactory conditions for milliped life are more frequently met with in the higher parts of the island than in the lower elevations, where the scarcity of forms may be at-

tributed to the more complete subjugation of the land to agriculture and other effects of dense human population.

A similar situation as regards the humus fauna probably exists in Barbados, the most completely cultivated island in the West Indies, but one not included in the itinerary of the expedition, so that direct observations were impossible. However, the only reason that can be advanced as to why there are but two species of millipeds known from Barbados is that the original species have been greatly localized or nearly exterminated by the intensive cultivation since European occupation. Both of the species reported, *Rhinocricus monilicornis* and *Orthomorpha coarctata*, are widely distributed through the West Indies, and it is much more likely that they were introduced into Barbados in modern times than that they represent the remnants of the aboriginal milliped fauna of the island, as the native home of neither species is definitely known.

In the following part of this paper are given descriptions of the new genera and species collected by the expedition; notes on the structure, distribution, and taxonomy of others previously known; line drawings of essential structural features of many species; and magnified photographs of some of the most outstanding species, which show to a slight extent the remarkable diversity, not only among the various orders of millipeds involved, but also within the orders themselves.<sup>2</sup>

Class DIPLOPODA  
Subclass PSELAPHOGNATHA  
Order ANCYROTRICHA  
Family POLYXENIDAE

**POLYXENUS LONGISETIS** Pocock

*Polyxenus longisetis* Pocock, Journ. Linn. Soc. London, vol. 24, p. 474, 1894.

Pocock's assignment of this species to the genus *Polyxenus* appears definitely open to question, as the description is exceedingly short and contains few important details, and none of these relates to peculiarities of the genus. There is no indication that eyes are present, but the very long antennae suggest that the species should have been referred

<sup>2</sup>With the exceptions of *Lophoproctus comans*, photographed in water, and *Inodesmus peduncularis*, the millipeds used in illustrating this paper were lightly coated with ammonium chloride to bring out details of sculpturing in the photographs.

to *Lophoproctus*. This view is furthered by the illustration, which shows but a single row of hairs along the posterior margin of each segment, as in *Lophoproctus*, instead of two rows, as in *Polyxenus*. In other respects the disposition of the hairs is very similar to that in *Lophoproctus niveus* Loomis, except that segment 1 is not even indicated in the drawing and its two clusters of hairs apparently are shown as being on the back of the head. In neither of the above genera is there a row of hairs at the back margin of the head or of the first segment.

Specimens from Cuba and others collected by the Armour Expedition from Mount Misery, St. Kitts, January 24, 1932, have been referred to *P. longisetis*.<sup>3</sup> These specimens are without eyes but in other respects answer the description of the species. An examination of the type is necessary to determine its genus and whether the above specimens have been correctly determined.

#### LOPHOPROCTUS COMANS, n. sp.

Plate 1, fig. 1

One female from the Maracas Valley, Trinidad, February 13, 1932.

*Diagnosis*.—The large size of the body, its exceedingly shaggy appearance, due to the long hairs of the lateral prominences and those on each side of the dorsum; and the broad, very dense fascicle of uniformly long hairs, are the outstanding characters by which this species may be recognized.

*Description*.—Body very shaggy; gray; quite large and stout; about 5.5 mm long, including the terminal brush of hairs; 1.2 mm wide; terminal brush a little more than 1 mm long and over half as broad; number of segments 11, with 13 pairs of legs.

Head oval, eyeless, with long, slender antennae; joint 1 short; joint 2 equal to 4, a third longer than 3, but little longer than 5, and noticeably shorter than joint 6, which is as long as the 2 subequal outer joints combined. Labrum deeply and narrowly notched at middle. From the outer margin of the head, just above the antennae and reaching across the front, the surface is densely beset with long, slightly curved, erect, clavate, barbed hairs, most closely set above the antennae; on each side of the middle of the front the hairy area extends forward considerably but at the middle the transverse band of hairs is narrow. Above this band of scattered hairs there is a single crescentic series of similarly shaped hairs on each side of the head, and near the outer end of the series there are three tiny round

<sup>3</sup> Bull. Mus. Comp. Zool., vol. 75, pp. 357-358, 1933.

pits forming a triangle, each pit containing a very fine erect sensory hair; remainder of head glabrous.

First segment small and inconspicuous, a very narrow transverse ellipse not reaching the lateral limits of the body. On either side of the middle there is a very large transversely oval cluster of long erect radiating hairs; remainder of surface glabrous. Some writers appear not to have noted the first segment as distinct from the second segment but have combined the two in describing segment 1.

Second segment with the lateral prominence on each side produced forward about opposite the lateral angle of segment 1. Near the posterior margin on each side is a very narrowly oval cluster of long hairs, the two dorsal clusters connected by a submarginal row of much shorter depressed hairs.

Ensuing eight segments with vestiture similar to segment 2. Segment 3 with the lateral prominences somewhat directed forward, but on the other segments they are directed backward. Each of these lateral prominences bears a dense brush of very long, barbed hairs, some hairs being as long or even longer than any two segments combined. In general, these hairs are directed obliquely backward and show much less tendency to radiate in all directions than is usual in this family.

Last segment with a very large and exceedingly dense brush of slender, uniformly long, straight hairs lying parallel to each other, each hair with one to three tiny hooks on one side near the apex. The brush of hairs is about as wide as the last segment, the sides are almost parallel, and the end is squarely truncate.

Legs rather stout; joint 1 as long as broad; joint 2 about half as long as broad; joint 3 longer than broad; joints 4, 5, and 6 decreasing in length; joint 7 longer than any other joint, narrowly conical, with a spine beneath the apical third which is stouter than the terminal claw. Ventral-posterior face of joints 1, 2, and 3 with two to five short, clavate hairs in a single longitudinal series.

*Type*.—U.S.N.M. no. 1084.

#### LOPHOPROCTUS NIVEUS, n. sp.

Two females were collected in dry leaf-litter near the rocky cliffs on the southwest coast of Beata Island, January 18, 1932.

*Diagnosis*.—The smaller size, lighter color, shorter and more definitely radiating hairs of the lateral prominences, and the compound terminal pencil of hairs distinguish this species from *L. comans*, the only other named species in the West Indies.

*Description.*—Body of medium size; length without the terminal pencil of hairs, which is missing, 3.5 mm, width over 1 mm. Living color almost pure white. Segments 11, number of legs 13.

Head with the hairs distributed much as in *L. comans*, but they are somewhat shorter, and the two anterior areas are not so widely separated. Antennae with joints of different proportions from those of *L. comans*, as shown in figure 1.

First segment small and with two clusters of hairs as in *L. comans*.

Segment 2 with the lateral prominences slightly produced forward, but those on the other segments extend outward; the hairs on these prominences are straight and radiate in all directions, not curving backward as in *L. comans*, nor are they as long as in that species,



FIG. 1.—*Lophoproctus niveus*. Antenna.

although some of the longest hairs seem to have been lost from the specimens. Near the side of each segment, close to the posterior margin, is a small cluster of erect, radiating hairs, and along the posterior margin there is a close-set series of rather long hairs pointing backward.

Last segment with all hairs lost, but it is apparent that the terminal pencil was composed of two parts, as there is a round folliculate area above, and a larger reniform folliculate area below it. This caudal pencil of hairs probably was very similar to that of the following undetermined species from Nassau.

Legs resembling those of *L. comans*, except that the spine beneath the distal third of the last joint is smaller than the terminal claw.

*Type.*—U.S.N.M. no. 1085.

#### LOPHOPROCTUS sp.

Many specimens were collected at Nassau, New Providence Island, January 3, 1932.

All the specimens are so badly rubbed that it is impossible to gain a complete conception of the vestiture. However, the caudal pencil of hairs is composed of two definite parts, an upper round cluster of very long, light-colored, parallel hairs, beneath which there is a brush of equally dense, dark, parallel hairs about two thirds the length of the upper group but forming a cluster more than twice as wide and considerably thicker. The antennae and other structural characters

are very similar to those of *L. niveus*, but the living color was darker. The advisability of attempting to name this species is questioned until specimens with vestiture intact can be examined.

**LOPHOPROCTUS sp.**

Five specimens collected near Orangetown, St. Eustatius, January 22, 1932.

They appear to differ slightly from *L. niveus* and the Nassau species but are so badly rubbed that only a very incomplete description is possible, and this would complicate rather than aid future systematic work on the genus.

**Subclass CHILOGNATHA**

**Order LIMACOMORPHA**

**Family GLOMERIDESMIDAE**

**GLOMERIDESMUS TRINIDADENSIS, n. sp.**

Plate 1, fig. 2

Two males were collected in the Maracas Valley, Trinidad, February 13, 1932.

*Diagnosis.*—This is decidedly the largest member of the genus. The uncolored head and the shape of the pleurae are additional differences between it and *G. marmoreus* Pocock, its closest relative.

*Description.*—One male 10 mm long, the other one 11 mm long, and both 2 mm in diameter.

Head and ventral surfaces uncolored, yellow in the alcoholic specimens; the color of the segments above as in *G. marmoreus* Pocock.

Pleurae striate in front, their posterior margin simple, not at all serrate, transverse, with the inner corner slightly more than a right angle and not produced as is shown in Pocock's figure. The posterior lateral margin of the first joint of the legs simple, nonserrated.

The penes are soft, flexible, unchitinized structures, and in specimens just removed from alcohol they are distended, and four or five narrow, longitudinal, glabrous areas are to be seen in alternation with transversely striate, setiferous areas of similar width. On drying somewhat, the glabrous areas contract laterally and appear as deep furrows. The distended penes are capable of reaching back over the coxae of seven or eight pairs of legs and are much stouter than after a little drying.

*Type.*—U.S.N.M. no. 1086.

## Order COLOBOGNATHA

## Family SIPHONOPHORIDAE

*SIPHONOPHORA MILLEPEDA*, n. sp.

A single mature female and a number of tiny young were found beneath a rock in a cacao grove on the hills above Charlottstown, Man-of-War Bay, Tobago Island, February 20, 1932.

*Diagnosis.*—In this species the number of segments greatly exceeds that of any other known member of the genus. Other distinctive characters include the shape of the third antennal joint and the vestiture of the antennae; the very short, deeply emarginate hypostomal plate; and the reduced size of the first few pairs of legs.

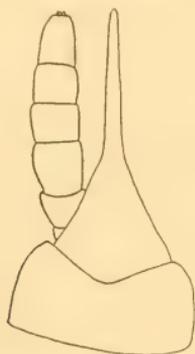


FIG. 2.—*Siphonophora millepeda*. Head, antenna, and first segment, dorsal view.

*Description.*—Length of the type 58 mm, width 1.3 mm. Number of segments 190. Living animals cream-colored.

Head shorter than the beak, narrow, triangular, the sides almost straight (fig. 2). Beak very long and slender, nearly straight, hardly deflexed, the tip approximating the ends of the antennae. Hypostomal plate very short, broad, deeply emarginate. Antennae stout with joint 3 thickest, equalling joint 6 in length, the other joints shorter; joints 1 to 5 beset with hairs of various lengths; joints 6 and 7 much more densely covered with shorter hairs of uniform length.

Body densely beset with straight, erect hairs varying in length from moderately short to ones 4 or 5 times as long. Segments very strongly convex longitudinally, dorsum moderately depressed transversely. Posterior margin of segments finely and uniformly serrate.

The anal valves together are hemispherical and covered with hairs similar to those on the segments. Preanal scale transverse behind, with fewer and shorter hairs than the valves.

First few pairs of legs smaller and weaker than those farther back, gradually increasing in size on the first few segments. Coxae of first pair of legs each produced into a small, inconspicuous, triangular lobe at the distal end on the dorsal side.

The unconscious rivalry between millipeds for the greatest number of segments becomes keener with the finding of this Tobago Island species. Several years ago another species of this order was described from California,<sup>4</sup> one of the specimens having 192 segments but the others falling considerably below this number. Although 192 segments is the greatest number thus far known for a milliped, it is not unlikely that specimens of the present species or the California one will be found exceeding this number.

*Type*.—U.S.N.M. no. 1087.

#### SIPHONOCYBE HARTI (Pocock)

Plate I, fig. 3

*Siphonorhinus harti* Pocock, Ann. and Mag. Nat. Hist., ser. 6, vol. 15, p. 313, 1895.

*Siphonophora nigrosignata* Silvestri, An. Mus. Nac. Buenos Aires, vol. 6, p. 54, 1898.

Specimens of this species were collected in the Maracas Valley and in the Arena Forest area of Trinidad, February 1932.

Living color light golden brown with a broad dark brown line reaching from the first to almost the last segment. The anterior end of the body is slightly darker than the posterior end. Head and antennae pure white, in conspicuous contrast to the anterior segments. The dense pubescence of the segments gives the body a velvety appearance in life. The animals are very sluggish and move with great deliberation.

The gonopods are of the same general type as those of *Siphonophora progressor* Chamberlin, as shown in Chamberlin's drawing.<sup>5</sup>

There appear to be no grounds for maintaining Silvestri's species as distinct from *harti* Pocock.

#### Family POLYZONIIDAE

##### SIPHONOTUS PURPUREUS Pocock

*Siphonotus purpureus* Pocock, Journ. Linn. Soc. London, vol. 24, p. 479, 1894.

*Siphonotus virescens* Silvestri, An. Mus. Nac. Buenos Aires, vol. 6, p. 55, 1898.

This species was collected in the following places. Roseau, Dominica; Port-of-Spain, Trinidad; Tobago Island; Fort-de-France, Martinique; Point-à-Pitre, Guadeloupe; Paramaribo, Dutch Guiana.

<sup>4</sup> *Illacme plenipes* Cook and Loomis. Proc. U.S. Nat. Mus., vol. 72, pp. 10-12, 1928.

<sup>5</sup> Proc. U.S. Nat. Mus., vol. 60, pp. 1-71, illus., 1922.

Pocock's description states that the head is "apparently furnished on each side with two large, black, prominent eyes, the upper of which are covered by, though visible through, the first tergite." In none of the specimens I have examined, several of which have been dissected, has there been more than one eye on each side, although the surface behind the eye, beneath the first segment, is sometimes dark-colored.

The dorsum of the segments has two transverse rows of short, rather widely spaced, erect setae; one row crossing the middle of the subsegment, the other in its posterior margin. First segment with setae more numerous and scattered over the entire surface.

## Order MONOCHETA

### Family STEMMIULIDAE

#### STEMMIULUS SURINAMENSIS, n. sp.

One male was collected 70 kilometers from Paramaribo, Dutch Guiana, beside the railway to the Cable Station, March 3, 1932.

*Diagnosis.*—The form of the gonopods, and the first and second legs, as shown in figure 3, *b* to *e*, distinguish this species.

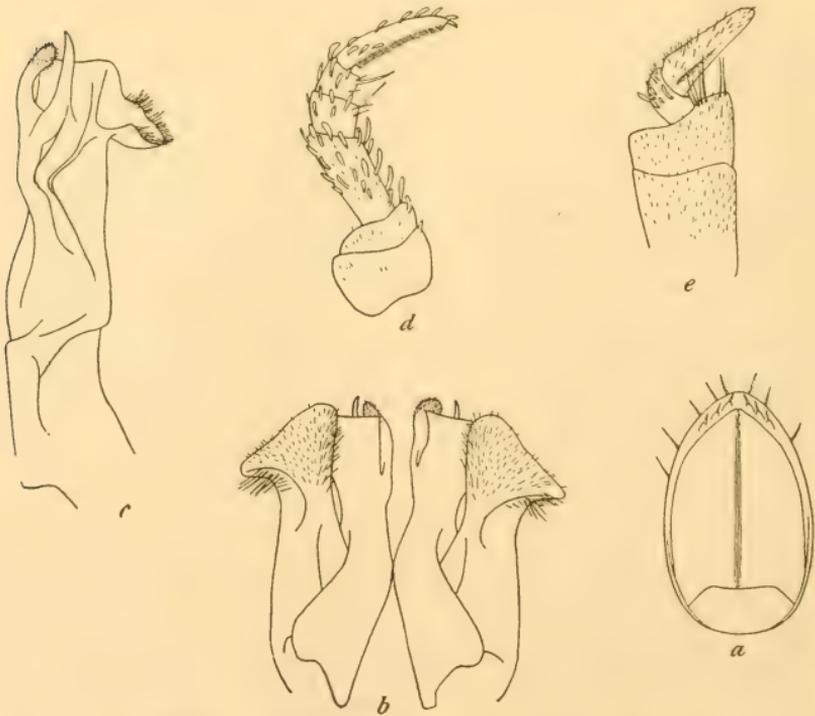


FIG. 3.—*Stemmiulus surinamensis*. *a*, last segment, anal valves and scale, ventral view; *b*, gonopods, anterior view; *c*, right posterior gonopod, posterior view; *d*, first male leg, anterior view; *e*, second male leg, anterior view.

*Description*.—Length about 20 mm. Number of segments 48.

Body with the first three segments broad, followed by a slight constriction. Posterior end of the body gradually narrowed, moderately compressed laterally.

Head rather dark; first and last segment light; color darkening from in front; segments with a narrow longitudinal median light band, on each side of which the dark color is nearly solid to a large lateral rounded spot of light maculations. Surface of the segments sculptured with numerous distinct irregular scratches in addition to the usual striations.

Single ocellus on each side large and strongly pigmented.

First segment with two strong lateral striae; margin rounded on the sides.

Last segment with apex slightly exceeding the valves. Valves with thin raised margins. Preanal scale truncate behind, the sides oblique (fig. 3, *a*).

Gonopods, first and second male legs as shown in figure 3, *b* to *c*.

*Type*.—U.S.N.M. no. 1088.

#### STEMMIULUS INSULANUS Chamberlin

*Stemmiulus insulanus* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, p. 178, 1918.

Three males and four females were collected in the Arena Forest area, Trinidad, and near King's Bay, Tobago Island, in February 1932.

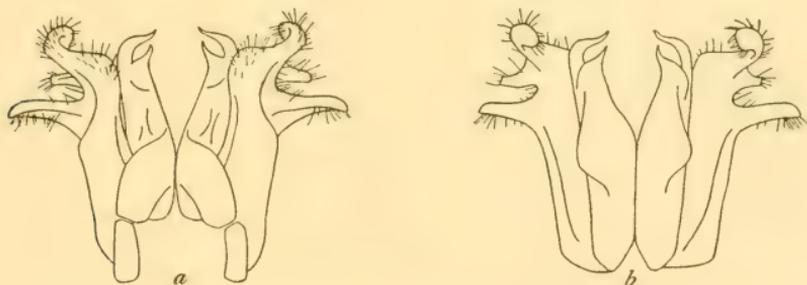


FIG. 4.—*Stemmiulus insulanus*. *a*, gonopods, anterior view; *b*, gonopods, posterior view.

All the above specimens are smaller than Chamberlin's type, which was a male. A 14-millimeter male and a female of the same length were the largest specimens collected by the writer. The living color notes state that the head, the first three segments, and the anal segment are light red, with the posterior half of segment 3 and succeeding segments dark colored.

The gonopods are shown in figure 4, *a* and *b*.

**PROSTEMMIULUS WHEELERI (Silvestri)**

*Diopsiulus wheeleri* Silvestri, Bull. Amer. Mus. Nat. Hist., vol. 24, pp. 568-569, 1908.

Numerous specimens were collected at Roadtown, Tortola, March 19, 1932.

The number of segments given by Silvestri for this species, on the basis of broken specimens, is too low, as the range observed in the Tortola specimens is from 40 to 45.

The largest female is 18 mm long.

The bodies are strongly compressed laterally in spite of Silvestri's statement to the contrary.

**Order DIPLOCHETA****Family EPINANNOLENIDAE****EPINANNOLENE HAITIENSIS Chamberlin**

*Epinannolene haitiensis* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, pp. 179-180, 1918.

A mature and an immature female were collected at the Citadel, near Cape Haitien, Haiti, March 27, 1932.

**Family SPIROSTREPTIDAE****ORTHOPORUS ANTILLANUS (Pocock)**

*Spirostreptus antillanus* Pocock, Journ. Linn. Soc. London, vol. 24, pp. 483-484, 1894.

A number of specimens were collected at Hillsborough, Carriacou Island, February 8, 1932.

The largest specimen, a female, was 100 mm long with 60 segments; the largest male was 98 mm long with 63 segments.

**ORTHOPORUS NITIDUS (Daday)**

*Spirostreptus nitidus* Daday, Term. Füzetek, vol. 14, p. 137, 1891.

Two female specimens, collected in Trinidad without definite locality, were presented by Dr. F. W. Urich, of Port-of-Spain.

These specimens agree with Pocock's description, except that each has a greater number of segments than credited to the species, one having 64 segments, the other 68 segments.

## ORTHOPORUS TRACTUS, n. sp.

A single female was collected in the Aripo Savannah, Trinidad, February 14, 1932.

*Diagnosis.*—The small size of the body and the median light stripe extending its full length distinguish this species from other members of the genus.

*Description.*—Length 30 mm, width 2 mm. Number of segments 51.

Body with a very definite, uniformly narrow, longitudinal median line of light color continuous from the front margin of segment 1 to the apex of the last segment; posterior quarter of segments transparent but the remainder brownish, areolate with light spots. Head areolate on the vertex, with a solid brown band between the eyes; remainder of the head and the antennae light colored.

Head smooth and shining and with a median furrow visible on the front of the vertex. Eyes composed of about 30 ocelli in 6 rows forming a triangle. Structure of the gnathochilarium typical of the genus.

First segment with two very strong lateral striae reaching from the eye around to the posterior margin. Laterad of these is a submarginal stria reaching from near the lower corner of the eye to the posterior margin.

Ensuing segments with a simple, very sharply impressed, transverse median line on the front segments, but following segment 6 or 7 it contains a single series of uniformly close-set, short, longitudinal striae beginning well below the pores. Ventral striae not reaching beyond the limits of the legs except on a few anterior segments. Dorsally, the surface of the segments is brilliantly shining and very sparsely and minutely aciculate-punctate. The front half of the anterior subsegments is finely striate-reticulate, but the posterior half is less sculptured.

Pores beginning on segment 6.

Last segment ending in a thin, rounded-triangular production surpassed by the valves. Dorsal surface rather coarsely and densely punctured, the sides smoother.

Anal valves punctate throughout but more strongly so near the smooth raised margins.

The assignment of this species to the genus *Orthoporus*, on the basis of only female characters, is somewhat tentative, and final judgment must be withheld until a male is examined.

*Type.*—U.S.N.M. no. 1089.

**ANETHOPORUS CLARKI** Chamberlin

*Anethoporus clarki* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, pp. 184-185, 1918.

Three females were collected at the eastern end of the Island of Tobago, February 20, 1932.

**ANETHOPORUS GRACILIOR** Chamberlin

*Anethoporus gracilior* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, pp. 185-186, 1918.

A single female specimen, 53 mm long and 3.5 mm broad, with 56 segments was collected with the foregoing species. The specimen has a distinct depression on each side of the head between the eye and the antenna.

## Order ANOCHETA

## Family SPIROBOLIDAE

**RHINOCRICUS LIMATULUS**, n. sp.

Ten specimens were collected at St. Claude, above Basse Terre, Guadeloupe, March 13, 1932, by P. H. Dorsett and H. F. Loomis.

*Diagnosis.*—Closest relationship seems to be with *R. socius* Chamberlin, which has not been examined, but *R. limatulus* appears to differ in its smaller size, more uniform coloration, scobina in a shorter series, and in the form of the gonopods.

*Description.*—Length of the largest specimen, a male, 68 mm, width 6.5 mm; the females are stouter, one measuring 60 mm in length being 7 mm wide. Number of segments 46 to 49.

The living animals have a rather dull sheen and are dark slate-gray throughout, except for the narrowly colorless posterior margin of the segments.

Head with a definite furrow on the vertex and on the clypeal area but not between the antennae on the front, which is crossed transversely by a considerable number of fine impressed lines originating near the antennae and arching upward across the middle of the head. Antennal cones numerous.

First segment with a short but prominent marginal rim below the lower corner of the eye and not passing beyond the lower limit of the segment; sides broadly and evenly rounded.

Ensuing segments strongly convex, especially at each end of the body; the transverse depression scarcely evident on any segment. Pores very evident, each being placed in the bottom of a small pit which is bounded behind by a short, deep impression. Surface of the

segments smooth and with a dull sheen except just along the posterior margin, which shines in contrast. Ventral striations not reaching to the last joint of the legs. Scobina present from segment 12 or 13 to within 15 or 16 segments of the posterior end of the body, the scobina small and represented by a round pit followed by a narrow attenuated striate area.

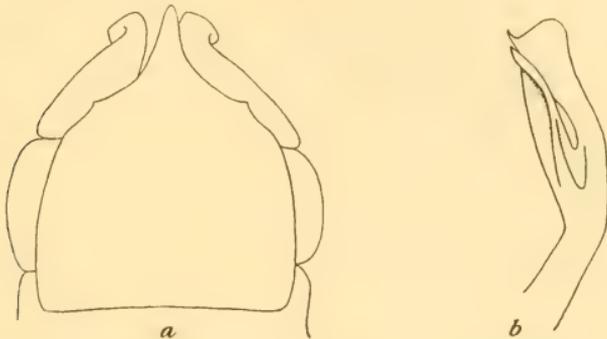


FIG. 5.—*Rhinocricus limatulus*. *a*, gonopods, anterior view; *b*, apex of inner gonopod, mesial view.

Last segment with the rather sharply angled tip equaling the valves. Anal valves of some specimens show a faint indication of having compressed margins. Preanal scale broadly rounded behind, the sides emarginate.

Gonopods as shown in figure 5, *a* and *b*.

Males without special modifications of the pregenital legs.

*Type*.—U.S.N.M. no. 1090.

#### RHINOCRICUS GRENADENSIS Pocock

*Rhinocricus grenadensis* Pocock, Journ. Linn. Soc. London, vol. 24, pp. 498-499, 1894.

Several specimens of this species were collected near Grand Etang, Grenada, February 10, 1932.

#### RHINOCRICUS ARBOREUS Saussure

*Rhinocricus arboreus* Saussure, Linn. Ent., vol. 13, p. 331, 1859.

Many specimens were collected from the branches and trunks of low bushes and trees on the high hills back of Roadtown, Tortola Island, March 19, 1932.

The living animals are brilliantly shining, black, and in the sunlight they show a slight bluish or greenish reflection. The labrum of these

specimens is without teeth in the emargination, a character not observed in other species of the genus.

#### RHINOCRICUS LEUCOSTIGMA Pocock

*Rhinocricus leucostigma* Pocock, Journ. Linn. Soc. London, vol. 24, pp. 500-501, 1894.

This species was found to be common in the vicinity of Roseau, Dominica, in January 1932, but with a range of size less than that credited to the species; the largest specimen was 45 mm long and many were less than 30 mm in length.

Chamberlin<sup>6</sup> incorrectly assigned this species to the island of St. Lucia instead of Dominica.

#### RHINOCRICUS MARTINIQUENSIS Chamberlin

*Rhinocricus martiniquensis* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, p. 199, 1918.

Five specimens were found beside the road from Fort-de-France to St. Pierre, Martinique, March 10, 1932.

Although none of these specimens exceeds 30 mm in length, they agree with Chamberlin's description in other particulars. His as-

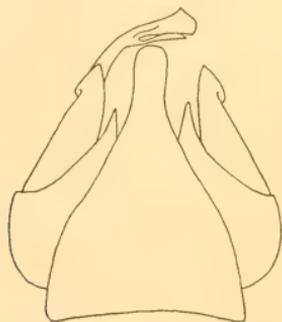


FIG. 6.—*Rhinocricus martiniquensis*. Gonopods, anterior view.

sumption of the difference between the anal segment in this species and *R. leucostigma* is correct, as was shown by direct comparison of specimens. *R. martiniquensis* has the margins of the anal valves much less compressed, and the median plate of the gonopods has the tip longer, more slender, and the apex rounded. In *R. leucostigma* the apex is almost squarely truncate.

Gonopods as shown in figure 6.

<sup>6</sup> Bull. Mus. Comp. Zool., vol. 62, p. 199, 1918.

Males with the coxae of the third legs produced into triangular lobes; similar lobes, decreasing in size, are found on the next four legs. Joints 2 to 5 of legs 3 to 7 have a swollen pad on the under side.

**RHINOCRICUS LATICOLLIS, n. sp.**

Seven specimens were collected on the roadside between Fort-de-France and St. Pierre, Martinique, March 10, 1932.

*Diagnosis.*—The broad first segment, the reduced or entirely obsolete posterior stria on the dorsum of the segments, and the shape of the median plate of the gonopods distinguish this species from its closest relative, *R. martiniquensis*.

*Description.*—Length of the largest specimen, a female, 34 mm, width 3.5 mm. Number of segments 39 to 42.

Color much as in *R. martiniquensis*, but the median spots are broadly triangular with the base in front, the apex not quite reaching the posterior margin of the segment.

Antennae with numerous sense cones.

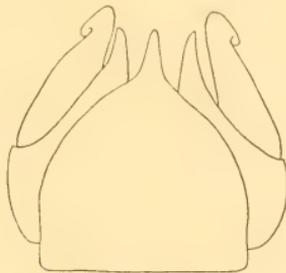


FIG. 7.—*Rhinocraticus laticollis*. Gonopods, anterior view.

First segment noticeably wider than any other segment; the lateral margin on each side broadly rounded and with a very narrow, inconspicuous raised rim.

Segments 2 to 4 decreasing in width behind the first segment; the other segments of uniform width to near the posterior end of the body, which narrows rather gradually. Segments with two transverse striae, the anterior one rather prominent on the dorsum, curving back far below the pore to join the posterior one, which becomes very faint or is lacking on the dorsum a short distance above the pore. Scobina present. Last segment, anal valves, and preanal scale as in *R. martiniquensis*.

Males with the median plate of the gonopods broad to beyond the middle, the distal extremity narrowly produced, with the acute tip reaching no farther than the tips of the lateral lobes and not as far as the tips of the posterior gonopods (fig. 7).

Coxae of legs 3 and 4 moderately produced into triangular lobes. Joint 3 of legs 3 to 7 sometimes with a lobe or swollen prominence on the under side, the other joints nearly normal.

*Type*.—U.S.N.M. no. 1091.

#### RHINOCRICUS MONILICORNIS (Porath)

*Spirobolus monilicornis* Porath, Bih. Svensk. Vet.-Akad. Handl., vol. 4, p. 31, 1876.

Specimens were collected in St. Martins; Martinique; Trinidad; Georgetown, British Guiana; and Paramaribo, Dutch Guiana.

From these specimens and closely related forms it seems likely that with a larger number of specimens from more localities it would be found advisable to reduce *R. consociatus* Pocock, *R. juxtus* Chamberlin, and possibly *R. tobagoensis* Chamberlin, at least to the rank of varieties of *R. monilicornis*, rather than to maintain them as species distinguished by what appear to be intergrading characters of color, size, and structure.

#### RHINOCRICUS CONSOCIATUS Pocock

*Rhinocricus consociatus* Pocock, Journ. Linn. Soc., London, vol. 24, p. 500, 1894.

Many specimens were collected on Bequia Island and at Hillsborough, Carriacou Island, in February, 1932. Both islands were very dry, and the specimens usually were found congregated beneath flat stones, logs, or pieces of boards on moderately exposed hillsides.

#### RHINOCRICUS CONSOCIATUS ECAUDATUS, n. var.

Specimens collected near Grand Anse, Grenada, February 10, 1932, show slight variations from the true *R. consociatus*. The last segment equals, but does not exceed, the anal valves, and the median plate of the gonopods has the sides slightly emarginate instead of being straight, but the inner gonopods of the two forms are similar. Although such differences are not considered sufficient for establishing another species, it seems advisable to call attention to them by recognizing the animals as a distinct variety.

*Type*.—U.S.N.M. no. 1092.

#### RHINOCRICUS GRAMMOSTICTUS Pocock

*Rhinocricus grammostictus* Pocock, Journ. Linn. Soc. London, vol. 24, p. 501, 1894.

A number of specimens were found in the Cul de Sac Valley, and on the Bar de l'Isle, above Castries, St. Lucia, February 2, 1932.

None of the specimens exceeds the limit of size given by Pocock for this species, which increases the probability that *R. serpentinus*

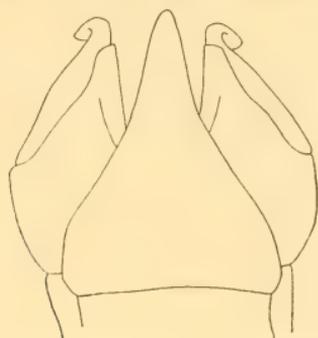


FIG. 8.—*Rhinocricus grammostictus*. Gonopods, anterior view.

Pocock is a valid species, although no specimens of it have been seen since it was described.

The gonopods of *R. grammostictus* are shown in figure 8.

#### NESOBOLUS MALTZANI (Pocock)

*Rhinocricus maltzani* Pocock, Journ. Linn. Soc. London, vol. 24, pp. 495-496, 1894.

Collected along the trail to Christoph's Citadel, Haiti, March 27, 1932.

#### CUBOBOLUS RAMAGEI (Pocock)

*Rhinocricus ramagei* Pocock, Journ. Linn. Soc. London, vol. 24, p. 489, 1894.

A number of specimens of this species were collected in the Cul de Sac Valley, St. Lucia, February 3, 1932.

As Pocock's description was based on a single female specimen, and the species has not subsequently been reported, the following notes are given.

Length varying from 42 to 55 mm.

Living color almost completely black above, except the head and the first two or three segments, which are light yellowish brown. The first segment has a small black area behind the middle of the anterior margin. Mucro of the last segment light brown. Antennae, legs, and ventral surfaces almost pure white. Pocock's statement that there is a light spot in the middle of the dorsum of each segment applies only to a few specimens after they have been preserved in alcohol, none being seen in living animals.

Antennal cones numerous.

Males with first two pairs of legs conspicuously smaller than the adjacent legs, otherwise unmodified. From the third pair of legs to within a few pairs of the posterior end of the body the fifth joint

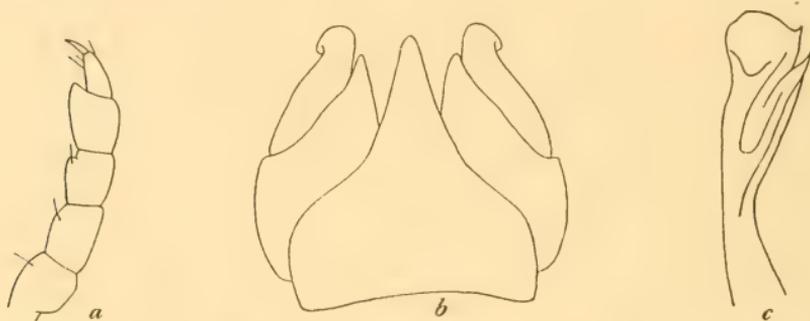


FIG. 9.—*Cubobolus ramagei*. *a*, seventh male leg, anterior view; *b*, gonopods, anterior view; *c*, apex of inner gonopod, mesial view.

of the legs is produced ventrally beneath the last joint (fig. 9, *a*). Coxae of the third legs somewhat triangularly produced.

Gonopods as shown in figure 9, *b*, the apical divisions of each inner gonopod separated for only a short distance (fig. 9, *c*).

#### MICROSPIROBOLUS SIGILLATUS, n. sp.

Male type was collected on Morne Pilboreau, above Ennery, Haiti, May 28, 1926, by O. F. Cook. A female specimen was collected in the same locality May 13, 1927, and another at the Citadel near Cape Haitien, March 27, 1932, by H. F. Loomis.

*Diagnosis*.—The most outstanding character of this species is the dorsal median marking, which consists of a solid band on the first few segments but thereafter the band is divided on the front of each segment to form a Y-shaped figure, with its stem on the hindbelt.

*Description*.—Length of the largest specimen, a female, 27 mm, breadth 2.5 mm. Number of segments 43.

In life the head is dark except at the labrum. First segment nearly white with a blackish spot behind at the middle and another on each side half way to the lateral margin. Ensuing segments with a broad black median band which is solid on the first few segments but on each segment thereafter is split widely apart to the hindbelt, forming a Y-shaped figure with the basal stem crossing the hindbelt; this figure pink along the sides and in the cleft. Laterad of the dark median figure is a broad cream band, below which is a still broader black band somewhat areolate with small light spots, and below this band the color is nearly white. Last segment dark, with a large semicircular

cream-colored spot on each side in front. Anal valves and preanal scale dark, antennae moderately so. Pleurae and basal joints of the legs light-colored, the outer joints darker.

Head with nearly circular eyes, composed of 21 or 22 large, convex ocelli in 5 or 6 series. Median groove faintly marked on the clypeus and lower part of the front. Clypeal fovea four on each side.

First segment narrowly rounded on the sides, subacute, the raised rim extending from opposite the eye around to the posterior margin.

Ensuing segments with the lateral suture sometimes faintly impressed beyond the pore, the other sutures not impressed but frequently showing as light lines in the integument. Transverse constriction marked by a pronounced sulcus extending across the dor-

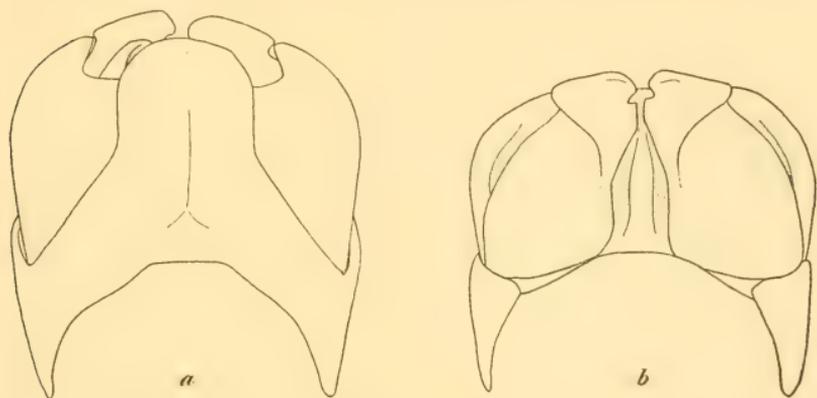


FIG. 10.—*Microspirobolus sigillatus*. *a*, gonopods, anterior view; *b*, gonopods, posterior view.

sum of all but five or six of the caudal segments; surface behind the sulcus definitely convex. Pores of moderate size, opening from the intersection of the lateral suture with the transverse suture, between the midbelt and hindbelt, and not quite half way between the impressed sulcus and the posterior margin. Surface of the segments lightly aciculated; ventral striae on the first few segments reaching three quarters of the way to the line of the pores, on the other segments becoming restricted to the vicinity of the base of the legs.

Last segment rather suddenly rounded at the apex, which equals, but does not exceed, the summit of the valves. Valves not margined. Preanal scale shorter and more broadly rounded than in the other species examined.

Males with the coxae and other joints of the pregenital legs unmodified. Gonopods as shown in figure 10, *a* and *b*.

*Type*.—U.S.N.M. no. 1093.

**MICROSPIROBOLUS DORSETTI, n. sp.**

Two males and two females were collected near Roadtown, Tortola Island, by P. H. Dorsett, March 18, 1932.

*Diagnosis.*—This species may be rather closely related to *M. richmondi* Chamberlin, as shown by the gonopods, but its principal differences are the larger size, greater number of segments, different coloration, and the lack of an impressed sulcus across any of the segments except a few near the head.

*Description.*—Length of the largest specimen, a female, 32 mm, width 2.7 mm. Number of segments 46 to 50.

Living colors: Head solid black; first segment salmon in front, changing to cream behind, the posterior margin narrowly black. Segments 2 to 6 dark throughout. Ensuing segments dark; in the females with a small transverse oval spot of salmon on each side of the forebelt, partly covered by the segment in front but showing through its transparent margin, another similar spot behind it on the midbelt (in alcoholic specimens the two spots appear more or less joined together); in the males the light spots of the midbody region are reduced in size, the anterior one sometimes missing on each segment, and the coloration otherwise is less vivid than in the females, the males being darker. Last segment with the exposed portion black, but on each side there is a large salmon spot showing through the overlapping penultimate segment. Behind segment 6 or 7 the ventral surface becomes increasingly lighter and is conspicuously salmon-colored on the last segments.

Head with a fine impressed median line on the vertex and another on the clypeal region. Clypeus with four fovea on each side.

First segment narrowly but evenly rounded on the sides, with a broad, low raised rim.

Ensuing segments with the transverse impression very faint on the dorsum of all but six or eight of the anterior segments, where it is marked by a very pronounced stria, which vanishes suddenly between segments 7 to 10. Exposed portion of the anterior half of the segments with surface similar to the posterior half, being rather coarsely reticulated and with a few fine scratches. Ventral striations not reaching beyond the tips of the legs.

Last segment with the tip usually exceeding the valves a little.

Males with the first five pairs of legs considerably heavier than the others, the sixth and seventh pairs intermediate in size. Legs 3 to 5 with coxae produced backward into broad, thick, rounded lobes; those of the fourth pair of legs a little larger than the others.

