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# BULLETIN

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Bulletin of the Museum of Comparative Zoölogy  
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VOL. XXXVII. No. 1.

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DESCRIPTIONS OF NEW AND LITTLE-KNOWN MEDUSÆ  
FROM THE WESTERN ATLANTIC.

BY ALFRED GOLDSBOROUGH MAYER.

WITH SIX PLATES.

CAMBRIDGE, MASS., U. S. A. :  
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No. 1. — *Descriptions of New and Little-known Medusa from the Western Atlantic.* BY ALFRED GOLDSBOROUGH MAYER.

## LIST OF SPECIES.

### SCYPHOMEDUSÆ.

*Bathyluca solaris*, nov. gen. et sp.

### HYDROMEDUSÆ.

*Bougainvillia Gibbsi*, nov. sp.

*Lymnorea borealis*, nov. sp.

*Oceania carolinæ*, nov. sp.

*Oceania singularis*, nov. sp.

*Octonema gelatinosa*, nov. sp.

*Orchistoma tentaculata*, nov. sp.

*Stomotoca apicata*, L. AGASSIZ.

*Stomotoca rugosa*, nov. sp. = *Stomotoca apicata*, FEWKES.

*Syndictyon angulatum*, nov. sp.

### CTENOPHORÆ.

*Mnemiopsis McCradyi*, nov. sp.

THE Medusæ described in the following paper were obtained by the author as assistant to Mr. Alexander Agassiz in collecting new material for a work upon the Medusa-fauna of the Atlantic Coast of North America. The descriptions of Western-Atlantic Medusæ herein given will eventually be published also in the new edition of *The North American Acalephæ* now in preparation by A. Agassiz and A. G. Mayer.

Eight species are new; of these one is a Scyphomedusa, one a Ctenophore, and six are Hydromedusæ. In addition to these there is one Hydromedusa (*Stomotoca rugosa*) that we have redescribed under a new name.

The Scyphomedusa (*Bathyluca solaris*) is, judging from its structural affinities, a deep-sea type, although the single specimen from which our figures were obtained was found upon the surface of Narragansett Bay, Rhode Island.

The Medusæ described in this paper were collected at different times at Eastport, Maine; Newport, Rhode Island; Charleston, South Carolina; and in the Bahama Islands during visits made to the above localities at the suggestion of Mr. Agassiz.

## SCYPHOMEDUSÆ.

### BATHYLUCA, nov. gen.

#### *Bathyluca solaris*, nov. gen. et sp.

##### Figs. 1, 2, Plate 1.

A single specimen of a new genus of Discomedusa belonging to the family Ephyridæ was found in Narragansett Bay, Rhode Island, on July 27, 1896, by R. W. Hall, Esq. The medusa was found floating upon the surface, but as it was very much torn and battered, and as it differs widely from any of the hitherto known pelagic medusæ of our coasts, we are inclined to suspect that it may prove to be a deep-sea form, a specimen of which has wandered to the surface.

*Generic Characters.*—*Bathyluca*, nov. gen. Discomedusæ with a simple cruciform, central mouth opening, without mouth-arms or palps. There are 16 wide, radial, gastro-vascular pouches (8 ocular and 8 tentacular). There is no ring canal. There are 8 marginal sense-organs and 16 marginal tentacles. There are 4 gonads in the oral floor of the disk, and there are 4 sub-genital pits.

*Specific Characters.*—The umbrella is flat, and the gelatinous substance is quite thick. It is 45 mm. in diameter, and about 10 mm. in height. The aboral surface of the umbrella is sprinkled over with small clusters of nematocysts. There are 8 marginal sense-organs that are deeply sunken within small niches between the lappets. The entoderm of these sense-organs contains no pigment, but instead there are small white granules (Figure 2). There are 24 marginal lappets and 16 long hollow tentacles. The mouth opening is cruciform in shape, and there appear to be no mouth-arms or palps. We may, however, be mistaken in regard to this, for our specimen was much torn and battered, and it is possible that the palps may have disappeared. There are 4 wide sub-genital pits. The gonads are found in the entoderm of the lower floor of the gastro-vascular cavity, and their position is marked by 4 horseshoe-shaped ridges upon the lower floor of the sub-umbrella. There are a number of long gastric cirri that arise from the regions of the gonads

and project slightly beyond the mouth opening. The stomach is large, its diameter being about  $\frac{1}{2}$  that of the umbrella itself. Sixteen wide, simple radial pouches extend outward from the stomach cavity into the peripheral regions of the umbrella. Eight of these pouches go to the marginal sense-organs, and 8 to the tentacles which are hollow throughout almost their entire length. There are 8 radial bands of muscle fibres in the ex-umbrella. These go to the marginal sense-organs. The gelatinous substance of the disk is translucent but slightly bluish in color. The clusters of nematocysts over the aboral surface are dull yellowish brown, and the tentacles are slightly green in color.

Single specimen, Narragansett Bay, Rhode Island.

## HYDROMEDUSÆ.

**STOMOTOCA**, L. AGASSIZ, 1862.

**Stomotoca apicata**, L. AGASSIZ.

Fig. 3 ♂, Fig. 4 ♀, Plate 2.

- |        |   |   |
|--------|---|---|
| Male   | { | Saphenia apicata, McCrady, J., 1857, Gymn. Charleston Harbor, p. 27, Pl. VIII. Figs. 2, 3.  |
|        |   | Stomotoca apicata, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. p. 347.  |
| Female | { | Stomotoca apicata, Agassiz, A., 1865, North Amer. Acal., p. 168.  |
|        |   | Dinematella cavosa, Fewkes, J. W., 1881, Bull. Mus. Comp. Zool. Harvard Coll., Vol. VIII. p. 151, Pl. II. Figs. 2, 3; Pl. IV. Fig. 3. |
|        |   | Dinematella cavosa, Fewkes, J. W., 1884, Amer. Nat., Vol. XIX. p. 195, Fig.   |

*Stomotoca apicata*, L. Agassiz, is distinguished by the fact that the entoderm of the proboscis in the male is emerald green, or straw-colored; and in the female dull ochre. Also the tentacle bulbs in the male are purple, and in the female dull ochre. This species has been confounded by Brooks, 1883, and Fewkes, 1881, with another form in which the entoderm of the proboscis and tentacle bulbs is brick-red in both sexes. For this brick-red form we propose the name *Stomotoca rugosa*.

*Specific Characters.* — *Stomotoca apicata*. In the adult medusa the bell is about 4 mm. high and 2 mm. broad. It is provided with a prominent apical projection that is solid in the males, but usually hollow in the females, the gastro-vascular space leading upward into it. There are two long tentacles with large, hollow basal bulbs. In addition to the two long tentacles there are usually 6 small rudimentary tentacle bulbs upon the bell margin. The proboscis is flask-shaped, there is no peduncle, and the 4 lips are curved slightly upward. The ectoderm of the upper portion of the proboscis, under the 4 radial tubes, is thrown into folds or convolutions, and it is in this region that

one finds the gonads. There are 4 broad radial tubes and a broad circular vessel with somewhat jagged outlines. The velum is well developed. The color of the proboscis in the male varies from intense green to dull ochre-yellow, or cream-color; and the basal bulbs of the tentacles vary from faint to deep purple. In the females, the proboscis and tentacle bulbs are usually dull ochre-yellow, or cream-color, but in some few individuals the proboscis is faintly straw-colored, and the tentacle bulbs faint purple. In the female the apical projection of the bell is hollow, while in the male it is usually solid.

Common at Newport, Rhode Island, from July 15-September. Rare at Charleston, South Carolina.

The young medusa resembles the adult excepting that the apical projection to the bell is wanting, or is but little developed. There are 2 tentacles and 2 rudimentary tentacle bulbs. The sexual color difference is seen in the youngest medusæ we have observed. The hydroid stock is unknown.

### *Stomotoca rugosa*, nov. sp.

Fig. 5, Plate 2.

*Stomotoca apicata*, Fewkes, J. W., 1881, Bull. Mus. Comp. Zoöl., Vol. VIII. p. 152, Pl. II. Figs. 1, 4, 9.

*Amphinema apicatum*, Brooks, W. K., 1883, Studies Biol. Lab. Johns Hopkins Univ., Vol. II. p. 473.

The bell is 5 mm. high and 3 mm. broad; it bears an apical projection which in some specimens is long and slender, and in others is short and blunt. The substance of this projection is solid throughout. There are 2 long, well-developed tentacles and 14 small rudimentary ones. The basal bulbs of the long tentacles are large and hollow. When fully stretched, the long tentacles attain a length of 4-6 times the bell height. The velum is well developed. There are four broad radial tubes, and a broad circular vessel with jagged outlines. The proboscis is flask-shaped, the lips being flanged and quite prominent. The sexual products are found in the ectoderm of the upper portion of the proboscis where the outer surface is folded into a complex series of ridges. The bell is transparent, and the entoderm of the tentacle bulbs and of the proboscis is brick-red. In some individuals the 4 radial tubes and the circular vessel are faint red.

There is a well-marked southern variety of this species, found at the Tortugas, Florida, in which the proboscis and the tentacle bulbs are brick-red streaked with black. In some individuals, indeed, the proboscis and tentacle bulbs are coal-black.

Brooks, 1883, has described the hydroid and young medusa of this species from Beaufort, North Carolina. According to him, the hydroid stock is a *Perigonimus* very much like *P. minutus*, Allman, 1871, p. 324, Plate XI. Figures 4-6.

This medusa is common at Newport, Rhode Island, and is also found at Charleston, South Carolina. It is rare at the Tortugas, Florida.

## SYNDICTYON, A. AGASSIZ, 1862.

*Syndictyon angulatum*, nov. sp.

Figs. 6-8, Plate 3.

*Specific Characters.* — The bell is almost square in cross-section and is not quite as broad as it is high. The bell height in the specimens found by us was about 2.5 mm. There are 4 stiff tentacles that are about three-fourths as long as the bell height. The distal halves of these tentacles are conical in shape, and are covered thickly with clusters of nettle cells. The basal bulbs of the tentacles are large and swollen, and contain each a single well-developed ectodermal ocellus. This ocellus is formed by a cup-shaped invagination of ectodermal cells that are deeply stained with dark-brown pigment granules. It is probable that this structure constitutes a very primitive udoscopic eye. The velum is small. There are 4 narrow, straight, radial tubes and a slender circular vessel. The proboscis is spindle-shaped, and the mouth is a simple circular orifice. The gonads are situated within the ectoderm of the proboscis. The entoderm of the proboscis and of the tentacle bulbs varies from turquoise to blue-green in different specimens.

Several specimens of this medusa were found off Turks Islands, Bahamas, January 20, 1893.

## BOUGAINVILLIA, LESSON, 1836.

*Bougainvillia Gibbsi*,<sup>1</sup> nov. sp.

Figs. 14, 15, Plate 4.