Seventh segment of the males with the ventral median ridge high, thickened on the sides but rather thin at the middle.

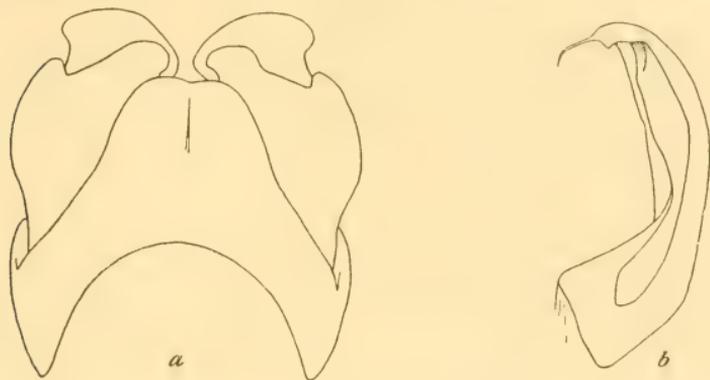


FIG. 11.—*Microspirobolus dorsetti*. *a*, gonopods, anterior view; *b*, inner gonopod, posterior view.

In spite of the fact that there are three legless segments at the posterior end of the body of the male type and four legless ones in the other, indicating that the animals are not quite mature, the gonopods of both seem to be fully developed, as shown in figure 11, *a* and *b*.

*Type*.—U.S.N.M. no. 1094.

#### APOROBOLUS, n. gen.

*Type*.—*Aporobolus crusoii*, n. sp.

*Diagnosis*.—This genus is unique in the Anocheta in that there are no repugnatorial pores on segment 7. In all other members of the order, pores extend from segment 6 to the penultimate segment in an unbroken series. The unusually low number of segments and the large basal joint of the antennae are other noteworthy characters. Relationship with *Microspirobolus* is indicated.

*Description*.—Body moderately slender, composed of fewer segments than is usual for the order.

Head with four fovea on each side of the clypeus. Antennae set in deep recesses on the sides of the head, the basal joint as large or larger than any other joint. Sense cones four.

First segment narrowed on the sides.

Second segment not markedly different from the next segment.

Ensuing segments bisected by a strong transverse constriction. Repugnatorial pores beginning on segment 6 and present on all other segments to the penultimate with the exception of segment 7, a con-

dition not known to occur in any other member of the order. Lateral or ventral striae not extending beyond the tips of the legs.

Last segment with the entire margin thickened, including the apex, which equals or just exceeds the valves.

Anal valves meeting in a deep groove, the margins not compressed.

Gonopods somewhat intermediate between those of *Rhinocricus* and *Microspirobolus*, but other characters point to closer relationship with the latter genus.

**APOROBOLUS CRUSOI, n. sp.**

One male and six females were collected February 20, 1932, at Man-of-War Bay, Tobago, the site of Robinson Crusoe's shipwreck.

*Description*.—Length of the largest specimen, a female, 20 mm, width 2 mm. Number of segments 35 to 38.

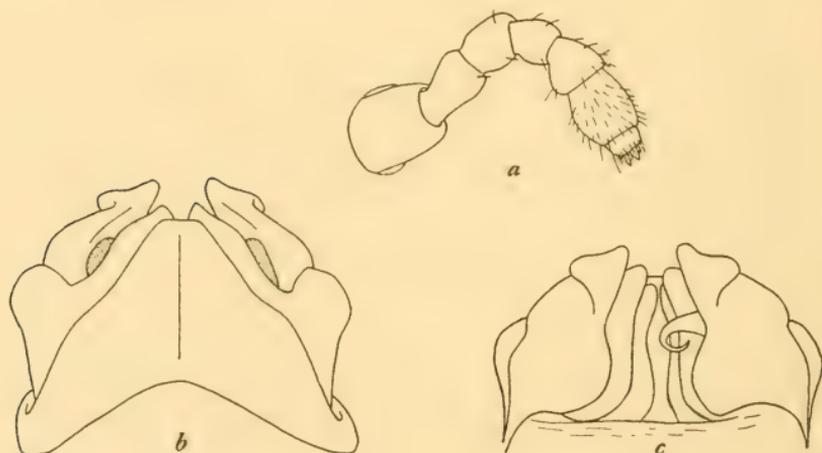


FIG. 12.—*Aporobolus crusoi*. *a*, antenna; *b*, gonopod, anterior view; *c*, gonopod, posterior view.

Living color white with a black stripe along the middle of the dorsum and another along each side.

Head with a short, deep furrow on the vertex; clypeus with four fovea on each side; ocelli rather large, 15 to 19 in number and arranged in three series; antennae deepset on the sides of the head, the cardo of the mandibles broadly and deeply excavated for their reception, basal joint long and thick, equaling or slightly exceeding joint 6 in both dimensions (fig. 12, *a*); sense cones four.

First segment with the sides narrowed, slightly emarginate in front and back just above the lateral margin. Anterior margin with a strong

raised rim reaching from the eye to the posterior corner of the segment.

Second segment continuing below segment 1 with scarcely any angulation of the surface, hardly differing from segment 3 in appearance.

Ensuing segments divided into halves by a strong transverse constriction containing a series of crescentic impressions reaching from the tips of the legs across the dorsum. Lateral striae confined to the ventral surfaces, not extending beyond the tips of the legs. Exposed dorsal surface of the segments smooth and shining, with a few short, fine longitudinal scratches. Anterior division of the segments almost flat longitudinally, posterior divisions moderately convex. Pores large, borne well behind the constriction. Pores of segment 6 larger than the others and lower on the body. Segment 7 without pores.

Anal valves strongly convex, smooth, without compressed margins, meeting in a deep groove.

Preanal scale broad, rounded-triangular.

The male type has 36 segments, of which the last 3 are without legs, but in spite of this the gonopods seem to be fully developed, as shown in figure 12, *b* and *c*. The gonopods bear some resemblance to those of the genus *Microspirobolus*, but the median plate is more triangular, and the inner gonopods are decidedly more simple, being slender and attenuated.

The pregenital legs of the male show no marked modifications, but the first two pairs of legs are nearly as long as the third pair and are considerably heavier.

*Type*.—U.S.N.M. no. 1095.

#### AZYGOBOLUS, n. gen.

*Type*.—*Azygobolus tumidus*, n. sp.

*Diagnosis*.—The location of the pore far behind the transverse depressions of the segments associates this genus with *Microspirobolus* and *Aporobolus*, but otherwise the relationship is remote, for the body is remarkably slender and submoniliform; the pores are borne on slight but evident swellings; and most unusual of all, the gonopods are devoid of a median plate, the generic name alluding to this unique condition. The posterior gonopods bend back over the coxae of the eighth pair of legs and appear incapable of being retracted into the body.

*Description*.—Body long, narrow, submoniliform, resembling *Nanolene* or some of the other cambalids rather than a spirobolid.

Head without a median sulcus on the vertex; clypeal setae four on each side; antennae short (fig. 13, *a*) and widely separated. Gnathochilarium as shown in figure 13, *b*.

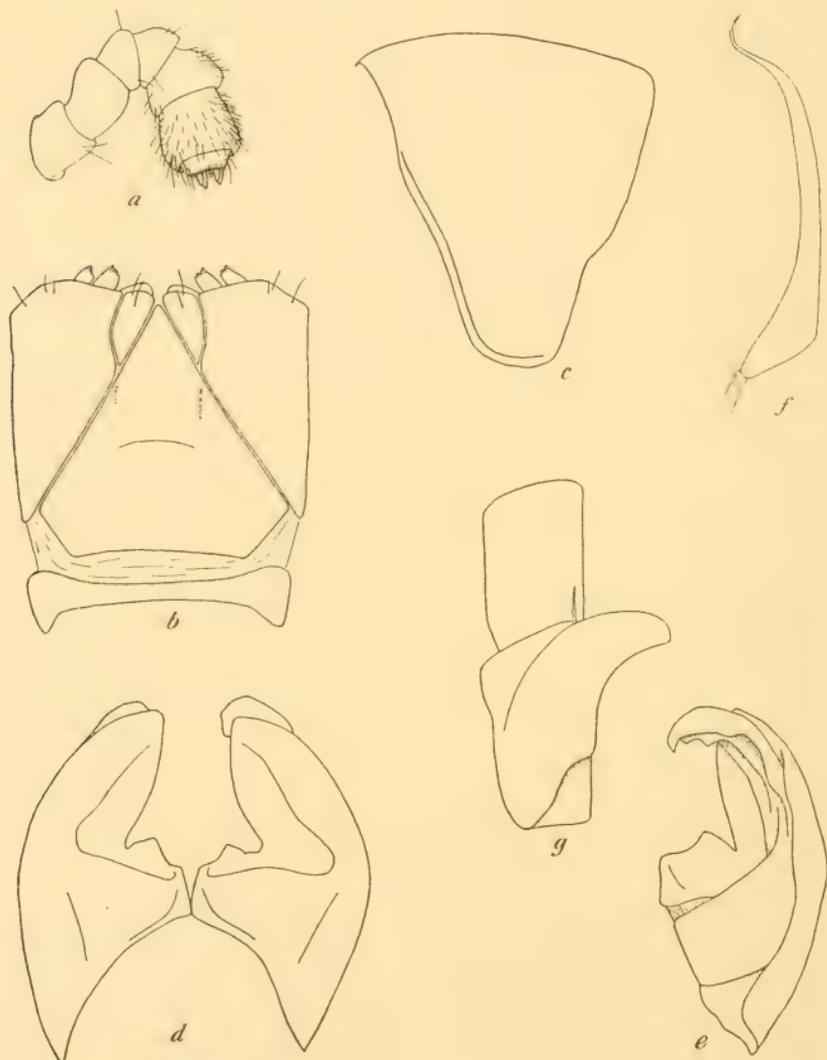


FIG. 13.—*Azygobolus tumidus*. *a*, antenna; *b*, gnathochilarium; *c*, first segment, lateral view; *d*, gonopods, anterior view; *e*, posterior gonopod, posterior-lateral view; *f*, inner gonopod; *g*, coxa and second joint of fifth male leg, mesial view.

First segment narrowed on the sides; slightly emarginate behind the eye, the posterior border more definitely emarginate above the angle (fig. 13, *c*).

Second segment with a pronounced anterior corner or shoulder obscured from the side by the first segment.

Ensuing segments each with a strong transverse median depression, in front of which the surface is sculptured with circular and crescentic impressions; the posterior half of the segment smooth, higher, and much more strongly convex, the large pore half way to the back margin and opening from the apex of a broad but distinctly evident swelling. Legs and pores terminating on the antepenultimate segment, possibly indicating that the animals lack one moult of maturity.

Last segment with the apex slightly exceeded by the moderately inflated anal valves, which meet in a deep groove and lack compressed margins.

Gonopods completely lacking a median plate, the mesial junction of the lateral lobes fully exposed in front. Apical halves of the posterior lobes bent back and carried outside the body, and their shape indicates that they are incapable of retraction within the body at any time.

Coxae of the fifth male legs with prominent lobes.

#### AZYGOBOLUS TUMIDUS n. sp.

Plate 2, figs. 1 and 2

Many specimens, including the male type, were collected at Marigot, St. Martins Island, March 17, 1932. Other specimens were found at Point-à-Pitre, Guadeloupe, March 11, 1932.

*Description.*—Length of the largest specimen 29 mm, width 1.2 mm. Number of segments 42 to 46.

Living color dark brown throughout.

Head smooth and shining throughout; vertex without a sulcus; clypeus with eight setae, the interval between the second and third setae on each side greater than that between the first and second or the third and fourth; labrum shallowly emarginate, the teeth inconspicuous; antennae too short to reach the posterior margin of segment 1, sense cones four; ocelli 28 to 34, in five or six series paralleling the first segment and forming a subtriangular patch.

First segment with a very pronounced, narrow raised rim extending from the lower corner of the eye to the posterior margin; surface smooth.

On the remainder of the body the strongly convex posterior halves of the segments give the animals a submoniliform appearance much like that of *Nannolenc*. The pore swellings are not very apparent from above, but when viewed from the side they are immediately evident.

Apex of the last segment rather broadly rounded and not separately produced, being exceeded by the anal valves, which lack compressed margins.

Preanal scale large, broad, the posterior margin rounded-transverse, the lateral angle on each side somewhat thickened or inflated.

Gonopods as shown in figure 13, *d* and *e*. They lack a median plate, and the distal half of the posterior lobes are bent back outside the body with their tips reaching above the coxae of the next pair of legs. Inner gonopods simple, the tips greatly drawn out, almost hairlike (fig. 13, *f*).

Coxae of the fifth male legs each with an erect lobe bent forward at the apex (fig. 13, *g*).

*Type*.—U.S.N.M. no. 1096.

#### TRIGONIULUS LUMBRICINUS (Gerstaecker)

*Spirobolus lumbricinus* Gerstaecker, Gliederthier-fauna Sansibar, p. 516, 1873.

This widespread tropical species was found in St. Kitts, Dominica, Martinique, British Guiana, and Dutch Guiana.

#### SPIROSTROPHUS NARESI (Pocock)

*Spirobolus naresei* Pocock, Ann. and Mag. Nat. Hist., vol. 11, p. 252, 1893.

This species was found in abundance in Dominica, Martinique, Guadeloupe, and St. Lucia.

### Order MEROCHETA

#### Family STRONGYLOSOMIDAE

#### ORTHOMORPHA COARCTATA (Saussure)

*Polydesmus coarctata* Saussure, Mem. Myr. Mex., p. 297, 1860.

This milliped was found in St. Eustatius, St. Kitts, St. Martins, Antigua, Guadeloupe, Dominica, Martinique, St. Lucia, Bequia, Carriacou, Trinidad, and Dutch Guiana.

#### ONCIUROSOMA sp.

Three 19-segmented specimens of this genus were collected about 70 kilometers from Paramaribo, Dutch Guiana, near the railway to the Cable Station on the Surinam River, March 3, 1932.

Although they probably represent a new species, as none exceeds 11 mm in length, their structural characters, particularly those of the male, have not fully developed and it is inadvisable to give them specific designation. From the form of the lateral keels and the last seg-

ment it is apparent that they are most closely related to the genotype, *O. neotropicum* Silvestri.

### Family CHELODESMIDAE

#### AMPHELICTOGON BIDENS, n. sp.

Plate 1, fig. 4

A male type and two females were found near Arthurstown, Cat Island, January 4, 1932, in a natural pit in the limestone rock, locally called a "banana hole" from the fact that bananas are planted in these pits, which afford protection from the constant winds.

*Diagnosis.*—Judging from Chamberlin's description<sup>1</sup> *A. bahamiensis* is closely related to *A. bidens* but has only a single tooth on the inner side of the posterior or ventral division of each gonopod, whereas *A. bidens* has two teeth. Moreover, it is inferred that *A. bahamiensis*

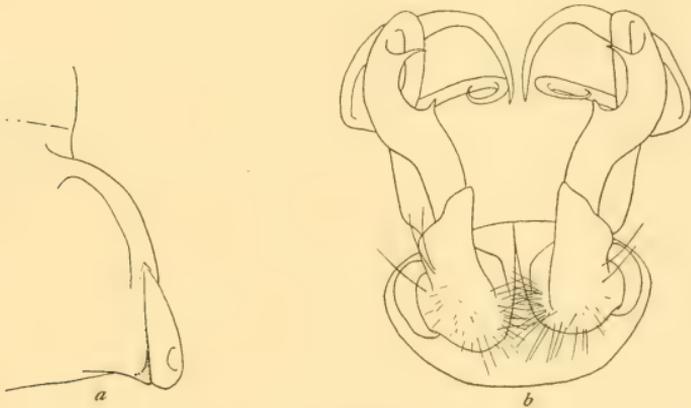


FIG. 14.—*Amphelictogon bidens*. a, lateral keel of segment 15, male; b, gonopods.

conforms to the generic description in having one or two teeth on the posterior margin of the keels, but the keels of *A. bidens* are without marginal teeth.

*Description.*—Length 20 mm, width 2.5 mm. Male a little more slender than the female. Body widest at the second segment in both sexes.

In live specimens the head is chestnut-brown with a darker area between the antennae; first segment brown with the lateral angles almost white; segments 2 to 4 chestnut-brown with the posterior angles nearly white, the other nonporiferous segments, including seg-

<sup>1</sup> Bull. Mus. Comp. Zool., vol. 62, pp. 231, 232, 1918.

ment 20, uniform chestnut-brown throughout, as are the antennae and legs; poriferous segments with the entire keels and some of the adjacent area of the dorsum white. The median line of the body is darkened by the internal ganglion showing through the body wall.

Head with a very deep median furrow on the vertex.

Segments with the keels well developed and without any teeth on the caudal margin as ascribed to members of this genus. Pore swelling long and thick (fig. 14, *a*).

Gonopods as shown in figure 14, *b*.

Sternum between the third legs of the male with two small, forwardly directed processes. The fourth sternum with processes more rounded and not produced forward.

*Type*.—U.S.N.M. no. 1097.

#### ANTILODESMUS VINCENTI (Pocock)

*Odontopeltis vincenti* Pocock, Journ. Linn. Soc. London, vol. 24, p. 514, 1894.

*A. grenadanus* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, pp. 236, 237, 1918.

Three males and three females were collected in Grenada, February 10, 1932.

Comparison of my Grenada specimens with Chamberlin's description of *A. grenadanus* and Pocock's description and figures of



FIG. 15.—*Antilodesmus vincenti*. Gonopod.

*Odontopeltis vincenti* leads to the conclusion that but one species is involved.

The living color of the animals is chestnut-brown with the keels and a triangular area on each segment yellow, the base of the triangle extending along the posterior margin contrary to the description of *A. grenadanus*, but Pocock stated that the color varies considerably, so that differences in color pattern are of little weight.

One of the gonopods is shown in figure 15.

## BEATADESMUS, n. gen.

*Type*.—*Beatadesmus utowani*, n. sp.

*Diagnosis*.—Although no males have been seen, the validity of this genus seems well substantiated by the combination of characters represented by the very strong teeth of the lateral and posterior margins of the segments near the middle of the body, and the different coloration of the poriferous and nonporiferous segments.

*Description*.—Body with the dorsum moderately convex, the sides parallel to about segment 16. Posterior subsegments smooth above or with one or two tiny tubercles on the surface of the keels.

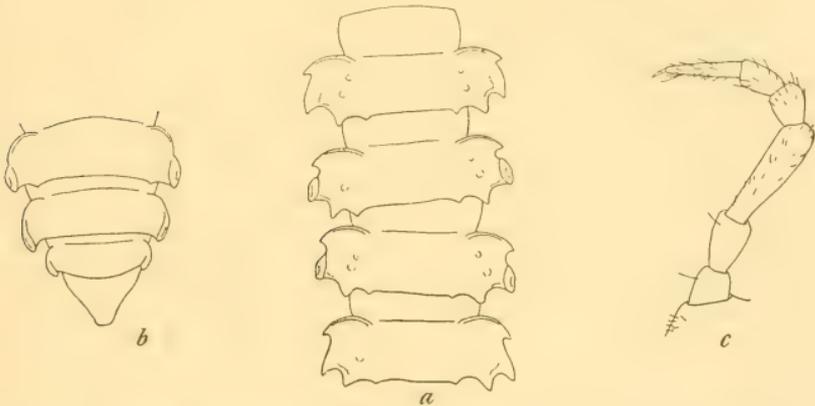


FIG. 16.—*Beatadesmus utowani*. *a*, segments 8 to 11, dorsal view; *b*, segments 17 to 20, dorsal view; *c*, first leg of segment 8, female.

Head wider than the body, the cardo of the mandibles especially prominent, long, subrectangular; antennae long and slender, joints 2 to 6 inclusive of uniform thickness.

First segment semicircular, with an erect seta on each side of the middle close to the front margin.

Ensuing segments with a sharp, prominent tooth at the anterior corner of each keel from segment 2 to segment 16 (fig. 16, *a*), behind which the tooth vanishes (fig. 16, *b*); on the middle segments the tooth is larger and is produced outward and backward; posterior angles of the nonporiferous segments all strongly produced caudad, especially in the midbody region; on the poriferous segments the thickened rim surrounding the pore occupies much of the lateral margin of the keel and replaces the produced angle. Posterior margin of the segments with a large tooth mesad of the posterior angle of each keel and usually with a much smaller tooth mesad of it; these teeth dis-

appearing on the last few segments. Poriferous segments differing in color from the others.

Anal valves subrectangular, flattened, with prominent margins.

Joint 3 of the legs much longer than any of the other joints (fig. 16, *c*); sterna near the middle of the body wider than the length of the third leg joint.

#### BEATADESMUS UTOWANI, n. sp.

A number of fragments of dead specimens and a single live but immature female (18 segments) were found January 18, 1932, under rocks on Beata Island, off the south coast of Haiti. The name given this animal associates the island where it was found with the yacht *Utowana*, on which the members of the expedition lived during three months of exploration in the West Indies.

*Description*.—Length of females probably about 25 mm, width 3.5 mm; males shorter and more slender. Body with the sides parallel from near the head to about segment 16; dorsum not strongly arched.

The immature female was entirely white in life, but the dead specimens obviously retained much of the color of the living animals, and although none of these had the head or first three segments, all of the poriferous segments are present and usually have a narrow brown area along the transverse sulcus on each side of the middle, the remainder of the surface white; nonporiferous segments with a median light area which is broader at the posterior margin than in front, the remainder of the segment brown or with a narrow portion of the longitudinal margin of the keels white.

Anterior half of all segments brown below, the dorsum with a white median area, widest at the anterior margin, extending backward and on some of the last segments joining with the white portion of the posterior subsegment. Last segment, valves, preanal scale, and legs entirely dark colored.

The sterna have 30 to 40 tiny, short hairs scattered over the surface but with slightly greater density in front than on the back half.

Other characters have been given in the generic description.

*Type*.—U.S.N.M. no. 1098.

#### BELONODESMUS THAXTERI Chamberlin

Plate 1, fig. 5

*Belonodesmus thaxteri* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, pp. 246-247, 1918.

This species is very abundant in the forests near Port-of-Spain, Trinidad, and probably is common throughout the island. Its range

also includes Tobago Island, near the eastern end of which, at Man-of-War Bay, it was collected in February 1932.

This species was erroneously placed in the Polydesmidae instead of the present family, where all its characters indicate that it belongs. The pores are not "near the margin of the keels on the dorsal side" but are actually in the thickened rim of the margin, the oblique elevation of the keels allowing the pores to be plainly seen from above. The gonopods, one of which is shown in figure 17, are definitely chelodesmid.



FIG. 17.—*Belonodesmus thaxteri*. Gonopod.

In addition to the characters given in the original description, it was noted that there is a serrate-tubercular ridge on the side of each segment from 2 to 17 located a short distance above the base of the legs. The sterna are high and wide with the legs lateral to them; there is a distinct tooth behind each coxal joint on the segments from just in front of the middle of the body to its rear end.

In the male the fifth joint of the first leg is produced distally into a lobe reaching almost to the claw of the last joint; the succeeding four pairs of legs have similar ventral lobes decreasing in size. Sternum between the fourth legs with two thin, high, transverse tubercles; that between the fifth legs with two smaller conic tubercles; and that between the sixth legs with two higher tubercles.

#### PRIODESMUS ACUS Cook

Plate 2, fig. 3

*Priodesmus acus* Cook, Proc. U.S. Nat. Mus., vol. 18, pp. 55, 56, 1895.

A mature female and a nearly mature male were collected about 70 kilometers from Paramaribo, Dutch Guiana, beside the railway leading to the Cable Station on the Surinam River, March 3, 1932.

Since the female of this species closely follows the description and drawings of the male of *P. acus*, the validity of *P. parae* Cook, erected with some question as to its distinctness from *P. acus*, is substantiated.

A character not noted in the description of *P. acus* is the presence of slender tubercles that project beyond the margin of the segment just above each posterior leg on segments 2 to 18. The female measures 20 mm in length.

### Family EURYURIDAE

#### APHELIDESMUS DIVERGENS Chamberlin

Plate I, fig. 6

*Aphelidesmus divergens* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, p. 249, 1918.

Numerous specimens were collected in Trinidad and Tobago, February 1932.

The antennae are separated by less than the diameter of one of the sockets. Front of the head conspicuously swollen between the antennae and immediately below them.



FIG. 18.—*Aphelidesmus divergens*. Gonopod.

Segments 2, 3, and 4 with a small but distinct tooth at the anterior corner of each keel.

Segments coarsely tuberculate along the posterior margin below the keels; on the anterior segments this tuberculation is not confined to the marginal area alone but extends onto the lateral surface. Anterior corner of the keels, beginning with segment 5, beset with many sharply conic tubercles, as is also the posterior margin of each keel.

In both sexes there are two conic tubercles on each side of the sternum opposite each leg with the exception of the first two pairs of legs.

One of the gonopods is shown in figure 18.

## Family PLATYRHACHIDAE

## NANORRHACUS LUCIAE (Pocock)

Plate 1, fig. 7

*Platyrhachus luciae* Pocock, Journ. Linn. Soc. London, vol. 24, pp. 511-512, 1894.

Numbers of specimens were found in the forest on the Bar de l'Isle above Castries, St. Lucia, February 2, 1932.

## Family POLYDESMIDAE

## AETHEANDRA, n. gen.

*Type*.—*Aetheandra multiplex*, n. sp.

*Diagnosis*.—The relationship of this genus may be close to *Polydesmus*—at least the females suggest this possibility—but the males exhibit more diverse secondary sexual characters than previously associated with this family, such as the greatly broadened labrum, the posterior productions of segments 2 and 3, and the expanded joints of legs 2 and 3. In remarkable contrast to the diversity of the secondary characters, the gonopods show a degree of simplicity probably not equaled by any other member of the order.

*Description*.—Small, very agile millipeds with the body of the proportions of a small *Polydesmus*. Number of segments 20. Lateral carinae horizontal, marked off from the body proper by a broad longitudinal depression; a more definite, transverse depression across the dorsum. Dorsum and lateral margins of the keels with a few thickened setae, but lacking any polygonal areas or tubercles, the surface finely granular. Pores in the usual sequence, opening on the dorsal surface from the base of the produced posterior angles. Males exhibiting unusual secondary sex characters in various parts of the body.

Head with the antennae long and slender; joints 2 to 6 subequal in length but joint 6 suddenly widened on the outer side beyond the small base. Vertex medianly impressed, glabrous behind, but in front to the upper limits of the antennal sockets it is finely pubescent. Males with a prominent transverse tubercle on the front just below the antennae; also with a continuous ridge connecting the lateral angles of the head; on each side the ridge begins at the angle and passes in front of the antenna and curves up between it and the frontal tubercle, joining the ridge from the other side high on the vertex where it is less prominent; labrum broadened, the front margin nearly straight

or slightly emarginate from the abruptly angled lateral corners (fig. 19, *a*); the labrum of the female of the usual narrowed polydesmid type.

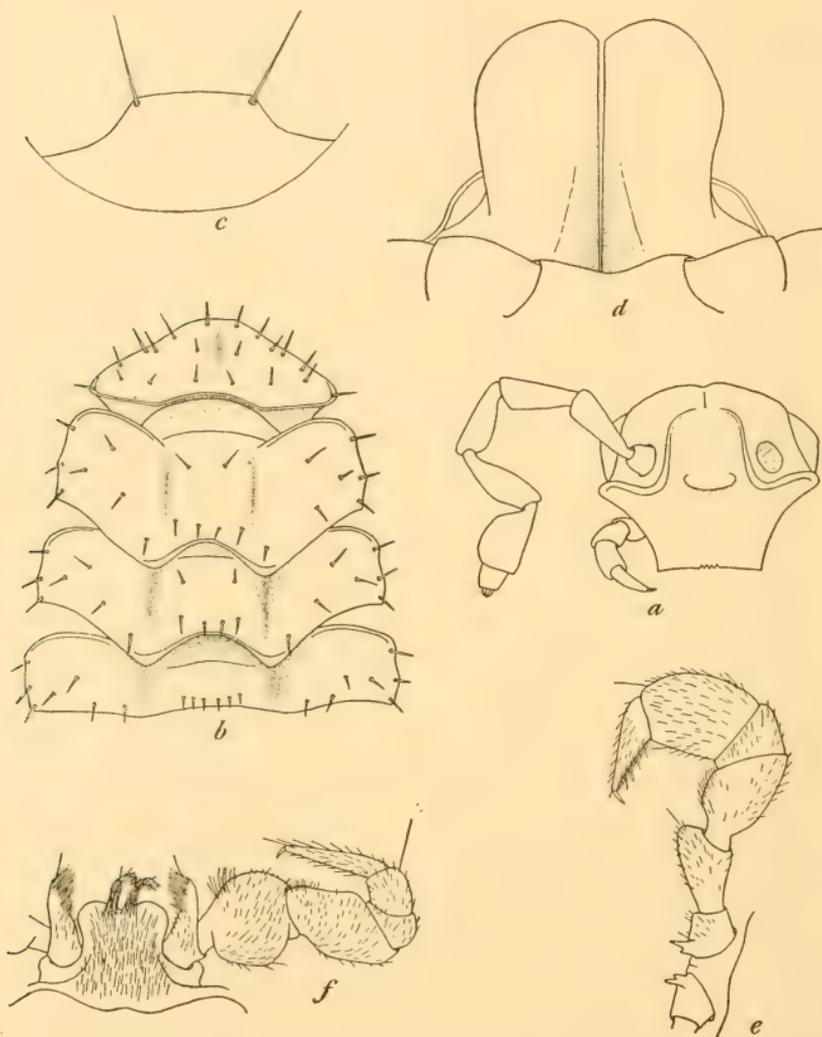


FIG. 19.—*Acteandra multiplex*. *a*, head and antenna of male, anterior view; *b*, segments I to 4 of male, dorsal view; *c*, preanal scale; *d*, gonopods; *e*, sternum and second male leg, anterior view; *f*, sternum and third male leg, anterior view.

First segment subsemicircular, broadly depressed along the middle; surface with 20 erect thickened setae.

Second segment longer than any other; the keels produced forward, lateral margins each with 3 thickened setae, the dorsal surface of the

segments including the keels with 14 erect thickened setae. Setae similarly disposed on the other segments. Males with the lateral keels more sharply produced forward, the posterior margin of the segment carried back on either side of the middle into a broadly triangular lobe extending over the next segment (fig. 19, *b*). The third male segment also has two similar lobes extending over segment 4. The fourth male segment with the dorsum very short, depressed below the level of the segments on either side of it, the keels strongly ascending, the six setae between the keels in a single row along the posterior margin instead of there being two in front and four behind as on the other segments.

Ensuing segments similar in the sexes, the posterior ones narrowing gradually, the posterior angles increasingly more produced to segment 17, after which they decrease in size and are scarcely apparent on segment 19. The setae along the posterior margin of segment 19 are about double the length of those on the other segments.

Last segment small, ending in a short, horizontal, truncated cone; sides emarginate.

Anal valves strongly convex, with thin, raised margins.

Preanal scale broad at base, the sides emarginate, the apex broadly truncated with a seta at each corner (fig. 19, *c*).

Gonopods exceedingly simple, consisting of two broad, thin, erect, apically rounded plates resembling tiny tombstones, the basal portion of each broadened; the plates oblique-transverse and in contact along their mesial sides (fig. 19, *d*). The opening in the segment through which the gonopods project is widest in front, with the posterior margin raised into a high rim.

First male legs smaller than those of the female.

Second male legs with each coxal joint bearing a small tubercle near the base; second joint somewhat produced at the apex posteriorly; joints 3, 4, and 5 thin but greatly expanded vertically; joint 6 thickened at the base, narrowing distally, with a comb of fine hairs along the ventral side (fig. 19, *e*).

Third male legs with each coxal joint produced into a high process with long hairs behind and along the inner side to the tip; joints 2 and 3 thin but greatly expanded vertically; the three distal joints nearly normal, the terminal one lacking a ventral comb of hairs; sternum very greatly elevated transversely into a broad, thin, posteriorly concave prominence, very woolly in front and topped by two locks of long, twisted hairs; the posterior concave face of the elevation is glabrous and shining (fig. 19, *f*).

**AETHEANDRA MULTIPLEX**, n. sp.

Plate 2, figs. 4 and 5

Three males, four females, and four young were collected in the heavy forest near the top of the ridge back of Kings Bay, Tobago, February 20, 1932. They were found among very moist, decaying sheaths and leaves from a huge cabbage palm, and on being disturbed ran rapidly for shelter.

*Description.*—The living color was bright light brick-red and the thickened hairs were quite apparent in spite of the rather small size of the animals. The largest specimen was 9 mm long and 1.5 mm broad. Structural characters have been sufficiently set forth in the generic description.

This is a very remarkable millipede in several particulars. The females are not strikingly different from many other small polydesmids, but the males differ from them so much that had the sexes been collected separately they would have been considered as distinct species, or even as representing different genera, for the secondary sexual modifications of the male not only greatly affect the anterior legs and sterna, but the shape of the head and anterior segments is changed in a very unusual manner. Outstanding differences of the head and dorsum are not expected between male and female in the Polydesmidae, but this species is exceptional in these particulars, for the head and first four segments are very dissimilar in the sexes. Although it is usually found that some of the legs in advance of the gonopods differ from the corresponding female legs in this family, the modifications seldom are as extreme or numerous as those of the second and third male legs of *A. multiplex*, and the sternum between the latter legs is remarkably developed. In view of the many secondary modifications it is surprising not to find complex gonopods as a corollary, but instead they are of a simplicity not paralleled in any other member of the family and probably not even surpassed within the order Merocheta.

*Type.*—U.S.N.M. no. 1099.

**AGENODESMUS**, n. gen.

*Type.*—*Agenodesmus reticulatus*, n. sp.

*Diagnosis.*—The general appearance of the animal is that of a small polydesmid, and although the dorsum lacks tubercles or broad, convex areas, the setae are rather typical. The shape of the first and last segment and of the lateral carinae, the dorsally placed pores, and the structure of the gonopods are definitely suggestive of the smaller Poly-

desmidae, but the tiny, 18-segmented body distinguishes it from all other forms except the 18-segmented *Hexadesmus*, which has the dorsal setae slender instead of definitely clavate.

*Description*.—Body very small, about eight times as long as broad; composed of but 18 segments; dorsum lacking tubercles or convex areas but definitely reticulated and with transverse series of strongly clavate setae.

Head with no median furrow evident, the surface reticulated and with many tiny, erect bristles, those of the vertex shorter than elsewhere. Cardo of each mandible with short bristles similar to those of the vertex. Antennae strongly clavate, with joint 6 longest and broadest; joints 4, 5 and 6 each with a very long extremely fine hair on the outer side near the end.

First segment oval; narrower than the head or the ensuing segments; surface relatively coarsely reticulated, as is the surface of all the other segments; a series of 10 large, clavate bristles along the anterior margin, and behind this is a median series of 4 similar bristles, and a third row of bristles along the posterior margin.

Second segment with the lateral carinae a little longer than those of the next two segments, distinctly produced forward, the carinae of the ensuing segments decreasingly so; anterior and posterior corners of all carinae rounded, except on the three segments preceding the last, which have the posterior corners acute and moderately produced backward; lateral margins simple, convex in outline.

Posterior subsegments moderately convex, with a distinct transverse depression; surface reticulated; the lateral carinae slightly depressed, not very strongly produced. Along the anterior margin of each segment is a series of 10 erect, strongly clavate setae, and a series of 8 similar ones along the posterior margin, the bristles of both series directed forward. On the four segments in front of the last some of the bristles of the anterior row are moved back and form a submedian row. Penultimate segment with six very long, slightly clavate hairs projecting straight back from the posterior margin.

Last segment as long or longer than the penultimate segment; definitely produced into a slightly down-curved, papillate mucro.

Repugnatorial pores large, rimless, opening from the top of a slight conic swelling of the dorsal surface close to the posterior corner of segments 5, 7, 9, 10, 12, 13, 15, 16, and 17.

Anal valves moderately convex, with raised margins.

Preanal scale long, rounded-triangular.

Sterna wider than the length of the first joint of a leg; crossed each way by a deep median depression.

Gonopods with basal joints large, galeate; each apical joint rather small, biramous at tip, curving outward and backward from the inner side of the basal joint.

**AGENODESMUS RETICULATUS, n. sp.**

A male (type) and several females were collected at Fond des Negre, Haiti, June 28, 1927, and on the same date two females were found between Petit Goave and Leogane, by O. F. Cook and H. F. Loomis. A female that does not differ strikingly from the more southern specimens was collected at Le Borgne, on the north coast of Haiti on March 26, 1930, by O. F. Cook. A mature female and a younger specimen were collected on the north slope of Mount Misery, St. Kitts, January 24, 1932. Four mature females were found on the Bar de l'Isle, above Castries, St Lucia, February 2, 1932, and two young were found at Roseau, Dominica; and two others from near Grand Etang, Grenada, the same year. These specimens do not differ among themselves or from Haitian specimens.

*Description.*—Length of the largest specimen 2 mm, width .25 mm. Number of segments 18.

Living color white with a slight tinge of pink.

Head large, strongly convex; surface distinctly reticulated and hirsute, vertex without a median furrow. Antennae strongly clavate, joints 2 and 3 subequal, each longer than joint 4; joint 5 broader than long, about the same length as joint 2 or 3, considerably shorter than joint 6, which also slightly exceeds it in thickness; joints densely hairy, especially the outer ones; joints 4, 5, and 6 each with a long and extremely fine hair on the outer side distally.

First segment about twice as wide as long, with a broad, transverse depression at middle, otherwise as given in the generic description.

Ensuing segments with characters as given in the generic description.

Last segment as long or longer than the penultimate segment, the apex produced into a slightly downcurved papillate mucro, the lateral margin on each side with three setae; dorsal surface with a transverse row of four long, erect bristles near the middle, and between this row and the mucro are two additional bristles.

Gonopods with each basal joint galeate, the surface somewhat hispid; apical joint arising from an opening in the inner surface of the basal joint near the front and curving upward and backward, the joint rather simple, terminating in two branches subequal in length but with

the anterior one heavy and definitely foliate near the apex, the posterior branch slender, attenuated (fig. 20).

Anterior male legs without lobes or other secondary specializations.

The discovery of this tiny species was of particular interest because of its having only 18 segments, a condition never before observed in the Merocheta, no mature member of which had previously been found with more than 20 or less than 19 segments.

Another closely related 18-segmented millipede was later found in Cuba and given the name of *Hexadesmus lateridens*.<sup>8</sup> This species is now known from Haiti, St. Kitts, and Carriacou of the Grenadines.

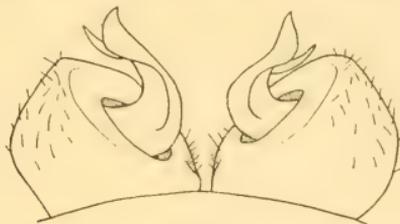


FIG. 20.—*Agenodesmus reticulatus*. Gonopods.

With the exceptions of the Oniscomorpha, in which 13 segments is the maximum, and the Limacomorpha with 20 or 21 segments, none of the remaining orders of Chilocheta contains animals with so few segments as in the Merocheta. In the Merocheta, species with only 19 segments are the exception rather than the rule, by far the largest number having the full complement of 20 segments. In some of the small forms, such as *Brachydesmus* and *Bactrodesmus*, the possession of only 19 segments is believed to be a depauperate condition, and this view seems to be supported and supplemented by *Agenodesmus* and *Hexadesmus*.

Not only is *A. reticulatus* nearly the shortest of all known millipeds, but it is decidedly more slender and delicate than any other yet discovered, the proportions of a polydesmid having been closely maintained in spite of the greatly reduced length.

*Type*.—U.S.N.M. no. 1100.

#### HEXADESMUS LATERIDENS Loomis

*Hexadesmus lateridens* Loomis, Bull. Mus. Comp. Zool., vol. 75, pp. 362, 363, illus., 1933.

Four female specimens, two of which are young, were collected beneath rocks on the grassy hills south of Basse Terre, St. Kitts,

<sup>8</sup> Bull. Mus. Comp. Zool., vol. 75, pp. 362, 363, illus., 1933.

January 23, 1932. They were in company with two other species of millipeds, *Dilophops bullatus* Loomis and *Psochodesmus granulofrons* (Chamberlin). Two mature (18-segmented) females were collected also near Hillsborough, Carriacou Island, February 8, 1932. A young specimen was collected at Petite Riviere de Artibonite, Haiti, July 1927, by H. F. Loomis.

#### CHILAPHRODESMUS, n. gen.

*Type*.—*Chilaphrodesmus rubellus*, n. sp.

*Diagnosis*.—Relationship to the 19-segmented African genus *Bactrodesmus* is shown by the structure of the gonopods; in both genera the basal joint is large and hollowed out to receive the apical joint, much as in the Stiodesmidae or Chytodesmidae. The dorsum in *Chilaphrodesmus*, however, is not definitely tuberculate; the repugnatorial pores open from the side of the posterior angle of the keel rather than from the dorsal surface of the keel; and the posterior margin of the penultimate segment is straight between the produced angles of the keels, not toothed as in *Bactrodesmus*.

*Description*.—Body about 7 times as long as broad, with 20 segments; dorsum flattened, slightly convex; lateral carinae projecting as in *Polydesmus*.

Head large, greatly exposed from above; surface quite densely hairy, the hairs of the vertex shorter than elsewhere; groove of the vertex fine and faint. Antennae rather slender, scarcely clavate, densely hirsute, especially the three outer joints; joint 6 broadest but not exceeding joint 3 in length; next in order of length come joints 2, 5, and 4, with 1 and 7 the shortest and subequal, each half as long as joint 2.

First segment oval, much narrower than the head or the adjacent segments; anterior margin with a thin, raised rim extending from one lateral angle to the other; behind this rim is a series of 10 very long erect setae arising from tiny, inconspicuous swellings or granules; behind this series are two others, the median containing four setae, the posterior six setae; surface elsewhere definitely reticulated, as is the surface of all the other segments.

Second segment with the carinae longer than those of the segments immediately following, especially segments 3 and 4.

Second and ensuing segments with an anterior row of four long erect setae and a posterior row of six smaller setae arising from granules similar to those on the first segment; each granule being in the center of an indefinite low, convex area; all segments except the first and last with six setae projecting horizontally backward from

the posterior margin, their length intermediate between the two dorsal series; in the male the setae are on small marginal teeth which are obsolete on the last few segments; the females with teeth indefinite or lacking. Beginning with the second segment the posterior margin of each segment has a broad triangular sinus or emargination on each side adjacent to the carina, causing the posterior angle of each carina to appear definitely produced backward, whereas on only the last segments do the corners of the carinae extend farther back than the median portion of the posterior margin of the dorsum and on these segments the sinus is reduced or lacking and the margin straight from side to side. All nonporiferous segments, except the first and last, have the lateral margin on each carina tridentate, each tooth bearing a long seta; poriferous segments with four setiferous teeth on the lateral margin of the carinae and the pore opens outward and backward from the margin of the posterior angle between the last two teeth. Pores on the customary segments; posterior angles of segment 19 much shorter than those of segment 20.

Last segment with a transverse median row of six setae and two setae near the papilliform apex which is short and almost horizontal.

Anal valves strongly convex; the margins thinly elevated.

Preanal scale rather long, triangular.

Sterna wide, about as in *Polydesmus*.

Basal joint of each gonopod large, subtriangular, hollowed to receive the long, curved apical joint. When the apical joints are exerted, one crosses the other, and each is directed toward the opposite side of the body.

In the male specimen the outer joints of the anterior legs are missing, but the coxal joints are present and show no specializations distinguishing them from the coxae of the legs farther back. The sterna between the seventh and eighth pair of legs are not definitely wider than the adjacent sterna.

This is an active little creature, apparently of much the same habit as *Bactrodesmus*, running swiftly for shelter when disturbed, with the antennae held nearly parallel in front of it. Because of the small size and rapid movements several specimens escaped in the litter of leaves; the ones collected were found on the underside of a stone which was upturned, and from which they were unable to escape.

**CHILAPHRODESMUS RUBELLUS** n. sp.

Plate 2, fig. 6

A male (type) and two females were collected near the road on the summit of Morne Pilboreau, above Ennery, Haiti, July 24, 1927,

by H. F. Loomis. A 17-segmented female was collected from the same locality, March 21, 1930, by O. F. Cook. Two females were collected within the Citadel, Cape Haitien, Haiti, March 27, 1932.

*Description*.—Length of the largest specimen, a female, 5.5 mm, width .8 mm.

Living color definitely pink.

Head with the three teeth of the labrum small but acute; the surface of the labrum and clypeus less hirsute and more distinctly shining than the rest of the head; antennae as shown in figure 21, *a*.

Behind segment 4 the seta at each end of the posterior row is usually reduced in size or is entirely lacking, leaving only the four inner setae. On the poriferous segments a small seta rises from the top of the posterior projection of the lateral margin of each carina above and just behind the pore. The entire dorsal surface of all the segments



FIG. 21.—*Chilaphrodesmus rubellus*. *a*, antenna; *b*, gonopod.

is rather coarsely reticulated as seen with high magnification, with the bottom of each cell strongly shining.

Gonopods with each basal joint large and strongly convex, sub-triangular, hollowed and apparently capable of receiving the outer joint when retracted. In the type these outer joints are projected laterally, one crossing the other and hiding much of it. Each outer joint is moderately stout, evenly curved, with a very large, acutely triangular lobe at the middle of the inner side; outer portion of the joint more slender, subspatulate, the apex rather thin and rather broadly emarginate (fig. 21, *b*).

The two females collected in Christoph's Citadel, are each 8 mm long, and although considerably larger than the specimens from the type locality, they agree very well in other particulars; however, examination of males from near the Citadel might show that they represented a second species.

*Type*.—U.S.N.M. no. 1101.

## Family CHYTODESMIDAE

**DOCODESMUS HAITIENSIS** Chambe. lin

Plate 3, figs. 1 and 2

*Docodesmus haitiensis* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, p. 216, 1918.

A number of specimens were found within the walls of Christoph's Citadel, near Cape Haitien, Haiti, March 27, 1932.

**DOCODESMUS SCULPTURATUS**, n. sp.

Plate 4, fig. 1

Many specimens, including the male type, were collected in a "banana hole" 3 or 4 miles from Nassau, New Providence, Bahama Islands, January 3, 1932.

*Diagnosis.*—This is the smallest and relatively the most coarsely sculptured of the genus. The dorsal tubercles are large and conspicuous and the sulci in the margins of the segments are particularly apparent; the posterior margins of the segments, especially segments 18 and 19, are strongly scalloped.

*Description.*—Length varying from 5 to 7 mm, width from 1 to 1.3 mm.

Living color cinnamon-brown above, lighter beneath.

Body more convex than in the other species and the sculpturing coarser; the sulci between the areas of the front margin of the first segment and the lateral and posterior margins of the other segments are particularly deep; the transverse convex areas on the dorsum of the body segments are not especially evident but the tubercle at the center of each area is large and high. Lobation of the lateral carinae as in the other species.

Head with a slightly elevated, granular area on the vertex, crossed by a median depression; clypeus continuous with the front.

First segment relatively longer at the middle than in the other species, the posterior margin on each side of the median portion directed forward more obliquely, surface with 10 large tubercles in 2 rows, with additional finer granulations.

Ensuing segments with four longitudinal rows of large tubercles, apparently three tubercles in each row, but in reality the third elevation is formed by an enlarged elevated area of the margin, immediately behind the row; the other marginal areas are smaller and project as distinct scallops. Between each pair of the enlarged areas of the posterior margin there are two smaller areas on all but the last three segments; on segments 18 and 19 the posterior margin is wholly occu-

pied by the four large areas, which are even more conspicuous than on the preceding segments. Anterior rim of the subsegments conspicuous on the carinae but less evident across the dorsum. Posterior angles of the carinae not definitely produced backward until segment 16 or 17.

Last segment with two prominent dorsal tubercles.

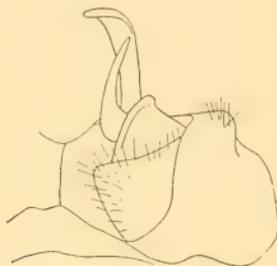


FIG. 22.—*Docodesmus sculpturatus*. Gonopod.

Gonopods as shown in figure 22, the basal joint large, hemispherical.

Legs of the males without special modifications except that the sternum between the fourth legs bears two tiny rounded tubercles.

Females with the anterior ventral margin of segment 3 elevated for a long distance into a very prominent ridge directed obliquely backward, the median portion thin-edged, the lateral angle on each side higher and several times as thick.

*Type*.—U.S.N.M. no. 1102.

#### DOCODESMUS TRINIDADENSIS Chamberlin

Plate 4, fig. 2

*Docodesmus trinidadensis* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, p. 219, 1918.

Specimens were collected in Trinidad at Sangre Grande, in the Aripo Valley, and in the Arena Forest area; others were found at Scarborough and Man-of-War Bay, Tobago.

The largest specimen was 12 mm long and 2.2 mm wide. The living color ranged from black with the carinae deep reddish-brown to entirely black with the exception of a narrow reddish area along the front margin of segment 1.

Body moderately convex; rather coarsely sculptured but relatively less prominent than *D. sculpturatus*; the transverse convex polygonal areas of the dorsum are more pronounced and there are more fine, irregular granulations in addition to the large tubercles. The areas separated by sulci along the posterior margin of the segments project

as faint crenulations but are produced into acute projections only on segment 19.

Head with a deep median impression across the coarsely granular area of the vertex which is separated from the front of the head by a deep channel just above the antennae; clypeal region elevated above and separated from the front by a deep furrow, especially evident on the sides.

Segments with raised anterior rim strongly evident on the carinae and adjacent dorsum but broken into erect crenations across the middle of the dorsum.



FIG. 23.—*Docodesmus trinidadensis*. Gonopod.

Gonopods as shown in figure 23, the basal joint relatively small, subangularly compressed, not forming an almost true hemisphere.

Males with the sternum between the fourth legs bearing two small, rounded tubercles. First joint of the fourth legs with a rounded setiferous tubercle in front, the second joint with the distal anterior corner continued into an acute lobe.

Females with the anterior ventral margin of segment 3 carried up into a high, thin, slightly reflexed ridge, highest at the middle and without prominent lateral angles.

In spite of the fact that my specimens are smaller, it seems evident that this is Chamberlin's species, although few distinctive characters were given in its description.

#### **DOCODESMUS ROBUSTUS, n. sp.**

Plate 4, fig. 3

A male (type) and a female were found at Kings Bay, Tobago Island, February 20, 1932.

*Diagnosis*.—Besides being much shorter in proportion to its width than any other species of *Docodesmus*, the irregular, cuspidate tuberculation of the dorsum and the lack of series of large tubercles make this the most easily recognized member of the genus. It may be remotely related to *D. trinidadensis*, as the structure of the head and the gonopods seem to indicate.

*Description.*—Body elongate-oval and less than four times as long as broad; both specimens measuring 13 mm in length and 3.7 mm in width. Dorsum strongly convex, much more so than in *trinidadensis*, and the lateral carinae descend more obliquely.

The living animals were dull black above throughout, lighter beneath.

Head with a very pronounced, broad, deep furrow just above the antennae separating the frontal region from the raised, medianly furrowed, granular vertex; clypeal region suddenly elevated above the frontal region, smooth and shining.

First segment about a third narrower than the midbody segments; anterior margin evenly rounded, the surface behind the marginal areas with densely scattered small granules.



FIG. 24.—*Docodesmus robustus*. *a*, last 2 segments, anal valves and scale, ventral view; *b*, side view of a gonopod from above and slightly behind.

Ensuing segments without longitudinal or transverse lines dividing the surface into large polygonal areas, and without any definite series of large tubercles; instead, the dorsal surface, except the usual smooth sulcate areas of the posterior margin and the lateral carinae, is densely scattered with small tubercles of various sizes, the median ones somewhat rounded but those on the sides of the dorsum and adjacent carinae are definitely cuspidate and each is surmounted by a very tiny and very short seta. Posterior marginal areas at the middle of the dorsum very short, not projecting beyond the margin as crenations except on several of the last segments. Anterior raised rim continuous across the dorsum, where its apex is slightly undulated.

Last segment with two large appressed, triangular tubercles above. Lateral lobes large, the median one broad, rounded-transverse behind. Ventrally, the four apical setae are protected on each side by a strong conic tubercle which projects backward (fig. 24, *a*).

Anal valves flattened, with moderately raised margins; disk of each valve with an angular fold or ridge extending upward from the lateral corner of the scale. Preanal scale triangular, the setiferous tubercles exceeding the median angle.

Gonopods shaped somewhat like those of *D. trinidadensis*, but the median portion of the long inner arm is expanded just below the distal half (fig. 24, *b*).

Males with the fourth sternum bearing two rounded, finely hispid tubercles; first joint of each fourth leg with a tubercle of about the same size.

Females with the anterior ventral margin of the third segment gradually raised from each side to form a low ridge or rim, which is highest at the middle of the body.

*Type*.—U.S.N.M. no. 1103.

#### IOMOIDES, n. gen.

*Type*.—*Iomoides hispidus*, n. sp.

*Diagnosis*.—This genus seems to be closely related to *Iomus* Cook, but is more convex and more compact; the lateral carinae are not as broad or as deeply incised, although with the same number of marginal lobes. The rows of large dorsal tubercles converge caudad instead of diverging or running parallel, and the third joint of the legs is longer than the last joint.

*Description*.—Body very compact, about four times as long as wide, the dorsum very strongly arched; lateral carinae broad, exceeding the legs, the anterior corners lower than the bottom of the body cavity. Surface of the carinae and the dorsum roughened, including the four longitudinal rows of large tubercles. Segments 2 to 5 inclusive gradually widening, the ensuing segments to the sixteenth of uniform width, after which they narrow rapidly. The posterior subsegments are abruptly raised high above the anterior subsegments, the face of the elevation being distinctly recessed, receiving the posterior edge of the foregoing segment when the body is held straight; anterior margin of the segments with a definite scallop between the outer and inner row of tubercles on each side, and two other scallops between the inner rows of tubercles.

Head quite convex, completely hidden beneath the first segment; surface between and above the antennae elevated and roughened, below the antennae the surface is somewhat shining and hispid. Antennae strongly clavate, geniculate, joint 5 broadest and longest.

First segment subhexagonal, greatly exceeding the head in front, narrower than the second segment, twice as broad as long; central

portion sharply raised above the broadly expanded anterior margin, which is divided by radiating lines into 10 elongate areas; disk with two transverse rows of large tubercles, entire dorsal surface, including the tubercles and the expanded margin, very finely roughened.

Second segment with the lateral margin of the carinae half again as long as segment 3, divided into three lobes by two very long, narrow, usually dirt-filled slits; front lobe of each keel raised; its anterior margin partly covering the oblique posterior margin of the first segment; middle lobe depressed below the level of the others.

Dorsum of segments 2 to 19 inclusive with four longitudinal rows of slightly convex, transverse areas, there being two such areas in each row and in the center of each area is a large, rounded-conic tubercle. The two rows of tubercles on each side of the faintly indicated median line extend obliquely mesad toward the back of each segment, especially the outer row. On the antepenultimate segment the last tubercle in each inner row is larger than the tubercles on any other segment and projects up and back, slightly exceeding the posterior margin. The lateral margin of each carina has a deep, narrow incision; the anterior and posterior margin each with three sublageniform incisions; these incisions, and particularly the one in the lateral margin, usually filled with dirt. Pores very inconspicuous, apparently present on segments 5, 7, 9, 10, 12, 13, 15-18, near the posterior corner of the carina.

Penultimate segment with the outer margins of the carinae converging backward very sharply, the posterior margin of each carina very short, the posterior corner only slightly produced, exceeded by the two projecting median tubercles of the dorsum.

Last segment almost or entirely hidden by the penultimate segment; posterior margin with three rounded, setiferous tubercles on each side; the papilliform process beneath the apical margin. Ventral margin on each side with a conic tubercle opposite the middle of the valve.

Anal valves slightly convex, margins broad and slightly elevated.

Preanal scale truncated at apex, a setiferous tubercle at each angle of the truncation.

Legs not reaching beyond the lateral carinae; joint 3 equaling or exceeding joint 6. No secondary sexual differences noted in the legs.

Sterna narrower than the length of a basal joint of a leg, crossed in each direction at middle by a deep furrow; without special modifications in either sex.

Gonopods with a large, clypeate basal joint opening inward, the terminal joint with an enlarged base supporting an erect process below which, on the inner side, a sicklelike blade projects backward, the tip turned upward.

Females with a very short ventral crest on the third segment just behind the second pair of legs.

**IOMOIDES HISPIDUS, n. sp.**

Plate 3, figs. 3 and 4

Two males, one the type, and two females were collected beneath a mango tree on the lower slope of Morne Brigand, near Bayeux, Haiti, July 16, 1927, by H. F. Loomis. The animals were sluggish in their movements, usually remaining motionless for a while after being exposed and were very difficult to see except when turned on their backs, thus exposing the light-colored ventral surfaces. Other specimens were collected at Le Borgne, Haiti, March 26, 1930, by W. H. Jenkins and O. F. Cook.

*Description.*—Length of the largest specimen, a female, 9 mm, width 2.2 mm.

In living specimens the dorsum is dull coal-black and usually somewhat incrustated with dirt; the under side of the posterior subsegments also is dark-colored to the sterna, and the elevated portion of the head between and above the antennae is coal-black; the remainder of the head, the antennae, the legs, sterna, anal valves, preanal scale, papilliform apex of the last segment, and the entire anterior subsegments are uniformly white or uncolored.

Head with an inconspicuous median furrow on the vertex. Antennae with joints 1, 2, and 3 gradually increasing in length; joint 4 about as long as joint 2, joint 5 twice as thick as joint 3 and somewhat longer, equaling joints 6 and 7 together, of which the latter is the shortest. In figure 25, *a*, the head and first two segments are shown in ventral view.

First segment with the median anterior margin nearly straight across, the sides extending obliquely outward and backward; lateral portions of the back margin directed inward and backward to the straight, transverse median margin. Central area of the segment subglobular, very abruptly raised above the greatly expanded anterior border, with an anterior row of four large conic tubercles and a posterior row of six smaller ones, each tubercle surmounted by a long seta in addition to the many tiny, erect setae scattered over the entire surface of the segment. A small seta in the middle margin of each of the areas of the expanded anterior margin.

On the ensuing segments the dorsal surface, including the large tubercles, is hispid with each of the large tubercles supporting a long bristle.

The outer lobes of the keels, to just in front of the middle of the body, each have a single seta in the margin; the outer lobes of the keels of the remaining segments each have two setae in the margin. Posterior margin of the keels with the incisions deeper than those of the front margin and with the outer incision more remote from the base of the keel than that of the front margin. On the posterior margin the lobe adjacent to the one at the outer corner contains a conic, bristle-tipped tubercle. Close to the base of each carina on segment 2 is a bristle-tipped tubercle; similar tubercles are found on the

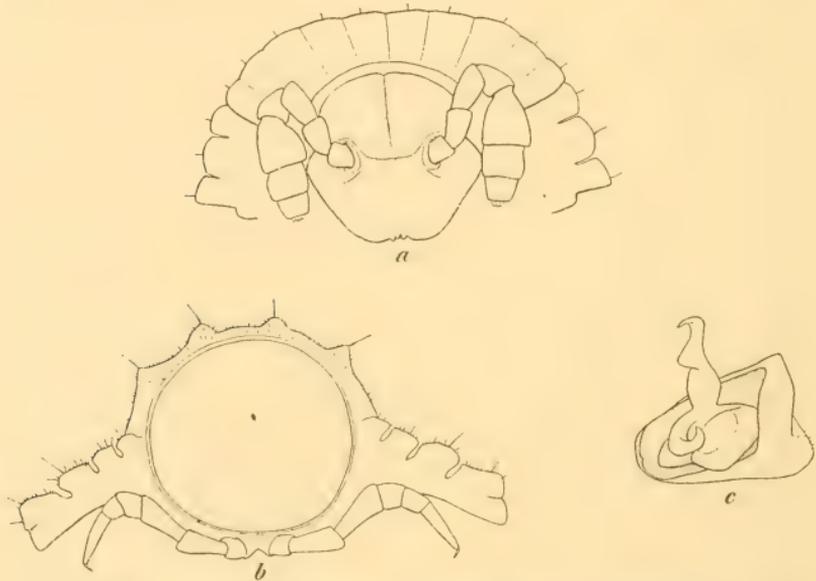


FIG. 25.—*Iomoides hispidus*. *a*, head and first 2 segments, ventral view; *b*, eighth segment, posterior view; *c*, gonopod, meso-posterior view.

carinae of segments 3 and 4, but increasingly farther removed from the base of the carinae, and on segments 6, 8, 11, and 14 the tubercles are near the middle of the carinae, poriferous segments without such tubercles. Posterior view of segment 8 shown in figure 25, *b*.

Penultimate segment with the tubercles reduced in size, especially those of the outer rows, the last tubercle in each inner row projecting a little way behind the back margin.

Last segment with the two apical marginal tubercles very close together.

Gonopods as shown in figure 25, *c*.

*Type*.—U.S.N.M. no. 1104.

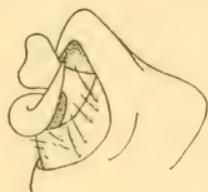
**IOMOIDES GLABRA**, n. sp.

Plate 3, fig. 5

A male (type) and a female were collected at Christoph's Citadel, Cape Haitien, Haiti, March 27, 1932.

*Diagnosis.*—This species may be instantly distinguished from *I. hispidus* by the complete lack of hairs on the dorsum or along the outer margins of the segments. The tubercles of segment I are relatively larger and more distinct. In addition the following differences occur:

The body is smaller and narrower, the male being 5.5 mm long and 1.2 mm broad, the female 7 mm long and 1.5 mm broad. The incisions of the keels are narrower and dirt-filled in both specimens.

FIG. 26.—*Iomoides glabra*. Gonopod.

Segment I has the anterior margin more definitely rounded although still somewhat subhexagonal. Of the anterior row of four tubercles, the inner two are double the size of the outer ones. There are but four tubercles in the posterior row, the outer ones of the same size as the corresponding ones in front but the inner two half the size of the outer, hence contrasting very strikingly in size with the pair in front.

The gonopods show further differences, as seen in figure 26.

*Type.*—U.S.N.M. no. 1105.

**PSOCHODESMUS** Cook

*Psochodesmus* Cook, Brandtia, p. 25, 1896.

*Xerodesmus* Chamberlin, Proc. California Acad. Sci., vol. 12, p. 403, 1923.

*Tidopteris* Chamberlin, Zoologica, New York Zool. Soc., vol. 3, no. 21, p. 420, 1923.

*Dominicodesmus* Chamberlin, Proc. Biol. Soc. Washington, vol. 36, p. 189, 1923.

After examining a number of specimens of *Psochodesmus crescentis* Cook from the type locality in Florida, and comparing them with descriptions, illustrations, or specimens representing the above genera, it is apparent that all these genera are synonyms of *Psochodesmus*. Specimens of *Dominicodesmus geophilus* from many Haitian localities

are obviously congeneric with *P. crescentis*, and in comparison with the paratype specimens of *Trescolobus granulofrons* Chamberlin no specific differences whatever were discovered. As the description of this latter species outranks *Dominicodesmus geophilus* in time of publication, the Haitian species must now stand as *Psochodesmus granulofrons* (Chamberlin). The following generic notes were made from specimens of the Florida and Haitian species:

Head with the granular area of the vertex traversed by a distinct median furrow. First segment somewhat flattened, much less strongly convex than the next segment and with the margin and lateral angles notably higher than the keels of that segment. Segments 2, 3, and 4 slightly shorter at the middle than segment 5. As viewed from the side the keels of the segments do not reach below the ventral third of the body. Anal valves distinctly convex and with thin, raised margins. Sterna narrower than the diameter of the basal joint of the leg on either side and with a definite median groove.

Inasmuch as the original description of *P. crescentis* is extremely brief, the following characterization has been prepared in order to place it on a comparable basis with the other species.

#### PSOCHODESMUS CRESCENTIS Cook

*Psochodesmus crescentis* Cook, *Brandtia*, p. 25, 1896.

Numerous specimens with 19 segments were collected between Crescent City and Palatka, Florida, May 16, 1927, by O. F. Cook. One 20-segmented male and three females were collected at Vero Beach, Florida, April 22, 1933, by H. F. Loomis. Other specimens



FIG. 27.—*Psochodesmus crescentis*. *a*, first segment, dorsal view; *b*, keels of segments 9 and 10, dorsal view.

have been collected at the United States Plant Introduction Garden, Coconut Grove, Florida, by O. F. Cook and H. F. Loomis.

First segment with the scalloped anterior margin broadly rounded, the scallops short and broad, not separated by incisions (fig. 27, *a*); surface with numerous small indistinct granules and two transverse rows of round tubercles, four in the anterior row and six in the posterior row.

Second segment with the lateral margin of each keel but little longer than the margins of the keels of the next two segments, the marginal lobes not conspicuously larger than on those segments.

All segments from the second to the penultimate inclusive with four longitudinal rows of large rounded tubercles, three tubercles of subequal size in each row; surface elsewhere covered with rather indefinite granules, those in the interval between the inner rows of tubercles in two longitudinal rows.

Nonporiferous segments in front of segment 15 with three lateral lobes on each keel, segments 16-19, with the keels 4-lobed; segment 5 with a single lobe in front of the pore process, all other pore-bearing segments with two lobes in front of the process, which projects from the posterior corner of the keel (fig. 27, *b*). Segments 2 to 18 with two lobes on the posterior margin laterad of the outer row of large dorsal tubercles, the outer lobe the largest and slightly elevated.

Last segment with a long tubercle on each side of the middle bent caudad and slightly exceeding the posterior margin.

Females with scarcely any crest on the ventral side of the third segment immediately behind the second pair of legs.

From the description and the drawings of *P. sequens* (Chamberlin) it is evident that it is closely related to *P. crescentis* but is of larger size; the basal joints of the gonopods of the 19- and 20-segmented specimens of *P. crescentis* are broader than long, but in *P. sequens* the basal joints are distinctly longer than broad; apical joint of the gonopods not showing in the immature Florida specimens and broken in the mature one.

Specimens of *P. granulofrons* (Chamberlin) have been found in several localities in Haiti, and a description has been prepared from them, which allows comparison with *P. crescentis*.

#### PSOCHODESMUS GRANULOFRONS (Chamberlin)

*Treseolobus granulofrons* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, p. 221, 1918.

*Dominicodesmus geophilus* Chamberlin, Proc. Biol. Soc. Washington, vol. 36, p. 189, 1923.

Examination of the paratypes of *T. granulofrons* showed it to be a species of *Psochodesmus* and, furthermore, in comparison with specimens of *D. geophilus* it was obvious that but a single species was involved. The type of *T. granulofrons* seems to be no longer in the Museum of Comparative Zoology, Cambridge, Mass.; hence the examination had to be from the paratype material.

Numerous specimens, all of which are females with not more than 19 segments, were collected by O. F. Cook and H. F. Loomis in the following localities in Haiti; Thor, near Port-au-Prince; Ennery; near Plaisance; Petite Riviere de Artibonite; and on Morne Pilboreau. Armour Expedition localities include Orangetown, St. Eustatius; Basse Terre, St. Kitts; Boggy Peak, Antigua; St. Claude above Basse Terre, Guadeloupe; Arena Forest, Trinidad.

Length of the largest specimen 5 mm, width .7 to .8 mm.

Living color light pink to buffish-pink or light brownish-red.

First segment with the anterior margin more nearly straight across than in *P. crescentis*, with the usual 10 lobes or scallops separated from each other by deep incisions, except the two outer lobes on each side, which are very shallowly separated or not at all (fig. 28, *a*). Surface with the 10 tubercles larger and higher than in *P. crescentis*, the granules also larger and more definite in shape.

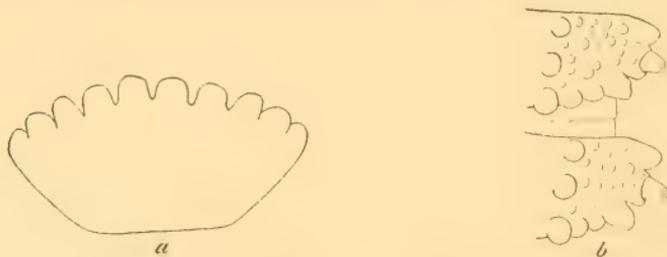


FIG. 28.—*Psochodesmus granulofrons*. *a*, first segment, dorsal view; *b*, keels of segments 9 and 10, dorsal view.

Second segment with the lateral margin of each keel half again as long as the margins of the keels of either the third or fourth segment, and the marginal lobes conspicuously larger.

Ensuing segments with the large tubercles in the dorsal rows higher and more definitely shaped than in *P. crescentis*, the middle tubercle in each row a little smaller than the one on either side of it; remainder of the surface covered with sharply defined granules of various sizes, those in the interval between the inner rows of tubercles irregularly disposed except on several of the anterior segments, the interval itself wider than that in *P. crescentis*.

Nonporiferous segments with the keels lobed as in *P. crescentis*, although behind segment 15, the keels may appear 3-lobed; all the poriferous segments with a single lobe in front of the pore process, which projects outward and slightly backward from near the middle of the lateral margin and apparently replaces both the middle and posterior lobes (fig. 28, *b*). On each segment the posterior margin

laterad of the outer row of large tubercles has three lobes, of which the outer one is much the largest, conspicuously elevated, and is close to the posterior corner of the keel. Lateral keels not projecting as far from the sides of the body as in *P. crescentis* and placed somewhat higher on the side of the body.

Last segment with the two dorsal tubercles narrower than those of *P. crescentis*.

Females with a definitely raised, back-curving crest on the ventral side of the third segment in front, immediately behind the second pair of legs.

Just how this species differs from *P. sequens* (Chamberlin) is not known, for aside from the characters of the gonopods, no characters are mentioned for *P. sequens* that allow it to be distinguished from the Haitian species.

### Family STIODESMIDAE

#### HOMODESMUS PARVUS Chamberlin

*Homodesmus parvus* Chamberlin, Bull. Mus. Comp. Zool., vol. 62, pp. 222, 223, 1918.

A male, similar in all particulars to specimens of this species from Haiti, was collected in the crater of the extinct volcano known as "The Quill" near Orangetown, St. Eustatius, January 22, 1932.

Chamberlin has reported this species from Puerto Rico. It is abundant in Haiti, from which country it may have been dispersed to these other islands in comparatively recent times, as it has not been found there in numbers.

#### GASATOMUS EMERSONI Chamberlin

Plate 3, fig. 6

*Gasatomus emersoni* Chamberlin, Zoologica, New York Zool. Soc., vol. 3, pp. 417-419, 1923.

A male was collected in the Maracas Valley, Trinidad, February 13, 1932.

It coincides in all particulars with Chamberlin's description and illustration except in size, for it is 6.5 mm long and 1.3 mm broad.

The anterior legs and sterna show no secondary sexual modifications. The sterna behind the gonopods, however, are strongly elevated, narrow, deeply depressed in each direction, and the posterior sternum of each segment is produced behind on each side into a rounded lobe.

The gonopods are somewhat of the type of those of *Cynedesmus simplex* Loomis, but the inner piece of each is shorter, heavier, and more simple.

## CYNEDESMUS Cook

This genus was erected to accommodate a species from Grand Canary, and later *Cryptodesmus ornamentatus* Karsch, from Cuba, was added to it. Several West Indian species described under *Trescolobus* by Chamberlin were reallocated by him in *Cynedesmus*, but it now appears that none of them belongs in this genus. His assumption that *Lophodesmus* Pocock is a synonym of this genus does not appear justified after a careful review of the characters of the two genera. The statement that no description of the type of *Cynedesmus* has been published is erroneous, as *C. formicola* was described in the Proceedings of the Academy of Natural Sciences of Philadelphia, 1896, page 267.

One difference between *Lophodesmus* and *Cynedesmus* is that the outer margins of the keels of segments 3 to 19 inclusive are bilobed in *Lophodesmus*, whereas in *Cynedesmus* some of the keels have three or even four distinct lobes. The dorsal tuberculation in both genera is of specific rather than generic value, for in each genus there are species with two dorsal rows of large tubercles, and others have four rows. In *Lophodesmus* the apical structure of each gonopod is enclosed within the hollowed, hemispherical basal joint, whereas in *Cynedesmus* the basal joint is smaller and the apical structure is less crassate and rises above the base.

## CYNEDESMUS SIMPLEX, n. sp.

A single male was collected about 70 kilometers from Paramaribo, Dutch Guiana, March 3, 1932, beside the railway to the Cable Station.

*Diagnosis*.—The smaller size differentiates this species from the others. None of the nonporiferous segments after the first has more than three lobes on the keels, and the keels of the penultimate segment are reduced in size and without sulci forming lateral lobes as on the other segments.

*Description*.—Length 5 mm, width .8 mm.

Head with the apex of the vertex smooth, but the anterior part is coarsely and irregularly granular to the upper limits of the antennal sockets. Antennae with joint 5 longest and broadest.

First segment with 10 scallops of equal size along the front margin; surface of the disk with 10 high, rounded tubercles arranged in a transverse ellipse, the rest of the surface somewhat granular.

Ensuing nonporiferous segments to segment 17 with the lateral keels 3-lobed; on segment 18 the lobes are indistinct, and the keels of segment 19 are small and without any semblance of lobes. Keels of

segments 5, 7, 9, 10, 12, 13, 15, and 16 with two distinct, equal lobes in front of the pore tubercle. Surface of the segments with four longitudinal rows of four high, rounded tubercles; on the caudal segments the lateral rows of tubercles are reduced in size, and the median rows are increased; surface elsewhere indistinctly granular, the gran-



FIG. 29.—*Cynedesmus simplex*. Gonopod, lateral view.

ules nowhere in regular series. The entire surface of the animal is more or less dirt-incrusted.

Last segment without dorsal tubercles, the posterior margin 6-lobed. Gonopods shown in lateral view in figure 29.

Anterior legs and sterna of the male without special modifications.  
*Type*.—U.S.N.M. no. 1106.

#### CYNEDESMUS sp.

An 18-segmented female 3.5 mm long and .7 mm broad was found on the Aripo Savannah, Trinidad, February 14, 1932.

Although several characters appear to distinguish this animal from other species of the genus, mature specimens should be seen before it is assigned a specific name.

#### LOPHODESMUS CARAIBIANUS (Chamberlin)

*Trescolobus caraibianus* Chamberlin, Bull. Mus. Comp. Zool. vol. 62, pp. 220-221, 1918.

One female specimen, which in comparison with Haitian specimens of this species showed no striking differences other than being slightly more slender, was collected under a stone near the Grantstown section of Nassau, New Providence, January 3, 1932.

#### Family HERCODESMIDAE

##### DILOPHOPS, n. gen.

*Type*.—*Dilophops bullatus*, n. sp.

*Description*.—Body very strongly arched; keels projecting downward and outward for a moderate distance, their extremities almost on a level with the basal joints of the legs, margins with a heavy, thickened rim.

Head with a distinct median depression on the vertex, on either side of which there is a high, very broad, rough, longitudinal ridge rising just above and mesad of the antenna, the upper half split and forming two diverging smaller ridges. Antennae short and moderately clavate; joints 1, 3, and 4 subequal in length, broader than long; joint 2 nearly as long as joints 3 and 4 together; joint 5 broadest and not quite half again as long as the two preceding joints together, approximately twice as long as joint 6; joint 7 half as wide as 6, slightly longer than broad.

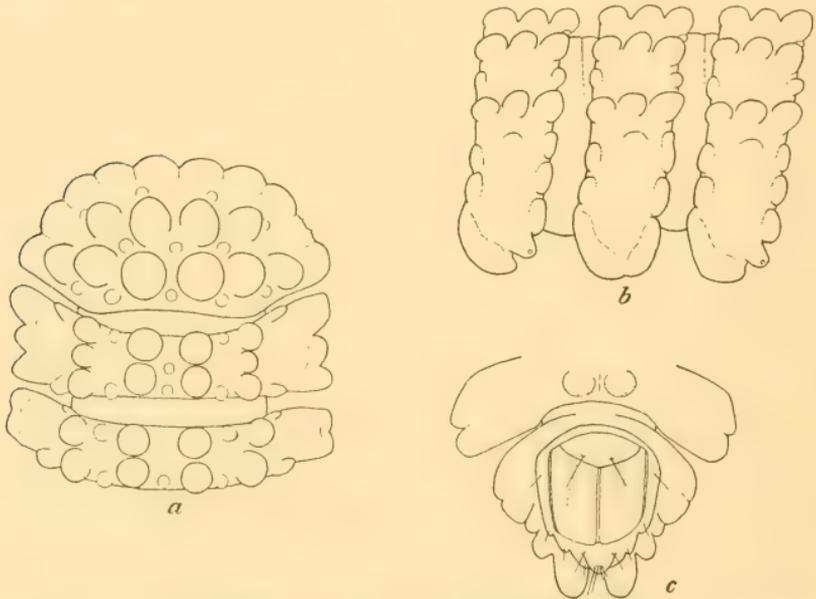


FIG. 30.—*Dilophops bullatus*. *a*, first 3 segments, dorsal view; *b*, segments 13 to 15, oblique lateral view; *c*, last 3 segments, anal valves and scale, ventral view.

First segment very strongly convex, completely covering the head from above; the narrow horizontal margin slightly higher than the margin of the keels of the second segment, with 10 marginal scallops; surface almost entirely occupied by two transverse rows of very large and high tubercles, four tubercles in the anterior and six in the posterior row; in addition, there are a few small granules arranged in three transverse rows with the rows separated by the rows of larger tubercles. Segments 1, 2, and 3 are shown in figure 30, *a*.

Ensuing segments with four longitudinal rows of large tubercles which are considerably smaller than the tubercles of the first segment. On segment 2 there are three tubercles in each outer row and two

tubercles in each inner row, whereas on segments 3 and 4 there are but two tubercles in any row, and on the segments following these there are three tubercles in each row. One or two small granules are present between each pair of rows of large tubercles.

Second segment with the lateral margin of each keel 3-lobed and over half again as long as the margin of the keels of segment 3 or 4. Nonporiferous segments, from the third to the nineteenth inclusive, with the outer margin of the keels weakly bilobed, the anterior lobe usually the largest except on segments 3 and 4, where the lobes are equal. Poriferous segments with two lobes in addition to the poriferous tubercle, which separates the two lobes and projects from near the posterior corner of the keel, the posterior lobe small and more nearly on the posterior margin of the keel than on the lateral margin. Segments 13, 14, and 15 are shown in figure 30, *b*. Pores present on segments 5, 7, 9, 10, 12, 13, 15, and 16.

Nineteenth segment considerably longer than those preceding it, completely concealing the last segment from above. Surface with the large tubercles of the inner rows almost completely coalesced to form two high ridges, in each of which the last tubercle is produced far behind the posterior margin; each outer row of tubercles reduced in size but not coalesced, the last tubercle in each row projecting slightly behind the margin; between this tubercle and the lateral keel is a small granule also projecting beyond the margin. Posterior corner of the lateral keel on each side reaching about half way to the apex of the produced median ridge. Ventral view of segments 18, 19, 20, anal valves and scale are shown in figure 30, *c*.

Last segment small and completely hidden from above by the penultimate segment; posterior margin with three small setiferous lobes on each side; under the apex there is a large setiferous cone almost obscuring the two apical lobes.

Anal valves lacking definitely raised margins; median portion of each valve somewhat depressed longitudinally, on each side of which the surface is slightly convex.

Preanal scale subtriangular, with the customary two setae.

Sterna very narrowly separating the legs.

Third segment of the females very short behind the second pair of legs and slightly more elevated than the fourth segment but without a separate, definitely delimited crest.

#### **DILOPHOPS BULLATUS, n. sp.**

##### **Plate 4, fig. 4**

A single female (type) was collected from beneath a log an eighth of a mile from the beach at Bayeux, Haiti, July 15, 1927, by H. F.

Loomis. A mature female and one with 19 segments were collected on Morne Pilboreau, March 21, 1930, by O. F. Cook. A female was collected under a rock with specimens of *Psochodesmus granulofrons* (Chamberlin) on one of the grassy hills south of Basse Terre, St. Kitts, January 23, 1932.

*Description*.—Length 4.5 mm, width .7 mm.

Living colors recorded as dirty white throughout.

In addition to the characters given in the generic description the following features are of value.

On the first segment in front of each large tubercle of the anterior series there is a small, rounded granule or tubercle, and a similar granule is located just behind each interval between the tubercles of both rows; thus there are three granules behind the anterior row and five behind the posterior row.

On the ensuing segments there usually is a small granule on the anterior and posterior border between the outer and inner row of tubercles on each side, and another lower, less conspicuous granule laterad of the median tubercle of the outer row. On the median line of these segments there is a small granule close to the posterior margin, and on segment 2 there is also another half way to the anterior margin. These segments also with two low, transverse prominences on the anterior and posterior margin between the outer row of large tubercles and the keel, those on the posterior margin projecting farther beyond the margin than those in front.

*Type*.—U.S.N.M. no. 1107.

## Family STYLODESMIDAE

### **BOTRYDESMUS**, n. gen.

*Type*.—*Botrydesmus lutosus*, n. sp.

*Diagnosis*.—This genus is rather closely related to the African *Napodesmus* Cook but is smaller and does not have the penultimate segment produced and hiding the last segment from above; and probably the body is much more convex.

*Description*.—Body slender, very convex; composed of head and 19 segments, of which the last is not obscured from above by the penultimate segment; keels low on the sides of the body, descending almost to the level of the legs (fig. 31, a); dorsal surface incrustated with dirt; pore formula normal.

Head with the vertex slightly elevated above the front from a point between the bases of the antennae, the surface coarsely granular, depressed at middle.