*Specific Characters.* — Adult medusa; Figure 14. The bell is about 4 mm. in height and 3.8 mm. in diameter. The gelatinous substance is very thick, so that the bell cavity is only about one half as deep as the height of the animal. There are 4 clusters of marginal tentacles which arise from 4 large bulbous swellings, situated at the bases of the 4 radial canals. Each bulbous swelling gives rise to 4 or 5 long slender tentacles. There is a single dark-brown ocellus at the base of each tentacle upon the centripetal (lower) side. The velum is small. There are 4 straight, narrow, radial canals. The proboscis is wide and cruciform in cross-section, and the radial canals arise from the 4 corners of the cross. The proboscis is short and does not extend quite one half the distance from the inner apex of the bell cavity to the velar opening. The mouth is situated at the extremity of a short tubular neck, and there are no prominent lips. Four radially situated oral tentacles arise from the sides of the neck of the proboscis. Each one of these branches dichotomously about twice. The gonads are developed upon the sides of the stomach, and

<sup>1</sup> Named for Mrs. Theodore K. Gibbs.

in the female the ova are large and prominent. The proboscis is pearl-colored, or of a delicate green. The entodermal cores of the tentacle bulbs are red surrounded by a delicate yellow-green. The supporting lamella of the bell often displays a faint greenish tinge.

*Young Medusa.* — In the young medusa there are but 8 tentacles, 2 from each tentacle bulb. The bell is a little higher than a hemisphere and the gelatinous substance is not very thick, being of about uniform thickness everywhere instead of being very thick at the aboral pole, as in the adult. The proboscis is short and quadratic, and there are 4 short, unbranched, knob-shaped oral tentacles. When the medusa is about 3 mm. in height, the bell is still hemispherical. The proboscis is wide, shallow, and quadratic, and the oral tentacles branch once dichotomously. About 4-5 marginal tentacles arise from each tentacle bulb.

This medusa is found in Newport Harbor, Rhode Island, from July until October.

This species is distinguished from *Margelic carolinensis*, L. Agassiz, by the greater height and less width of its bell. Also in *M. carolinensis* the proboscis is long and slender, while in *B. Gibbsi* it is short, wide, and cruciform in cross-section. The proboscis of *M. carolinensis* is widest at about the middle point of its length, while that of *B. Gibbsi* is widest at its proximal base.

## LYMNOREA, PÉRON and LESUEUR, 1809.

### *Lymnorea borealis*, nov. sp.

Figs. 16-18, Plate 5.

*Specific characters.* — The bell is 3 mm. in height. The bell walls are thin, and there is a slight apical projection. There are 32 well-developed marginal tentacles with large basal bulbs. These tentacles are about  $\frac{1}{2}$  as long as the bell height, and are curled slightly upward. They are not very flexible. The velum is well developed. There are 4 straight, narrow radial tubes. The proboscis is pyriform and the mouth is surrounded by 4 short, dichotomously branching, oral tentacles. Each of these oral tentacles branches 2 times, thus giving rise to 4 tentacle tips (see Figure 18). These tips are short and knob-like and are covered with long slender nematocyst capsules borne upon thread-like filaments (see Figure 17). The gonads occupy 4 radially situated, longitudinal swellings upon the proboscis. The entoderm of the proboscis, and of the bulbs of the marginal tentacles, is red.

Three specimens, all of them being males, were found in Eastport Harbor, Maine, on September 19, 1898.

## OCEANIA, PÉRON and LESUEUR, 1809.

*Oceania carolinæ*, nov. sp.

Figs. 9-11, Plates 3, 4.

*Specific Characters.* — The bell is not quite a hemisphere, and is 1.4 mm. in diameter. The cavity of the bell is shallow, so that the gelatinous substance is quite thick. There are 16 well-developed marginal tentacles with large, hollow basal bulbs. These are only about half as long as the bell diameter, but as they are usually carried coiled in a close helix they appear much shorter. In addition to these well-developed tentacles there are 48 small rudimentary tentacle bulbs that probably never develop into tentacles. There are 64 otocysts, 4 between each adjacent pair of large tentacles (see Figure 11). Each otocyst contains 2 spherical otoliths. The velum is well developed. There are 4 narrow, straight, radial canals. The mature proboscis (Figure 10) is flask-shaped, and there are 4 simple curved lips. The gonads are developed upon the radial tubes at about one quarter the distance from the circular vessel to the proboscis. In the female the ova are very conspicuous. The entoderm of the tentacle bulbs and proboscis and of the radial tubes in the region of the gonads is bright yellow-green.

This species was extremely abundant in Charleston Harbor in the early part of September, 1897, and in June, 1898.

*Oceania singularis*, nov. sp.

Figs. 12, 13, Plate 4.

*Specific Characters.* — The bell is 2 mm. in diameter and the sides are quite straight and sloping. Near the apex of the bell there is a sharp constriction, above which there is a lens-shaped apical projection. There are 16 well-developed marginal tentacles with large, hollow, conical-shaped basal bulbs. The lashes of the tentacles are short and are covered with nematocystic cells. In addition to the 16 functional tentacles there are 16 intermediate rudimentary ones. There are 32 otocysts, each containing a single highly refractive spherical otolith. There are 4 straight radial tubes. The proboscis is quadrangular in cross-section, and there are 4 simple lips. The 4 gonads are developed upon the 4 radial canals near the base of the proboscis. The entoderm of the proximal part of each tentacle bulb is turquoise-green, and the distal part is brownish-red. The entoderm of the proboscis and of the radial tubes in the neighborhood of the gonads is of a delicate turquoise tinge.

A single specimen of this medusa was found in Newport Harbor, Rhode Island, on August 22, 1896.

## OCTONEMA, HAECKEL, 1879.

*Octonema gelatinosa*, nov. sp.

Figs. 20, 21, Plate 6.

*Specific Characters.*—Young medusa? The bell is 3.5 mm. in diameter and somewhat flatter than a hemisphere. The gelatinous substance is quite thick. In the single specimen examined there were 4 tentacles with long hollow basal bulbs. These tentacles were about 2 times as long as the bell diameter. Within the entoderm of the inner side of each tentacle bulb there was a single dark-colored pigment spot. In addition to these long tentacles there were 12 rudimentary tentacle bulbs upon the bell margin. It is possible that these might have in time developed tentacles; in the specimen observed by us, however, they were very small and apparently rudimentary. A dark-colored pigment spot was found in the entoderm of each of these tentacle bulbs. There were 8 marginal clubs, 2 in each quadrant. A dark-brown entodermal pigment spot was situated at the base of each (see Figure 21). The velum was well developed. There were 4 straight radial canals upon the upper regions of which the gonads were situated. The proboscis was a simple tube with 4 simple lips. The color of the entoderm of the 4 large tentacle bulbs, and of the radial tubes in the region of the gonads was green.

A single specimen was found in Charleston Harbor, South Carolina, September 14, 1897.

## ORCHISTOMA, HAECKEL, 1879.

*Orchistoma tentaculata*, nov. sp.

Fig. 19, Plate 5.

*Specific Characters.*—Young medusa: The bell was 6 mm. in height. The sides near the margin were slightly flanged outward. The gelatinous substance of the upper portion of the bell was very thick, so that the concavity was shallow. There were thirty-two marginal tentacles in various stages of development, the longest being about 1.5 times as long as the bell height. The tentacles possessed long, hollow basal bulbs. There were no marginal sense-organs. There were sixteen functional radial tubes, and sixteen others in process of development. The radial tubes were straight, and there were no traces of gonads upon them. The velum was well developed. The proboscis was flat and shallow, and there were 8 lips. The entoderm of the basal bulbs of the tentacles was of a delicate green. Only one immature specimen of this medusa has ever been seen; it was found at Newport, Rhode Island, August 18, 1896. The genus is closely related to *Melicertum*.

## CTENOPHORÆ.

MNEMIOPSIS, L. AGASSIZ, 1860.

**Mnemiopsis McCradyi**,<sup>1</sup> nov. sp.

Figs. 22, 23, Plate 6.

*Specific Characters.* — *Mnemiopsis McCradyi*: This species is closely allied to *Mnemiopsis Leidyi*, A. Agassiz, but differs from it chiefly in the much greater complexity of the ramifications of the chymiferous tubes within the lappets; and also in the very decided amber color of the gelatinous substance of the animal. It is also remarkable that in this species the gelatinous substance of the body is of so tough a nature that the creature may be removed from the water by hand without suffering injury. Indeed, we know of no Ctenophore that is as resistant as this species. The animal is 100 mm. in length, our figures being natural size. There are eight longitudinal rows of ciliated plates. Four of these rows, that extend down the lateral lappets, are about twice as long as are the four others that lead from the apex to the auricles. The body is markedly compressed, the broad lateral axis, extending through the lappets, being about twice as great as the auricular axis. (Compare Figures 22 and 23.) The lateral lappets are about as long as the remaining portion of the body, and are similar in shape and size to those of *M. Leidyi*, and much longer than in *M. Gardeni*. (See A. Agassiz, 1865; North American Acalephæ, Figures 20, 21 and 22, 23.) The apical sense-organ is found at the bottom of a deep cleft at the aboral pole of the body, and is similar in structure to that of *M. Leidyi*. The chymiferous tubes that wind through the lateral lappets are of a decided purple color and their ramifications are very complex. The mature ova are similar in appearance to those of *M. Leidyi*.

A single perfect specimen of this species was found in Charleston Harbor, South Carolina, September 15, 1897.

<sup>1</sup> This species is named in honor of Professor John McCrady in recognition of his important researches upon the medusæ of Charleston Harbor.

PLATE 1.

- Fig. 1. *Bathyluca solaris*, nov. gen. et sp. Oral view of the medusa.  
Fig. 2. *Bathyluca solaris*. Oral view of one of the marginal sense-organs.

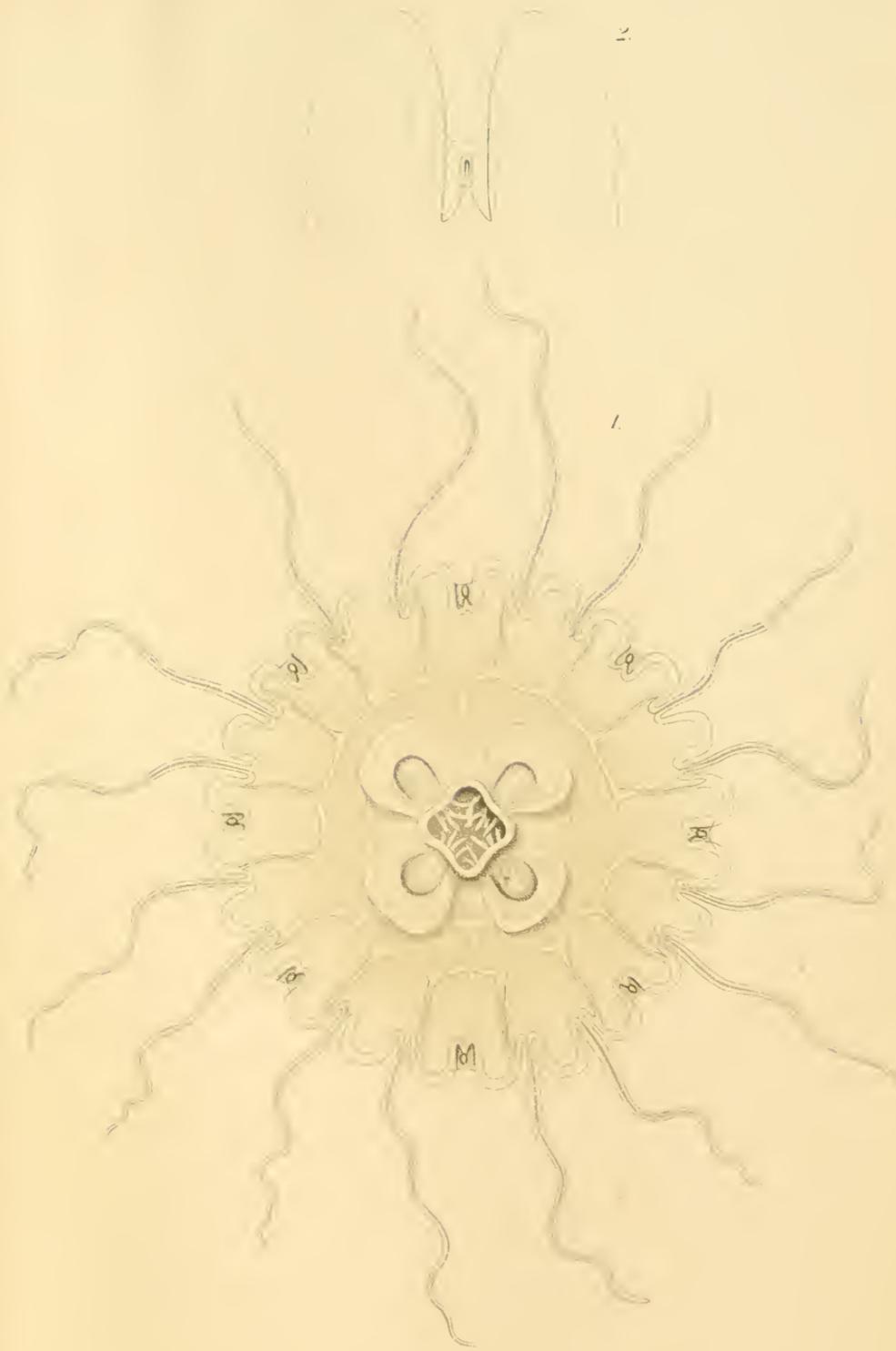






PLATE 2.

Fig. 3. *Stomotoca apicata*, L. Agassiz. Male medusa.

Fig. 4. *Stomotoca apicata*. Female medusa.

Fig. 5. *Stomotoca rugosa*, Mayer = *Stomotoca apicata*, Fewkes, 1881.

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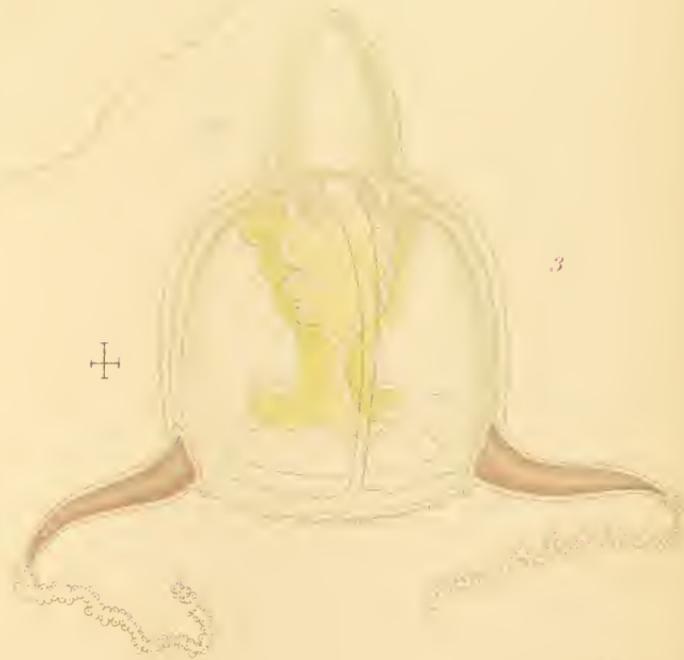
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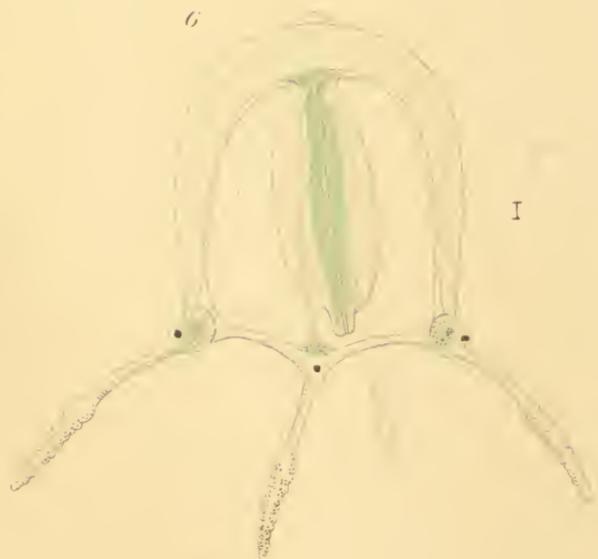
PLATE 3.

- Fig. 6. *Syndictyon angulatum*, nov. sp. Side view of medusa.  
Fig. 7. *Syndictyon angulatum*. Side view of one of the tentacle bulbs, showing the ocellus.  
Fig. 8. *Syndictyon angulatum*. Surface view of tentacle bulb.  
Fig. 9. *Oceania carolinæ*, nov. sp.

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PLATE 4.

- Fig. 10. *Oceania carolinæ*, nov. sp. Side view of proboscis and radial canal.  
Fig. 11. *Oceania carolinæ*, nov. sp. View of bell margin.  
Fig. 12. *Oceania singularis*, nov. sp.  
Fig. 13. *Oceania singularis*. View of bell margin.  
Fig. 14. *Bougainvillia Gibbsi*, nov. sp. Mature medusa.  
Fig. 15. *Bougainvillia Gibbsi*, nov. sp. Young medusa.

11.



10.



12.



13.



14.



15.



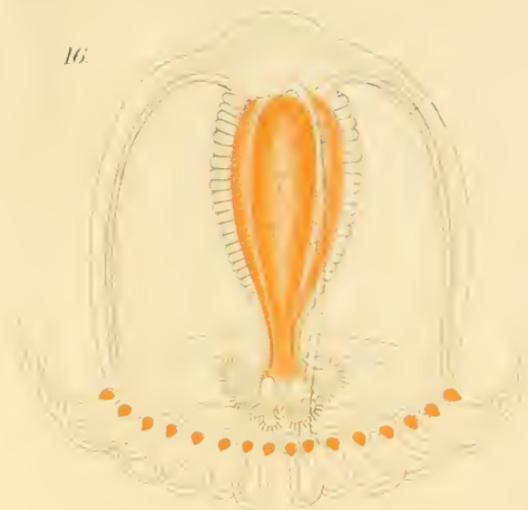




PLATE 5.

- Fig. 16. *Lymnorea borealis*, nov. sp.  
Fig. 17. *Lymnorea borealis*, nov. sp. View of nematocyst capsules upon the oral tentacles.  
Fig. 18. *Lymnorea borealis*. Side view of proboscis, showing the oral tentacles.  
Fig. 19. *Orchistoma tentaculata*, nov. sp.

16.



17.



18.



19.







PLATE 6.

- Fig. 20. *Octonema gelatinosa*, nov. sp.  
Fig. 21. *Octonema gelatinosa*, nov. sp. Marginal sense club.  
Fig. 22. *Mnemiopsis McCradyi*, nov. sp. View of broad side. Natural size.  
Fig. 23. *Mnemiopsis McCradyi*, nov. sp. View of narrow side. Uncolored figure,  
natural size.



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23



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The following Publications of the Museum of Comparative Zoölogy  
are in preparation:—

Reports on the Results of Dredging Operations in 1877, 1878, 1879, and 1880, in charge of ALEX-  
ANDER AGASSIZ, by the U. S. Coast Survey Steamer "Blake," as follows:—

- E. EHLERS. The Annelids of the "Blake."  
C. HARTLAUB. The Comatulæ of the "Blake," with 15 Plates.  
H. LUDWIG. The Genus *Pentacrinus*.  
A. E. VERRILL. The Alcyonaria of the "Blake."

Illustrations of North American MARINE INVERTEBRATES, from Drawings by BURK-  
HARDY, SONREL, and A. AGASSIZ, prepared under the direction of L. AGASSIZ.

- A. AGASSIZ. The Islands and Coral Reefs of the South Seas. "Albatross" Expedition  
of 1899-1900.  
LOUIS CABOT. Immature State of the Odonata, Part IV.  
E. L. MARK. Studies on Lepidosteus, continued.  
" On *Arachmaetis*.  
R. T. HILL. On the Geology of the Windward Islands.  
W. McM. WOODWORTH. On the Bololo or Palolo of Fiji and Samoa.  
A. AGASSIZ and A. G. MAYER. The *Acalephs* of the East Coast of the United States.  
A. G. MAYER. Some *Acalephs* from the South Pacific.  
A. G. MAYER. *Acalephs* from the Tortugas, Florida.  
AGASSIZ and WHITMAN. Pelagic Fishes Part II., with 14 Plates.

Reports on the Results of the Expedition of 1891 of the U. S. Fish Commission Steamer  
"Albatross," Lieutenant Commander Z. L. TANNER, U. S. N., Commanding, in charge of  
ALEXANDER AGASSIZ, as follows:—

- |  |  |
|--|--|
| A. AGASSIZ. The Pelagic Fauna.                               | J. P. McMURRICH. The Actinarians.                  |
| " The Echini.  | E. L. MARK. Branchiocerianthus.                    |
| " The Panamic Deep-Sea Fauna.                                | JOHN MURRAY. The Bottom Specimens.                 |
| J. E. BENEDICT. The Annelids.                                | ROBERT RIDGWAY. The Alcoholic Birds.               |
| K. BRANDT. The Sagittæ.                                      | P. SCHIEMENZ. The Pteropods and Hete-<br>ropods.   |
| " The Thalassicolæ.  | W. PERCY SLADEN. The Starfishes.                   |
| C. CHUN. The Siphonophores.                                  | L. STEJNEGER. The Reptiles.                        |
| " The Eyes of Deep-Sea Crustacea.                            | THEO. STUDER. The Alcyonarians.                    |
| W. H. DALL. The Mollusks.                                    | M. P. A. TRAÜTSTEDT. The Salpidæ and<br>Doliolidæ. |
| H. J. HANSEN. The Cirripeds.                                 | E. P. VAN DUZEE. The Halobatidæ.                   |
| W. A. HERDMAN. The Ascidians.                                | H. B. WARD. The Sipunculids.                       |
| S. J. HICKSON. The Antipathids.                              | H. V. WILSON. The Sponges.                         |
| W. E. HOYLE. The Cephalopods.                                | W. McM. WOODWORTH. The Nemerteans.                 |
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VOL. XXXVII. No. 2.