First segment with the produced anterior margin divided into four large, scalloped, widely separated lobes, the two middle ones most widely separated and the anterior margin of each divided into three scallops, the lateral lobes each with two scallops on the anterior margin. Disk with 10 prominent conic tubercles. The dorsal surface and all the margins are incrustated with dirt (fig. 31, *b*).

Second segment with four narrow longitudinal ridges, the apex of each being divided into three sections; all margins of the segment

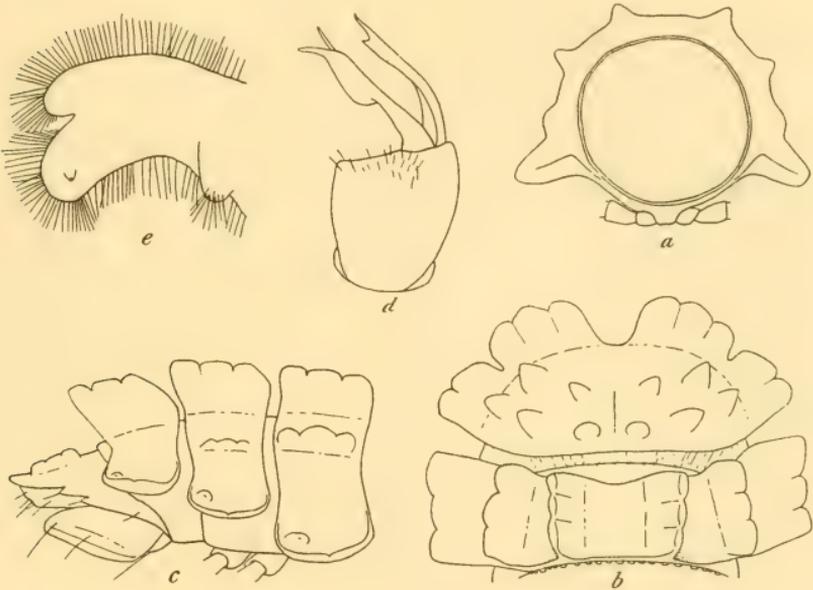


FIG. 31.—*Botrydesmus lutosus*. *a*, segment from near middle of body, end view; *b*, first 2 segments, dorsal view; *c*, last 4 segments and valves, lateral view; *d*, gonopod, lateral view; *e*, keel of segment 7 with coating of dirt removed, dorsal view.

elevated, thin, especially on the keels; lateral margin of the keels 3-lobed.

Ensuing segments with the dorsal surface and raised margins as on the second segment; the keels all 2-lobed; the actual surface sculpturing of the segments is obliterated by the very general incrustation of dirt. As the posterior end of the body is approached, the two median ridges increase in height and each lateral ridge decreases until on the penultimate segment the lateral ridges are not evident but the dorsal ones are very high, though not greatly produced backward (fig. 31, *c*).

Last segment fully exposed from above; the dorsum with two ridges; the posterior margin widely rounded at middle and with two lateral lobes, of which the lowest is the largest.

Anal valves slightly convex, with rather broad, low margins; surface sparsely and minutely hispid.

Preanal scale triangular, the surface also minutely hispid.

Gonopods as shown in figure 31, *d*.

Sterna narrow and similar in the sexes.

Third male legs with the middle joints slightly more swollen than those of the adjacent legs.

The incrustation of dirt on the dorsum is removed with difficulty, but when this is accomplished, the surface of the segment is shown to be strongly shining and with a faintly impressed median line present. The dorsal ridges in reality are each seen to be composed of three separate tubercles tipped with numerous fine setae; and the raised margins of the segments are formed of closely placed hairs which catch and hold dirt; these hairs are longest on the lateral keels (fig. 31, *e*). The tubercles of segment 1 are hispid at the apex, and the margins of the anterior lobes have a continuous series of long hairs similar to the margins of the keels of the ensuing segments. Pores opening from tiny conic prominences on the posterior lobe of the keels; this lobe is longer and broader than the anterior lobe; the posterior margin of the keel is deeply emarginate, and there is a lobe or tubercle on the posterior margin of the dorsum at the base of each keel.

#### BOTRYDESMUS LUTOSUS, n. sp.

A single male and over a score of females were found on the under side of a log in a clearing of the Arena Forest, Trinidad, February 16, 1932.

*Description*.—Length from 4 to 4.5 mm, width from .5 to .6 mm.

The living animals were buff-colored, the color being derived from the incrustation of earth rather than from any pigment in the body, which probably was pure white as in the cleaned alcoholic specimens.

Other characters given in the generic description.

*Type*.—U.S.N.M. no. 1108.

#### Family COMODESMIDAE

##### INODESMUS Cook

*Lasiodesmus* Silvestri, Bull. Amer. Mus. Nat. Hist., vol. 24, pp. 575, 576, 1908.

## INODESMUS PEDUNCULARIS, n. sp.

Plate 4, figs. 5 and 6

Over a score of female specimens were found on the under side of a log near Paramaribo, Dutch Guiana, March 1, 1932.

*Description*.—Length 7 mm, width .6 mm.

Living animals white and remaining so in alcohol.

Head exposed from above; densely beset with short hairs to the clypeal region; vertex with a median furrow; front crossed by a deep transverse furrow just below the antennal sockets; clypeal region elevated, smooth, with four long setae near base and about eight others along the margin; antennae separated by a distance equal to the diameter of one of the sockets.

First segment narrower than the head or ensuing segments, oval in shape.

Ensuing segments without any definite projecting lateral carinae, these being indicated by rather prominent shoulders on the anterior segments which become less obvious toward the back end of the body. Dorsal surface of the segments finely granular and beset with long, erect, but flexuous hairs.

Second segment extending farther ventrad than any other segment; the sides in front produced forward and covering the posterior lateral margin of segment 1. There is a definitely produced, rounded prominence at the posterior corner, opposite the lateral limit of segment 3.

Segment 5 with a definitely pedunculate pore on each side close to the anterior margin of the subsegment. On the other segments the pores are on smaller peduncles and are near the middle of the segments.

Last segment with a deflexed mucro surpassing the valves except when they are open.

Other characters given by Silvestri in the generic description of *Lasiodesmus* are exhibited by this animal.

*Type*.—U.S.N.M. no. 1110.

After comparing the present species, from a generic standpoint, with Silvestri's description of *Lasiodesmus* and with the brief characterization of *Inodesmus* Cook,<sup>9</sup> there appears to be no reason for maintaining Silvestri's genus. Chamberlin's assumption that *Lasiodesmus* belongs to the Strongylosomidae<sup>10</sup> is erroneous. The question of the distinctness of *Inodesmus jamaicensis* Cook and *I. caraibicus* (Silvestri) cannot be decided until comparison is made of the types or of specimens undoubtedly similar to the types.

<sup>9</sup> Brandtia, p. 25, 1896.

<sup>10</sup> Bull. Mus. Comp. Zool., vol. 62, p. 246, 1918.

From the descriptions of *I. jamaicensis* and *I. caraibicus* the following inferences are possible: *I. peduncularis* differs from both in having stalked pores, the first of which is adjacent to the front margin

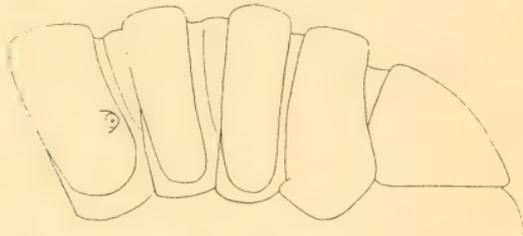


FIG. 32.—*Inodesmus peduncularis*. First 5 segments, lateral view.

of segment 5; it differs further from *I. caraibicus*, as shown in Silvestri's illustration, in the shape of the second segment, which overlaps the posterior-lateral part of the first segment and which also has a produced lobe or tubercle on the posterior angle (fig. 32).

#### Family CYRTODESMIDAE

#### CYLIOCYRTUS OCREATUS, n. sp.

Plate 3, fig. 7

About 15 specimens were collected in the Maracas Valley and the Arena Forest, Trinidad, February 13, 1932.

*Diagnosis*.—Apparently differing from *C. asper* (Peters) in having the first segment entirely concealed from the side by the expanded sides of segment 2; and there are no large tubercles on the dorsum of the segments as shown in Cook's drawing.<sup>11</sup> It is possible that the radiating lines seen on the lateral lobes of segment 2 in this species also are present in *C. asper*, in which case they are a generic character; otherwise they constitute a specific difference.

*Description*.—Length 10 mm, width 2 mm.

Living animals dull black; the anterior subsegments black posteriorly, white anteriorly, the dividing line very definite, biarcuate. Head black to between the antennae, which, with the anterior part of the head, are white. Legs, anal valves, and preanal scale also white.

Head with the vertex eroded-granular, not hispid; two ridges above the antennae and most prominent near them; vertex and front joined at the same level; antennae strongly geniculate at the fourth joint (fig. 33, a).

<sup>11</sup> Proc. U.S. Nat. Mus., vol. 21, pp. 451-468, 1898.

First segment semicircular or somewhat crescentic; with the front margin transverse and slightly emarginate, the median third low and simple, the outer third on each side occupied by three elevated lobes, the outer of which is twice as broad as the two subequal inner ones combined; disk broadly depressed along the middle, finely erose-granular and hispid, each side somewhat inflated and coarsely granular, erose, and hispid but with some of the setae longer than those on the middle of the disk.

Second segment completely concealing the first segment from the side; the median portion of the dorsum depressed, the sides somewhat inflated; sculpturing of the dorsum similar to that of segment 1; expanded lateral lobes with the surface coarsely granular-erose, hispid, the granulations separated into definite triangular sections by de-

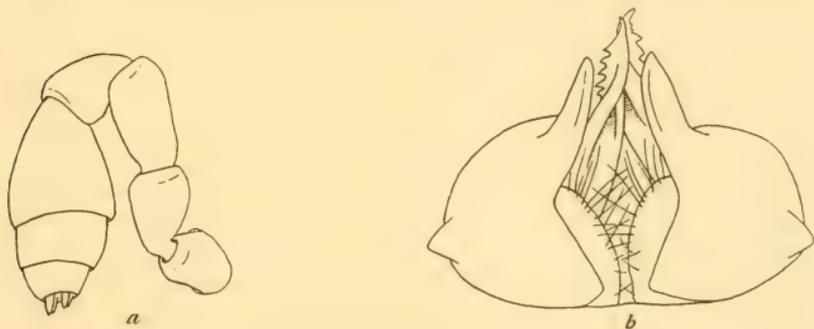


FIG. 33.—*Cyliocyrtus ocreatus*. a, antenna; b, gonopods.

pressed lines radiating from a central point of the lobe and extending to the raised rim of the anterior and lateral margins of the lobe and terminating in slight incisions of the rim, which give it a faintly scalloped appearance.

Ensuing segments coarsely granular-erose and strongly hispid with short and long setae intermixed, the entire surface usually with a moderate incrustation of dirt which hides the pores. There are no large tubercles present on the dorsum as shown in Cook's illustration of *C. asper*. The outer margin of the keels, following the second segment, is simple and sharply rounded, becoming more broadly rounded on the middle segments, where it is indistinctly 2-lobed, and on the posterior segments it finally becomes indistinctly 3-lobed. On the anterior subsegments the dark posterior portion is uniformly pitted, the surface including the pits very finely granulated; white anterior portion of the subsegment minutely honeycombed.

Last segment broadly rounded behind, the median third of the margin simple, each lateral third occupied by two lobes.

Gonopods with each enlarged basal joint continued at the apex of the inner side into a long, erect lobe nearly equaling the tip of the inner joint and guarding it on the outer side. Inner joint coarsely serrate along its outer margin, the tip acute (fig. 33, *b*).

Legs similar in both sexes. Males with the coxae of the sixth legs moderately separated; those of the seventh legs twice as widely separated, the sternum flat; legs following the gonopods moderately separated, the sternum bearing two round tubercles.

*Type*.—U.S.N.M. no. 1109.

Although the following species of millipeds were not collected by the expedition of 1932 it seems advisable to call attention to them here, inasmuch as they were not mentioned by Chamberlin in his list of the diplopods of the West Indies.<sup>22</sup>

#### **SPIROBOLUS BAHAMENSIS** Bollman

*Spirobolus bahamensis* Bollman, U.S. Nat. Mus. Bull. 46, p. 192, 1893.

Known only from the original collection from the island of San Salvador. This species may belong to the genus *Arctobolus*, as the number of clypeal foveolae apparently exclude it from the genus *Rhinocricus*. *Arctobolus* is common throughout the eastern United States, but no species are known from any of the Bahama or West Indian Islands.

#### **RHINOCRICUS MODESTIOR** Silvestri

*Rhinocricus modestior* Silvestri, Bull. Amer. Mus. Nat. Hist., vol. 24, p. 570, 1908.

Known only from Puerto Rico.

#### **RHINOCRICUS SERPENTINUS** Pocock

*Rhinocricus serpentinus* Pocock, Journ. Linn. Soc. London, vol. 24, pp. 501, 502, 1894.

Known only from St. Lucia.

#### **INODESMUS JAMAICENSIS** Cook

*Inodesmus jamaicensis* Cook, Brandtia, p. 25, 1896.

Known only from the original collection from Jamaica.

<sup>22</sup> Bull. Mus. Comp. Zool., vol. 62, no. 5, 1918.

## EXPLANATION OF PLATES

## PLATE 1

- FIG. 1. *Lophoproctus comans*, female, dorsal view.  $\times 13$ .  
FIG. 2. *Glomeridesmus trinidadensis*, male, latero-ventral view.  $\times 10$ .  
FIG. 3. *Siphonocybe harti*, female, dorsal view.  $\times 5$ .  
FIG. 4. *Amphelictogon bidens*, male, dorsal view.  $\times 5$ .  
FIG. 5. *Belonodesmus thaxteri*, head and first six segments of male, dorsal view.  
 $\times 10$ .  
FIG. 6. *Aphelidesmus divergens*, male, dorsal view.  $\times 4$ .  
FIG. 7. *Nanorrhacus luciae*, male, dorsal view.  $\times 4$ .

## PLATE 2

- FIG. 1. *Azygobolus tumidus*, male, lateral view.  $\times 7$ .  
FIG. 2. *Azygobolus tumidus*, another male, ventral view.  $\times 7$ .  
FIG. 3. *Priodesmus acus*, 19-segmented female, dorsal view.  $\times 7\frac{1}{2}$ .  
FIG. 4. *Aetheandra multiplex*, male, dorsal view.  $\times 10$ .  
FIG. 5. *Aetheandra multiplex*, female, dorsal view.  $\times 13$ .  
FIG. 6. *Chilaphrodesmus rubellus*, female, dorsal view.  $\times 10$ .

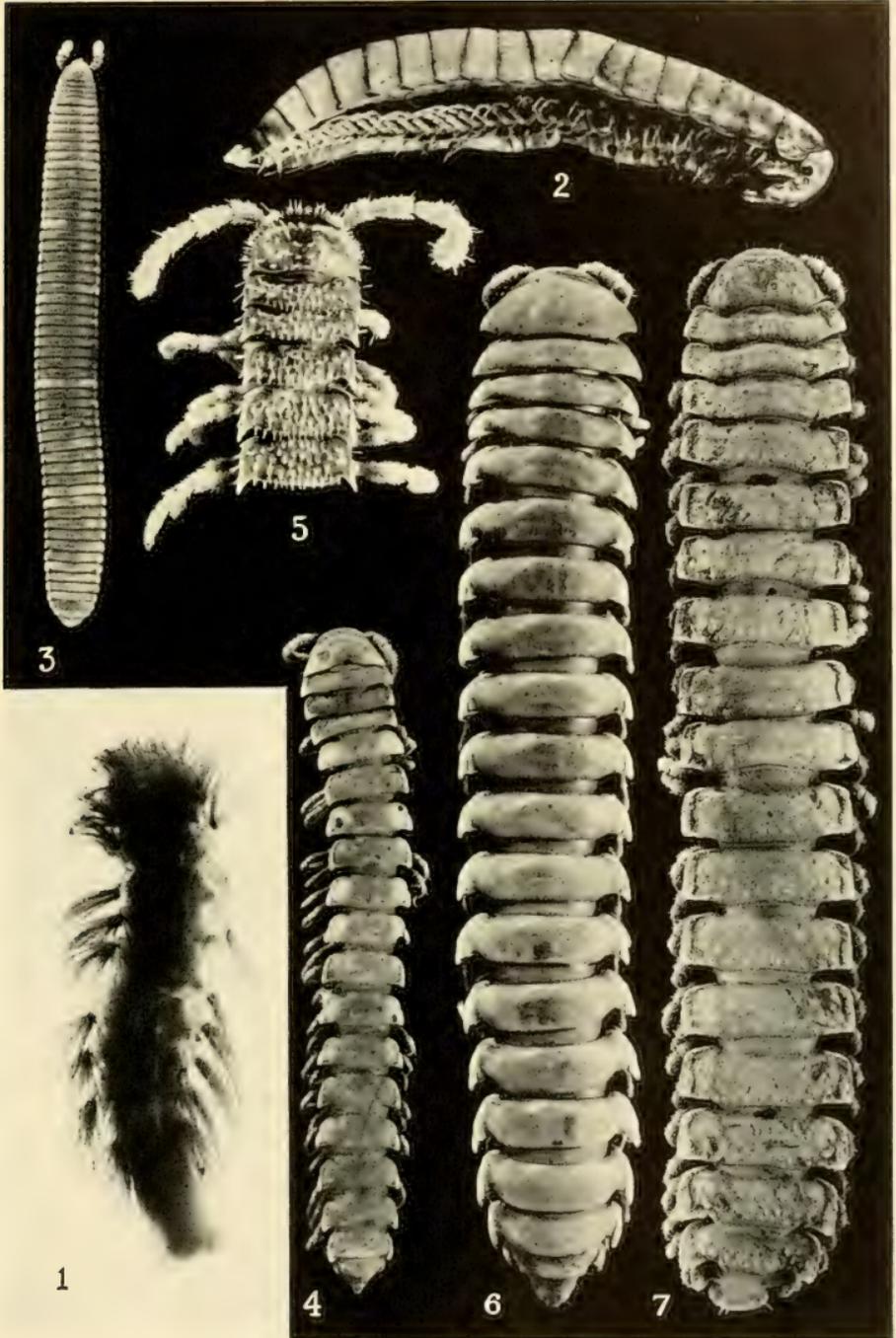
## PLATE 3

- FIG. 1. *Docodesmus haitiensis*, female, dorsal view.  $\times 7\frac{1}{2}$ .  
FIG. 2. *Docodesmus haitiensis*, male, ventral view.  $\times 7\frac{1}{2}$ .  
FIG. 3. *Iomoides hispidus*, female, dorsal view.  $\times 10$ .  
FIG. 4. *Iomoides hispidus*, male, ventral view.  $\times 10$ .  
FIG. 5. *Iomoides glabra*, female, dorsal view.  $\times 10$ .  
FIG. 6. *Gasatomus emersoni*, male, dorsal view.  $\times 13$ .  
FIG. 7. *Cylioxyrtus ocreatus*, loosely curled female, lateral view.  $\times 13$ .

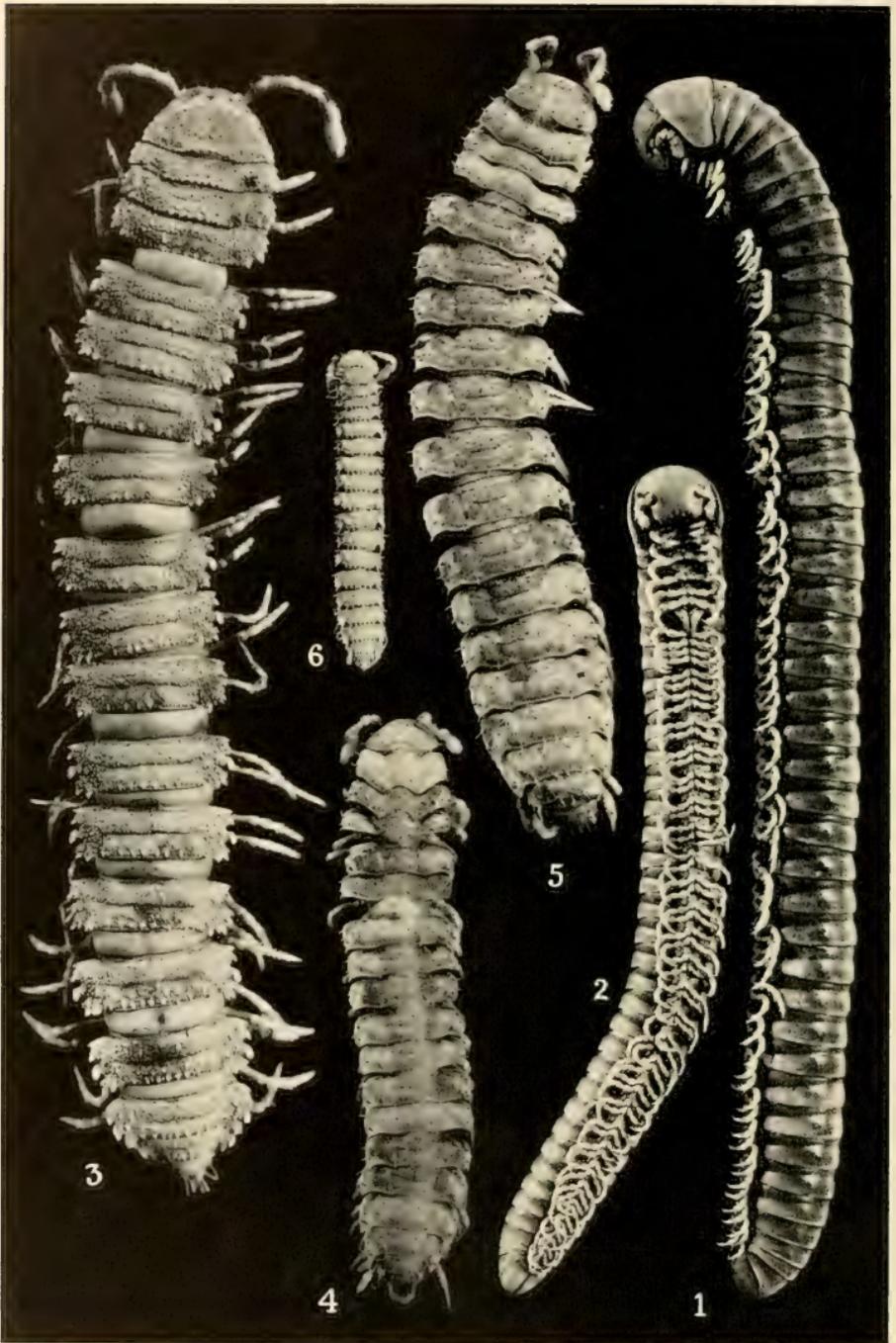
## PLATE 4

- FIG. 1. *Docodesmus sculpturatus*, male, dorsal view.  $\times 13$ .  
FIG. 2. *Docodesmus trinidadensis*, female, dorsal view.  $\times 13$ .  
FIG. 3. *Docodesmus robustus*, male, dorsal view.  $\times 13$ .  
FIG. 4. *Dilophops bullatus*, female, dorsal view.  $\times 13$ .  
FIG. 5. *Inodesmus peduncularis*, male, dorsal view.  $\times 13$ .  
FIG. 6. *Inodesmus peduncularis*, female, lateral view.  $\times 13$ .



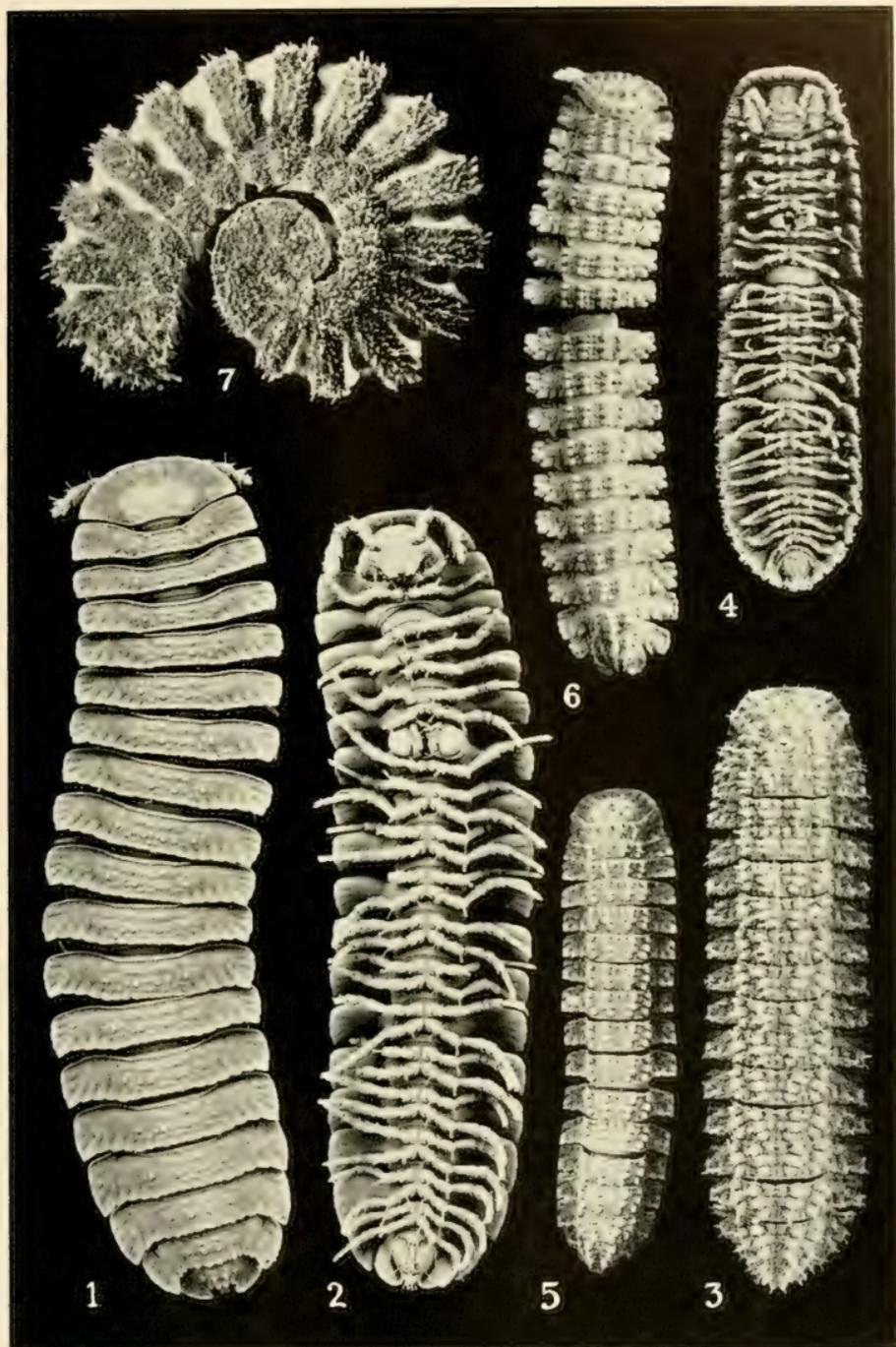


MILLIPEDS COLLECTED BY THE ALLISON V. ARMOUR EXPEDITION  
(For explanation, see page 69.)



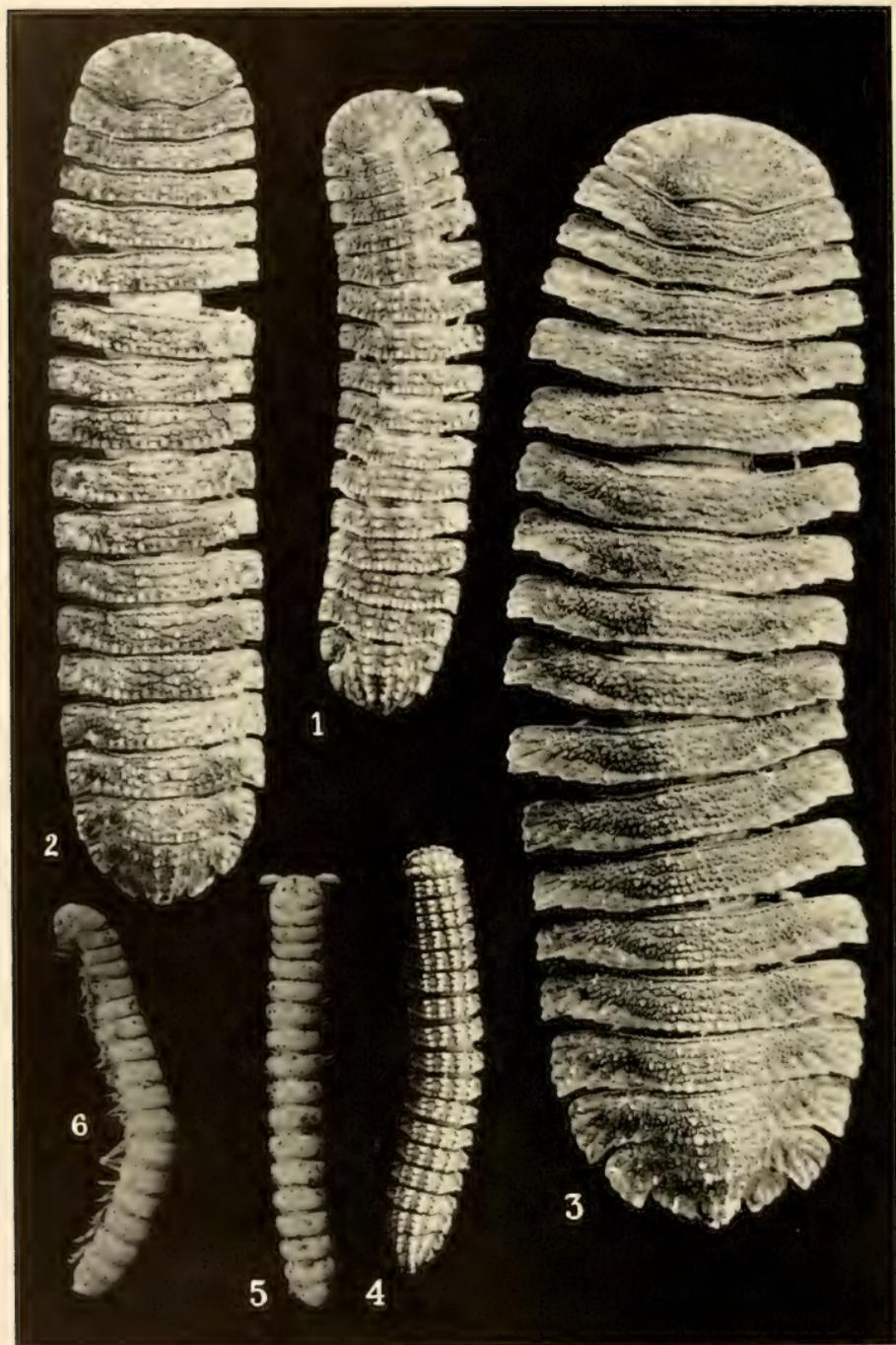
MILLIPEDS COLLECTED BY THE ALLISON V. ARMOUR EXPEDITION

(For explanation, see page 60.)



MILLIPEDS COLLECTED BY THE ALLISON V. ARMOUR EXPEDITION

(For explanation, see page 69.)



MILLIPEDS COLLECTED BY THE ALLISON V. ARMOUR EXPEDITION  
(For explanation, see page 69.)

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## Roebling Fund

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# WORLD WEATHER AND SOLAR ACTIVITY

BY

H. HELM CLAYTON



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### WORLD WEATHER AND SOLAR ACTIVITY

BY H. HELM CLAYTON

#### INTRODUCTION

This paper is the sixth of a series by the author giving the results of investigations of the relation of solar activity to atmospheric changes. The earlier ones were published as Smithsonian Miscellaneous Collections, vol. 68, no. 3; vol. 71, no. 3; vol. 77, no. 6; vol. 78, no. 4; and vol. 82, no. 7. The author wishes to express his appreciation for the continuance of the encouragement in these researches by Dr. C. G. Abbot and Mr. John A. Roebing. He also wishes to acknowledge the help of Miss M. I. Robinson in the protracted statistical work that has been necessary.

The features especially stressed in this paper are:

1. The world-wide correlations of atmospheric changes, as indicated by a similarity in these changes in both the Northern and Southern Hemispheres and in widely separated continents and oceans. In some cases the changes are directly similar, and in others the changes are directly opposite—that is, when one increases the other decreases.

2. A relationship is found between atmospheric changes and sun-spot activity, and an even closer relationship with changes in solar radiation.

3. Centers of action in the atmosphere are found to shift position under the influence of changes in the intensity of solar activity. This is a fact of great importance to be considered in correlating the weather between distant places, in studying the question of periodicity in the weather, and in tracing atmospheric movements of a wavelike nature.

#### WORLD-WIDE CORRELATION OF WEATHER CHANGES

In figure 1 a comparison is made between the mean annual rainfall in the interior of the United States and the height of the Parana River at Rosario, Argentina. By rainfall is meant the actual rainfall plus its equivalent in other forms of precipitation. The area used is the interior basin of the United States between the Allegheny and Rocky Mountains. The data were obtained from the Monthly Weather Review, and the mean annual values of the rainfall were computed for

each year from 1900 to 1932 from the mean rainfall given for each of the following 10 sections:

Ohio Valley and Tennessee, Lower Lake Region, Upper Lake Region. Upper Mississippi Valley, West Gulf States, North Dakota, Missouri Valley, Northern Slope, Middle Slope, Southern Slope. The values are given in inches in column (1), table I.

TABLE I.—*Fundamental Data*

| Year      | (1)   | (2)   | (3) | (4)  | (5)  | (6)  | (7)  |
|-----------|-------|-------|-----|------|------|------|------|
| 1889..... | ....  | ....  | ..  | 0.5  | 0.1  | 0.0  | -0.6 |
| 1890..... | ....  | ....  | ..  | 0.1  | -0.5 | -0.1 | -1.0 |
| 1891..... | ....  | ....  | ..  | -0.2 | 0.0  | 0.2  | 0.2  |
| 1892..... | ....  | ....  | ..  | -0.5 | -0.6 | -0.6 | -0.7 |
| 1893..... | ....  | ....  | ..  | -0.3 | -0.4 | -0.3 | -0.7 |
| 1894..... | ....  | ....  | ..  | -0.1 | -0.4 | -0.3 | -0.6 |
| 1895..... | ....  | ....  | ..  | -0.1 | -0.1 | -0.3 | -0.2 |
| 1896..... | ....  | ....  | ..  | -0.2 | 0.2  | 0.1  | 0.3  |
| 1897..... | ....  | ....  | ..  | 0.1  | -0.4 | -0.2 | -0.1 |
| 1898..... | ....  | ....  | ..  | -0.4 | -0.6 | -0.6 | -0.9 |
| 1899..... | ....  | ....  | ..  | -0.1 | 0.1  | 0.2  | 0.4  |
| 1900..... | 29.82 | 4.527 | ..  | -0.1 | 0.3  | 0.2  | 0.5  |
| 1901..... | 24.95 | 2.998 | ..  | -0.2 | 0.2  | 0.1  | 0.4  |
| 1902..... | 29.35 | 3.536 | ..  | 0.0  | -0.4 | 0.2  | 1.0  |
| 1903..... | 29.04 | 3.268 | ..  | 0.2  | -0.5 | -0.2 | 0.0  |
| 1904..... | 26.21 | 3.807 | ..  | 0.1  | 0.0  | 0.3  | 0.2  |
| 1905..... | 31.82 | 5.611 | ..  | 0.2  | -0.3 | 0.4  | 1.0  |
| 1906..... | 29.21 | 3.621 | ..  | -0.2 | 0.0  | 0.0  | 0.1  |
| 1907..... | 27.21 | 3.634 | ..  | -0.4 | -0.6 | 0.0  | 0.0  |
| 1908..... | 28.58 | 4.249 | 33  | -0.1 | -0.4 | 0.0  | 0.1  |
| 1909..... | 28.85 | 2.924 | 40  | -0.2 | -0.4 | -0.2 | -0.2 |
| 1910..... | 22.73 | 2.837 | 75  | -0.2 | 0.0  | -0.4 | -0.6 |
| 1911..... | 28.33 | 3.128 | 25  | 0.3  | 0.4  | 0.4  | 0.5  |
| 1912..... | 27.37 | 4.382 | 12  | 0.5  | 0.3  | 0.4  | 0.7  |
| 1913..... | 28.20 | 3.664 | 27  | 0.4  | 0.2  | 0.5  | 0.7  |
| 1914..... | 27.64 | 3.836 | 11  | 0.6  | 0.7  | 0.8  | 1.4  |
| 1915..... | 31.62 | 3.717 | 26  | -0.4 | 0.5  | 0.3  | 0.5  |
| 1916..... | 26.81 | 2.397 | 60  | -0.4 | -0.3 | -0.4 | -0.6 |
| 1917..... | 22.90 | 2.255 | 75  | -0.1 | -0.3 | -0.3 | -0.5 |
| 1918..... | 26.68 | 3.018 | 28  | -0.2 | 0.4  | 0.6  | 0.5  |
| 1919..... | 29.69 | 4.189 | 13  | 0.0  | 0.6  | 0.5  | 0.9  |
| 1920..... | 28.65 | 4.562 | 54  | 0.0  | 0.3  | 0.1  | -0.2 |
| 1921..... | 28.12 | 4.387 | 63  | 0.4  | 0.1  | 0.0  | -0.2 |
| 1922..... | 27.46 | 4.465 | 21  | 0.4  | 0.3  | -0.1 | -0.2 |
| 1923..... | 30.17 | 4.458 | 22  | 0.7  | 0.5  | 0.1  | 0.1  |
| 1924..... | 25.18 | 2.967 | 27  | 0.4  | 0.3  | 0.2  | 0.0  |
| 1925..... | 25.15 | 2.396 | 24  | 0.5  | 0.1  | 0.3  | 0.0  |
| 1926..... | 29.36 | 4.058 | 21  | 0.4  | 0.1  | 0.4  | 0.4  |
| 1927..... | 30.38 | 3.141 | 34  | 0.1  | 0.0  | 0.2  | 0.1  |
| 1928..... | 28.84 | 3.819 | 13  | 0.2  | 0.2  | 0.0  | 0.2  |
| 1929..... | 29.01 | 4.494 | 15  | 0.1  | 0.0  | 0.2  | 0.0  |
| 1930..... | 23.84 | 3.843 | 63  | 0.7  | 0.3  | 0.6  | 0.7  |
| 1931..... | 26.50 | 4.974 | 41  | ..   | ..   | ..   | ..   |
| 1932..... | 28.75 | 5.039 | 21  | ..   | ..   | ..   | ..   |

(1) Average rainfall in inches in interior basin of the United States between the Allegheny and Rocky Mountains.

(2) Average height in meters of the Parana River at Rosario, Argentina.

(3) Percentage of area of Australia above average rainfall.

(4) Departures of annual mean pressure from 42-year normal at Quixeramobim (values preceding 1897 were interpolated from Recife).

(5) Departures of annual mean pressure from 42-year normal at Antananarivo.

(6) Departures of annual mean pressure from 42-year normal at Colombo.

(7) Departures of annual mean pressure from 42-year normal at Darwin, Australia.

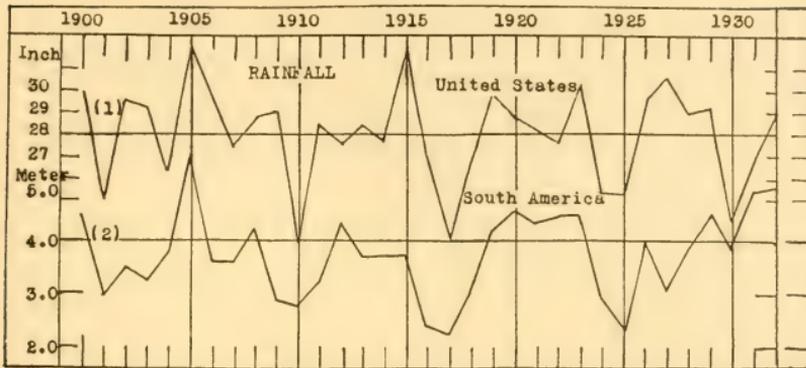


FIG. 1.—(1) Mean annual rainfall between the Allegheny and Rocky Mountains. (2) Mean annual height of the Parana River at Rosario, Argentina.