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SOME MEDUSÆ FROM THE TORTUGAS, FLORIDA.

BY ALFRED GOLDSBOROUGH MAYER.

WITH FORTY-FOUR PLATES.

CAMBRIDGE, MASS., U. S. A. :  
PRINTED FOR THE MUSEUM.  
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No. 2. — *Some Medusæ from the Tortugas, Florida.* By ALFRED GOLDSBOROUGH MAYER.

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## INTRODUCTION.

THE medusæ described in the following paper were obtained by the author while assistant to Mr. Alexander Agassiz in collecting for a work upon the Medusa fauna of the Atlantic Coast of North America. Three expeditions were made, for Mr. Agassiz, to the Tortugas, Florida, extending from June 10-22, 1897; June 25-August 19, 1898; and May 14-July 4, 1899. The manuscript has been submitted to him, and the descriptions herein given will ultimately be published also in the new edition of "North American Aculephæ" now in preparation by A. Agassiz and A. G. Mayer.

We wish to avail ourselves of this opportunity to express our appreciation of the cordiality and kindness of George R. Billbury, Esq., head

keeper of the lighthouse at Loggerhead Key, Tortugas, to whose intelligent and painstaking co-operation we owe much that may be of value in the following paper. We also wish to thank Major J. E. Sawyer, U. S. A., to whose permission we were indebted for the use of the government steamer, "George W. Childs," for transportation to and from between Key West and the Tortugas. We are also indebted for a like service to the officers of the Union Bridge Company in allowing the use of their steamer "Ambrosio Bolivar."

The Tortugas occupy what is probably the most favorable situation from which to study the pelagic life of the Tropical Atlantic. They lie upon the northern edge of the deep channel of the Gulf Stream as it issues from the Gulf of Mexico. Pure, deep ocean water surrounds them, and there are none of the shallow mud-flats that render the shore waters of Florida so turbulent, at times, that many of the more delicate pelagic animals are killed. As is well known, the Gulf Stream pours outward from the Gulf of Mexico through the Straits of Florida. The Gulf Stream does not occupy the whole cross-section of the strait, however, but according to the researches of Lieutenant, now Commander, J. E. Pillsbury (Report U. S. Coast and Geodetic Survey, 1885-87), it flows nearer to the Cuban coast than to the line of the Florida Keys. The northern limit of this great stream lies at least 28 miles south of Rebecca Shoal, the average edge being about 6 miles farther south, or 34 miles south of Rebecca Shoal (see U. S. Coast Survey Report, 1887, pp. 174, 175, Illustration 42).

The currents in the immediate vicinity of the Tortugas are extremely variable and are greatly under the influence of the tides and winds, while the tides themselves are small and easily influenced by extraneous circumstances. In the passage between Rebecca Shoal and the Tortugas the current sets practically north with the flood tide and south with the ebb. About five miles west of Loggerhead Key the southerly set of the ebb tide is stronger than the northerly current induced by the flood. There can be no doubt that the prevailing winds play an important part in setting up local currents in the immediate vicinity of the Tortugas. The prevailing E.-S.E. winds of the summer months cause a decided westerly surface drift, and this is evidenced by the fact that during this period sand is washed away from the eastern shore of Loggerhead Key and spread out into long cusped forelands<sup>1</sup> which extend from

<sup>1</sup> "Cusped foreland" is a term used by F. P. Gulliver (1896; Bull. Geol. Soc. America, Vol. VII.) to denote a sandy, projecting point of land which has cusped outlines, and is formed by the agency of currents.

both the north and south ends of the island in a westerly direction. The island thus assumes, roughly, the form of a crescent with its horns pointing westward. The north winds that occur during the winter months annually destroy these crescentic horns, but they are annually replaced by the summer breezes.

Although the northern edge of the *current* of the Gulf Stream probably never impinges against the Tortugas, a fresh south breeze is sufficient to drive its surface waters, unaccompanied by the current,<sup>1</sup> upon the islands, and under these conditions vast quantities of gulf-weed, and large numbers of *Physalia*, *Velella*, and other pelagic animals are cast up upon their shores. It is well known that the Gulf Stream bears along upon its surface vast numbers of floating animals that are drawn into it by winds and currents from the adjacent tropical regions of the Atlantic, and thus it comes about that pelagic animals from all over the Gulf of Mexico and West Indies are drifted past the Tortugas.

The temperature of the surface waters in the immediate vicinity of the Tortugas is remarkably high, being about 74°–77° F. in winter, and 80°–86° F. in summer, the average for the whole year being about 78° F. It is probably owing to this high temperature, and also to the great purity of the ocean water, that marine animals may be maintained alive in aquaria with remarkable success at the Tortugas; for the temperature of the laboratory is almost sure to be lower than that of the sea, and thus the animals in the aquaria are refreshed and thrive well.

#### COMPARISON OF THE TORTUGAS FAUNA WITH THAT OF THE SOUTHERN COAST OF NEW ENGLAND.

Ninety species of *Acalephs* have been found at the Tortugas. Of these, 62 are *Hydromedusæ*, 16 *Siphonophoræ*, 7 *Scyphomedusæ*, and 5 *Ctenophoræ*. Of these, 39 species are new to science, 33 being *Hydromedusæ*, 3 *Siphonophoræ*, 1 *Hydroid*, and 2 *Scyphomedusæ*.

The *Acalephian* fauna of the Tortugas is strictly tropical, and is totally different from that of the eastern coast of New England north of Cape Cod. A number of characteristic Tortugas forms are, however, blown northward every summer, and are thus found in considerable numbers upon the southern coast of New England, where they have been found in Newport Harbor and in Buzzard's Bay. Only three Tortugas species have, however, succeeded in establishing themselves

<sup>1</sup> See Lieutenant (now Commander) J. E. Pillsbury, 1886, Report of U. S. Coast and Geodetic Survey, Appendix No. 11, p. 287.

in Buzzard's Bay and Newport Harbor; these are: *Turritopsis nutricula*, *Margelis carolinensis*, and *Stomotoca rugosa*. But these northern specimens of the two latter forms display distinct and constant color differences which distinguish them from their near relatives in the Tortugas, and probably entitle them to rank as varieties one of the other. In addition to these three Hydromedusæ, there is one Scyphomedusa, *Dactylometra quinquecirra*, that is established in Tampa Bay, Florida, and also in the bays and estuaries of the southern coast of New England. It has not yet been found at the Tortugas, but, judging from its range of distribution, it probably will be discovered there.

There are a number of other characteristic Tortugas Acalephs that may be classed as occasional visitors to the southern coast of New England, upon which they are drifted by the agency of the prevailing S.-S.W. winds of the summer months. None of these appear to succeed in establishing themselves permanently upon the New England coast. Among these Hydromedusæ may be mentioned, *Eutima mira*, *Æquorea floridana*, *Glossocodon tenuirostris*, and *Liriope scutigera*; and among the Siphonophoræ, *Physalia pelagica*, *Velella mutica*, *Porpita Linnæana*, *Diphyes bipartita*, *Eudoxia campanula*, *Ersæa Lessonii*, *Diphyopsis campanulifera*, and *Diplophysa inermis*. No doubt further researches will increase this list of tropical Acalephs that are drifted far from their southern habitat and slowly perish in the colder waters of the north.

It is interesting to notice that the Acalephian fauna of Charleston Harbor, South Carolina, in latitude 32°, 20', is very different from that of the Tortugas, and may be said to be subtropical; for it is intermediate in character between the fauna of the Tortugas and that of the southern coast of New England. For example, the following 13 Acalephs are established both at Charleston, South Carolina, and on the southern coast of New England: *Dactylometra quinquecirra*, *Cyanea versicolor*, *Eucheilota duodecimalis*, *Epenthesis bicophora*, *Oceania languida*, *Willia ornata*, *Gemmaria gemmosa*, *Pennaria tiarella*, *Stomotoca rugosa*, *Stomotoca apicata*, *Turritopsis nutricula*, *Margelis carolinensis*, and *Nemopsis Bachei*; and the following 17 Acalephs are found both at Charleston and the Tortugas: *Dactylometra quinquecirra?* *Beroë Clarkii*, *Bolina vitrea*, *Margelis carolinensis*, *Stomotoca rugosa*, *Gemmaria gemmosa*, *Turritopsis nutricula*, *Halitiara formosa*, *Æquorea floridana*, *Eutima mira*, *Entimalphes cœrulea*, *Epenthesis folleata*, *Eucheilota ventricularis*, *Steenstrupia gracilis*, *Liriope scutigera*,

*Glossocodon tenuirostris*, and *Dyscannota gemmifera*. In addition to these there are a few *Acalephs* such as *Stomolophus meleagris* that are strictly subtropical, having been found neither at the Tortugas nor upon the southern coast of New England, but which are abundant at Charleston.

It is important to observe, also, that the *Acalephian* fauna of the Bermudas, like that of Charleston, is distinctly intermediate between the fauna of the Tortugas and that of the southern coast of New England. Of the 30 species described from the Bermuda Islands by Fewkes (1883; *Bull. Mus. Comp. Zoöl. at Harvard Coll.*, Vol. XI.), 9 are established at Newport, Rhode Island; and 16 at the Tortugas.

Not a single species of *acaleph* known from the Tortugas has been found established upon the eastern coast of New England north of Cape Cod. The fauna of the eastern coast of New England is, however, closely related to that of the northern coast of Europe (see Browne, 1895, *Trans. Liverpool Biol. Soc.*, 96; *Proc. Zoöl. Soc.*, London; Hartlaub, 1897; *Helgolands Medusen*, etc.).

To summarize, then, we have at the Tortugas a tropical fauna that gradually disappears, and is replaced by other forms, as we go northward along the coast of the United States. Only three species of the Tortugas fauna are established upon the southern coast of New England, and not one extends north of Cape Cod, Massachusetts. It appears that the great majority of the forms established at the Tortugas are incapable of surviving in the colder waters of the north, although individuals are annually driven far to the northward of their natural habitat by the agency of the Gulf Stream, and the prevailing S.-S.W. winds of the summer season.

#### COMPARISON OF THE TORTUGAS FAUNA WITH THAT OF THE TROPICAL ATLANTIC.

Very instructive facts are brought to light when we compare the *Acalephian* fauna of the Tortugas with that of the warm zone of the Atlantic Ocean. By the term "warm zone" we include all that region of the Atlantic lying between 30° N. Lat. and 10° S. Lat., and extending from the coast of Africa to the American shores. This "warm zone" includes the Canary and Cape Verde Islands, the Bahamas and West Indies, the Guinea Stream, the North and South Equatorial Currents, and the warmer parts of the Gulf Stream. At the present time about 130 species of *Hydromedusæ* are known to inhabit this "warm zone."

Haeckel, 1879, describes 30 species from the Canary Islands, 10 from the coast of Africa and Cape Verde Islands, and 10 from the "Tropical Atlantic." Maas, 1893, in his account of the Hydromedusæ of the Plankton Expedition, enumerates about 21 additional species; and 57 others have been made known by L. Agassiz, Brooks, Fewkes, and Mayer from the Bahamas, Florida Reefs, and Tortugas.

The Hydromedusan fauna of the Tortugas is so closely related to that of the Florida Reefs and the Bahama Islands, that they may be said to be practically identical; and we will therefore speak of it hereafter as the "Bahama-Tortugas" fauna.

When we come to compare the Hydromedusan fauna of the Bahama-Tortugas with that of the remaining portion of the "warm zone," exclusive of the West Indies, we are met with the remarkable fact that only 7 species are known to be common to both the Bahama-Tortugas region and the great remaining region of the "warm zone." Thus only 5 Hydromedusæ have been found in both the Canary Islands and Bahama-Tortugas region. These are *Æginella dissonema*, *Aglaura hemistoma*, *Aglaura hemistoma* var. *Nausicaa*, *Staurodiscus tetrastaurus*, and *Laodicea ulothrix*. Two other Hydromedusæ, *Glossocodon tenuirostris* and *Liriope scutigera*, are found in the midst of the ocean between the Canary Islands and the West Indies. It will be noticed that 5 out of these 7 forms that are common to both the eastern and western halves of the "warm zone" are Trachylina, or forms that develop through a free-swimming planula and pelagic actinula stage. The two others, *Laodicea ulothrix* and *Staurodiscus tetrastaurus*, belong to the Leptolinidæ and probably develop through a sessile hydroid stage with alternation of generations. In 1893 it was shown by Maas in "Die Craspedoten Medusen der Plankton-Expedition," and in *Natural Science*, Vol. II. pp. 92-99, that the great majority of the Hydromedusæ found in the midst of the Atlantic, far from land, belong to the Trachylina, and the few Leptolina discovered always show a relation to some neighboring coast. As is well known, it was the avowed object of Hensen's Plankton Expedition of 1889 to study the organic life of the high seas as free from the influence of coasts as possible. This expedition entered the region that we have designated the "warm zone" on August 20, and left it on October 20, 1889. During these two months the expedition remained for by far the greater part of the time upon the high seas, approaching land only at the Cape Verde Islands, Ascension, Fernando Noronha, and the mouth of the Amazon. As has been shown by Maas, 1893, the Hydromedusæ

found in this region consisted almost entirely of forms of Trachylina, composed of Trachynemidæ, Aglauridæ, and especially Geryonidæ. (See Craspedoten Medusen der Plankton Expedition, 1893, Taf. VII., VIII.)

The facts then appear to be that we have at the eastern extremity of our "warm zone," or in that region adjacent to the coast of Africa and in the neighborhood of the Canary Islands, a Hydromedusan fauna composed of both Trachylina and Leptolina, and the species which compose this fauna show a distinct relationship with Mediterranean forms. In the midst of the "warm zone," midway between the Canary Islands and the West Indies, the fauna is composed *almost entirely* of forms of Trachylina that are pelagic species *par excellence*, and are distributed widely over the high seas, and also reach the coasts of Africa and America. In the Bahama-Tortugas region we find a Hydromedusan fauna composed of both Trachylina and Leptolina, the Leptolina forms of which are *almost wholly distinct* from those of the Canary Islands.

We wish to call attention to the fact that a comparison of the Hydromedusan fauna of the Bahama-Tortugas with that of the Canary Islands is open to serious objections, and that the conclusions arrived at through such a comparison may be of but little value. The Canary Islands occupy a small area, and are surrounded by water of 1000-2000 fathoms in depth, while the temperature of the surface water in their neighborhood is about 10° F. colder than that of the Bahama-Tortugas region. We might then expect that a marked difference would be observed in the Hydromedusan faunæ of the two regions, for in the neighborhood of the Bahamas and Tortugas we find great areas of very shallow water having a very high temperature, while even the deepest parts of the Gulf of Mexico and Caribbean Sea have a temperature of 39½° F. It would be much fairer and far more conclusive, were we able to do so, to institute a comparison between the fauna of the Bahama-Tortugas and that of the Gulf of Guinea in the neighborhood of the Islands of Anno Bom, St. Thomas, and Fernando Po; for here the continental slope of the African coast is more gradual than at any other place, and the islands are surrounded by a depth of water not greater than 500 fathoms, having a bottom temperature of 39½° F.; which is exactly the same as that of the deep parts of the Gulf of Mexico. The temperature of the surface water is also nearly the same as that of the Bahama-Tortugas region. The conditions at the Tortugas in August and September are very similar to those in the Gulf of Guinea

in February and March, as will become clear through an inspection of Krümmel's Temperature Charts (Kettler's Zeitschrift, Bd. VI., Taf. II., III. Also, Bull. Mus. Comp. Zool. at Harvard Coll., Vol. XIV., pp. 240, 242, Figs. 168, 169). Unfortunately the Hydromedusan fauna of the Gulf of Guinea is unknown, but when we come to know it, we would not be surprised were it found that many Tortugas forms are established in this region.

The *Scyphomedusæ* of the Bahama-Tortugas region are, for the most part, distinctly West Indian types, and are quite different from the species found on the Atlantic Coast of Africa. - It is well known that these forms are much more abundant along coasts than they are in the open sea. The *Discomedusæ*, especially, are given to congregating in swarms in bays and estuaries. We are therefore not surprised to find that most of the Bahama-Tortugas species are peculiar to the West Indies and the adjacent warm coasts of North and South America. Vanhöffen (1888; *Bibliotheca Zoologica*, and 1892; *Acalephen der Plankton Expedition*) has given maps showing the geographical distribution of *Scyphomedusæ*, and from an inspection of his charts it becomes quite apparent how these forms are distributed along coasts, and that few of them have yet been found in the open sea. Indeed, according to Vanhöffen ('92) only six *Scyphomedusæ* were found by the Plankton Expedition of 1889, which confined its investigations, as far as possible, to the open sea far from coasts.

The following *Scyphomedusæ* appear to be restricted to the Bahama-Tortugas region and the West Indies: *Cassiopea frondosa*, Lamarek; *Cassiopea xamacana*, Bigelow; *Linerges mercurius*, Haeckel; *Linerges pegasus*, Haeckel; *Linuche unguiculata*, Eschscholtz; *Linuche vesiculata*, Haeckel; *Aurelia habanensis*, Mayer; *Aurelia marginalis*, L. Agassiz; *Charybdea xamacana*, Conant; *Tripedalia cystophora*, Conant; *Charybdea punctata*. In addition to these the following forms are established in the Bahama-Tortugas region, but extend also for a considerable distance northward along the coast of the United States: *Pelagia cyanella*, Péron and Lesueur; *Dactylometra quinquecirra*, L. Agassiz; *Tamoya haplonema*, F. Müller. The following species extend from the West Indies southward along the Brazilian coast; *Dactylometra lactea*, L. Agassiz; *Tamoya haplonema*, F. Müller.

There are also a few *Scyphomedusæ* of very wide distribution that are found in the region of the West Indies and Bahamas. Among these are: *Nausithoë punctata*, Kölliker, found in the Mediterranean, the Tropical Atlantic, and the Bahamas. A very close variety, *N.*

punctata var. pacifica, occurs in the Tropical Pacific. *Periphylla hyacinthina*, Steenstrup; found widely distributed throughout the whole Atlantic Ocean (see Vanhöffen, 1892; *Akalephen der Plankton Expedition*, Taf. V.). *Pelagia phosphora*, Haeckel; appears to be widely distributed over the Tropical Zone of the Atlantic Ocean (see Haeckel, 1879, p. 507, Vanhöffen, 1892, pp. 19, 20); *Atolla Bairdii*, Fewkes, is a deep sea form that has been found by the "Albatross" in the Gulf Stream, off the coast of the United States, and by Vanhöffen south of the Cape Verde Islands, off the African coast.

*The Siphonophoræ* of the Bahama-Tortugas region are almost all widely distributed Tropical Atlantic forms, and most of them have already been found by Haeckel, and by Chun, in the Canary Islands. The Siphonophoræ are pelagic animals *par excellence*, and as they undergo their development while floating within the ocean, and are quite, if not wholly, independent of the bottom, one finds them widely distributed by ocean currents. As was pointed out by Chun (1897, *Siphonophoren der Plankton Expedition*, p. 101, etc.), the Siphonophoræ of the warm regions of the Atlantic Ocean are widely distributed, distinctive species not being confined to particular regions. It is quite true, however, as Chun also shows (pp. 107-109), that, while many of the Atlantic Siphonophoræ are found in the Mediterranean, there are others which are peculiar to the Mediterranean and have not been seen in the Atlantic; while there are also a number of Atlantic species that do not appear in the Mediterranean. It is possible, as future researches may demonstrate, that there are a few Siphonophoræ that are restricted to the Gulf of Mexico, or the Bahama Banks, but as yet we are certainly not justified in making any such statement.

*The Ctenophoræ* of the Bahama-Tortugas region are not sufficiently well known, and too little has been discovered concerning their distribution to warrant us in drawing general conclusions in regard to their geographical range. *Beroë Clarkii* and *Bolina vitrea* appear to be confined to the West Indies and the southern Atlantic Coast of the United States, while *Ocyroë crystallina* probably has a wider distribution over the Tropical Atlantic. The so-called "*Eucharis multicornis*," "*Hormiphora plumosa*," and "*Beroë ovata*" of the Tortugas have not been studied with sufficient care to warrant our stating that they are actually identical with the Mediterranean species bearing the same names.

COMPARISON OF THE BAHAMA-TORTUGAS FAUNA WITH THAT OF THE  
FIJI ISLANDS AND TROPICAL PACIFIC.

In 1897, A. Agassiz and the author made a study of the Acalephian fauna of the Fiji Islands, South Pacific, in 18° S. Lat., 178° E. Long. from Greenwich. The results of our investigations have been published in the Bulletin of the Museum of Comparative Zoölogy at Harvard College, 1899, and we there show that the Hydromedusæ and Siphonophoræ of the Fiji Islands are very closely related to those of the Tortugas, Florida. All of the Hydromedusæ and Siphonophoræ found by us in the Fiji Islands belong to well-known Atlantic genera. In the case of the Hydromedusæ 4 Fijian species are so closely related to forms found at the Tortugas that we are unable to distinguish any specific difference between them, and therefore we venture to assert that they may be identical species. These forms are *Æginella dissonema*, *Halitiara formosa*, *Pandea violacea*, and *Æquorea floridana*. It will be observed that only one of these identical species belong to the Trachylina (*i. e.* *A. dissonema*), the other three being Leptolina forms. In addition to the species already mentioned, the following genera of Hydromedusæ are represented both in the Fiji Islands and in the Tortugas by very closely allied, although distinct species, — *Aglaura*, *Eutima*, *Laodicea*, *Oceania*, *Epenthesis*, and *Tiaropsis*.