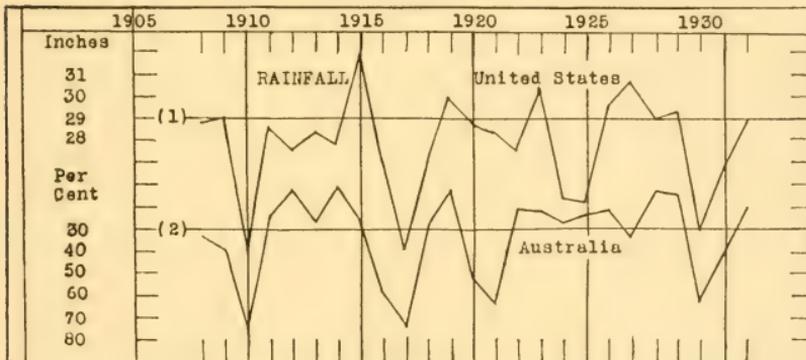


FIG. 2.—(1) Mean annual rainfall between the Allegheny and Rocky Mountains. (2) Percentage of Australia covered by excess of rainfall over normal.

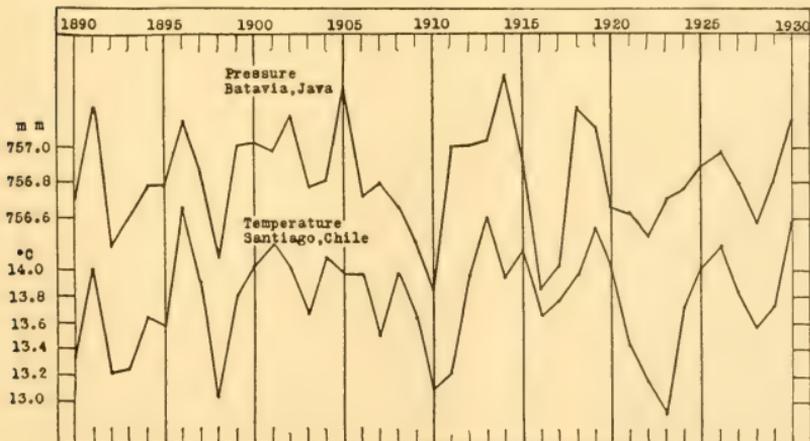


FIG. 3.—Comparison of pressure in the Indian Ocean with temperature in Chile.

The Parana River drains the interior of South America between about  $15^{\circ}$  S. and  $30^{\circ}$  S. The river heights used were those measured at Rosario, Argentina, near the mouth of the river. The mean annual height for each year from 1900 to 1932 is given in column (2) of table 1. The variations of height are believed to form a good index of the variations of rainfall over central South America, because there is no snowfall or ice to retard the flow of water into the river. The correlation between the rainfall of the interior of the United States and the variation in height of the Parana River is found to be  $+ .55 \pm .08$ .

It was shown in a preceding paper<sup>1</sup> that the annual variations of pressure at San Diego are similar to those at Buenos Aires.

In figure 2 a comparison is made between the rainfall of the interior of the United States and the rainfall of Australia. The rainfall of the United States was obtained as previously described. The rainfall of Australia is expressed in percentages of Australia covered by areas of rainfall in excess of the normal. These data were obtained from the Rain Map of Australia, 1931 and 1932, published by the Commonwealth Meteorologist and are given in column (3) of table 1. In this case there is an inverse relationship—that is, when the rainfall in the United States is low, that in Australia is high, and vice versa. For this reason the curve of Australia is inverted, the higher values being plotted downward. The correlation value is  $- .66 \pm .08$ .

In comparing the two sets of curves, it is seen that every marked depression in the rainfall in the interior of the United States was accompanied by low water in the Parana River except in 1930 and was coincident with a marked excess of rainfall in Australia, except in 1924.

In figure 3 is shown a comparison of the annual mean pressures at Batavia in the Indian Ocean with the annual mean temperatures at Santiago, Chile. There is clearly a similarity between them, showing that they tend to oscillate in the same way. The correlation between the two for 64 years, 1866 to 1930, is  $r = .43 \pm .03$ . An even closer relation is found between the pressure in the Indian Ocean as observed at Colombo, Ceylon, and that at Santiago, Chile. The correlation for the 29 years, 1871 to 1902, is  $r = -.68 \pm .08$ , and for the 28 years, 1903 to 1930, it is  $r = -.61 \pm .08$ . In other words, the pressure oscillates oppositely in the two regions except for occasional breaks in the sequence.

Many similar instances have been pointed out by others. Blandford, Teisserenc de Bort, Hildebrandsson, Lockyer, Mossman, Arctowski,

<sup>1</sup> Smithsonian Misc. Coll., vol. 78, no. 4, p. 43, 1926.

Exner, Walker, Groissmayr, Nansen, Mémery, and others have given instances of correlation in weather in widely separated areas even in opposite hemispheres. De Geer finds these widespread correlations as far back as the glacial epoch, and White's researches suggest them even at an earlier period.

It is evident that there is something in common in the weather in widely separated parts of the earth, even in countries on opposite sides of the earth, as is shown in figure 2 in a comparison between the

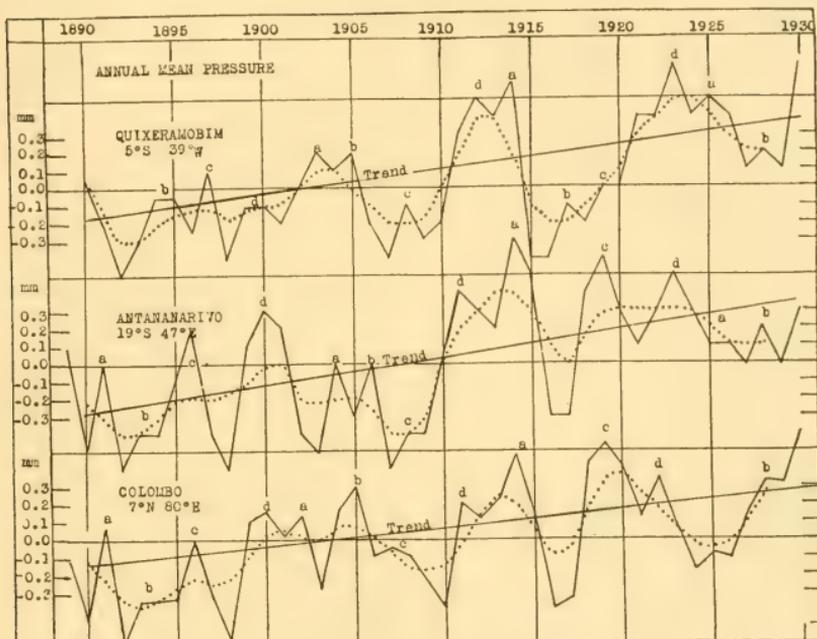


FIG. 4.—Annual means of pressure at widely separated tropical stations and smoothed means of several years, showing similarity of changes.

rainfall in the United States and in Australia. In fact, the weather changes are in some way related to each other over the entire world, as will be more fully seen from what follows.

In figure 4 the annual departures from normal pressure are plotted for three widely separated tropical stations, namely, Quixeramobim, Brazil; Antananarivo, Madagascar; and Colombo, Ceylon. The departures from 42-year normals are given in table 1, columns (4), (5), (6), and (7). The data for Quixeramobim were extended backward to 1889 by comparison with Recife. The oscillations of the annual pressures at these three stations show a similar pattern. More-

over, the general trend of the pressure during the past 50 years has been upward. This is true throughout the equatorial region from northern Brazil to northern Australia. It will be noted that there are maxima every 2 to 4 years, which in the plot are marked a, b, c, d. There are also longer oscillations, which may be brought out by smoothing the curves. Consecutive or overlapping means of 3, 4, and 5 years were tried; then a second smoothing of the means of 3 was tried, so that the formula became  $\frac{1}{3}\Sigma_i^3\Sigma_i^3$ . A second smoothing of the means of 4 was also tried with the formula  $\frac{1}{8}\Sigma_i^4\Sigma_i^2$ . The results

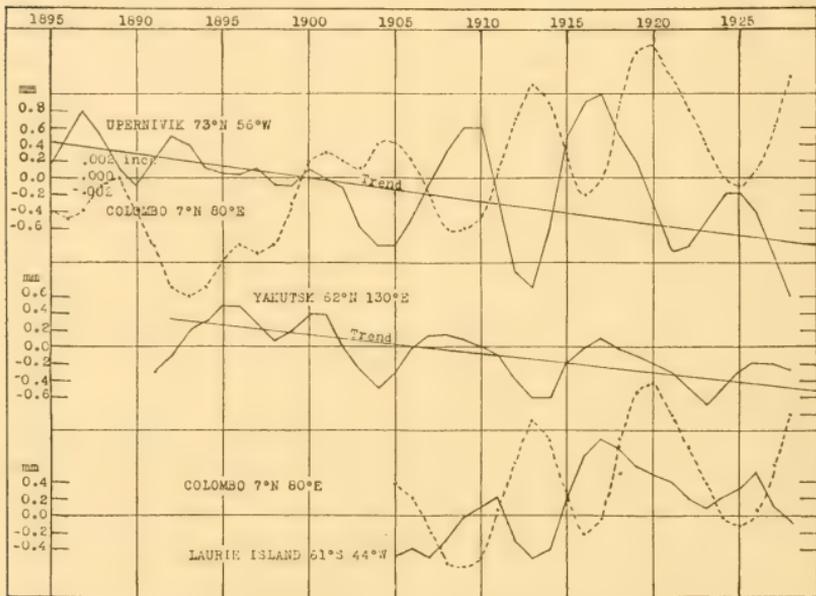


FIG. 5.—Smoothed means of pressure at stations in high latitudes (continuous lines) compared with smoothed means at a tropical station (dotted lines).

of this last formula gave the smoothest curves; but the second means of 3 were more easily obtained, so that the first formula was adopted for the smoothing, although in some cases the first means of 5 were used instead. The dotted curves given in figure 4 are from the second means of 3 (first formula). The data for these curves were obtained from World Weather Records, Smithsonian Miscellaneous Collections, vols. 79 and 90.

In figure 5 the smoothed means for Colombo are compared with similar smoothed annual means of pressure in high latitudes. The pressure oscillations are larger in high latitudes than in the Tropics, so that Colombo is plotted on a more open scale. It is seen that the

longer oscillations of pressure at Colombo are exactly opposite to those at Upernivik in Iceland and at Yakutsk in Siberia, and the trend of the pressure for the past 42 years is opposed. The comparison of Colombo with Laurie Island, the most southern station in the Southern Hemisphere, in the lowest curve in figure 5 shows that the pressure oscillations of long period in high latitudes in the Southern Hemisphere are also opposed to those at Colombo and are similar to those in high latitudes in the Northern Hemisphere. It should be noted that Colombo is only about  $7^{\circ}$  of latitude from the Equator and is within the warmest and most humid area of the earth, whereas Upernivik and Yakutsk are in the coldest regions of the Northern Hemisphere where the vapor content of the atmosphere is small.

This comparison indicates that there are marked changes in the Pole to Equator pressure gradients in the atmosphere and, hence, marked oscillations in the intensity of the atmospheric circulation. To this cause may reasonably be attributed the similarities of rainfall and temperature between such widely separated areas as the United States and South America, the United States and Australia, and the similarity between the pressure in the Indian Ocean and the temperature on the coast of Chile.

The general diminution in the pressure gradient between high and low latitudes during the past 42 years, as shown by the trend of the pressures in high and low latitudes, is indicative of a world-wide amelioration of climate during the same period. It has been pointed out by various research workers that glaciers in high latitudes are slowly retreating, that the waters in the Great Lakes and in other lakes farther west in the United States are receding to lower levels, and that there is an upward trend of the temperature in high latitudes in both hemispheres. This change has probably been in progress during most of the past century. The latest publication on this subject is by Kincer in the *Monthly Weather Review* for September 1933. These various researches indicate that the climate of the earth is on the whole becoming warmer and drier in some long period of solar change, the length of which is not yet known. The change of climate corresponds in character with the long-period oscillations of past epochs pointed out by C. E. P. Brooks, of London, in his book "Climate Through The Ages."

When the departures from normal pressure are plotted on charts, they are seen to be larger in certain regions than in others. The regions of greatest departure have been called centers of action, but they are not fixed in position. This fact is evident from figure 6. This figure gives a comparison of the smoothed annual means of pressure

at Upernivik, Iceland, and Gjesvaer, Norway. From 1885 to 1895 the pressure changes at Gjesvaer were opposed to those at Upernivik, from 1900 to 1924 they were similar, and from 1925 to 1930 they were

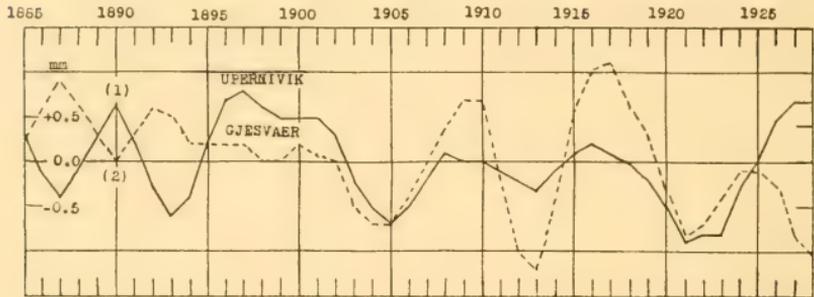


FIG. 6.—(1) Smoothed annual means of pressure at Upernivik, latitude  $73^{\circ}$  N., longitude  $56^{\circ}$  W. (2) Smoothed annual means of pressure at Gjesvaer, latitude  $71^{\circ}$  N., longitude  $25^{\circ}$  E.

again opposed. This difference indicates a shift in position of a center of action, which fact will be considered later in connection with its relation to solar activity.

#### SUN SPOTS AND WEATHER

The world-wide correlation of weather changes suggests some general cause, most probably a change in solar activity. The relation of weather to sun-spot changes has been a subject of investigation for many years by independent research workers. The most recent research is that of Schostakowitsch, a review of whose work appeared in the Bulletin of the American Meteorological Society for March 1933. These various investigations have brought out very clearly that when a mean of several years is taken in the Tropics, the pressure averages lower, the rainfall and cloudiness higher, and the surface temperatures lower near sun-spot maximum than near sun-spot minimum.

In order to illustrate this point, a mean is taken of the annual departures of pressure at Quixeramobim and Antananarivo given in table 1, columns (4) and (5). This mean was corrected for trend and plotted in figure 7 over the inverted sun-spot curve for the interval 1889 to 1930. The pressure curve is more variable than the sun-spot curve and usually shows about four maxima, a, b, c, d, in each sun-spot period. By smoothing out these secondary maxima by overlapping means of 5, the broken curve is obtained which is seen to run

almost exactly parallel with the sun-spot curve. This similarity indicates clearly a relation between the two.

No such parallel relation prevails between the smoothed annual means of pressure in high latitudes and the sun-spot curve. In comparing plots of the two, decade by decade, it is evident that in high latitudes the centers of action in the atmosphere varied in position over wide distances with variations of intensity of solar activity.

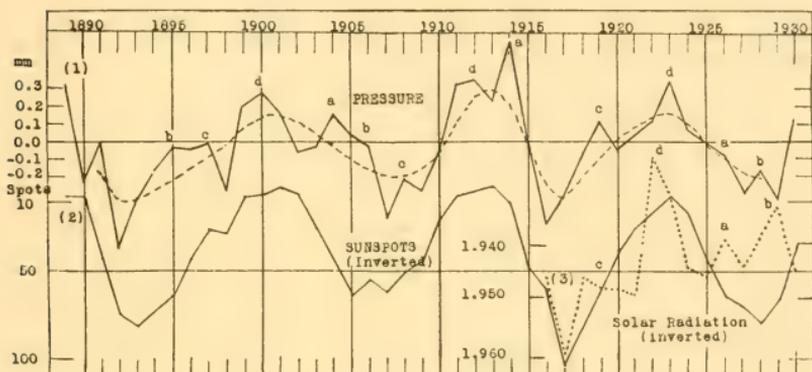


FIG. 7.—Comparison of mean pressures in Tropics with sun spots and solar radiation.

(1) Mean annual pressures at Quixeramobim and Antananarivo, corrected for trend. (2) Mean annual number of sun spots, inverted. (3) Mean annual values of solar radiation, in calories per minute, inverted.

This shifting of centers of action in high latitudes causes discontinuities and changes of phase in the sun-spot period and confuses relations that might otherwise appear.

The relative sun-spot numbers at successive sun-spot maxima differ greatly, as will be seen by the numbers in table 2.

TABLE 2.—Relative Sun-spot Numbers at Different Epochs

| Yearly means |              |           |        | 5-year means |             |            |        |
|--------------|--------------|-----------|--------|--------------|-------------|------------|--------|
| Maxima       |              | Minima    |        | Maxima       |             | Minima     |        |
| Year         | Number       | Year      | Number | Years        | Number      | Years      | Number |
| 1870.....    | <b>139.1</b> | 1867..... | 7.3    | 1868-72...   | <b>92.6</b> | 1865-69... | 33.1   |
| 1883.....    | 63.7         | 1878..... | 3.4    | 1881-85...   | 58.7        | 1876-80... | 13.1   |
| 1893.....    | <b>84.9</b>  | 1889..... | 6.3    | 1891-95...   | <b>67.1</b> | 1887-91... | 11.9   |
| 1905.....    | 63.5         | 1901..... | 2.7    | 1904-8 ...   | 54.0        | 1899-1903. | 10.7   |
| 1917.....    | <b>103.9</b> | 1913..... | 1.4    | 1915-19...   | <b>70.2</b> | 1911-15... | 13.5   |
| 1928.....    | 77.8         | 1923..... | 5.8    | 1926-30...   | 62.5        | 1921-25... | 21.0   |

The highest sun-spot numbers were in 1870, 1893, and 1917, and lesser maxima were observed in 1883, 1905, and 1928. The first

group of maxima are here called periods of high solar activity and the second group, periods of moderate activity. It will be noticed that periods of higher and lesser activity have occurred alternately,

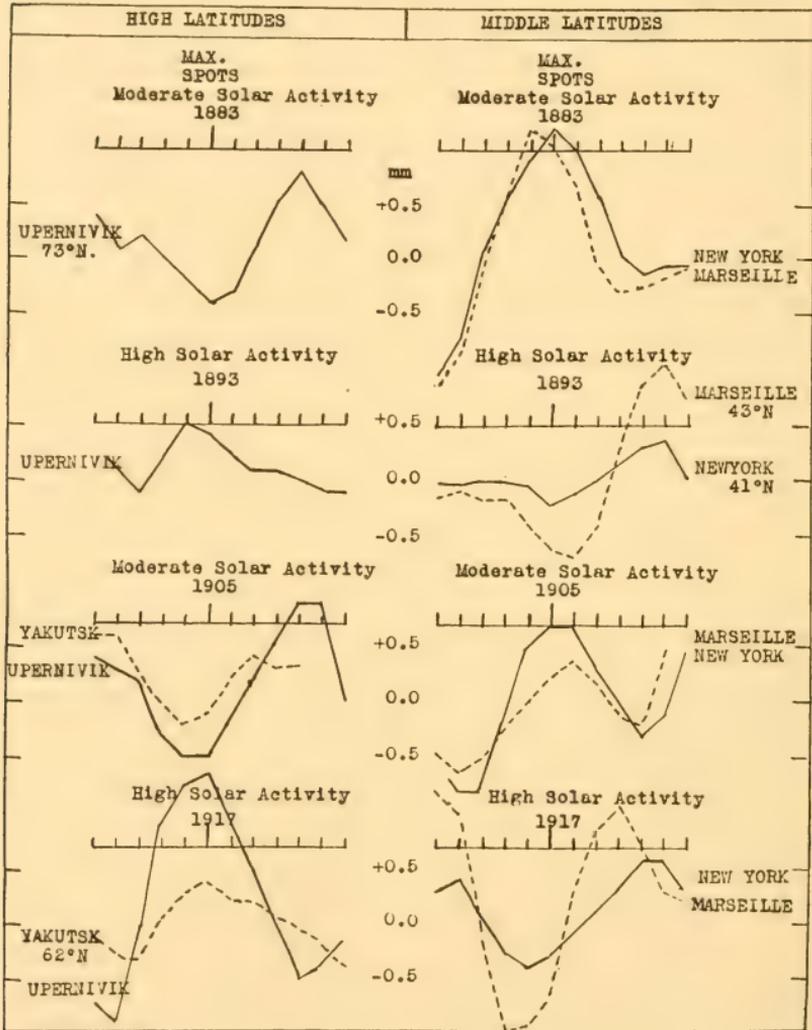


FIG. 8.—Smoothed annual means of pressure during the sun-spot period, Northern Hemisphere.

thus giving rise to a period of 22 to 24 years between similar states of activity. This alternation is found in the records since 1848 but not earlier.

In figure 8 the smoothed annual means of pressure at Upernivik and at Yakutsk have been plotted for successive periods of sun-spot

activity, in so far as observations permit, and are compared with the values observed simultaneously at New York and Marseille. The plots show that in 1883 with moderate solar activity the pressure was low at Upernivik and high at New York and Marseille. In 1893 with increased solar activity the pressure was high at Upernivik and low at New York and Marseille. In 1905 with moderate solar activity the pressure was low at Upernivik and also at Yakutsk and high at New York and Marseille. With greatly increased solar activity in

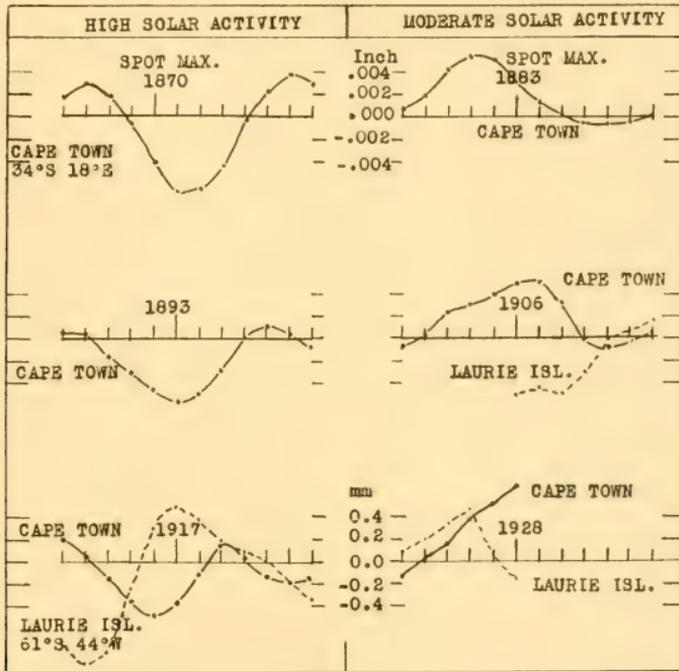


FIG. 9.—Smoothed annual means of pressure during the sun-spot period, Southern Hemisphere.

1917 the pressure was very high at Upernivik and low at New York and Marseille. These diagrams indicate that with high solar activity the centers of increased atmospheric pressure move northward to near 70° latitude, whereas with moderate solar activity they are found near 40° latitude. The same poleward oscillation of a center of increased pressure in the Southern Hemisphere with increased solar activity is indicated in figure 9. In this diagram the smoothed annual means of pressure at Cape Town are shown with high solar activity on one side of the diagram and with moderate solar activity on the

other side. During periods of high maxima of solar activity the pressure is low at Cape Town, whereas with moderate maxima of solar activity the pressure is high at Cape Town, just as it is at New York and Marseille in the Northern Hemisphere. At Laurie Island,  $61^{\circ}$  S. shown by the broken line, the pressure was high with high solar activity in 1917 and low with moderate solar activity in 1905-6 and 1928, just as it was at Upernivik and Yakutsk in high latitudes in the Northern Hemisphere. The observations at Laurie Island now cover two sun-spot periods, and great credit is due the Argentine Government for maintaining this station with great difficulty and with much expense in this high southern latitude. It is hoped that in the coming years other nations may find it possible to maintain a net of stations in high southern latitudes.

An effort was made to map the positions of the centers of action at different sun-spot epochs. For this purpose the data published in World Weather Records (Smithsonian Misc. Coll., vols. 79 and 90) were used. These volumes contain the most complete set of data available, but for vast areas of the world there are still no observations, and for this reason any map of world conditions must be incomplete.

Five-year means of pressure, with the central year the epoch of maximum sun spots, were obtained for all available stations and plotted on a world chart. Lines of equal departure from normal were drawn for each 0.3 mm in the Tropics and for larger intervals in higher latitudes. The areas where the pressure was above normal are shaded. These areas for three epochs of maximum sun spots are shown in figure 10. The epochs are arranged in the order of intensity of solar activity as indicated by the number of spots, 1915-19, 1891-95, 1904-8. (See table 2.) The data were insufficient for earlier epochs.

During the marked maximum of spots 1915-19 the pressures are shown very high in high latitudes in both the Northern and Southern Hemispheres, with centers of greatest departure over Greenland and northern Siberia in the Northern Hemisphere and secondary centers over the cold waters off the coast of Africa and of Lower California. In the equatorial belt and over the warm waters of the Gulf Stream and the Kuro Siva the pressures were generally below normal, with centers of low pressure over the North Atlantic and North Pacific between  $40^{\circ}$  and  $50^{\circ}$  N. Corresponding centers of low pressure are shown in the Southern Hemisphere between  $30^{\circ}$  and  $40^{\circ}$  S. With a lessened intensity of solar activity in 1891-95 the centers in high latitudes appear displaced toward the Equator, with the exception of a low-pressure area over northern Europe. The center of high pressure over Greenland has moved southward toward Hudson Bay, and

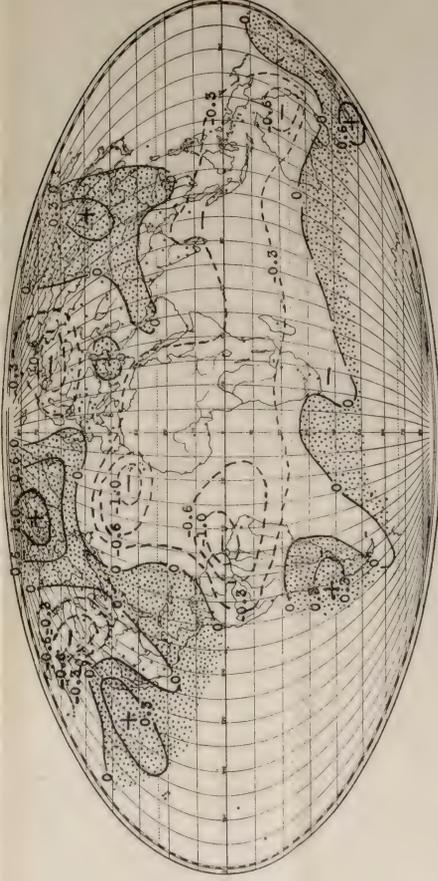




Sun-spot maximum 1915-1919. Mean number of spots 70.2.



Sun-spot maximum 1891-1895. Mean number of spots 67.1.



Sun-spot maximum 1904-1908. Mean number of spots 54.0.

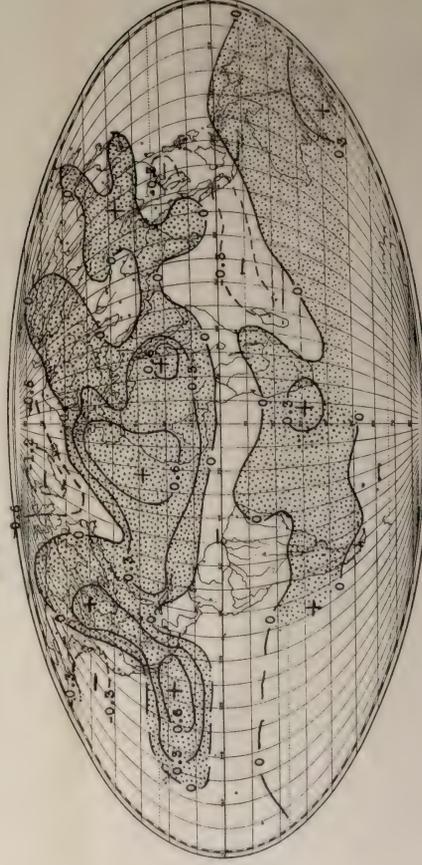


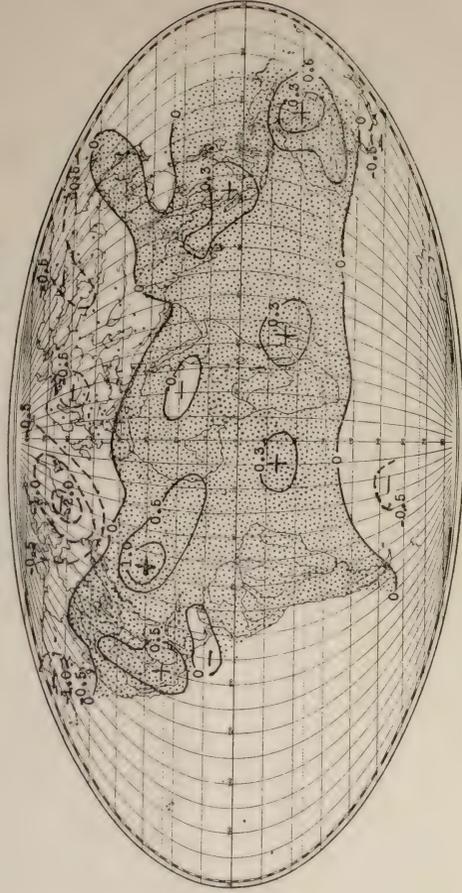
FIG. 10.—Departures of 5-year means of pressure from normal.







Sun-spot minimum 1910-1914. Mean number of spots 7.9.



Sun-spot minimum 1899-1903. Mean number of spots 10.7.



Sun-spot minimum 1887-1891. Mean number of spots 13.8.

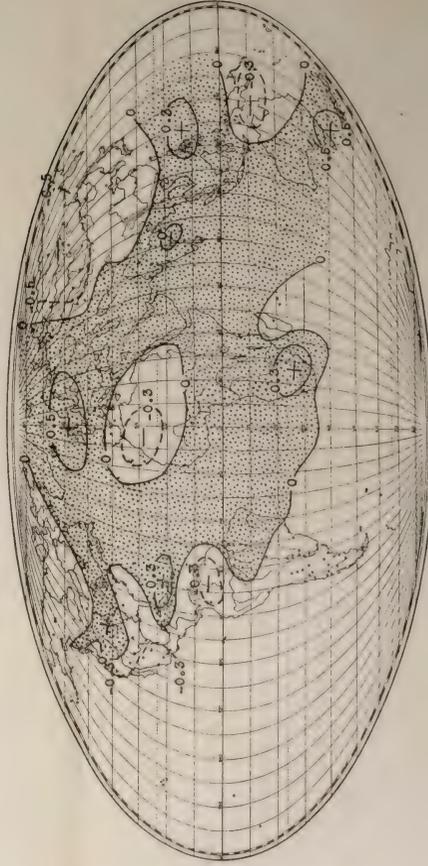
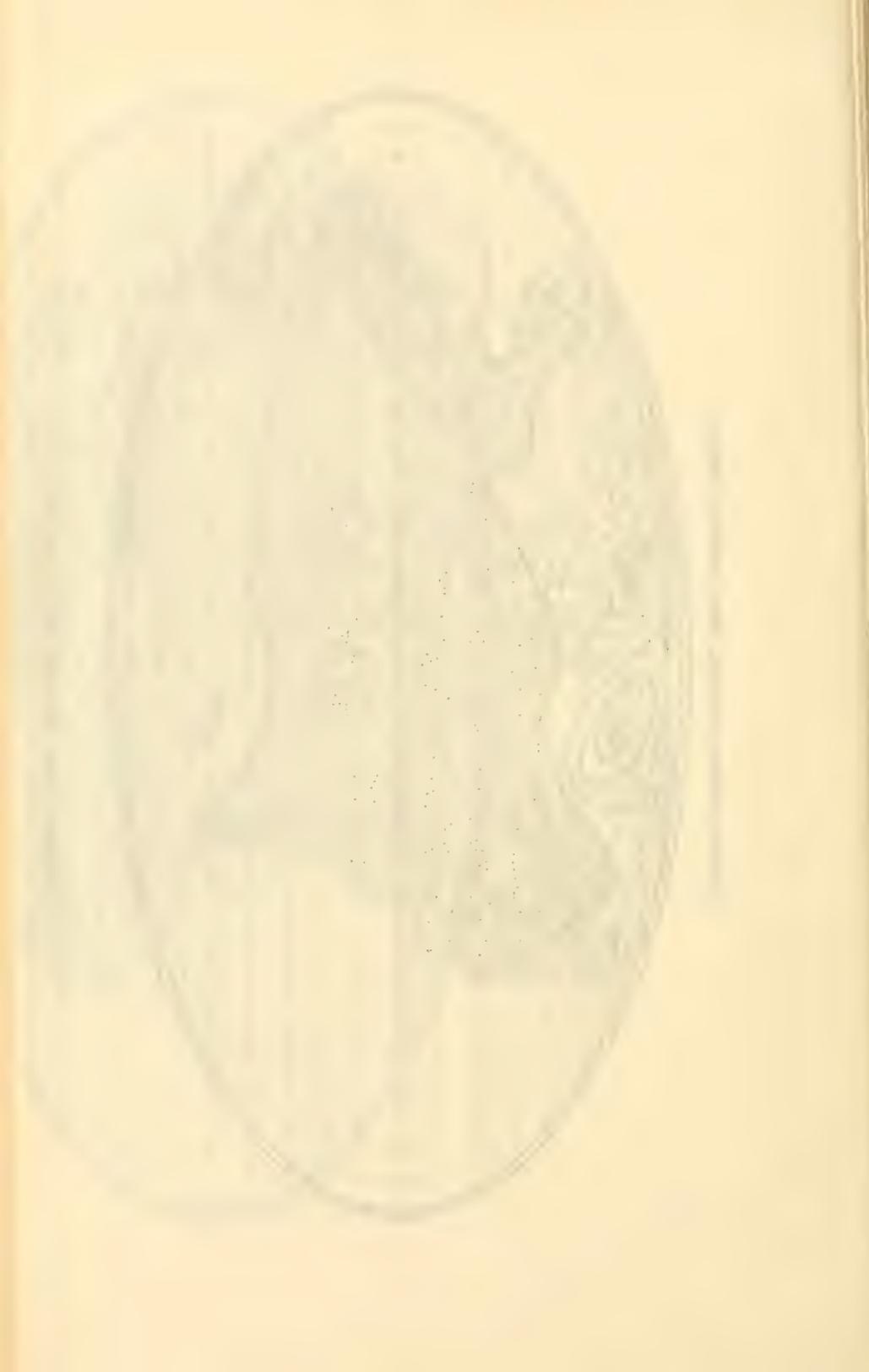


FIG. 11.—Departures of 8-year means of pressure from normal.



the center over northern Siberia has moved to a lower latitude. The center of decreased pressure over the North Atlantic has moved about  $10^\circ$  of latitude toward the Equator, and the decreased pressure over the North Pacific extends southeastward over the United States. Still referring to figure 10, with an even lower solar activity in 1904-8 the centers of excess pressure have moved southward to central North America and to Southern Siberia, respectively, and the centers off Lower California and northern Africa have increased in intensity; but the pressure continues low over the equatorial belt between the East Indies and northern South America. The centers of excess pressure in southern latitudes have been displaced to latitudes between  $30^\circ$  and  $40^\circ$  S., and areas of deficient pressure have appeared in latitudes between  $60^\circ$  and  $70^\circ$  in both hemispheres.

In figure 11 the departures of the 5-year means of pressure during epochs of minimum sun spots are arranged in reverse order to those shown in figure 10 for maxima of spots. During the period of very low sun-spot numbers in 1910-14 the distribution of the areas of excess and defect of pressure is almost the reverse of the distribution during the period of high solar activity in 1915-19. During the less marked solar minima of 1899-1903 and 1887-91 the reversal is less evident, but it should be noted that in each case there was an excess of pressure along the equatorial belt between the East Indies and South America.

#### CORRELATIONS BETWEEN VARIATIONS IN SOLAR RADIATION AND WEATHER

The dotted curve in figure 7 shows the annual mean values of the solar constant of radiation as measured by the Smithsonian astrophysical observatories. These data are plotted inverted—that is, with the higher values downward, as was the case with the sun spots. The curve formed in this way resembles the mean pressure curve for the two selected tropical stations much more nearly than does the sun-spot curve. The very low pressures in 1916-17 correspond with high values of solar radiation, and the high mean values of pressure in 1922-23 correspond with low values of solar radiation. It should be noted also that during the sun-spot period 1917-28 there were four maxima of solar radiation just as there were of pressure, although the extremes do not coincide exactly in time. From this we may infer that the pressure changes are caused by changes in solar radiation and follow changes in sun-spot numbers only in a general way.

Figure 12 shows the annual means of sun spots and solar radiation during two sun-spot periods. The continuous curve is plotted from the relative sun-spot numbers and the dotted curve from the mean values of solar radiation. During the period 1912-23 the long period oscillation of radiation is the same as that of the sun spots, but during the period 1923-33 this relation is not apparent.

At times the month to month variations of solar radiation and of atmospheric pressure are strikingly similar. In figure 13 the continuous curves are plotted from the departures from the 10-year averages of the monthly means of solar radiation observed in the same month

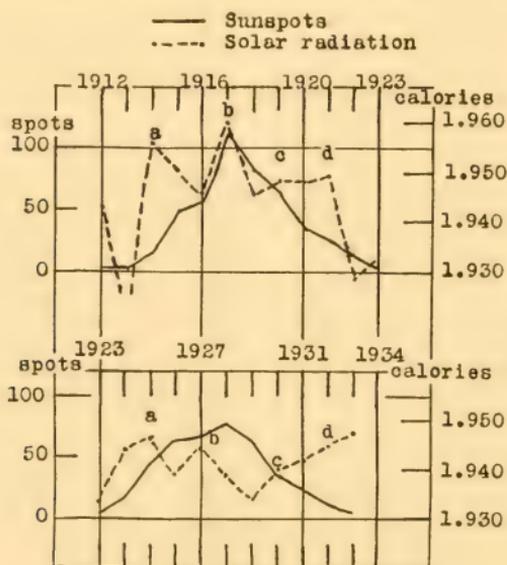


FIG. 12.—Sun spots and solar radiation annual means.

of succeeding years. The broken curves are plotted in the same way from monthly departures of atmospheric pressure in the centers of action in the atmosphere. The values of solar radiation are taken from table 45 of the *Annals of the Astrophysical Observatory of the Smithsonian Institution*, vol. V, p. 278, and the pressures are taken from *World Weather Records, 1921-1930*, Smithsonian Miscellaneous Collections, vol. 90.

It is seen in figure 13 that in the high-pressure center off the coast of Lower California in winter the solar radiation during the decade 1921-1930 varied in a general way in the same sense as the pressure, whereas in the Tropics during the interval from April to September it varied in an opposite way—that is, the pressure fell when the solar

radiation increased. For this reason the two lower plots of pressure departures from normal are inverted in figure 13. The correlation values vary between 0.60 and 0.70 for the 30 months covered by

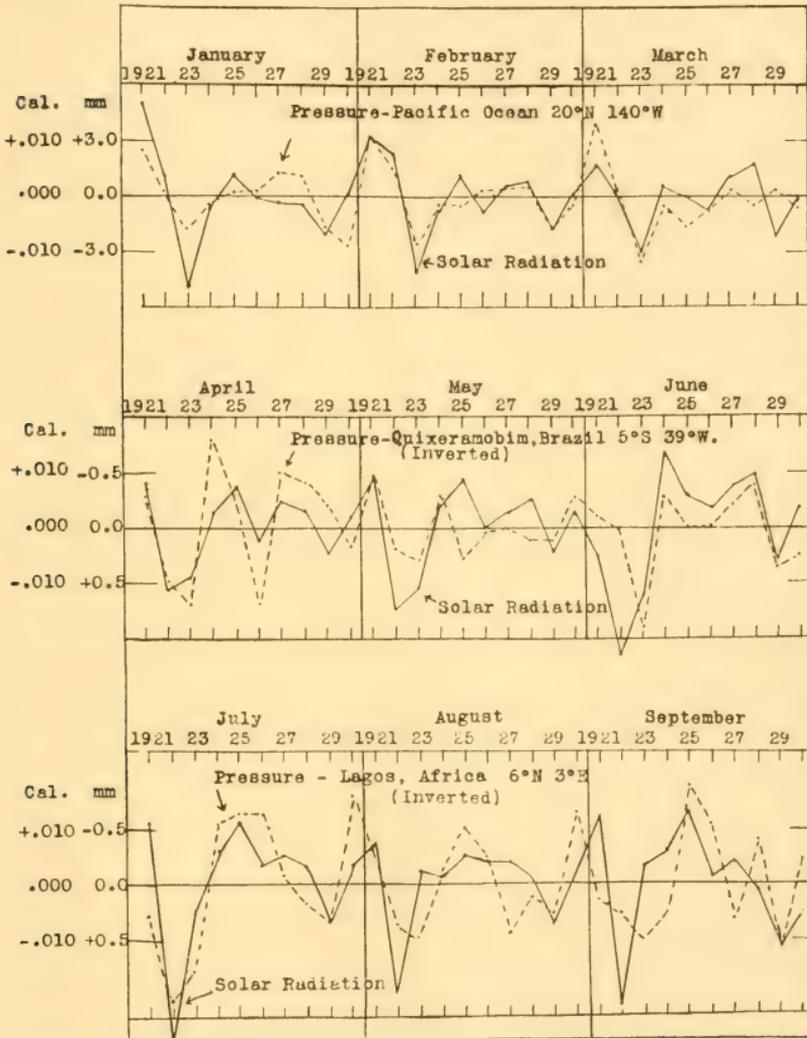


FIG. 13.—Monthly mean departures of solar radiation and of atmospheric pressure from 10-year normals (1).

each plot. The variations of atmospheric pressure are much larger in high latitudes than near the Equator. For that reason the variation of pressure for a given change in solar radiation is much greater in

high latitudes than at the Equator. This fact is illustrated by the upper plot in figure 13, where the pressure change for the same interval on the scale is six times as great as for the tropical stations; it is also shown in figure 14, where the centers of action are near  $50^{\circ}$  N. In this region the oscillations of pressure are 10 times greater than they are near the Equator.