Among the Siphonophoræ (*Abyla quincunx*, *Aglaisma quincunx*) and *Agalma Pourtalesii* are found both at the Tortugas and Fiji Islands. *Sphæronectes Köllikeri* of the Fiji Islands and Tropical Pacific is certainly very closely allied to *Sphæronectes gracilis* of the Tortugas and Tropical Atlantic; and the two species may eventually prove to be identical, and the same may be said of *Nectophysa Wyvillei*.

The Scyphomedusæ of the Fiji Islands are with two exceptions quite distinct from those of the Tortugas, for there are a number of characteristic Rhizostomata in the South Pacific that have no near allies in the Atlantic Ocean. We find, however, in the Fiji Islands a variety of *Nausithoë punctata* that may prove to be specifically identical with the form found at the Tortugas and in the Mediterranean. Another form, *Lineriges aquila*, of Fiji is closely allied to, although distinct from, *L. mercurius* of the West Indies.

Among the Ctenophoræ of Fiji, *Eucharis grandiformis* is a species that bears quite a close resemblance to *E. multicornis* of the Atlantic and Mediterranean, although it is certainly specifically distinct.

We must conclude, then, that the Acalephian fauna of the Fiji Islands is almost as closely related to that of the Tortugas as the latter is to

that of the Canaries. It should be borne in mind, however, that the physical conditions in the Fiji Islands are in many respects quite similar to those of the Tortugas, and are very different from those of the Canary Islands. In both the Fiji and Tortugas Islands we find luxuriant coral reefs and wide areas both of deep and shallow water, and in addition the temperature of the water in the two groups of islands is very nearly the same. In the Canaries, however, we find few corals, and no extensive shallow areas, the islands being surrounded by water of great depth. The temperature of the water there is also much lower than at the Fiji and Tortugas Islands.

We have shown that the Tortugas medusæ cannot survive in cold water, for not a single species is to be found upon the coast of New England north of Cape Cod. The Tortugas forms that are now established at the Fiji Islands must therefore have passed from the Atlantic into the Pacific Ocean somewhere within the tropical, or warm, regions of the Earth, and there can be but little doubt that the Tropical Atlantic was at one time in direct connection with the Pacific. Under these circumstances the Great Equatorial Current would pour from the Atlantic into the Pacific, and the pelagic life of the tropical regions of both oceans would become closely related. A fuller discussion of this subject, and of the researches of Hill, 1898 (Bull. Mus. Comp. Zoöl., Vol. 28) upon the geological history of the Isthmus of Panama will be found in our paper upon Fiji Acalephs in 1899.

In view of the close relationship that exists between the Acalephian faunæ of the Fiji and Tortugas Islands, one would be led to expect that the medusæ of the Gulf of Panama and the west coast of Mexico would also display a resemblance to those of the West Indies and Tropical Atlantic; and this is, indeed, the case. Maas, 1897, in his report upon the medusæ of the "Albatross" expedition of 1891, records 18 species of Hydro- and Scypho- medusæ belonging to 15 genera. All but one of the genera (*Chiarella*) are represented in the Atlantic by well-known species. Five of the Hydromedusæ from the Gulf of Panama and Galapagos Islands are represented in the Atlantic by species so closely related to them that, were they found existing side by side in the same region, they would probably be considered to be varieties one of the other. Thus:—

|                                      |                                       |   |  |
|--------------------------------------|---------------------------------------|---|--|
| <i>Stomotoca divisa</i> , Maas       | } is very<br>closely<br>related<br>to | { | <i>S. pterophylla</i> , of the Bahamas.        |
| <i>Homæonema typicum</i> , Maas      |                                       |   | <i>H. militare</i> , of the Atlantic.          |
| <i>Aglaura prismatica</i> , Maas     |                                       |   | <i>A. hemistoma</i> , of the Atlantic.         |
| <i>Liriope rosacea</i> , Eschscholtz |                                       |   | <i>L. cerasiformis</i> , of the Atlantic.      |
| <i>Geryonia hexaphylla</i> , Brandt  |                                       |   | <i>G. (Carmarina) hastata</i> , Mediterranean. |

The following table will serve to show the wide geographical range of some species of Medusæ found at the Tortugas, Florida. (0) indicates absence; (1) indicates that the species is identical with that found at the Tortugas. For example, (1) found in the column headed "Canary Islands" shows that the Canary species is identical with that found at the Tortugas. (1±) indicates the presence of a form that *may* prove to be identical with the Tortugas species. (A) indicates the presence of a closely allied but nevertheless distinct species from that found at the Tortugas.

| Name of Species.                   | Tortugas,<br>Florida,<br>24° 40' N. Lat.<br>82° 53' W. Long. | Canary Islands,<br>Atlantic Ocean,<br>28° 30' N. Lat.<br>15' W. Long. | Fiji Islands,<br>South Pacific,<br>18° S. Lat.<br>178° E. Long. | Mediterranean<br>Sea. |
|------------------------------------|--|---|---|-----------------------|
| <i>Hydromedusæ.</i>                |  |   |   |                       |
| <i>Æginella dissonema</i> . . .    | 1  | 1   | 1   | 0                     |
| <i>Aglaura hemistoma</i> . . .     | 1  | 1   | 1±  | 1                     |
| <i>Halitiara formosa</i> . . .     | 1  | 0   | 1   | 0                     |
| <i>Laodicea ulothrix</i> . . .     | 1  | 1   | A   | 0                     |
| <i>Pandea violacea</i> . . .       | 1  | 0   | 1   | 0                     |
| <i>Æquorea floridana</i> . . .     | 1  | 0   | 1±  | 0                     |
| <i>Staurodiscus tetrastaurus</i> . | 1  | 1   | 0   | 0                     |
| <i>Tiaropsis heliosa</i> . . .     | 1  | 0   | A   | A                     |
| <i>Scyphomedusæ.</i>               |  |   |   |                       |
| <i>Nausithoë punctata</i> . . .    | 1  | ?   | 1±  | 1                     |
| <i>Siphonophoræ.</i>               |  |   |   |                       |
| <i>Abyla pentagona</i> . . .       | 1  | 1   | 0   | 1                     |
| <i>Abyla quincunx</i> . . .        | 1  | 1   | 1   | 0                     |
| <i>Agalma Pourtalesii</i> . . .    | 1  | 0   | 1   | 0                     |
| <i>Diphyes bipartita</i> . . .     | 1  | 1   | 0   | 1                     |
| <i>Diphyopsis picta</i> . . .      | 1  | 1   | 0   | 0                     |
| <i>Physalia pelagica</i> . . .     | 1  | 1   | 0   | 1?                    |
| <i>Rhizophysa Eysenhardtii</i> .   | 1  | 1   | 0   | 0                     |
| <i>Rhizophysa Murrayana</i> .      | 1  | 1   | 0   | 0                     |
| <i>Sphæronectes gracilis</i> . .   | 1  | 1   | 1±  | 1                     |
| <i>Ctenophoræ.</i>                 |  |   |   |                       |
| <i>Eucharis multicornis</i> . . .  | 1?   | 1   | A   | 1                     |

## MORPHOLOGY OF TORTUGAS MEDUSÆ.

Among the new species described in this paper the following are worthy of special notice: *Pseudoclytia pentata*, a hydromedusa, is normally pentamerous, having 5 radial canals  $72^\circ$  apart, 5 gonads, and 5 lips to the proboscis. This curious species has probably been derived, phylogenetically, from a pentamerous sport of some form of Epenthesis, and represents the survival of a discontinuous, meristic variation.

*Multioralis ovalis* is a new genus of Hydromedusæ in which 4 separate manubria are situated upon a single straight chymiferous canal, which traverses the long diameter of the bell.

*Eucheilota paradoxa* is the only Leptomedusa known which gives rise to young medusæ by a direct process of budding.

*Niobia dendrotentacula* is a remarkable form of Hydromedusa in which the tentacles develop into new medusæ and are set free to propagate the species. This is accomplished through a process of growth, budding, and fusion of parts. After all of the tentacles have been cast off, the adult medusa reproduces by a sexual process.

In *Bougainvillia niobe*, Mayer, the medusa buds found upon the proboscis are formed entirely from the ectoderm, the entoderm taking absolutely no share in their construction.

*Oceania McCradyi* of Brooks, 1888, a hydromedusa that produces hydroid-blastostyles upon its gonads, has been found at the Tortugas.

In *Dysmorphosa dubia*, there appear to be 4 rudimentary gonads? upon the 4 radial canals. If future observations confirm this conjecture, the case will be almost unique among Tubularian medusæ.

## SUMMARY OF RESULTS.

There is at the Tortugas, Florida, a tropical Medusan fauna, only three species of which are established upon the southern coast of New England; and not one species of which is found upon the New England coast north of Cape Cod.

The Hydromedusæ of the Tortugas are more closely related to those of the Fiji Islands, South Pacific, than they are to those of the Canary Islands, off the Atlantic Coast of Africa.

In comparing the Hydromedusan fauna of the Tortugas with that of the Canaries, we see that the Leptolina forms of the Tortugas are almost wholly distinct from those of the Canary Islands. A number of Trachylina forms are, however, common to the two groups of islands.

As was shown by Maas, 1893, these Trachylina forms range widely over the open ocean; and this observation has been confirmed by us during the cruise of the U. S. F. C. S. "Albatross" in the Tropical Pacific, 1899-1900.

The Siphonophoræ of the Tortugas are *very* closely related to those of the Canary Islands. They also display a relationship to those of the Fiji Islands, South Pacific.

The Scyphomedusæ of the Tortugas are, for the most part, distinctly West Indian types, and are not closely related to forms known from the African coast.

33 Hydromedusæ, 3 Siphonophoræ, 1 Hydroid, and 2 Scyphomedusæ are new to science, and 44 forms are new to American waters.

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## DESCRIPTIONS OF SPECIES.

### I. HYDROMEDUSÆ.

#### DIPURENA, McCrady, 1857.

##### *Dipurena fragilis*, nov. sp.

##### Fig. 41, Plate 17.

*Specific Characters.* — The bell is 4 mm. in height, and is half egg-shaped. The bell walls are of only moderate thickness. There are 4 long slender tentacles each bearing upon its distal end a single knob-shaped mass of nematocyst cells. A single black ocellus is situated in the ectoderm of the outer surface of each tentacle bulb. The velum is prominent. There are 4 slender straight radial canals, and a narrow ring-canal. The proboscis is about 8 mm. in length, and exhibits two distinct annular swollen regions where the gonads are situated. The entoderm of the proboscis, and of the basal bulbs of the tentacles, is ochre-yellow. The entoderm of the distal nematocyst knobs of the tentacles is slightly orange. Several specimens were found at the Tortugas in June, 1897.

This species differs from *Dipurena strangulata* of Charleston (see McCrady, Proc. Elliott Soc., 1857, p. 33, Plate 9, Figures 1, 2) in that the tentacles are longer and much more slender; and the color of the entoderm of the proboscis and tentacles is light ochre-yellow instead of rich green and red as in the Charleston species.