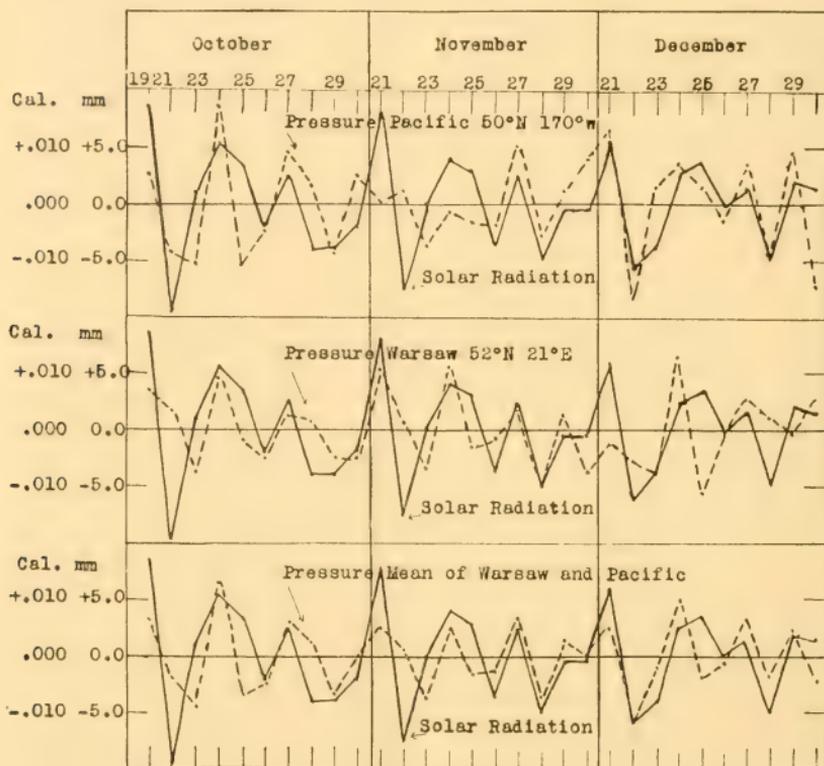


FIG. 14.—Monthly mean departures of solar radiation and of atmospheric pressure from 10-year normals (2).

Owing to the fact that the centers of action in the atmosphere show marked changes of position with variations of solar activity, as pointed out in the case of sun spots, it is not to be expected that any high degree of correlation between solar radiation and pressure can be expected for long intervals. It seemed worth while, however, to compute the correlation between the monthly values of solar radiation and of pressure for all parts of the world, using with the monthly values of solar radiation the pressure at selected stations taken from World Weather Records, Smithsonian Miscellaneous Collections,

vol. 90. The computed correlation coefficients and the amount of change in pressure for each change of 1 per cent in solar radiation are given in table 3 on page 36. The data all relate to the 10 years 1921-1930.

The correlation coefficients are plotted on maps, one for the whole period of 120 months in figure 15, and others for the seasons separately in figures 16, 17, 18, and 19. The correlations for the entire period of 120 months are not large, but the charted results show that minus correlations prevail over the Indian Ocean, equatorial Africa, the equatorial Atlantic, and along the Gulf Stream up to Iceland. The minus correlation signifies that with increased solar radiation the pressure falls within those areas where the pressure is normally low, and the plus correlation shows that it tends to rise within belts between  $20^{\circ}$  and  $40^{\circ}$  both north and south of the Equator. In other words, with increased solar radiation the normal areas of high and low pressure in the atmosphere are accentuated and the normal atmospheric circulation speeded up.

It is also to be noted that there are well-defined centers of plus and minus correlation. The center of plus correlation over Siberia may be called the Gobi Desert center; the one over northern Africa and the adjacent Atlantic, the Sahara center; the one over the Pacific west of lower California, the Pacific center; and the one over Labrador, the Labrador-Greenland center. It is significant that the areas of minus correlation, as pointed out in the case of sun-spot maxima, are in regions where the water temperatures and vapor pressures are high, and the centers of plus correlations are in regions where the vapor pressures are low. This fact suggests very strongly, if it does not prove, that the fall of pressure with increased solar radiation is due to the absorption of the increased radiation by the water vapor in the air, the heating of the air, a consequent lowering of the pressure, and an overflow of air to the colder and drier regions of the earth.

With the four seasonal charts the maximum correlation coefficients are large. Figures 16 to 19 show that although the areas of minus correlation vary in area and position with the seasons, the centers of greatest minus correlation are always found in regions of high vapor pressure. It is of especial significance that in June to August, when the sun is north of the Equator and the highest vapor pressures are also north of the Equator, the greatest minus correlations are found between the Gold Coast of Africa and the mouth of the Amazon River in South America; whereas in December to February, when the sun is in the Southern Hemisphere and the highest vapor pressures

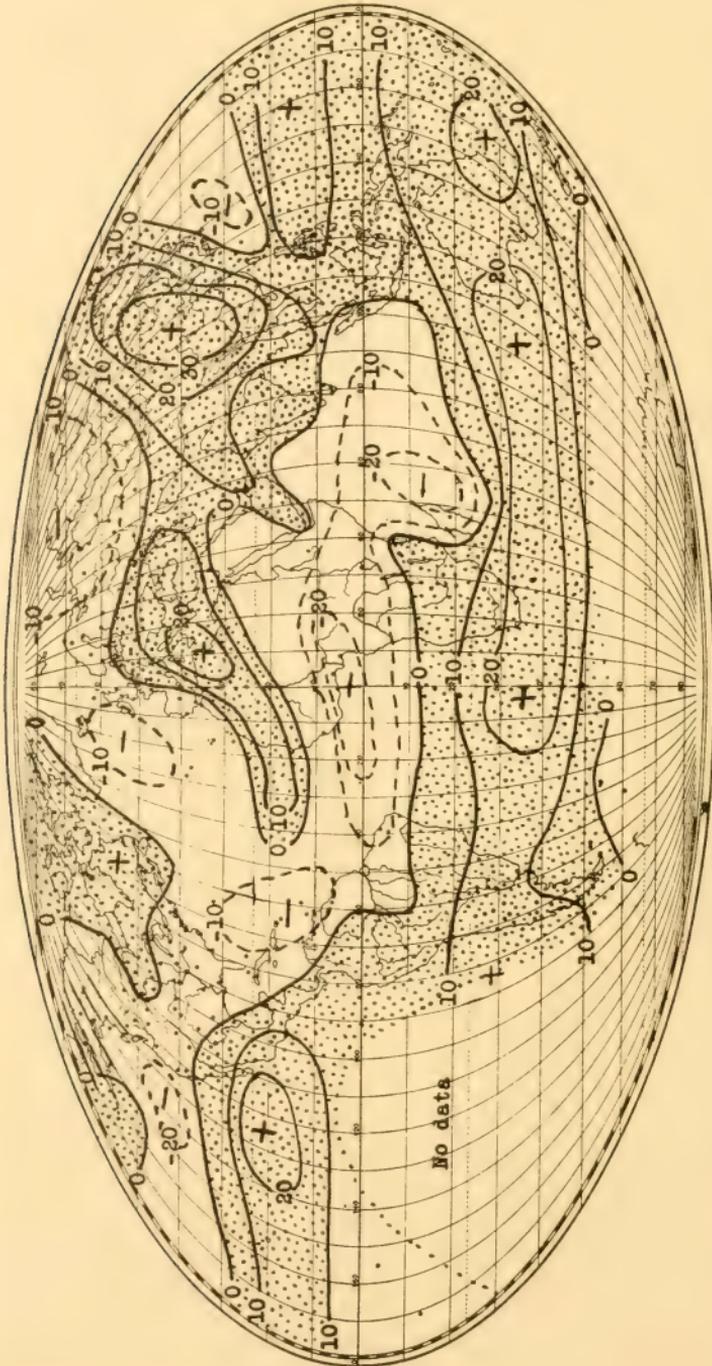


FIG. 15.—Correlations of monthly means of pressure and solar radiation. 1921-1930, 120 months.

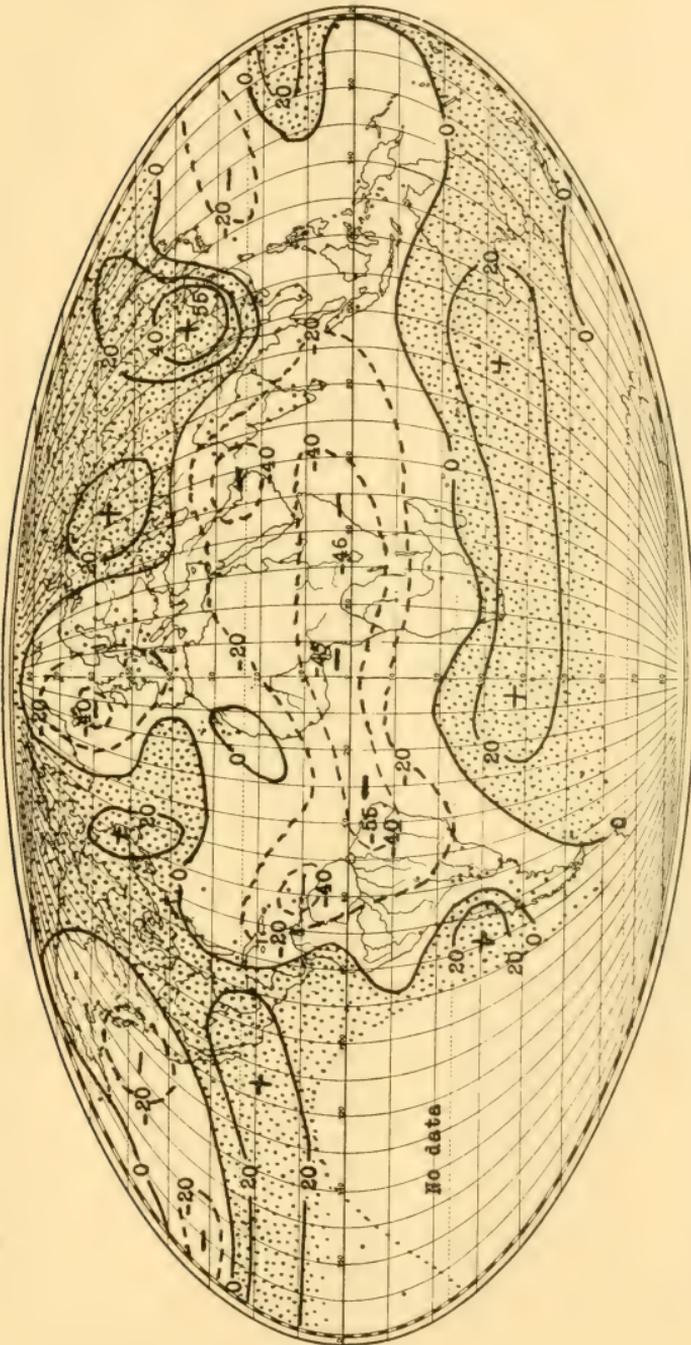


FIG. 16.—Correlations of monthly means of pressure and solar radiation. March to May, 1921-1930, 30 months.

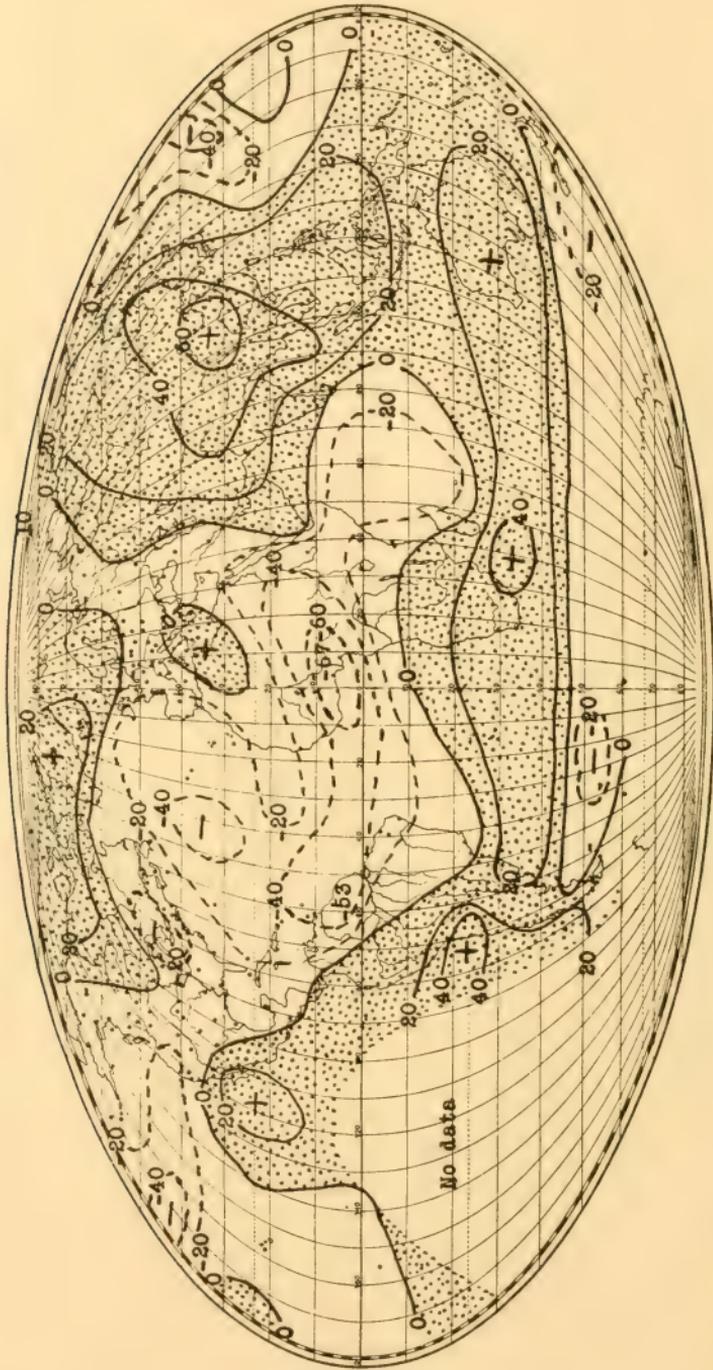


FIG. 17.—Correlation of monthly means of pressure and solar radiation. June to August, 1921-1930, 30 months.

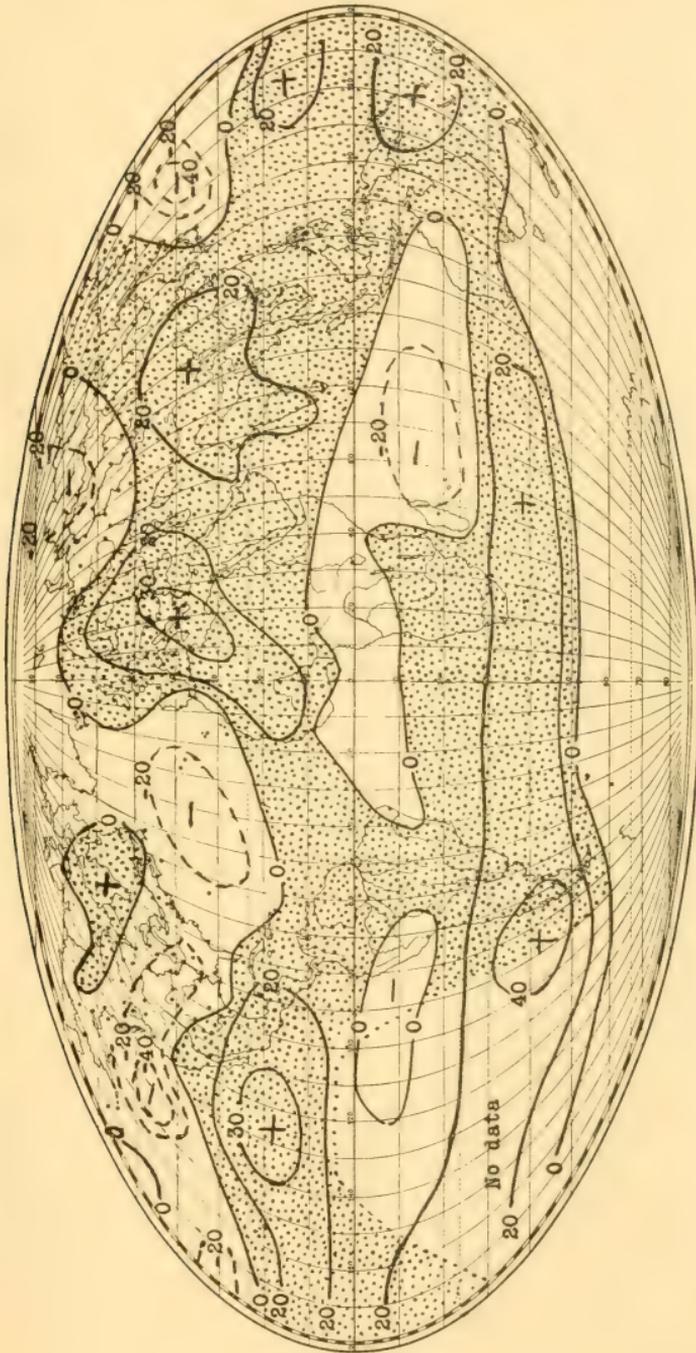


FIG. 18.—Correlation of monthly means of pressure and solar radiation. September to November, 1921-1930. 30 months.

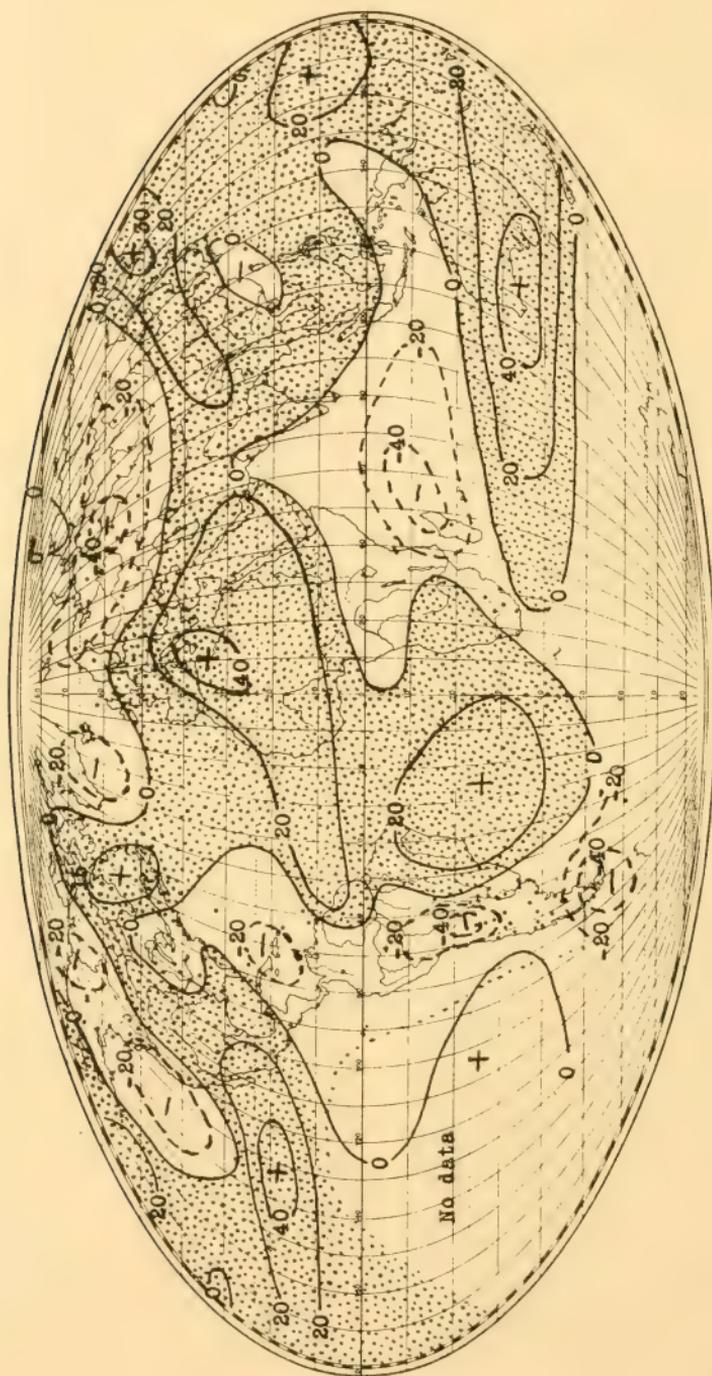


FIG. 19.—Correlations of monthly means of pressure and solar radiation. December to February, 1921-1930, 30 months.

are south of the Equator, the greatest minus correlations are found south of the Equator in the Indian Ocean near Madagascar and in central South America.

In Dr. G. C. Simpson's excellent paper on "Further Studies in Terrestrial Radiation,"<sup>2</sup> he considers what should be the effect of 1 percent change in solar radiation. He finds that such an increase might be balanced (1) by an increase of  $2^{\circ}$  C. in surface temperatures, or, (2) by an increase of  $1^{\circ}.5$  in the temperature of the stratosphere, or, (3) by an increase of .01 percent in cloudiness. However, what should not be overlooked in this connection is that an increase in cloudiness involves a coincident increase in temperature and a resulting decrease in pressure in order to produce the increase in cloudiness. This is particularly true in the equatorial belt. The calculations given in table 3, coefficient  $b$ , show that in the centers of action in that region the change of pressure for 1 percent change of solar radiation does not exceed  $-1.2$  mm. To produce this fall would require a rise in the mean temperature of the air column of about  $0^{\circ}.4$  C.<sup>3</sup> If there were no errors in the solar measurements, the correlation coefficients  $r$  and  $b$  would probably be larger, but in no case would the resulting temperatures exceed the amounts calculated by Simpson.

In high latitudes the coefficient  $b$  becomes larger and in the centers of action rises to 5 mm for 1 percent change in solar radiation; but in this region the air is approaching the axis of rotation of the earth, and the deflecting effect of the rotation plays a part in lowering the pressure within normal centers of low pressure which are intensified by the increased solar radiation. The height above the surface at which the greatest absorption of solar radiation by water vapor takes place is yet to be determined, but certainly in some cases it is within or above the cloud level.

In order to study the variation of position of the centers of action with varying intensity of solar radiation, the monthly departure from 10-year normals of solar radiation were arranged according to intensity in the following six classes: (1) over  $+ .010$  calories, (2)  $+ .006$  to  $+ .010$ , (3)  $+ .001$  to  $+ .005$ , (4)  $- .000$  to  $- .005$ , (5)  $- .006$  to  $- .010$ , (6) under  $- .010$ . The normal was taken as 1.940 calories per square centimeter per minute, and the absolute values may be obtained by adding this value to the departures given. The mean pressures for the 10 years 1921-1930 were then determined for each station in a world-wide net of stations for each class of solar radiation

<sup>2</sup> Mem. Roy. Meteorol. Soc., vol. 3, no. 21, pp. 19-22, 1928.

<sup>3</sup> See World Weather, p. 275, Macmillan and Co., 1923.

intensities. The data were taken from World Weather Records, 1921-1930. The results are given in table 4 on page 42 for each season and in table 5 on page 49 for the mean for the four seasons—that is, for the year.

Referring to table 5, the first step in investigating the relationships was to determine the correlation between the means of departures of pressures corresponding respectively to equal departures of solar radiation above and below normal. The results are as follows:

*Correlation between the Mean Departures of Pressure Corresponding  
Respectively to Equal Departures of Solar Radiation  
Above and Below Normal*

| Departures of solar radiation          | Correlation coefficients |                     |
|--|--------------------------|---------------------|
|  | Northern Hemisphere      | Southern Hemisphere |
| +.001 to +.005 and -.000 to -.005..... | $r = -0.35$              | $r = -0.51$         |
| +.006 to +.010 and -.006 to -.010..... | $r = -0.38$              | $r = -0.72$         |
| Over +.010 and under -.010.....        | $r = 0.27$               | $r = -0.23$         |
| Number of stations used.....           | $N = 119$ stations       | $N = 46$ stations   |

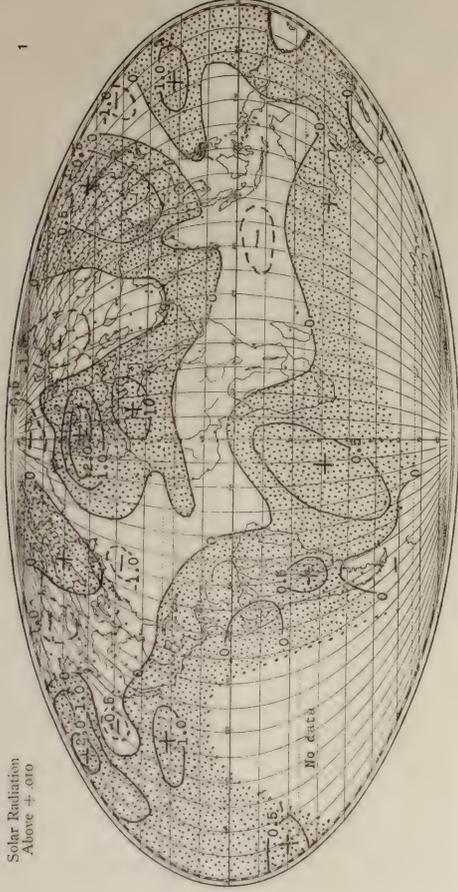
The meaning of this table is that for equal departures of solar radiation above and below normal the departures of pressure from normal in all parts of the world tend to have opposite signs. This relation holds for stations all over the world, not only in the means for the year, taken from table 5 as here given, but also in general with a few exceptions for the separate seasons given in table 4. This fact seems to leave no escape from the conclusion that this is a real and not an accidental relationship. In short, these extensive data, covering all parts of the world, prove that solar variation is an important weather factor, even the dominating one, as also appears from Figs. 13 and 14 and 23-26.

Figure 20 shows the areas of excess and of defect of pressure for three different values of solar radiation above normal, and figure 21 shows the areas for the different values of solar radiation below normal. The departures of radiation above and below normal were taken as nearly equal as possible. These charts show numerous centers of plus and of minus departures of pressure which appear to be related in the successive charts. For example, in figure 20 the upper chart (1), for solar radiation above +.010 calories, shows an area of excess pressure over Greenland and Labrador. In the next chart (2), for +.006 to +.010 calories, this area has extended southward with the center of greatest departure near Nova Scotia; and in the third chart (3), for +.001 to +.005 calories, the center of excess pressure is over the ocean to the south of Nova Scotia. In figure 21, with solar

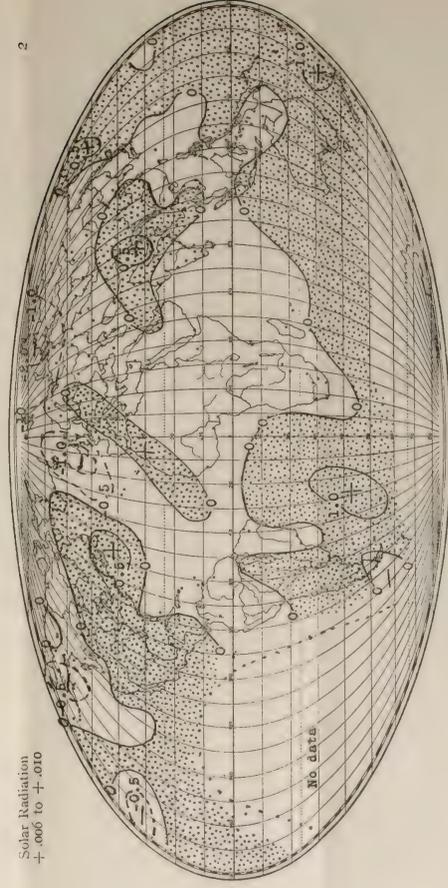




Solar Radiation  
Above  $\pm .010$



Solar Radiation  
 $+.006$  to  $+.010$



Solar Radiation  
 $+.001$  to  $+.005$

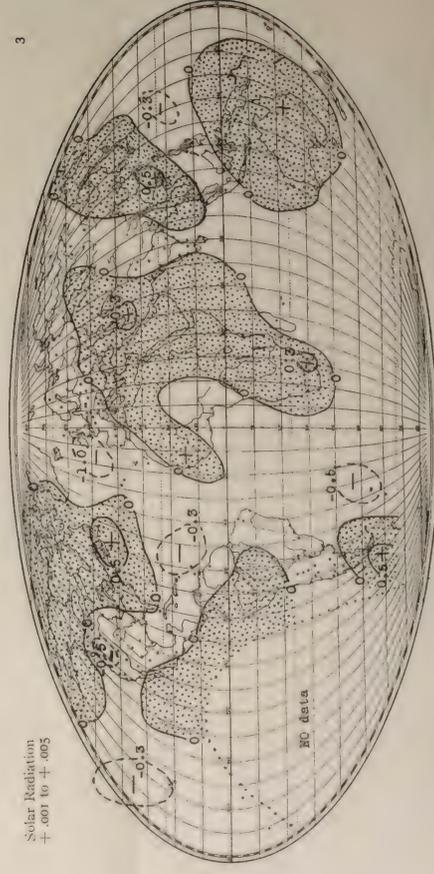


FIG. 20.—Mean departures from normal pressure in millimeters for different values of solar radiation above normal.

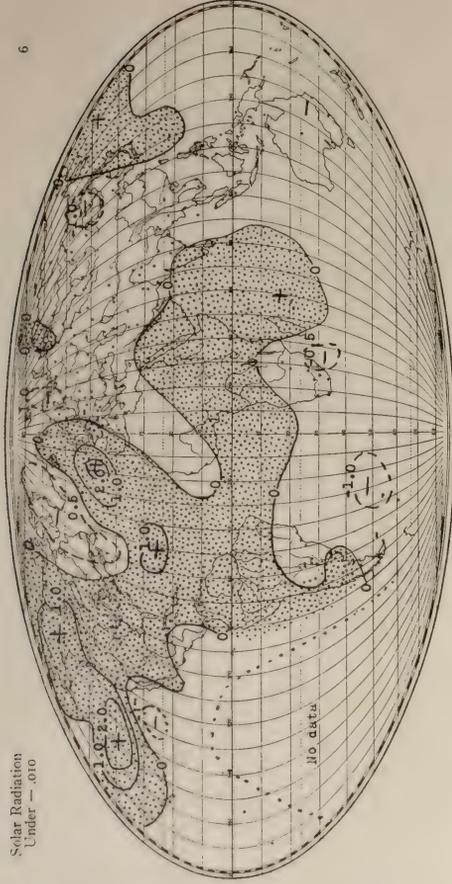






Solar Radiation  
Under  $-.010$

6



Solar Radiation  
-.006 to  $-.010$

5



Solar Radiation  
-.000 to  $-.005$

4

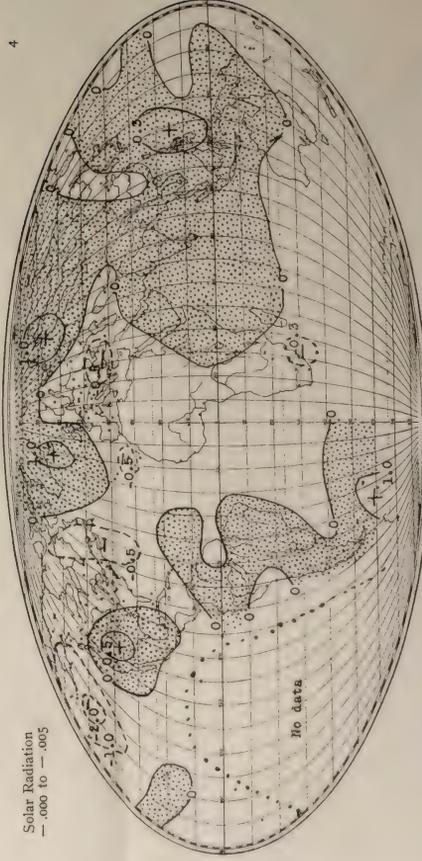


FIG. 21.—Mean departures from normal pressure in millimeters for different values of solar radiation below normal.



departures of  $-.000$  to  $-.005$  calories, chart (4), this area shows a defect of pressure with the minimum near Nova Scotia. Chart (5), for  $-.006$  to  $-.010$  calories, shows the center of defect northeast of Newfoundland, and chart (6), for values under  $-.010$  calories, shows the center of defect over Greenland and Labrador.

In the same way an area of excess pressure over Europe in chart 1 moves southward to the coast of Africa in chart 3, changes sign, and then moves northward over Europe with numerically increasing minus values of solar radiation. In chart 1 a center of minus pressures is found over the central Pacific west of California. This center shifts southwestward to latitude  $30^\circ$  in chart 3, changes sign with the change in radiation from plus to minus values, and then shifts northeastward with increasing minus values of solar radiation. The shift of centers does not appear quite so regular over the Atlantic. However, an area of defective pressure near Spitsbergen in chart 1 is found farther south in the two succeeding charts 2 and 3. With minus values of solar radiation it becomes an area of excess pressure covering the area between Greenland and Norway in charts 4 to 6. An area of excess pressure moves southward from northeastern Siberia to southern Siberia with decreasing positive values of radiation in charts 1 to 3, but the return northward of the minus area is not so evident in charts 4 to 6. A center of defective pressure near Bermuda in chart 1 shifts southward and is found near the West Indies in chart 3. It then changes sign with the change in solar radiation, and moves northward to the vicinity of Bermuda in chart 6.

In figure 22 an effort was made to plot the shift of the different centers of action. The position of the centers for different intensities are indicated by letters of the alphabet.

In general, when a center of action, either plus or minus, is found in a high latitude with high values of solar radiation, a center with an opposite sign is found about  $30^\circ$  farther south near the same longitude. Both these centers of action shift southward with decreasing plus values of solar radiation, change sign with the change in solar radiation from plus to minus, and then shift northward with increasing minus values of radiation. The only exception to this rule appears to be in the center of action in the Pacific, about  $20^\circ$  N. and  $140^\circ$  W., which apparently drifts eastward, changes sign, and then drifts westward again.

In the Southern Hemisphere the number of stations is too few to permit one to follow the shift in the centers of action, but the similarity of the changes north and south of the Equator, shown in the

study of the sun-spot relations, no doubt holds in the case of solar radiation changes of shorter period.

In order to study the seasonal shift in the centers of action, the data given in table 3 were plotted in a series of charts. It is not feasible to reproduce all of these charts, but they indicate that the centers of action for each intensity of solar radiation oscillate around their mean position as a result of seasonal changes. Hence, in order to determine the effect of any solar radiation change, both the solar intensity and the seasonal change must be considered.

In figures 23, 24, 25, and 26 the differences between the mean pressures for solar intensities of  $+ .006$  to  $+ .010$  and  $- .006$  to  $- .010$  are given for each season. The mean change in solar radiation is about  $.015$  calorie or  $0.8$  percent of the normal value,  $1.940$  calories. These charts show the direct effect of this change of solar radiation on the pressure as nearly as is possible with any arrangement of the data at present available. The changes shown by these charts are not small. They are sufficiently large to dominate the weather and to make their consideration imperative to anyone who would understand the weather and its causes.

The points of interest to be noted in these charts are: (1) With increased solar radiation there is a fall of pressure between Australia and Africa in December to February, when the sun is south of the Equator, and a fall of pressure between Malaysia and the West Indies in June to August, when the sun is north of the Equator; (2) with increased solar radiation there is a marked fall of pressure at all seasons in the North Atlantic, more marked and farther north in winter and spring and less marked and farther south in summer and autumn; (3) there is also a fall of pressure in the North Pacific west of North America; this area of fall is farther north and more marked in winter, but less pronounced than in the North Atlantic; (4) there is an increase of pressure over the Arctic region of North America at all seasons, although the center of greatest increase appears to oscillate back and forth across the continent; (5) there are two centers of increased pressure in northern Eurasia, one of the centers being found over eastern Asia and one between western Siberia and northern Europe, both showing large seasonal oscillations; (6) there are centers of increased pressure about  $10^{\circ}$  to  $30^{\circ}$  N.; one of these is found at all seasons between Hawaii and Mexico, another is in the Pacific about  $140^{\circ}$  E., and other more transient areas are near the west coast of Africa and near India. The stations in the Southern Hemisphere are too few to enable one to follow the shifting of the centers of action.

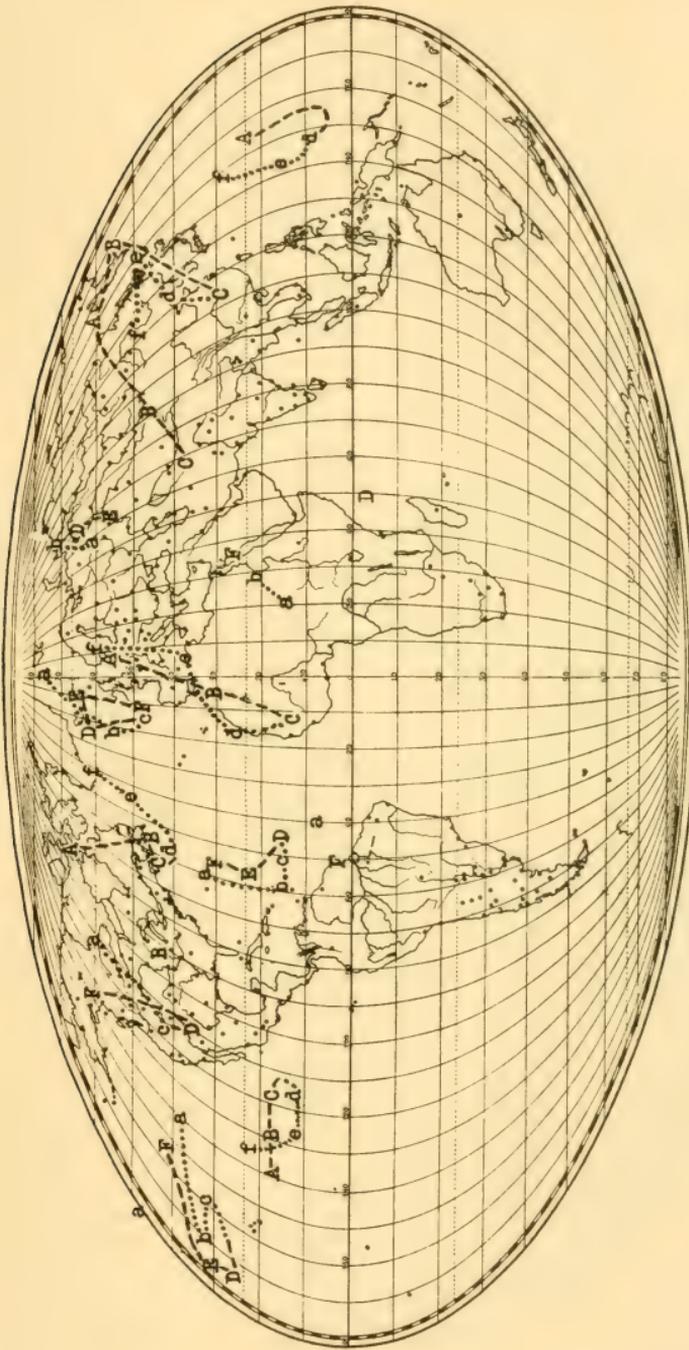


FIG. 22.—Movement of centers of action in the atmosphere with varying intensities of solar radiation.

|                                      |   |
|--------------------------------------|---|
| A = center of excess of pressure and | a = center of defect of pressure when solar radiation is over +.010 |
| B = " " " " " "                      | + .006 to +.010   |
| C = " " " " " "                      | + .001 to +.005   |
| D = " " " " " "                      | — .000 to —.005   |
| E = " " " " " "                      | — .006 to —.010   |
| F = " " " " " "                      | under .010  |

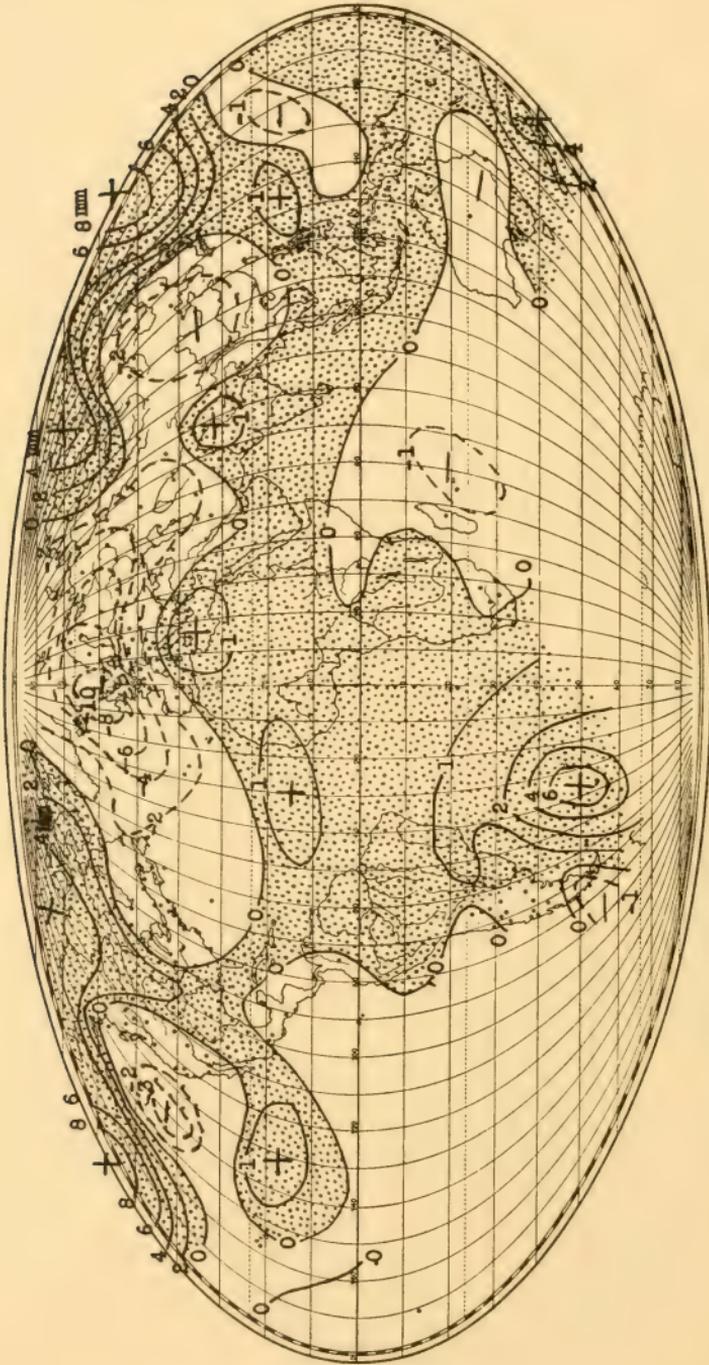


FIG. 23.—Differences between mean pressures with departures of solar radiation  $+.006$  to  $+.010$  and  $-.006$  to  $-.010$ , December to February.