**Dipurena picta**, nov. sp.

Figs. 45, 46, Plate 18.

*Specific Characters.* — The bell is cylindrical in shape and 3 mm. in height. The bell walls are very thick and of a tough gelatinous consistency. There are 4 slender tentacles that are not quite as long as the bell height. These tentacles bear from 3–5 bulb-shaped nematocystic swellings near their distal ends (see Figure 46). The basal bulbs of the tentacles are large, and each one bears a dark purple ocellus. There are 4 straight radial tubes and a narrow circular tube. The velum is not very well developed. The proboscis is about 5 mm. in length and exhibits two distinct annular swellings that mark the places where the gonads are situated. The entoderm of the proboscis and basal bulbs of the tentacles is of a beautiful custard-yellow. The entoderm of the nettle knobs of the tentacles is port-wine-colored.

Two specimens were found at the Tortugas, Florida, during the first week in August, 1898.

This species is closely allied to *Dipurena dolichogaster*, of the Mediterranean (see Haeckel, *Syst. der Medusen*, 1879, p. 25, Taf. II., Figures 1–7). It differs, however, from the Mediterranean form in that the bell is much thicker and more nearly cylindrical in shape, and there are fewer nematocyst-bearing bulbs upon the tentacles.

**STEENSTRUPIA**, FORBES, 1848.**Steenstrupia gracilis**, BROOKS.

Figs. 36, 37, Plate 16.

*Steenstrupia gracilis*, Brooks, W. K., 1882, *Studies Biol. Lab. Johns Hopkins Univ.*, Vol. II. p. 144.

*Specific Characters.* — The bell is 4.5 mm. in height, and is surmounted by a slender apical projection fully 2 mm. in length. There are 2 rudimentary tentacle bulbs, one short, stiff tentacle, and one long tentacle which is ringed with a number of annular swellings. The velum is well developed. There are 4 slender radial canals and a narrow ring-canal. A long slender canal runs up from the proboscis into the apical projection of the bell. In mature specimens (Figure 36) the proboscis extends a short distance beyond the velar opening. The proboscis is cone-shaped, and the mouth is a simple round opening without oral lappets. The entoderm of the proboscis is intense yellow-green and rose-color. The entoderm of the tentacles is either yellow-green or rose-colored. Found at the Tortugas, Florida, and on the North Carolina coast; in July and August.

## DINEMA, VAN BENEDEN, P. J., 1867.

*Dinema jeffersoni*,<sup>1</sup> nov. sp.

## Fig. 126, Plate 37.

*Specific Characters.* — The bell is dome-shaped and higher than it is broad; the height being about 1 mm. and the breadth 0.75 mm. The outer surface is sparsely sprinkled with nematocyst cells. There are 2 short marginal tentacles and 2 well-developed tentacle bulbs. The tentacles are covered with numerous small, wart-like, nematocyst-bearing swellings. The basal bulbs are well developed. There are 4 ocelli, one in each tentacle bulb. These ocelli are ectodermal and are situated on the centripetal sides of the bulbs. The velum is well developed. There are 4 straight narrow radial canals and a simple slender circular vessel. The proboscis is about as long as the height of the bell cavity. It is simple, round, and tubular, and the mouth-opening is situated at the extremity of a short cylindrical neck. A simple, short-style canal extends upward from the gastric cavity into the gelatinous substance of the bell. The entoderm of the tentacles and tentacle bulbs is of a delicate green. The ocelli are bright red-brown, and the entoderm of the proboscis is flesh-colored. This form is occasionally met with at the Tortugas late in May and early in June.

*Dinema floridana*, nov. sp.

*Specific Characters.* — The bell is about 4 mm. in height and 3 mm. in diameter. The gelatinous substance is thin and uniform, and the side walls of the bell are vertical. There are 2 well-developed, radially situated tentacles. Near the distal end of each of these tentacles there is a large knob-shaped swelling which terminates in a thin, nematocyst-bearing lash. The knob-shaped swelling is hollow and is connected with the general gastro-vascular system of the medusa by means of a narrow tube which extends throughout the length of the entodermal core of the tentacle. The basal bulbs are not large and there are no ocelli. In addition to the 2 long tentacles there are 2 simple rudimentary tentacle bulbs 90° from the well-developed tentacles. The velum is well developed. There are 4 straight narrow radial canals. The proboscis is flask-shaped, being narrower at its base than at the middle of its length. It extends a short distance beyond the velar opening, and the mouth is a simple round opening, at the extremity of a long narrow neck. The entoderm of the proboscis and tentacle bulbs is bright yellow. The entoderm of the swollen distal ends of the tentacles is yellow flecked with orange.

A single specimen of this medusa was found at the Tortugas, Florida, June 17, 1897.

<sup>1</sup> Named after Fort Jefferson, at the Tortugas, Florida.

**HALITIARA, FEWKES, 1882.****Halitiara formosa, FEWKES.**

*Halitiara formosa*, Fewkes, J. W., 1882, Bull. Mus. Comp. Zool. at Harvard Coll., Vol. IX. p. 276, Pl. IV. Fig. 2.

*Specific Characters.* — The bell is 3 mm. in height, and is provided with a solid apical projection. There are four long, radially situated tentacles, the distal ends of which are usually carried coiled in a tight helix. These tentacles are hollow, and have well-developed basal bulbs. In addition to these there are 24–35 short, solid tentacles that are usually carried tightly coiled. The velum is well developed. There are 4 straight, narrow radial tubes and a narrow, simple, circular vessel. The proboscis is pyriform, and extends for about half the distance from the apex of the bell cavity to the velar opening. The mouth is a simple round opening, and there are no prominent lips. The gonads are situated within the proboscis. In the case of the female the ova are very large and conspicuous. The entoderm of the proboscis and tentacle bulbs in the females is green; in the males, light brown. This medusa is certainly the commonest of all at the Tortugas, Florida, during the summer months. We have found this species in the Fiji Islands.

**ECTOPLEURA, AGASSIZ, L., 1862.*****Ectopleura minerva*, nov. sp.**

Fig. 38, Plate 16; and Fig. 125, Plate 37.

*Ectopleura*, sp., Fewkes, J. W., 1883, Bull. Mus. Comp. Zool. at Harvard Coll., Vol. XI. p. 85, Pl. I. Fig. 11.

This form possesses but two marginal tentacles instead of four, as in all other species of *Ectopleura*.

*Specific Characters.* — The bell is 2.5 mm. in height and is pear-shaped, having a well-developed apical projection. The gelatinous substance is of only moderate thickness. 8 rows of nematocyst cells extend from the tentacle bulbs to the bell apex. There are 2 well-developed tentacles, and 2 small tentacle bulbs. There are 6–9 separate, wart-like swellings upon the upper (aboral) side of each tentacle. These swellings are crowded with nettling cells. The velum is well developed. There are 4 straight, narrow, radial canals and a slender circular vessel. The proboscis is pear-shaped and is about  $\frac{2}{3}$  as long as the height of the bell cavity. A simple, short style-canal extends upward into the apical projection of the bell. The entoderm of the proboscis and tentacles is of a delicate purple, while the supporting lamella of the bell is of a

decided green. There are a large number of brilliant yellow spots in the radial canals and tentacle bulbs. This form is rare at the Tortugas, Florida. It was found by Fewkes, 1883, at the Bermudas.

## STOMOTOCA, AGASSIZ, L., 1862.

### *Stomotoca australis*, nov. sp.

#### Fig. 2, Plate 1.

*Specific Characters.* — The bell is about 2.5 mm. in height, and there is a well-developed, solid, conical projection upon the aboral surface of the umbrella. The bell walls are thin. There are 2 large diametrically opposed tentacles, which are situated at the foot of two of the radial canals. The basal bulbs of these tentacles are hollow, and are long and conical. In addition to the two long tentacles there are two rudimentary tentacle bulbs situated at the bases of the radial canals 90° away from the long tentacles. There are 8 ectodermal ocelli. 4 of these are situated upon the centrifugal surfaces of the 4 tentacle bulbs, and the 4 others occupy intermediate positions upon the bell margin. The velum is wide. The radial canals and circular tube are broad, and their edges are smooth and simple. The proboscis is short and urn-shaped, and extends about halfway from the inner apex of the bell cavity to the velar opening. The gonads occupy complexly folded and corrugated regions upon the sides of the stomach. The proboscis and tentacle bulbs are yellow, or greenish yellow. The ocelli are orange. The entodermal core of the proboscis often displays a faint orange tinge. This species is common throughout the summer at the Tortugas, Florida.

### *Stomotoca rugosa*.

*Stomotoca apicata*, Fewkes, J. W., 1881, Bull. Mus. Comp. Zoöl., Vol. VIII. p. 152, Pl. II. Figs. 1, 4, 9.

*Amphinema apicatum*, Brooks, W. K., 1883, Stud. Johns Hopkins Biol. Lab., Vol. II. p. 473.

This species has usually been confounded with *Stomotoca apicata*, L. Agassiz. *Stomotoca apicata*, L. Agassiz, is, however, distinguished from *S. rugosa* by the circumstance that the entoderm of the proboscis in the male is green, or straw-colored, and in the female, dull ochre; and the tentacle bulbs in the male are purple, and in the female, dull ochre. In the form described by Fewkes and Brooks, for which we propose the name *S. rugosa*, the entoderm of the proboscis and of the tentacle bulbs is always brick-red in both sexes.

*Specific Characters.* — The bell is 5 mm. high and 3 mm. broad. It bears an apical projection which in some individuals is long and slender and in others short and blunt. The substance of this projection is solid throughout. There are 2 long, well-developed tentacles and 14 small rudimentary ones.

The basal bulbs of the long tentacles are large and hollow. When fully stretched, the long tentacles attain a length of 4-10 times the bell height. The velum is well developed. There are 4 broad radial tubes, and also a broad circular vessel with jagged outlines. The proboscis is flask-shaped, the lips being flanged and quite prominent. The mature sexual products are found in the ectoderm of the proximal portion of the proboscis where the outer surface is folded into a complex series of ridges. The bell is transparent. The entoderm of the tentacle bulbs and of the proboscis is brick-red. In some individuals the entoderm of the 4 radial tubes and of the circular vessel exhibits a faint tinge of red. The specimens of this species from the Tortugas, Florida, are peculiar in that the red color of the proboscis and tentacle bulbs is streaked with black. In some cases, after the medusæ had been confined in aquaria for a number of days, the proboscis and tentacle bulbs became wholly black.

This medusa is very common at Newport, Rhode Island, but does not extend north of Cape Cod. It is found all along the southern coast of the United States, but is rare at the Tortugas, Florida.