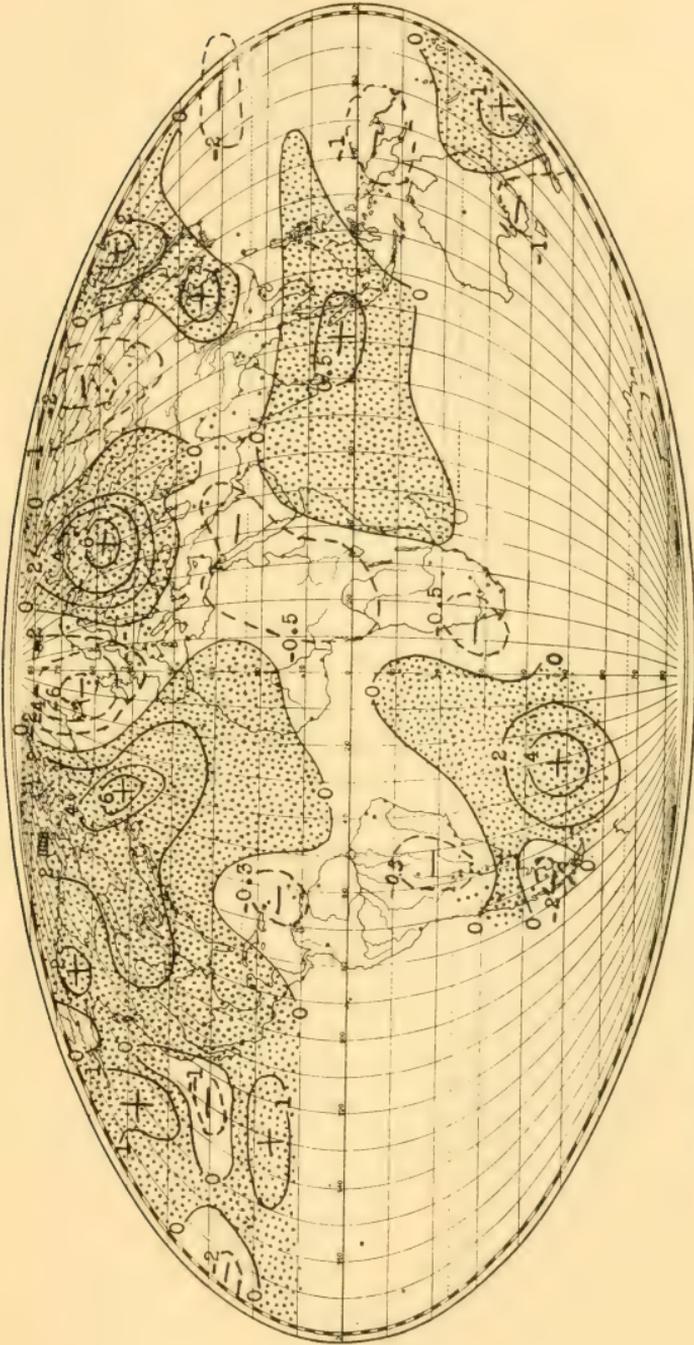


FIG. 24.—Differences between mean pressures with departures of solar radiation +.006 to +.010 and -.006 to -.010. March to May

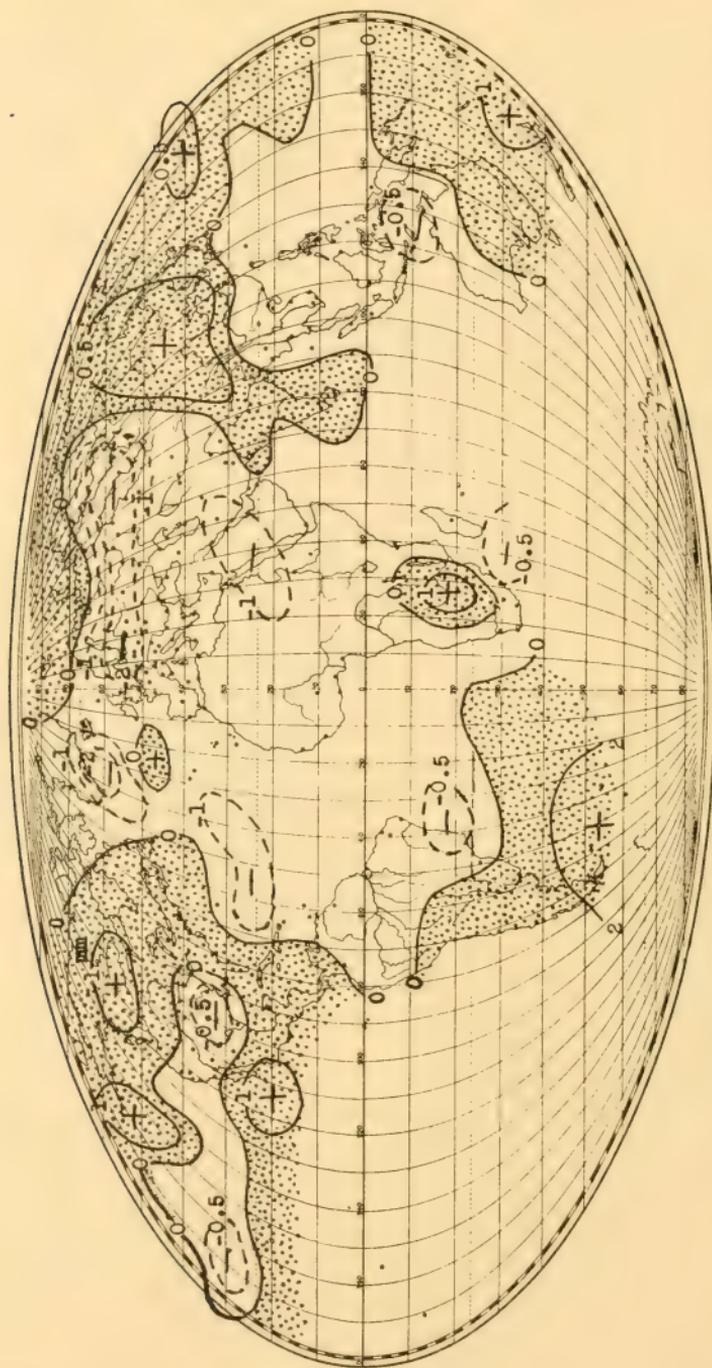


FIG. 25.—Differences between mean pressures with departures of  $+.006$  to  $+.010$  and  $-.006$  to  $-.010$ , June to August.

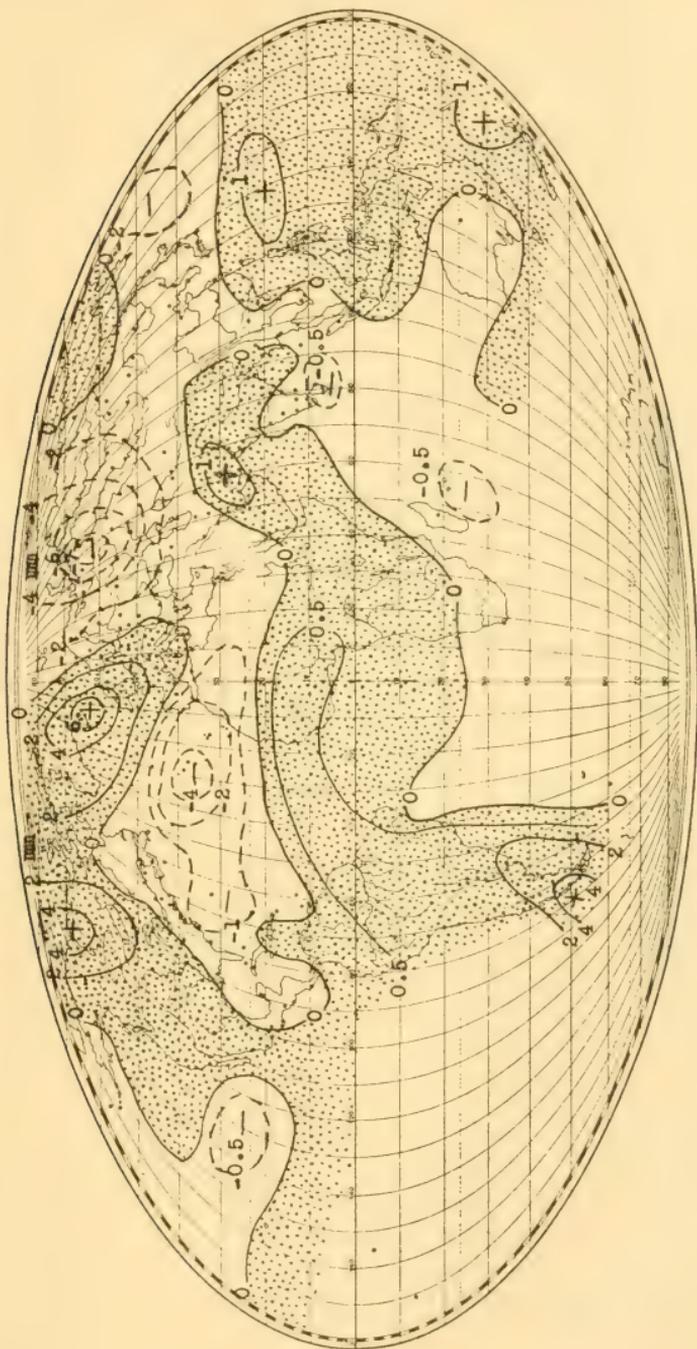


FIG. 26.—Differences between mean pressures with departures of solar radiation + .006 to + .010 and - .006 to - .010. September to November.

Similar charts for other intensities show that in general the northern centers of action are farther north with increased intensity of solar action and farther south with decreased intensity at all seasons. These charts show, as did the preceding charts, that with increase of solar radiation the pressure falls in those regions where the vapor pressure and the temperature are abnormally high for the latitudes in which they are found, whereas increases of pressure are found where the vapor pressure and temperature are below the normals for the latitude.

#### PROGRESSIVELY MOVING WEATHER WAVES

Numerous examples have been given in preceding papers of this series and in other publications of the progressive wavelike movements of weather areas in different parts of the world. These progressive movements can probably be explained in large part, at least, as due to the movements of the centers of action in the atmosphere with varying intensity of solar radiation. During each cycle of change in solar radiation the centers of excess pressure move from high latitudes to low latitudes and back again. These changes in position can be interpreted as waves that progress with a velocity inversely proportional to the length of the period of oscillation. In the shorter waves the west to east drift of the atmosphere in middle latitudes also plays an important part in the progressive motion.

#### SUMMARY

1. There is something in common in the weather in widely separated parts of the earth, even in countries on opposite sides of the earth, as for example the central United States and Australia. Changes in rainfall in central North America show a similarity to changes in central South America. Changes in pressure in the Indian Ocean show similarities to changes of temperature on the coast of Chile. Annual pressure means in San Diego vary in the same way as in Buenos Aires, and pressures in Ceylon vary inversely to those in Santiago, Chile. Many such relationships have been shown by other investigators.

It is suggested that these common features are brought about by changes in the intensity of the circulation of the earth's atmosphere. In confirmation of this view it is shown that there are periods lasting for several years when the pressure gradient between the equatorial region and the colder regions in high latitudes become greater than normal, and succeeding years when it becomes less than normal. This simultaneous change in the pressure gradient north and south of the

Equator indicates widespread oscillations in the circulation of the earth's atmosphere. In addition, for the past 42 years covered by the observations, there has been an upward trend of pressure in the equatorial belt and a downward trend in the cold areas of high latitudes, indicating a generally decreasing pressure gradient between high latitudes and the Equator, and an amelioration of the earth's climate.

2. In all latitudes, changes in pressure, temperature, and rainfall are most intense in certain areas, which have been called centers of action. In the equatorial region the centers of action are over the Indian Ocean and over the equatorial Atlantic between the Gold Coast of Africa and the Amazon River. In higher latitudes there are centers of action in the North Atlantic and North Pacific in which the pressure and rainfall change in the same way as in the equatorial centers of action.

Oppositely behaving centers of action are found over the cold lands of high latitudes such as Iceland, northern Canada, and northwestern Siberia, and over the cool waters of the middle latitudes such as the Pacific Ocean west of lower California and west of Chile and in the Atlantic ocean west of northern Africa. When the pressure and rainfall are in excess in this latter group of centers of action they are in defect in the equatorial and oceanic centers.

3. These centers of action are related in a general way to such major features of the earth's surface as the polar regions and the equatorial region and the distribution of land and water. Within regions of warm water and of high vapor content in the equatorial region, and over the oceans in high latitudes, the weather conditions in general oscillate oppositely to those over the cold land areas in high latitudes and the cool water areas of lower latitudes. These latter regions are also regions of low vapor pressure.

4. The centers of action are not stationary but tend to shift position, oscillating to and fro over wide areas, so that any given place on the earth's surface may be at one time within the influence of a field of action of one kind, and at another time under the influence of a field of action of an opposite kind.

This shifting of the centers of action in the atmosphere has been one of the most disconcerting and discouraging facts confronting research workers in meteorology. Relations have been found between distant regions which for a while gave high correlation coefficients,

either plus or minus, and then suddenly the relationship reversed in sign. Cycles have been found in the weather and have excited hope for a while that a key to weather changes had been discovered, but only to lead to disappointment by disappearing or by changing in phase. Wavelike movements in the atmosphere have been disclosed which continued for a short time and disappeared. A reason for these changes is now offered for the first time in the systematic changes of position in the centers of action in the atmosphere, under the influence of changing solar activity. With the removal of this outstanding difficulty, meteorology should show a marked advance, both in theory and in practical weather forecasting, more especially in forecasting for long periods in advance.

5. The changes in intensity and position of the centers of action in the atmosphere are intimately related to changes in solar activity, more especially to changes in solar heat radiation. The annual means of pressure in these centers of activity, when smoothed, follow in a general way the changes in annual values of sun spots, but there is no relation evident between the two in the changes of short period. Monthly and even shorter periods of change in the intensity of solar radiation show, however, an unmistakable relation to weather changes.

6. The picture presented in this paper is that of an atmosphere in which the regions of high vapor content in the tropical regions of the earth are strongly affected by changes of solar radiation (presumably by the absorption of the incoming heat rays by the water vapor in the air). The air therein becomes warmer, increases in volume per unit mass, and its pressure falls, attended by an increase in rainfall. Simultaneously, there are centers of action in high latitudes where opposite relationships are evident. These centers of action all sway back and forth under the influence of changing intensity of solar radiation and changing position of the sun with the season.

7. When solar radiation increases, the centers of action in high latitudes move farther north and increase in intensity. That is, the pressure over cold regions in these latitudes becomes abnormally high and the temperature falls, while simultaneously the belts of low pressure in equatorial regions widen and develop centers of low pressure in middle latitudes. These changes in pressure are attended by winds which markedly influence the temperatures in high latitudes.

8. The matter of especial importance considered in this paper is the shifting of the centers of action in the atmosphere under the influence of varying intensity of solar activity. If this is a fact, then no research worker in meteorology can afford to overlook it.

9. When the earliest investigations of the relations of solar activity and weather began, it was assumed that if the sun became warmer the temperature all over the earth would rise. Some confirmation of this view appeared to result from Köppen's finding that the mean temperature over all the regions from which he was able to obtain observations was higher when sun spots were at a minimum. But more recent investigations have disclosed that solar radiation is on the whole lower at sun-spot minimum and that with the increase of solar radiation there are regions of the earth which show opposite changes toward each other. Now it is shown that these regions of opposite change shift position on the earth's surface. This view adds complications, but brings us nearer the actual facts. In the meantime there has been a marked development in theory from the physical and mathematical viewpoint, as shown by the papers of Dr. G. C. Simpson on the heat balance in the atmosphere, and the studies of Brunt and Fowle on the absorptive powers of water vapor on solar radiation.

TABLE 3.—Correlation of Monthly Means of Solar Radiation and Atmospheric Pressure

| Station        | Lat.   | Long.   | Year,<br>120 months |         | Mar.-May,<br>30 months |         | June-Aug.,<br>30 months |         | Sept.-Nov.,<br>30 months |         | Dec.-Feb.,<br>30 months |         |
|----------------|--------|---------|---------------------|---------|------------------------|---------|-------------------------|---------|--------------------------|---------|-------------------------|---------|
|                |        |         | r                   | b<br>mb | r                      | b<br>mb | r                       | b<br>mb | r                        | b<br>mb | r                       | b<br>mb |
| PACIFIC OCEAN: |        |         |                     |         |                        |         |                         |         |                          |         |                         |         |
| Open Ocean     | 50° N. | 170° E. | -.05                | -0.5    | .14                    | 2.1     | -.24                    | -1.9    | -.34                     | -3.0    | .20                     | 2.8     |
| Open Ocean     | 50° N. | 170° W. | .12                 | 1.4     | .14                    | 3.0     | -.12                    | 0.9     | .10                      | 1.8     | .29                     | 5.4     |
| Open Ocean     | 50° N. | 150° W. | .02                 | 0.2     | .05                    | 0.6     | -.15                    | -1.2    | .24                      | 2.0     | -.03                    | -.05    |
| Open Ocean     | 40° N. | 160° E. | -.08                | -0.6    | -.07                   | -0.8    | .12                     | 0.4     | -.41                     | -2.7    | .11                     | 1.3     |
| Open Ocean     | 40° N. | 180°    | -.04                | -0.3    | .07                    | 0.9     | -.50                    | -2.4    | -.01                     | -0.1    | .15                     | 1.8     |
| Open Ocean     | 40° N. | 160° W. | -.05                | -0.6    | -.11                   | -1.3    | -.29                    | -1.4    | -.18                     | -1.5    | .10                     | 1.7     |
| Open Ocean     | 40° N. | 140° W. | -.24                | -2.1    | -.04                   | -0.5    | -.21                    | -3.1    | -.40                     | -3.3    | -.27                    | -3.0    |
| Open Ocean     | 30° N. | 150° E. | .08                 | 0.3     | -.02                   | -0.1    | .18                     | 0.4     | -.08                     | -0.3    | .17                     | 1.1     |
| Open Ocean     | 30° N. | 170° E. | -.07                | -0.4    | -.32                   | -2.2    | .00                     | 0.0     | -.26                     | -0.8    | .12                     | 1.2     |
| Open Ocean     | 30° N. | 170° W. | -.04                | -0.2    | -.28                   | -2.2    | -.10                    | -0.3    | -.05                     | -0.2    | .12                     | 1.4     |
| Open Ocean     | 30° N. | 150° W. | .04                 | 0.3     | -.08                   | -0.8    | .12                     | 0.6     | .10                      | 0.5     | .04                     | 0.4     |
| Open Ocean     | 30° N. | 130° W. | .01                 | 0.2     | -.10                   | -0.8    | .16                     | 0.5     | .26                      | 1.0     | -.16                    | -1.0    |
| Midway Island  | 28° N. | 177° W. | -.08                | -0.4    | -.28                   | -1.9    | .23                     | 0.7     | -.25                     | -0.8    | -.08                    | -0.6    |
| Omura          | 27° N. | 142° E. | -.12                | -0.4    | -.24                   | -0.8    | -.23                    | -0.8    | -.08                     | -0.2    | .08                     | 0.3     |
| Open Ocean     | 20° N. | 140° E. | .01                 | 0.1     | -.10                   | -0.6    | -.22                    | -0.8    | -.19                     | -0.8    | .18                     | 0.7     |
| Open Ocean     | 20° N. | 160° E. | .15                 | 0.5     | .13                    | 0.5     | .04                     | 0.1     | .25                      | 0.5     | .22                     | 0.9     |
| Open Ocean     | 20° N. | 180°    | .10                 | 0.3     | .26                    | 1.0     | .05                     | 0.4     | .00                      | 0.0     | .16                     | 0.6     |
| Honolulu       | 21° N. | 158° W. | .03                 | 0.1     | .16                    | 0.4     | -.10                    | -0.1    | .09                      | 0.2     | .00                     | 0.0     |
| Open Ocean     | 20° N. | 140° W. | .24                 | 1.1     | .26                    | 1.8     | .04                     | 0.1     | .31                      | 0.9     | .41                     | 2.4     |
| Ladrone Island | 13° N. | 145° E. | .12                 | 0.9     | .13                    | 1.2     | .10                     | 0.5     | .19                      | 1.1     | .07                     | 0.6     |
| Yap Island     | 9° N.  | 138° E. | .00                 | 0.2     | .05                    | 0.1     | .24                     | 0.3     | .06                      | 0.1     | .00                     | 0.0     |
| Ocean Island   | 1° S.  | 169° E. | .00                 | 0.2     | -.08                   | -0.5    | .02                     | 0.1     | .05                      | 0.2     | .24                     | 1.3     |
| Port Moresby   | 9° S.  | 147° E. | .13                 | 0.2     | -.03                   | -0.1    | .17                     | 0.3     | .24                      | 0.5     | .08                     | 0.2     |
| Samoa          | 14° S. | 172° W. | .13                 | 0.1     | .05                    | 0.1     | .02                     | 0.0     | .27                      | 0.4     | .11                     | 0.3     |
| NORTH AMERICA: |        |         |                     |         |                        |         |                         |         |                          |         |                         |         |
| Barrow         | 71° N. | 156° W. | -.22                | -3.3    | .19                    | 1.7     | .25                     | 1.0     | -.08                     | -0.6    | -.22                    | -3.3    |
| Fort Goodhope  | 66° N. | 129° W. | -.12                | -1.0    | -.25                   | -1.8    | .13                     | 0.6     | -.10                     | -1.1    | -.25                    | -3.3    |
| Eagle          | 65° N. | 141° W. | -.05                | -0.6    | -.19                   | -1.3    | -.18                    | -0.9    | .01                      | 0.2     | -.03                    | -0.6    |
| Nome           | 64° N. | 165° W. | -.05                | -0.3    | -.06                   | -0.6    | -.11                    | -1.1    | -.01                     | -0.0    | -.04                    | -0.6    |

NOTE.—r=correlation coefficient; b=amount of change in pressure for 1 percent change in solar radiation. b is in millibars but may be changed to percentages by moving the decimal point one place to left.

TABLE 3.—Correlation of Monthly Means of Solar Radiation and Atmospheric Pressure (continued)

| Station               | Lat.   | Long.   | Year,<br>120 months |         | Mar.-May,<br>30 months |         | June-Aug.,<br>30 months |         | Sept.-Nov.,<br>30 months |         | Dec.-Feb.,<br>30 months |         |
|-----------------------|--------|---------|---------------------|---------|------------------------|---------|-------------------------|---------|--------------------------|---------|-------------------------|---------|
|                       |        |         | r                   | b<br>mb | r                      | b<br>mb | r                       | b<br>mb | r                        | b<br>mb | r                       | b<br>mb |
| <b>NORTH AMERICA</b>  |        |         |                     |         |                        |         |                         |         |                          |         |                         |         |
| <i>(continued)</i> :  |        |         |                     |         |                        |         |                         |         |                          |         |                         |         |
| Kodiak                | 58° N. | 152° W. | -.04                | -0.2    | -.10                   | -1.0    | -.12                    | -0.6    | .07                      | 0.7     | -.01                    | -0.2    |
| Juneau                | 58° N. | 134° W. | -.06                | -0.5    | -.04                   | -0.4    | -.08                    | -0.3    | -.06                     | -0.4    | -.08                    | -1.3    |
| Dutch Harbor          | 54° N. | 166° W. | .02                 | 0.2     | .11                    | 1.5     | -.23                    | -1.0    | -.04                     | -0.3    | .20                     | 3.7     |
| Anticosti             | 40° N. | 63° W.  | .05                 | 0.4     | .17                    | 1.9     | -.18                    | -0.6    | .09                      | 0.0     | .15                     | 2.1     |
| Seattle               | 48° N. | 122° W. | -.15                | -0.8    | -.20                   | -1.7    | .10                     | 0.2     | -.21                     | -1.0    | -.16                    | -1.3    |
| Bismarek              | 47° N. | 101° W. | .01                 | 0.0     | .05                    | 0.4     | .02                     | 0.2     | -.09                     | -0.3    | .01                     | 0.1     |
| Cape Race             | 46° N. | 53° W.  | .05                 | ...     | .24                    | ...     | -.23                    | ...     | -.33                     | ...     | .05                     | ...     |
| Alpena                | 45° N. | 83° W.  | -.08                | -0.4    | .06                    | 0.4     | .36                     | -1.0    | -.03                     | -0.2    | -.05                    | -0.3    |
| New York              | 41° N. | 74° W.  | -.02                | -0.1    | .04                    | 0.3     | -.03                    | -0.1    | -.06                     | -0.2    | -.02                    | -0.2    |
| Red Bluff             | 40° N. | 122° W. | -.13                | -0.4    | -.28                   | -1.0    | -.34                    | -0.4    | .26                      | 0.5     | -.22                    | -1.0    |
| Denver                | 40° N. | 105° W. | -.10                | -0.4    | .01                    | 0.1     | -.07                    | -0.2    | -.35                     | -1.3    | .04                     | 0.2     |
| St. Louis             | 39° N. | 90° W.  | -.07                | -0.2    | .12                    | 0.6     | -.19                    | -0.4    | -.21                     | -0.7    | -.02                    | -0.1    |
| Charleston            | 33° N. | 80° W.  | -.07                | -0.2    | -.08                   | -0.5    | -.13                    | -0.3    | -.11                     | -0.3    | .02                     | 0.1     |
| San Diego             | 33° N. | 117° W. | .15                 | 0.3     | .01                    | 0.0     | .37                     | 0.5     | .17                      | 0.3     | .08                     | 0.2     |
| Abilene               | 32° N. | 100° W. | -.07                | -0.2    | .09                    | 0.4     | -.28                    | -0.6    | -.18                     | -0.4    | .06                     | 0.3     |
| Key West              | 25° N. | 82° W.  | -.05                | -0.1    | .20                    | 0.3     | -.21                    | -0.3    | .07                      | 0.1     | -.10                    | -0.2    |
| Mazatlan, Mex.        | 23° N. | 106° W. | .19                 | 0.3     | .20                    | 0.3     | .06                     | 0.1     | .30                      | 0.6     | .23                     | 0.5     |
| Merida                | 21° N. | 90° W.  | .13                 | 0.3     | .27                    | 0.8     | -.18                    | -0.2    | .30                      | 0.6     | .12                     | 0.4     |
| Colon                 | 9° N.  | 79° W.  | .07                 | 0.1     | .14                    | 0.2     | .07                     | 0.1     | .14                      | 0.2     | -.01                    | -0.0    |
| <b>SOUTH AMERICA:</b> |        |         |                     |         |                        |         |                         |         |                          |         |                         |         |
| Georgetown            | 7° N.  | 58° W.  | -.09                | -0.2    | -.36                   | -1.0    | -.53                    | -0.4    | .28                      | 0.5     | .21                     | 0.7     |
| Taperinka             | 2° S.  | 54° W.  | -.01                | -0.0    | -.21                   | -0.3    | -.17                    | -0.2    | .14                      | 0.2     | .18                     | 0.2     |
| Quixeramobim          | 5° S.  | 39° W.  | -.17                | -0.2    | -.55                   | -0.8    | -.35                    | -0.5    | .08                      | 0.1     | .02                     | 0.0     |
| Ondina                | 13° S. | 38° W.  | .05                 | 0.1     | -.23                   | -0.2    | -.02                    | 0.0     | -.22                     | 0.0     | .27                     | 0.6     |
| Cuyaba                | 16° S. | 50° W.  | .05                 | 0.1     | -.32                   | -0.6    | -.03                    | 0.0     | .02                      | 0.3     | .16                     | 0.3     |
| La Paz                | 16° S. | 68° W.  | .00                 | 0.0     | -.03                   | -0.2    | .12                     | 0.5     | -.12                     | -0.3    | -.02                    | -0.1    |
| Río de Janeiro        | 23° S. | 43° W.  | .01                 | 0.0     | -.23                   | -0.6    | -.10                    | -0.3    | .18                      | 0.3     | .22                     | 0.7     |
| Salta                 | 25° S. | 65° W.  | .15                 | 0.5     | .21                    | 0.7     | .45                     | 1.5     | .18                      | 0.5     | -.40                    | -1.4    |
| Asunción              | 25° S. | 58° W.  | .11                 | 0.3     | -.08                   | -0.3    | .12                     | 0.3     | .18                      | 0.5     | .16                     | 0.4     |
| Curitiba              | 25° S. | 49° W.  | .15                 | 0.3     | -.01                   | -0.0    | .16                     | 0.4     | .06                      | 0.1     | .33                     | 0.8     |
| Goya                  | 29° S. | 59° W.  | .15                 | 0.5     | -.13                   | -0.5    | .19                     | 0.8     | -.33                     | 0.9     | .06                     | 0.2     |

TABLE 3.—Correlation of Monthly Means of Solar Radiation and Atmospheric Pressure (continued)

| Station                          | Lat.   | Long.  | Year,<br>120 months |      | Mar-May,<br>30 months |      | June-Aug.,<br>30 months |      | Sept.-Nov.,<br>30 months |      | Dec.-Feb.,<br>30 months |       |
|----------------------------------|--------|--------|---------------------|------|-----------------------|------|-------------------------|------|--------------------------|------|-------------------------|-------|
|                                  |        |        | r                   | mb   | r                     | mb   | r                       | mb   | r                        | mb   | r                       | mb    |
| SOUTH AMERICA<br>(continued):    |        |        |                     |      |                       |      |                         |      |                          |      |                         |       |
| Córdoba                          | 31° S. | 64° W. | .12                 | 0.4  | .04                   | 0.2  | .18                     | 0.6  | .25                      | 0.7  | .12                     | 0.3   |
| Santiago                         | 33° S. | 71° W. | .09                 | 0.2  | -.03                  | -0.1 | .23                     | 0.5  | .02                      | 0.1  | .00                     | 0.1   |
| Buenos Aires                     | 35° S. | 58° W. | .14                 | 0.5  | -.07                  | -0.3 | .24                     | 0.9  | .25                      | 0.9  | -.06                    | -0.2  |
| Bahia Blanca                     | 39° S. | 62° W. | .08                 | 0.4  | -.04                  | -0.2 | .00                     | 0.0  | .33                      | 1.5  | -.15                    | -0.5  |
| Puerto Madryn                    | 43° S. | 65° W. | .07                 | 0.4  | -.09                  | -0.7 | -.01                    | -1.3 | .33                      | 1.8  | -.06                    | 0.4   |
| Sarmiento                        | 45° S. | 69° W. | .04                 | 0.2  | -.14                  | -1.1 | .20                     | 1.3  | .19                      | 1.1  | -.23                    | -1.7  |
| Islota de los Evangelistas       | 52° S. | 75° W. | .11                 | 1.0  | -.08                  | -1.1 | .23                     | 2.1  | .51                      | 3.7  | -.39                    | -3.8  |
| Santa Cruz                       | 50° S. | 68° W. | .05                 | 0.4  | -.05                  | -0.6 | .12                     | 1.0  | .38                      | 2.3  | -.42                    | -3.0  |
| Punta Arenas                     | 53° S. | 71° W. | .06                 | 0.2  | -.01                  | -0.2 | .10                     | 0.9  | .44                      | 3.0  | -.47                    | -3.8  |
| ATLANTIC OCEAN AND<br>GREENLAND: |        |        |                     |      |                       |      |                         |      |                          |      |                         |       |
| Upernivik                        | 73° N. | 50° W. | .05                 | 0.4  | .08                   | 0.9  | .25                     | 1.4  | -.05                     | -0.4 | -.02                    | -0.3  |
| Angmagalik                       | 66° N. | 37° W. | -.04                | -0.4 | -.04                  | -0.6 | .25                     | 1.9  | -.07                     | -0.6 | -.23                    | -4.0  |
| Stykkishólm                      | 65° N. | 23° W. | -.10                | -1.4 | -.20                  | -4.1 | .22                     | 1.3  | -.06                     | -0.7 | -.23                    | -5.3  |
| Berufjordur                      | 64° N. | 14° W. | -.07                | -1.0 | -.31                  | -4.7 | .20                     | 1.6  | .02                      | 0.2  | -.19                    | -4.4  |
| Open Ocean                       | 60° N. | 30° W. | -.09                | -0.6 | -.13                  | -3.5 | -.11                    | -0.8 | .19                      | 2.5  | -.35                    | -13.3 |
| Open Ocean                       | 60° N. | 15° W. | -.19                | -3.4 | -.46                  | -8.8 | -.46                    | -4.5 | .03                      | 0.4  | -.10                    | -3.0  |
| Open Ocean                       | 50° N. | 40° W. | -.05                | -0.4 | .17                   | 1.9  | -.38                    | -1.8 | -.02                     | -0.1 | -.01                    | -0.2  |
| Open Ocean                       | 50° N. | 30° W. | -.10                | -1.2 | -.03                  | -0.5 | -.31                    | -2.2 | -.10                     | -0.9 | -.01                    | -0.2  |
| Open Ocean                       | 50° N. | 20° W. | -.12                | -1.2 | -.15                  | -2.7 | -.26                    | -1.8 | -.02                     | -0.2 | -.02                    | -0.4  |
| Open Ocean                       | 40° N. | 60° W. | .00                 | 0.0  | .17                   | 1.9  | -.11                    | -1.4 | -.19                     | -0.9 | .09                     | 0.7   |
| Open Ocean                       | 40° N. | 50° W. | -.01                | -0.1 | .22                   | 3.1  | -.21                    | -1.0 | -.20                     | -0.8 | .11                     | 0.9   |
| Open Ocean                       | 40° N. | 40° W. | -.06                | -0.5 | .11                   | 1.4  | -.40                    | -1.7 | -.26                     | -1.4 | .12                     | 1.7   |
| Open Ocean                       | 40° N. | 20° W. | -.07                | -0.6 | .08                   | 0.9  | -.29                    | -1.0 | -.19                     | -1.2 | .02                     | 0.0   |
| Ponta Delgada                    | 38° N. | 26° W. | -.10                | -0.8 | .03                   | 0.4  | -.37                    | -1.3 | -.30                     | -1.7 | .06                     | 0.8   |
| Open Ocean                       | 35° N. | 70° W. | -.02                | -0.3 | -.03                  | -0.6 | -.14                    | -0.6 | .01                      | 0.1  | -.01                    | -0.1  |
| Madeira                          | 33° N. | 17° W. | -.10                | -0.8 | -.06                  | -0.5 | -.46                    | -1.1 | -.14                     | -0.4 | .01                     | 0.1   |

TABLE 3.—Correlation of Monthly Means of Solar Radiation and Atmospheric Pressure (continued)

| Station                                   | Lat.   | Long.  | Year,<br>120 months |         | Mar.-May,<br>30 months |         | June-Aug.,<br>30 months |         | Sept.-Nov.,<br>30 months |         | Dec.-Feb.,<br>30 months |         |
|---|--------|--------|---------------------|---------|------------------------|---------|-------------------------|---------|--------------------------|---------|-------------------------|---------|
|   |        |        | r                   | b<br>mb | r                      | b<br>mb | r                       | b<br>mb | r                        | b<br>mb | r                       | b<br>mb |
| ATLANTIC OCEAN AND GREENLAND (continued): |        |        |                     |         |                        |         |                         |         |                          |         |                         |         |
| Open Ocean                                | 30° N. | 50° W. | -.09                | -.5     | -.04                   | -.4     | -.30                    | -.9     | -.08                     | -.2     | -.09                    | -.6     |
| Open Ocean                                | 30° N. | 40° W. | -.10                | -.6     | -.04                   | -.3     | -.19                    | -.1     | -.30                     | -.9     | .11                     | .9      |
| La Laguna                                 | 28° N. | 10° W. | -.05                | -.2     | -.01                   | -.1     | -.32                    | -.4     | -.20                     | -.5     | .09                     | .5      |
| Open Ocean                                | 25° N. | 05° W. | -.19                | -.6     | -.17                   | -.9     | -.34                    | -.1     | -.15                     | -.4     | -.14                    | -.5     |
| Port-au-Prince                            | 19° N. | 72° W. | -.14                | -.2     | -.21                   | -.5     | -.34                    | -.1     | .10                      | .2      | -.26                    | -.5     |
| São Vicente                               | 17° N. | 25° W. | .11                 | .2      | .14                    | .3      | -.05                    | .18     | .04                      | .4      | .21                     | .6      |
| Richmond Hill                             | 12° N. | 02° W. | -.13                | -.2     | -.52                   | -.1     | -.18                    | -.2     | .07                      | .1      | -.07                    | -.2     |
| St. Helena                                | 16° S. | 6° W.  | .05                 | .4      | -.01                   | -.1     | .02                     | .2      | .07                      | .7      | .12                     | .8      |
| Cape Pembroke                             | 52° S. | 58° W. | .07                 | .8      | .13                    | .2      | .09                     | 1.1     | .27                      | .5      | -.37                    | -.1     |
| South Georgia                             | 54° S. | 37° W. | -.07                | -.7     | .14                    | 1.8     | -.22                    | -.1     | -.08                     | -.6     | -.03                    | -.5     |
| South Orkneys                             | 61° S. | 45° W. | .01                 | .1      | .18                    | 2.6     | .13                     | 1.0     | -.05                     | -.4     | -.20                    | -.2     |
| EUROPE:                                   |        |        |                     |         |                        |         |                         |         |                          |         |                         |         |
| Spitsbergen                               | 78° N. | 14° E. | -.09                | -.9     | -.09                   | -.1     | .04                     | 0.2     | -.06                     | -.5     | -.21                    | -.6     |
| Malye Karmakouly                          | 72° N. | 53° E. | -.04                | -.5     | -.03                   | -.5     | -.06                    | -.4     | -.17                     | -.2     | .07                     | 1.2     |
| Mehavn-Stetnes                            | 71° N. | 28° E. | -.02                | -.2     | -.00                   | -.9     | .24                     | 1.6     | .07                      | .7      | -.24                    | -.13    |
| Bodo                                      | 67° N. | 14° E. | -.05                | -.6     | -.09                   | -.5     | .10                     | 0.9     | .07                      | .8      | -.26                    | -.5     |
| Leningrad                                 | 60° N. | 30° E. | .00                 | 0.0     | .05                    | 0.9     | .12                     | 0.7     | 1.4                      | 1.4     | -.27                    | -.7     |
| Perm                                      | 58° N. | 56° E. | -.12                | -.9     | .33                    | 3.9     | .04                     | 0.2     | -.24                     | -.2     | -.41                    | -.6     |
| Aberdeen                                  | 57° N. | 2° W.  | -.04                | -.5     | -.23                   | -.3     | .04                     | 0.2     | .06                      | .8      | -.14                    | -.7     |
| Moscow                                    | 56° N. | 37° E. | -.02                | -.1     | .22                    | 2.7     | -.02                    | 0.1     | .05                      | -.28    | -.4                     | -.7     |
| Utrecht                                   | 52° N. | 5° E.  | .02                 | .2      | -.23                   | -.2     | -.08                    | -.4     | .21                      | 1.8     | .05                     | .8      |
| Warsaw                                    | 52° N. | 21° E. | .10                 | .8      | -.10                   | -.1     | -.05                    | -.2     | .37                      | 2.6     | .04                     | .5      |
| Valentia                                  | 52° N. | 16° W. | -.07                | -.1     | -.21                   | -.3     | -.22                    | -.2     | .05                      | .4      | -.02                    | -.4     |
| Marseille                                 | 43° N. | 5° E.  | .14                 | .9      | -.21                   | -.1     | .02                     | 0.0     | .33                      | 1.6     | .30                     | 3.2     |
| Rome                                      | 42° N. | 12° E. | .24                 | 1.7     | -.06                   | -.6     | .12                     | 0.4     | .30                      | 2.3     | .46                     | 4.7     |
| Tiflis                                    | 42° N. | 45° E. | .12                 | .5      | .01                    | 0.1     | -.01                    | -.0     | .27                      | 1.0     | .16                     | 1.2     |
| Krasnovodsk                               | 40° N. | 53° E. | .06                 | .3      | .02                    | 0.1     | -.02                    | -.1     | .02                      | .4      | .11                     | 1.9     |
| Lisbon                                    | 39° N. | 9° W.  | -.08                | -.4     | -.07                   | -.5     | -.30                    | -.5     | -.15                     | -.6     | .02                     | .2      |
| Beirut                                    | 34° N. | 35° E. | .10                 | 0.2     | -.17                   | -.6     | -.01                    | -.0     | .26                      | 0.4     | .26                     | 1.2     |

TABLE 3.—Correlation of Monthly Means of Solar Radiation and Atmospheric Pressure (continued)

| Station           | Lat.   | Long.   | Year,<br>120 months |         | Mar.-May,<br>30 months |         | June-Aug.,<br>30 months |         | Sept.-Nov.,<br>30 months |         | Dec.-Feb.,<br>30 months |         |
|-------------------|--------|---------|---------------------|---------|------------------------|---------|-------------------------|---------|--------------------------|---------|-------------------------|---------|
|                   |        |         | r                   | b<br>mb | r                      | b<br>mb | r                       | b<br>mb | r                        | b<br>mb | r                       | b<br>mb |
| AFRICA:           |        |         |                     |         |                        |         |                         |         |                          |         |                         |         |
| Helwan            | 30° N. | 31° E.  | -.05                | -.01    | -.29                   | -.09    | -.28                    | -.03    | .05                      | .01     | .16                     | 0.6     |
| Khartoum          | 16° N. | 33° E.  | -.06                | -.01    | -.18                   | -.05    | -.41                    | -.05    | .06                      | 0.1     | .24                     | 0.7     |
| Free town         | 8° N.  | 13° W.  | -.06                | -.01    | -.10                   | -.02    | -.33                    | -.04    | -.05                     | -.01    | .24                     | 0.4     |
| Lagos             | 6° N.  | 3° E.   | -.20                | -.03    | -.48                   | -.09    | -.07                    | -.10    | .20                      | 0.3     | .11                     | 0.2     |
| Entebbe           | 0° N.  | 32° E.  | -.16                | -.02    | -.46                   | -.10    | -.11                    | -.01    | -.13                     | -.01    | -.06                    | -.02    |
| Zanzibar          | 6° S.  | 39° E.  | .03                 | 0.0     | -.04                   | -.01    | -.09                    | -.01    | .19                      | 0.2     | .07                     | 0.1     |
| Salisbury         | 18° S. | 31° E.  | .08                 | 0.0     | -.09                   | -.01    | .23                     | 0.1     | .08                      | 0.0     | .05                     | 0.0     |
| Bulawayo          | 20° S. | 29° E.  | .10                 | 0.2     | -.07                   | -.01    | .19                     | 0.4     | .20                      | 0.2     | .02                     | 0.1     |
| Kimberley         | 29° S. | 25° E.  | .10                 | 0.1     | .07                    | 0.1     | .38                     | 0.2     | .18                      | 0.1     | -.36                    | -.01    |
| O'Okiep           | 30° S. | 18° E.  | .15                 | 0.3     | -.07                   | -.02    | .34                     | 0.6     | .19                      | 0.2     | .03                     | 0.0     |
| Durban            | 30° S. | 31° E.  | .25                 | 0.2     | .16                    | 0.2     | .42                     | 0.4     | .26                      | 0.1     | -.04                    | -.01    |
| Port Elizabeth    | 34° S. | 26° E.  | .23                 | 0.8     | .23                    | 1.0     | .32                     | 1.2     | .32                      | 0.7     | -.04                    | -.01    |
| ASIA:             |        |         |                     |         |                        |         |                         |         |                          |         |                         |         |
| Dickson           | 73° N. | 80° E.  | -.13                | -.15    | .01                    | 0.2     | -.38                    | -.27    | -.34                     | -.28    | .14                     | 27      |
| Yakutsk           | 62° N. | 129° E. | -.04                | ...     | .02                    | ...     | .05                     | ...     | .05                      | ...     | -.17                    | ...     |
| Yeniseysk         | 58° N. | 92° E.  | -.10                | -.07    | .11                    | 0.8     | .14                     | 0.4     | -.21                     | -.09    | -.35                    | -.37    |
| Tomsk             | 50° N. | 85° E.  | -.11                | -.07    | .18                    | 1.1     | .23                     | 0.8     | -.23                     | -.12    | -.39                    | -.39    |
| Barnaul           | 53° N. | 84° E.  | -.07                | -.03    | .21                    | 1.2     | .27                     | 0.6     | -.15                     | -.06    | -.34                    | -.27    |
| Irkutsk           | 50° N. | 104° E. | -.04                | -.01    | .05                    | 0.2     | .27                     | 0.7     | .07                      | 0.3     | -.31                    | -.19    |
| Petropavlovsk     | 53° N. | 159° E. | .25                 | 2.8     | .17                    | 4.5     | -.18                    | -.13    | .38                      | 2.7     | .35                     | 4.3     |
| Blagovyeshtchensk | 50° N. | 127° E. | .34                 | 0.8     | .27                    | 0.8     | .47                     | 1.4     | .22                      | 0.8     | -.02                    | -.01    |
| Nemuro            | 43° N. | 145° E. | .00                 | 0.3     | -.01                   | -.01    | .20                     | 0.6     | -.14                     | -.06    | .22                     | 1.6     |
| Vladivostok       | 43° N. | 132° E. | .19                 | 0.3     | .05                    | 0.3     | .41                     | 1.0     | -.11                     | -.08    | .10                     | 0.8     |
| Tashkent          | 41° N. | 69° E.  | .02                 | 0.0     | .05                    | 0.2     | .00                     | 0.0     | .05                      | 0.1     | .00                     | 0.0     |
| Joshin            | 41° N. | 129° E. | .10                 | 0.4     | .00                    | 0.3     | .45                     | 0.9     | -.00                     | -.02    | .01                     | 0.0     |
| Leh               | 34° N. | 78° E.  | .13                 | 1.2     | -.12                   | -.05    | .53                     | 0.6     | .22                      | 0.3     | .18                     | 1.0     |
| Nagasaki          | 35° N. | 130° E. | -.05                | -.01    | -.04                   | -.01    | .09                     | 0.4     | -.20                     | -.05    | -.07                    | -.02    |
| Nanking           | 32° N. | 119° E. | .39                 | 1.8     | .55                    | 4.0     | .00                     | 2.0     | .32                      | 1.3     | .13                     | 0.7     |
| Bushire           | 29° N. | 51° E.  | -.09                | -.02    | -.41                   | -.13    | .01                     | 0.0     | -.07                     | -.01    | .13                     | 0.3     |

TABLE 3.—Correlation of Monthly Means of Solar Radiation and Atmospheric Pressure (continued)

| Station   | Lat.   | Long.   | Year,<br>120 months |         | Mar.-May,<br>30 months |         | June-Aug.,<br>30 months |         | Sept.-Nov.,<br>30 months |         | Dec.-Feb.,<br>30 months |         |
|---|--------|---------|---------------------|---------|------------------------|---------|-------------------------|---------|--------------------------|---------|-------------------------|---------|
|   |        |         | r                   | b<br>mb | r                      | b<br>mb | r                       | b<br>mb | r                        | b<br>mb | r                       | b<br>mb |
| <b>ASIA (continued) :</b>                         |        |         |                     |         |                        |         |                         |         |                          |         |                         |         |
| Hyderabad   | 25° N. | 68° E.  | .08                 | 0.2     | -.37                   | -1.1    | .38                     | 0.8     | .17                      | 0.3     | -.08                    | -0.2    |
| Jask  | 20° N. | 58° E.  | .19                 | 0.5     | -.47                   | -1.3    | .45                     | 1.1     | .20                      | 0.5     | .28                     | 0.8     |
| Calcutta  | 23° N. | 88° E.  | .07                 | 0.1     | -.35                   | -1.2    | .34                     | 0.6     | .16                      | 0.3     | -.05                    | 0.1     |
| Hongkong  | 22° N. | 114° E. | .07                 | 0.2     | -.12                   | -0.5    | .20                     | 0.5     | .15                      | 0.3     | -.01                    | -0.1    |
| Bombay  | 19° N. | 73° E.  | .06                 | 0.1     | -.31                   | -0.4    | .07                     | 0.0     | .35                      | 0.3     | .00                     | 0.0     |
| Manila  | 15° N. | 121° E. | .13                 | 0.3     | -.15                   | -0.3    | .26                     | 0.4     | .25                      | 0.5     | .02                     | 0.1     |
| Aden  | 13° N. | 45° E.  | .04                 | 0.1     | -.34                   | -0.4    | .11                     | 0.1     | .10                      | 0.1     | .09                     | 0.2     |
| Port Blair  | 12° N. | 93° E.  | .16                 | 0.3     | -.10                   | -0.3    | .44                     | 0.5     | .26                      | 0.4     | .04                     | 0.1     |
| Amni Diwi   | 11° N. | 73° E.  | .08                 | 0.3     | -.24                   | -1.4    | .05                     | 0.2     | .34                      | 1.4     | .06                     | 0.3     |
| Saigon  | 11° N. | 107° E. | .01                 | 0.0     | -.11                   | -0.3    | .34                     | 0.4     | -.11                     | -0.3    | -.05                    | -0.1    |
| Iloilo  | 11° N. | 123° E. | .14                 | 0.3     | -.08                   | -0.1    | .28                     | 0.4     | .17                      | 0.3     | .10                     | 0.5     |
| Colombo   | 7° N.  | 80° E.  | -.08                | -0.1    | -.22                   | -0.5    | -.16                    | -0.2    | .06                      | 0.1     | -.07                    | -0.1    |
| <b>INDIAN OCEAN, AUSTRALIA, AND NEW ZEALAND :</b> |        |         |                     |         |                        |         |                         |         |                          |         |                         |         |
| Batavia   | 6° S.  | 107° E. | .15                 | 0.2     | -.00                   | -0.2    | .30                     | 0.3     | .30                      | 0.3     | .10                     | 0.2     |
| Christmas Island                                  | 10° S. | 106° E. | -.01                | 0.0     | .10                    | 0.2     | .17                     | 0.2     | -.15                     | -0.3    | -.13                    | -0.2    |
| Darwin  | 12° S. | 131° E. | .12                 | 0.1     | -.03                   | -0.1    | .19                     | 0.1     | .03                      | 0.1     | -.01                    | -0.1    |
| Antananarivo                                      | 10° S. | 48° E.  | -.14                | -0.3    | -.00                   | -0.2    | .11                     | 0.2     | -.16                     | -0.2    | -.40                    | -1.2    |
| Mauritius   | 20° S. | 57° E.  | -.22                | -0.6    | -.05                   | 0.0     | -.29                    | -0.5    | -.30                     | -0.3    | -.29                    | -1.2    |
| Alice Springs                                     | 24° S. | 134° E. | .12                 | 0.4     | .16                    | 0.6     | .29                     | 0.7     | -.05                     | -0.1    | .13                     | 0.5     |
| Sydney  | 27° S. | 153° E. | .23                 | 1.0     | .19                    | 1.1     | .34                     | 1.1     | .10                      | 0.4     | .34                     | 1.7     |
| Adelaide  | 34° S. | 151° E. | .21                 | 0.5     | .18                    | 1.4     | .28                     | 1.4     | .06                      | 0.4     | .39                     | 2.5     |
| Auckland  | 35° S. | 139° E. | .18                 | 0.5     | .19                    | 1.3     | .33                     | 1.8     | -.10                     | -0.6    | -.33                    | 1.8     |
| Wellington  | 37° S. | 175° E. | .06                 | 0.5     | .24                    | 2.5     | -.02                    | -0.2    | -.06                     | -0.5    | .23                     | 1.8     |
| Dunedin   | 41° S. | 175° E. | .05                 | 0.4     | .10                    | 1.1     | -.10                    | -0.8    | -.08                     | -0.8    | -.38                    | 3.7     |
|   | 46° S. | 170° E. | .02                 | 0.2     | .05                    | 0.6     | -.19                    | -1.0    | -.07                     | -0.8    | -.36                    | 4.0     |















TABLE 5.—Mean Departures of Pressure from Normal in Millimeters for Different Departures of Solar Radiation from Normal in Calories

| Station          | Lat. | Long. | Over<br>+.010 | Year                      |                           |                    |                      | Under<br>-.010 |
|------------------|------|-------|---------------|---------------------------|---------------------------|--------------------|----------------------|----------------|
|                  |      |       |               | + .006<br>to<br>+.010     | + .001<br>to<br>+.005     | 000<br>to<br>-.005 | -.006<br>to<br>-.010 |                |
|                  |      |       |               | Latitude 70° N. to 79° N. |                           |                    |                      |                |
| Barrow           | 71   | 156   | -1.4          | .3                        | .6                        | -.5                | -1.6                 | 1.0            |
| Upernivik        | 73   | 56    | 0             | -.3                       | .4                        | .4                 | -.9                  | -.3            |
| Spitsbergen      | 78   | E. 14 | -.6           | -.4                       | -.1                       | .8                 | 1.6                  | -.7            |
| Mehavn-Stetnes   | 71   | 28    | 0             | -1.2                      | .1                        | .3                 | 1.4                  | -1.0           |
| Malye Karmakouly | 72   | 53    | .9            | -1.4                      | -.2                       | .7                 | .5                   | -.2            |
| Waigatz          | 70   | 58    | -1.5          | -.8                       | -.2                       | 1.1                | .8                   | -.3            |
| Dickson          | 73   | 80    | -.6           | -2.1                      | .3                        | .6                 | .1                   | .6             |
|                  |      |       |               |                           |                           |                    |                      |                |
|                  |      |       | N.            | W.                        | Latitude 60° N. to 69° N. |                    |                      |                |
| Nome             | 64   | 165   | -.2           | -.7                       | .7                        | -.8                | -.3                  | 1.1            |
| Eagle            | 65   | 141   | .1            | .1                        | .8                        | -.1                | -1.3                 | 1.9            |
| Ft. Good Hope    | 66   | 129   | -1.6          | -.3                       | .2                        | -.7                | -.8                  | 1.4            |
| Angmagsalik      | 66   | 37    | -.6           | 0                         | -.4                       | .9                 | 1.4                  | -.7            |
| Atlantic         | 60   | 30    | .3            | -.2                       | -.7                       | .9                 | 1.1                  | -2.4           |
| Stykkishólm      | 65   | 23    | 0             | -.9                       | -.7                       | 1.1                | 1.6                  | 0              |
| Berufjördur      | 64   | 14    | .8            | -1.0                      | -.6                       | .5                 | 1.7                  | .1             |
| Bodö             | 67   | E. 14 | -.2           | -.4                       | -.1                       | -.1                | 1.9                  | -.5            |
|                  |      |       |               |                           |                           |                    |                      |                |
|                  |      |       | N.            | W.                        | Latitude 50° N. to 59° N. |                    |                      |                |
| Pacific          | 50   | 170   | 2.7           | .3                        | -.1                       | -1.4               | -1.1                 | .2             |
| Dutch Harbor     | 54   | 166   | 1.7           | -.2                       | .3                        | -1.3               | -2.4                 | 1.4            |
| Kodiak           | 58   | 152   | 1.0           | -.8                       | .3                        | -1.6               | -1.0                 | 1.8            |
| Pacific          | 50   | 150   | 1.8           | -.1                       | .2                        | -2.0               | -.9                  | .9             |
| Juneau           | 58   | 134   | -.4           | -.3                       | .3                        | -1.0               | -.5                  | 1.2            |
| Atlantic         | 50   | 40    | 0             | 0                         | -.1                       | .3                 | -.5                  | .4             |
| Atlantic         | 50   | 30    | .9            | -.7                       | -.6                       | .7                 | -1.3                 | 1.7            |
| Atlantic         | 50   | 20    | 2.3           | -.8                       | -1.2                      | .6                 | -.1                  | 2.0            |
| Valentia         | 52   | 10    | 2.3           | -1.1                      | -1.2                      | .6                 | .7                   | 1.4            |
| Aberdeen         | 57   | 2     | 2.4           | -.7                       | -.9                       | .3                 | 1.1                  | .6             |
| Utrecht          | 52   | E. 5  | 2.5           | -.3                       | -.7                       | -.2                | .8                   | .4             |
| Warsaw           | 52   | 21    | 1.2           | .4                        | -.2                       | 0                  | .7                   | -.2            |
| Moscow           | 56   | 37    | 0             | -.1                       | 0                         | -.1                | 1.1                  | -.4            |
| Leningrad        | 60   | 30    | .2            | .1                        | -.2                       | -.3                | 1.3                  | -.4            |
| Perm             | 58   | 56    | -1.2          | -.8                       | -.1                       | 1.0                | 1.5                  | -.2            |
| Barnaul          | 53   | 84    | -.4           | -.5                       | 0                         | .7                 | .6                   | -.3            |
| Tomsk            | 56   | 85    | -.9           | -.4                       | 0                         | .6                 | 1.3                  | -.4            |
| Yeniseysk        | 58   | 92    | -.4           | -.5                       | 0                         | .6                 | .1                   | -.2            |
| Irkutsk          | 52   | 104   | .2            | -.5                       | -.1                       | .5                 | .3                   | -1.2           |
| Blagovyeshchensk | 50   | 127   | .6            | -.4                       | .3                        | 0                  | .4                   | -1.0           |
| Petropavlovsk    | 53   | 159   | 1.6           | .8                        | .1                        | -.3                | -2.6                 | .5             |
| Pacific          | 50   | 170   | -.3           | .3                        | -.1                       | .2                 | -.9                  | .6             |
|                  |      |       |               |                           |                           |                    |                      |                |
|                  |      |       | N.            | W.                        | Latitude 40° N. to 49° N. |                    |                      |                |
| Pacific          | 40   | 180   | .6            | .6                        | -.5                       | -.2                | -.2                  | 1.0            |
| Pacific          | 40   | 160   | 1.3           | .2                        | -.3                       | -1.8               | .1                   | 2.3            |
| Pacific          | 40   | 140   | -.7           | -.1                       | -.1                       | -.9                | .1                   | 2.1            |
| Seattle          | 48   | 122   | -.1           | -.2                       | -.3                       | .4                 | -.2                  | .7             |
| Red Bluff        | 40   | 122   | 0             | 0                         | -.2                       | .1                 | 0                    | .3             |
| Bismarck         | 47   | 101   | -.2           | .5                        | 0                         | -.5                | -.5                  | .4             |
| Alpena           | 45   | 83    | -.1           | .1                        | .2                        | -.4                | -.4                  | .7             |
| New York         | 41   | 74    | -.1           | .3                        | .4                        | -.1                | .2                   | .5             |
| Father Point     | 48   | 68    | .3            | -.2                       | .3                        | -.8                | -.6                  | 1.3            |
| Anticosti        | 49   | 63    | 0             | -.2                       | .7                        | -.8                | -.6                  | -.1            |
| Atlantic         | 40   | 60    | -1.2          | .6                        | .5                        | -.6                | .2                   | -.7            |
| Cape Race        | 46   | 53    | -.8           | .5                        | .6                        | -.4                | -.2                  | -.9            |

TABLE 5.—Mean Departures of Pressure from Normal in Millimeters for  
Different Departures of Solar Radiation from  
Normal in Calories (continued)

| Station       | Lat. | Long. | Over<br>+.010 | Year                      |                      |                    |                      | Under<br>-.010 |
|---------------|------|-------|---------------|---------------------------|----------------------|--------------------|----------------------|----------------|
|               |      |       |               | +.006<br>to<br>+.010      | +.001<br>to<br>+.005 | 000<br>to<br>-.005 | -.006<br>to<br>-.010 |                |
|               |      |       |               | Latitude 40° N. to 49° N. |                      |                    |                      |                |
| Atlantic      | 40   | 50    | -.7           | .9                        | .2                   | -.4                | 0                    | -.4            |
| Atlantic      | 40   | 40    | 0             | 0                         | .2                   | -.2                | .2                   | .4             |
| Atlantic      | 40   | 20    | .8            | -.2                       | -.5                  | -.2                | .3                   | .7             |
| Marseille     | 43   | E. 5  | .9            | 0                         | 0                    | -.5                | -.1                  | -.2            |
| Rome          | 42   | 12    | 1.8           | -.2                       | .2                   | -.4                | -.7                  | -.6            |
| Tiflis        | 42   | 45    | .2            | 0                         | .2                   | -.4                | .6                   | -.8            |
| Krasnovodsk   | 40   | 53    | -.3           | -.2                       | .3                   | -.2                | .7                   | -.8            |
| Tashkent      | 41   | 69    | -.1           | -.1                       | .2                   | -.1                | .7                   | -.5            |
| Joshin        | 41   | 129   | .5            | 0                         | 0                    | -.4                | 0                    | -.2            |
| Vladivostok   | 43   | 132   | 0             | -.3                       | .1                   | .4                 | -.5                  | -.3            |
| Nemuro        | 43   | 145   | .5            | 0                         | .1                   | .5                 | -.3                  | .2             |
| Pacific       | 40   | 160   | -1.2          | .3                        | 0                    | .1                 | .2                   | .2             |
|               | N.   | W.    |               | Latitude 30° N. to 39° N. |                      |                    |                      |                |
| Pacific       | 30   | 170   | 1.3           | -.5                       | -.3                  | -.5                | .3                   | .8             |
| Pacific       | 30   | 150   | .6            | 0                         | -.2                  | -.4                | .5                   | 1.2            |
| Pacific       | 30   | 130   | -.3           | -.4                       | .2                   | 0                  | .4                   | -.5            |
| San Diego     | 33   | 117   | .5            | .1                        | 0                    | -.1                | 0                    | -.1            |
| Denver        | 40   | 105   | -.5           | -.1                       | -.1                  | .5                 | -.2                  | .1             |
| Abilene       | 32   | 100   | -.3           | 0                         | -.2                  | .3                 | -.3                  | .1             |
| St. Louis     | 39   | 90    | -.5           | .2                        | 0                    | 0                  | -.2                  | .2             |
| Charleston    | 33   | 80    | -.2           | 0                         | 0                    | -.3                | .1                   | .2             |
| Atlantic      | 35   | 70    | -.1           | .1                        | .1                   | -.5                | .4                   | .2             |
| Atlantic      | 30   | 50    | -.1           | 0                         | -.1                  | -.4                | .2                   | 1.0            |
| Atlantic      | 30   | 40    | -.3           | -.1                       | .1                   | -.3                | .4                   | .6             |
| Ponta Delgada | 38   | 26    | .6            | -.3                       | -.3                  | -.3                | .5                   | .7             |
| Madeira       | 33   | 17    | .5            | -.2                       | -.1                  | -.6                | .2                   | 1.0            |
| Lisbon        | 39   | 9     | .3            | -.4                       | -.1                  | -.2                | .3                   | .5             |
| Beirut        | 34   | E. 35 | .4            | -.2                       | .1                   | -.2                | -.2                  | 0              |
| Leh           | 34   | 78    | .3            | .3                        | -.1                  | 0                  | 0                    | -.2            |
| Nanking       | 32   | 119   | .5            | .3                        | .4                   | 0                  | .3                   | -1.9           |
| Nagasaki      | 33   | 130   | 0             | -.1                       | -.1                  | .1                 | .4                   | 0              |
| Pacific       | 30   | 150   | .6            | .2                        | -.3                  | .2                 | .3                   | -.3            |
| Pacific       | 30   | 170   | -.4           | -.2                       | 0                    | .1                 | .6                   | -.1            |
|               | N.   | W.    |               | Latitude 20° N. to 29° N. |                      |                    |                      |                |
| Pacific       | 20   | 180   | .6            | .2                        | -.1                  | -.1                | 0                    | -.2            |
| Midway Island | 28   | 177   | .1            | -.6                       | -.1                  | .4                 | .9                   | -.2            |
| Honolulu      | 21   | 158   | .2            | .1                        | -.1                  | 0                  | 0                    | 0              |
| Pacific       | 20   | 140   | 1.2           | .6                        | -.2                  | -.1                | -.5                  | -.3            |
| Mazatlan      | 23   | 106   | .5            | .1                        | 0                    | -.3                | -.5                  | .1             |
| Merida        | 21   | 90    | .4            | .1                        | -.1                  | 0                  | 0                    | -.1            |
| Atlantic      | 25   | 65    | -.1           | -.1                       | -.3                  | -.3                | .7                   | .6             |
| Key West      | 25   | 82    | .1            | .1                        | 0                    | 0                  | -.1                  | .1             |
| La Laguna     | 28   | 16    | 0             | -.2                       | .1                   | -.4                | .2                   | .2             |
| Helwan        | 30   | E. 31 | .3            | -.3                       | .1                   | -.1                | 0                    | .2             |
| Bushire       | 29   | 51    | 0             | -.4                       | 0                    | .1                 | .1                   | 0              |
| Jask          | 26   | 58    | 0             | -.2                       | .2                   | .2                 | -.3                  | -.3            |
| Hyderabad     | 25   | 68    | 0             | -.1                       | 0                    | .1                 | -.2                  | -.1            |
| Calcutta      | 23   | 88    | .1            | -.1                       | 0                    | .1                 | -.2                  | -.1            |
| Yunnanfu      | 25   | 102   | .3            | -.4                       | 0                    | 0                  | .6                   | -.2            |
| Hongkong      | 22   | 114   | .3            | -.1                       | .6                   | 0                  | .1                   | -.1            |
| Pacific       | 20   | 140   | 1.0           | 0                         | -.4                  | .2                 | -.3                  | .3             |
| Omura         | 27   | 142   | 0             | -.1                       | -.2                  | .3                 | .2                   | .2             |
| Pacific       | 20   | 160   | 1.0           | .1                        | -.1                  | 0                  | .1                   | -.4            |

TABLE 5.—Mean Departures of Pressure from Normal in Millimeters for  
Different Departures of Solar Radiation from  
Normal in Calories (continued)

| Station          | Lat. | Long. | Over<br>+.010 | Year                      |                       |                    |                      | Under<br>-.010 |
|------------------|------|-------|---------------|---------------------------|-----------------------|--------------------|----------------------|----------------|
|                  |      |       |               | + .006<br>to<br>+.010     | + .001<br>to<br>+.005 | 000<br>to<br>-.005 | -.006<br>to<br>-.010 |                |
|                  |      |       |               | Latitude 10° N. to 10° N. |                       |                    |                      |                |
| Port-au-Prince   | 19   | 72    | .2            | 0                         | -.1                   | -.1                | -.1                  | .3             |
| Richmond Hill    | 12   | 62    | 0             | -.1                       | -.1                   | .3                 | .1                   | .2             |
| São Vicente      | 17   | 25    | .3            | .2                        | -.1                   | -.2                | -.1                  | 0              |
| Khartoum         | 16   | E. 33 | 0             | -.3                       | .1                    | 0                  | .1                   | 0              |
| Aden             | 13   | 45    | .1            | -.1                       | .1                    | 0                  | -.2                  | .1             |
| Bombay           | 19   | 73    | .3            | -.3                       | 0                     | .1                 | -.2                  | .1             |
| Amini Divi       | 11   | 73    | .3            | -.2                       | 0                     | .1                 | -.3                  | 0              |
| Port Blair       | 12   | 93    | 0             | 0                         | .1                    | .2                 | -.1                  | -.4            |
| Saigon           | 11   | 107   | -.3           | 0                         | 0                     | .2                 | .2                   | -.3            |
| Manila           | 15   | 121   | 0             | .1                        | -.1                   | .3                 | -.2                  | -.3            |
| Iloilo           | 11   | 123   | -.1           | 0                         | 0                     | .4                 | -.2                  | -.5            |
| Guam             | 13   | 144   | -.1           | -.1                       | .1                    | .4                 | -.3                  | -.3            |
|                  | N.   | W.    |               | Latitude 0° to 9° N.      |                       |                    |                      |                |
| Colon            | 9    | 79    | .3            | 0                         | 0                     | -.1                | -.1                  | 0              |
| Georgetown       | 7    | 58    | .7            | .1                        | -.3                   | -.2                | -.3                  | .7             |
| Freetown         | 8    | 13    | -.2           | -.1                       | .1                    | -.1                | .2                   | -.1            |
| Lagos            | 6    | E. 3  | .1            | -.1                       | -.1                   | -.2                | -.1                  | .5             |
| Entebbe          | 0    | 32    | -.2           | -.2                       | .1                    | .1                 | -.1                  | .1             |
| Colombo          | 7    | 80    | .1            | -.1                       | 0                     | 0                  | 0                    | .1             |
| Yap Island       | 9    | 138   | -.1           | 0                         | 0                     | .3                 | .1                   | -.4            |
|                  | S.   | W.    |               | Latitude 0° to 9° S.      |                       |                    |                      |                |
| Taperinha        | 2    | 54    | .1            | 0                         | 0                     | 0                  | 0                    | 0              |
| Quixeramobim     | 5    | 39    | 0             | 0                         | -.1                   | .1                 | 0                    | .3             |
| Zanzibar         | 6    | E. 39 | 0             | -.1                       | .1                    | .1                 | -.2                  | 0              |
| Batavia          | 6    | 107   | 0             | .1                        | 0                     | .2                 | -.1                  | -.2            |
| Port Moresby     | 9    | 147   | .1            | 0                         | 0                     | .4                 | -.2                  | -.3            |
| Ocean Island     | 0    | 169   | .5            | .1                        | 0                     | .1                 | -.3                  | 0              |
|                  | S.   | W.    |               | Latitude 10° S. to 19° S. |                       |                    |                      |                |
| Apia             | 13   | 171   | .5            | .1                        | -.1                   | -.2                | .1                   | -.1            |
| La Paz           | 16   | 68    | 0             | 0                         | .1                    | 0                  | -.4                  | .1             |
| Cuiabá           | 16   | 56    | .3            | 0                         | 0                     | 0                  | -.1                  | 0              |
| Ondina           | 13   | 38    | 0             | 0                         | .1                    | 0                  | .1                   | -.1            |
| St. Helena       | 16   | 6     | .8            | .1                        | 0                     | -.2                | -.2                  | 0              |
| Salisbury        | 18   | E. 31 | -.2           | -.1                       | .2                    | -.2                | 0                    | .2             |
| Antananarivo     | 19   | 48    | -.1           | -.1                       | -.1                   | .2                 | 0                    | .2             |
| Christmas Island | 10   | 106   | -.1           | 0                         | 0                     | 0                  | 0                    | 0              |
| Darwin           | 12   | 131   | -.2           | -.1                       | 0                     | .4                 | -.3                  | -.3            |
|                  | S.   | W.    |               | Latitude 20° S. to 29° S. |                       |                    |                      |                |
| Catamarca        | 28   | 65    | .6            | .1                        | 0                     | .2                 | -.4                  | .1             |
| Goya             | 29   | 59    | .7            | .3                        | -.2                   | .3                 | -.4                  | -.2            |
| Asunción         | 25   | 58    | .7            | .3                        | -.2                   | .2                 | -.4                  | -.1            |
| Curitiba         | 25   | 49    | .2            | -.2                       | .1                    | .2                 | -.1                  | -.4            |
| Rio de Janeiro   | 23   | 43    | .4            | -.1                       | 0                     | .1                 | -.5                  | 0              |
| Salta            | 25   | 65    | .6            | .2                        | -.2                   | .2                 | -.4                  | -.1            |
| O'Okiep          | 30   | E. 18 | .1            | -.1                       | .2                    | -.2                | -.1                  | -.2            |
| Kimberley        | 29   | 25    | .1            | -.1                       | .2                    | -.3                | .3                   | -.3            |

TABLE 5.—*Mean Departures of Pressure from Normal in Millimeters for Different Departures of Solar Radiation from Normal in Calories (continued)*

| Station                            | Lat. | Long.  | Over<br>+.010 | Year                      |                       |                    |                      | Under<br>-.010 |
|------------------------------------|------|--------|---------------|---------------------------|-----------------------|--------------------|----------------------|----------------|
|                                    |      |        |               | + .006<br>to<br>+.010     | + .001<br>to<br>+.005 | 000<br>to<br>-.005 | -.006<br>to<br>-.010 |                |
|                                    |      |        |               | Latitude 20° S. to 29° S. |                       |                    |                      |                |
| Bulawayo .....                     | 20   | 29     | 0             | -.1                       | .2                    | -.1                | -.3                  | -.1            |
| Durban .....                       | 30   | 31     | .1            | -.1                       | .4                    | -.4                | .2                   | -.7            |
| Mauritius .....                    | 20   | 57     | -.2           | -.2                       | -.1                   | .2                 | .2                   | .4             |
| Alice Springs .....                | 24   | 134    | 0             | 0                         | .1                    | .3                 | 0                    | -.7            |
| Brisbane .....                     | 27   | 153    | .4            | .4                        | .1                    | -.3                | -.1                  | -.8            |
|                                    | S.   | W.     |               | Latitude 30° S. to 39° S. |                       |                    |                      |                |
| Santiago .....                     | 33   | 71     | .3            | 0                         | -.1                   | .1                 | -.1                  | 0              |
| Córdoba .....                      | 31   | 64     | .6            | .3                        | -.3                   | .1                 | -.4                  | -.1            |
| Bahía Blanca .....                 | 39   | 62     | .7            | .4                        | -.2                   | 0                  | -.8                  | .2             |
| Buenos Aires .....                 | 35   | 58     | 1.0           | .3                        | -.1                   | .2                 | -.5                  | .1             |
| Port Elizabeth .....               | 34   | E. 26  | 0             | 0                         | 0                     | -.1                | 0                    | -.1            |
| Adelaide .....                     | 35   | 139    | 0             | .1                        | 0                     | 0                  | 0                    | -.1            |
| Sydney .....                       | 34   | 151    | .1            | .1                        | 0                     | .1                 | 0                    | -.1            |
| Auckland .....                     | 37   | 175    | .1            | 1.5                       | -.3                   | .1                 | -.2                  | -.6            |
|                                    | S.   | W.     |               | Latitude 40° S. to 49° S. |                       |                    |                      |                |
| Sarmiento .....                    | 45   | 69     | -.2           | .2                        | .1                    | .3                 | -.5                  | -.2            |
| Puerto Madryn .....                | 43   | 65     | .8            | .2                        | 0                     | 0                  | -.1.3                | .6             |
| Dunedin .....                      | 46   | E. 170 | -.1           | .2                        | 0                     | -.1                | 0                    | -.1            |
| Wellington .....                   | 41   | 175    | 0             | .2                        | 0                     | -.1                | 0                    | -.1            |
|                                    | S.   | W.     |               | Latitude 50° S. to 59° S. |                       |                    |                      |                |
| Islota de los<br>Evagelistos ..... | 52   | 75     | -.1           | -.1                       | .5                    | .2                 | -.1.0                | -.8            |
| Punta Arenas .....                 | 53   | 71     | -.4           | 0                         | .5                    | .2                 | -.1.0                | -.3            |
| Santa Cruz .....                   | 50   | 68     | -.2           | -.1                       | .4                    | .3                 | -.1.0                | -.3            |
| Cape Pembroke .....                | 52   | 58     | .1            | .5                        | .1                    | .4                 | -.1.9                | -.1            |
| South Georgia .....                | 54   | 37     | .7            | 1.2                       | -.8                   | 1.3                | -.1.9                | 2.0            |
|                                    | S.   | W.     |               | Latitude 60° S. to 69° S. |                       |                    |                      |                |
| South Orkneys .....                | 61   | 45     | -.5           | 1.0                       | -.1                   | 2.5                | -.1.5                | -.2            |











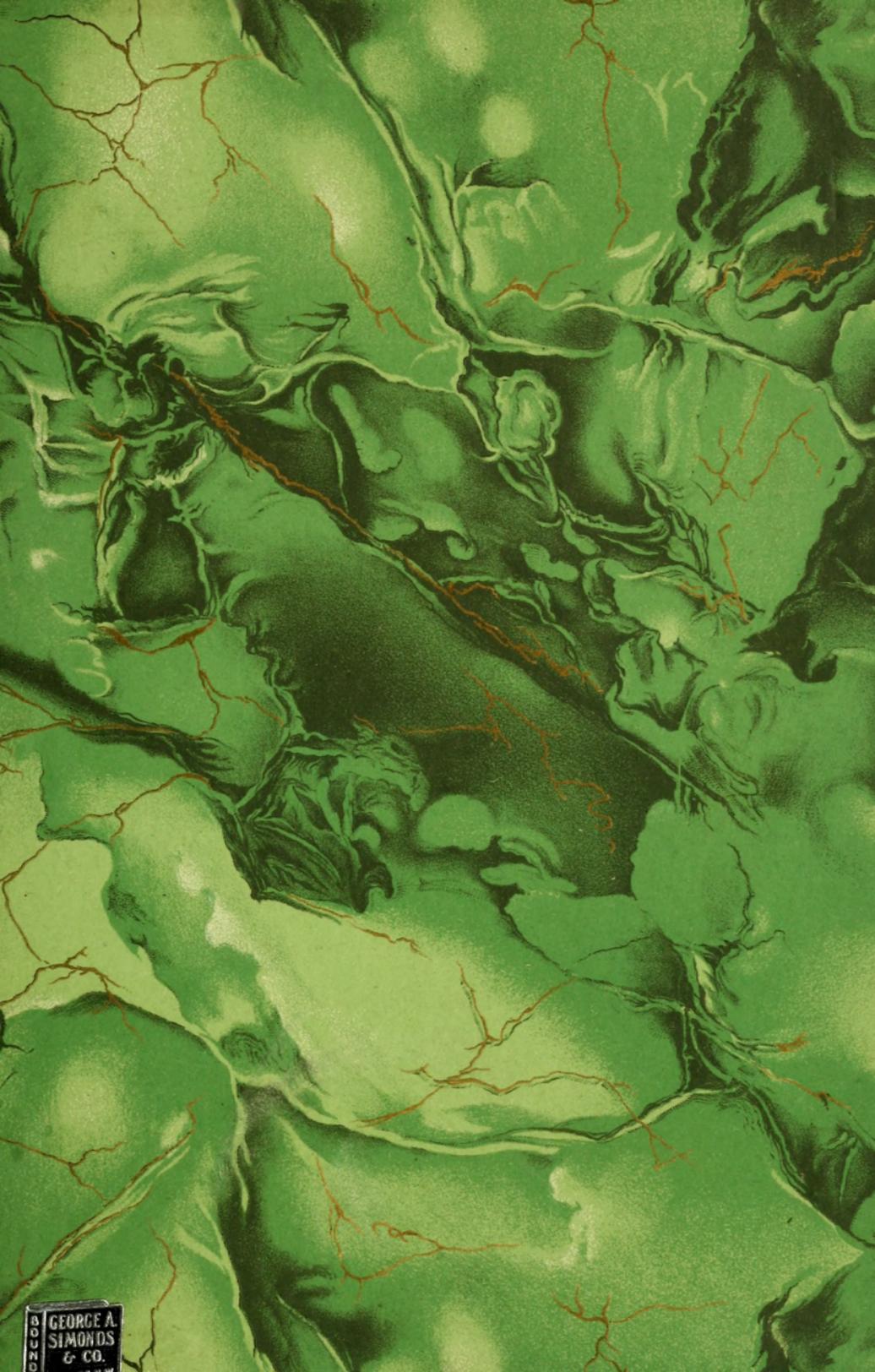












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