*Hydroid, and young medusa.* — Brooks, 1883, describes the hydroid of this species. It is a *Perigonimus*, very much like *P. minutus*, Allman (1871; *Tubularian Hydroids*, p. 324, Plate XI. Figures 4-6). It was found growing upon the lower surface of the shell of *Limulus*, fastened to the sand tubes of *Sabellaria*. The stems are simple and unbranched and are about 0.2 mm. in height. The stems are covered for about two thirds of their length by a delicate, closely adherent film of perisarc to which foreign particles become attached. The stomach occupies about one fourth or one fifth of the stem, from which it is separated by a slight constriction. Each polypite possesses ten tentacles, which point alternately backwards and forwards, those pointing forwards being a little longer than the others. The medusæ are attached by very short peduncles to the sides of the stems. When the medusa is set free it is about 0.5 mm. in height, and there is no trace of the apical projection, which develops in the course of about 8 days.

In an abnormal individual of this species found at Newport, Rhode Island, in July, 1892, there were 4 long tentacles, one at the base of each radial canal. This medusa was maintained alive in an aquarium for more than a month. When first found it had but two diametrically opposed tentacles, each at the foot of a radial canal. The other pair of large tentacles developed later, after the first pair had attained their full length. The medusa then possessed 4 long tentacles and 12 small rudimentary tentacle bulbs. This variation is interesting, as it illustrates the close relationship between *Stomatoca* and *Modeeria*.

## PANDEA, LESSON, 1837.

*Pandea violacea*, AGASSIZ and MAYER.

Fig. 1, Plate 1.

*Pandea violacea*, Agassiz, A., and Mayer, A. G., 1899, Bull. Mus. Comp. Zoöl. Harvard Coll., Vol. XXXII. p. 160.

*Specific Characters.*—The bell is pear-shaped and 4 mm. in height. The bell walls are only of moderate thickness. There are 32 tentacles, 8 of these are each about 3 times as long as the bell height, and 24 are small and rudimentary. The basal bulbs of the long tentacles are hollow. There are 32 ocelli, one on each tentacle bulb. The velum is well developed. The proboscis is flask-shaped, its proximal portion being distended by the 4 gonads. The lips are simple and cruciform. There are 4 straight radial tubes, and a broad circular vessel. The entoderm of the proboscis and tentacle bulbs is of a delicate pink. A green streak runs along the outer surface of the entodermal lining of the radial canals. The ocelli are purple in color. The medusa is common at the Tortugas, Florida, throughout the summer. We have found a species at the Fiji Islands that appears to be identical with the Tortugas form. Our figure is drawn from a specimen found at the Tortugas.

## TIARA, LESSON, 1843.

*Tiara superba*, nov. sp.

Fig. 39, Plate 16.

*Specific Characters.*—The bell is 5 mm. in height and possesses a small apical projection. There are 4 long hollow tentacles and 12 small rudimentary tentacles. A brilliant red eye-spot is found in the ectoderm of the outer surface of each tentacle bulb. The velum is well developed. There are 4 broad straight-edged radial tubes and a broad circular vessel. The proboscis is very broad and the lips are surrounded by complexly fimbriated lappets. The gonads are found in 4 sharply folded, radially arranged regions in the upper portion of the proboscis. The proboscis is bound to the radial tubes by means of 4 mesenteries. The entire gelatinous substance of the medusa is of a delicate rose-pink. The entoderm of the proboscis and tentacles is of a rich rose-color, and the entodermal core of the proboscis is emerald-green. This medusa makes its appearance in June and continues to be common throughout the summer at the Tortugas, Florida.

## GEMMARIA, McCRADY, 1857.

*Gemmaria dichotoma*, nov. sp.

Fig. 40, Plate 17.

*Specific Characters.* — The bell is 3 mm. in height and there is a solid mitre-shaped apical projection. The bell walls are thin. There are two rudimentary tentacle bulbs and two well-developed tentacles. The entodermal core of these large tentacles is hollow. They terminate in a bulb-shaped nematocyst swelling, which in some individuals is provided with delicate bristles. A number of tentaculæ arise from the upper or "dorsal" side of the tentacle, and each one of these terminates in a bulb-shaped swelling similar to that at the distal end of the main tentacle. The youngest and least-developed of these side branches is always found nearest the bell. The basal bulbs of the tentacles are large, and there is a single deep red ocellus in the outer surface of the ectoderm of each. The velum is quite well developed. There are 4 straight radial canals and a narrow circular canal. The proboscis is pyriform and extends about half the distance from the apex of the bell cavity to the velar opening. The entoderm of the proboscis and tentacles is ochre-yellow. Several specimens were found at the Tortugas early in July.

*Gemmaria gemmosa*, McCRADY.

Figs. 137, 138, Plate 41.

*Gemmaria gemmosa*, McCrady, J., 1857, *Gynn.* Charleston Harbor, p. 49.

*Zanclea gemmosa*, McCrady, J., 1857, *Gynn.* Charleston Harbor, p. 48, Pl. 8, Figs. 4, 5.

*Specific Characters.* — Hydroid stock; *Gemmaria gemmosa*. The hydroid was found at the Tortugas, Florida, growing upon a piece of floating gulf-weed (*Sargassum*). The hydrorhiza is creeping and net-like, and gives rise at irregular intervals to short, more or less twisted hydrocauli. Both the hydrorhiza and hydrocauli are covered with a horny, chitinous perisarc, which in the hydrocaulus displays a number of annulations. The hydrocaulus is corrugated, and opaque in color, throughout its length; and in this respect differs from the European *G. implexa* described by Allman (1871, *Tubularian Hydroids*, p. 290, Plate VII.). The fully developed hydranths are only 1.5 mm. in height. They are elongate, and the diameter near the proximal end is a little greater than at the free oral extremity. The tentacles arise in 5-8 whorls from the side of the hydranth. Each whorl contains 4-6 short tentacles. Each tentacle terminates in a distal knob which is armed with a dense cluster of nematocysts. The cells of the shafts of the tentacles are vacuolated, and the tentacles themselves quite stiff and inflexible. 4-8 medusa-buds arise from the side of the hydranth immediately below the proximal whorl of tentacles.

When set free the young medusa possesses 2 well-developed diametrically opposed tentacles and 2 rudimentary tentacle bulbs (Figure 137). The 4 radial, nematocyst-bearing swellings upon the ex-umbrella extend halfway up the sides of the bell from the margin toward the apex. The bell walls are uniform, and very thin and flexible. There are 4 slender radial canals, and the proboscis is a short simple tube with no trace of gonads. Before being set free, the tentacles are carried coiled inward so that they lie protected within the bell cavity. Soon after liberation, however, the tentacles are turned outward. (Compare Figures 137 and 138.) The deep-lying entoderm of the hydranth is of a delicate creamy pink, while the more superficial entoderm is of a translucent milky color. The entodermal cells of the superficial entoderm are large and vacuolated. The hydrorhiza is of a horny yellow color. This species is quite different from *Gemmaria implexa* of Allman. It is probably the hydroid of *Zanclaea gemmosa*, McCrady, of Charleston Harbor, but not having been able to raise the medusæ we must remain in some doubt concerning its identity.

### NIOBIA, nov. gen.

#### *Niobia dendrotentacula*, nov. sp.

**Figs. 141-143, Plate 42 ; Fig. 144, Plate 43.**

*Generic Characters.* — *Niobia*. Cladonemidæ with 2 simple and 2 bifurcated radial canals. There are 4 simple lips to the proboscis, but no oral tentacles. The marginal tentacles develop into free-swimming medusæ.

There is no place in the system of Haeckel (1879; p. 101) for this genus. It cannot be placed among the *Dendronemidæ*, for it has no oral tentacles, and as it has branched radial canals it cannot be classed among the *Pteronemidæ*. It combines the essential characters of both of these subfamilies, however, and forms a good connecting link between them.

*Specific Characters.* — Adult medusa. The bell is slightly flatter than a hemisphere, and is about 4 mm. in diameter. The gelatinous substance is quite thin and uniform, but not very flexible. The tentacles are arranged in bilateral symmetry, the axis being in the diameter of the two simple radial canals (see Figure 144, Plate 43). The oldest tentacle is situated at one end, and the youngest at the other end of this axis. (Figures 142, 144.) Each half of the medusa is a reflection of the other, and the order in age of the tentacles is given by the following diagram, the oldest tentacle being numbered (1) and the youngest (7): —



Tentacles (1) and (7) are situated at the bases of the simple radial canals, while tentacles (2, 2) and (3, 3) are found at the bases of the two bifurcate canals. In addition to these there are the intermediate sets of tentacles (4, 4), (5, 5), and (6, 6); and thus the medusa possesses 12 tentacles, each successive pair being  $30^\circ$  apart. It is very remarkable that through a peculiar process of growth each tentacle bulb is developed into a young medusa which resembles the adult, and is finally set free into the water. Various stages of this process will be seen by an inspection of Figures 141, 142, and 144. The oldest tentacle is the first to be transformed into a new medusa, and the others follow in the order of their age until all of the tentacles have been cast off. The first stage in this process is the development of a hernia-like outgrowth, involving both entoderm and ectoderm, adjacent to and on the centripetal side of each tentacle bulb upon the floor of the sub-umbrella. Soon after this two pointed outgrowths appear on both sides of each tentacle bulb, and finally develop into new tentacles. These outgrowing tentacles become larger, and soon a still younger pair make their appearance centrifugal to the first, and these are soon followed by two others which lie centripetally from the oldest pair. Before this, however, 4 short canals (the radial canals of the future medusa) develop, and place the gastric cavity of the future proboscis into communication with the circular vessel. An opening then appears in the velum of the adult medusa immediately below the proboscis of the future medusa, and this constitutes the velar opening of the new animal. The proboscis becomes cruciform in cross-section, and finally the new medusa is constricted off and becomes free in the condition represented in Figure 142. Here we see that the simple radial canals, the circular canal, the velum, and the oldest tentacle are stolen directly, so to speak, from the parent medusa. The forked canals, proboscis, and younger tentacles are new growths. Even before the outgrowing medusa is detached from the old one, hernia-like outgrowths appear upon the

sub-umbrella wall near the bases of *its* tentacles, and thus the process of forming new medusæ is repeated in the next generation. The medusæ are very hardy when detached and grow rapidly, and proceed at once to develop new medusæ from their own tentacle bulbs. When detached, the bell of the new medusa is about 1.5 mm. in diameter. It is difficult to comprehend the phylogenetic history of this curious and fortuitous combination of local growth, fusion, and budding which results finally in the formation of a medusa exactly resembling the adult. It is probable, however, that it has been derived from the usual budding process so common in hydromedusæ, but that in this case a greater and greater number of parts have been taken directly from the adult medusa, until the present state has been arrived at. After the original tentacles have been cast off, new ones grow out in their places, and thus the old medusa always has 12 tentacles. After every one of the original 12 tentacles has been cast off, however, the process of forming new medusæ becomes less active and finally ceases altogether. Then the gonads develop in 4 separate interradial regions on the wall of the gastric part of the proboscis. In the female the ova become very prominent, and are finally debised into the water. I was unable to raise them, however, and know nothing of the development of the sexual generation. The proboscis is flask-shaped, and there are 4 simple cruciform lips. The entoderm of the proboscis tentacle bulbs and circular canal is ochre-yellow, all other parts of the medusa being transparent. The medusa is very active and thrives well in confinement. Large numbers of them appeared at the Tortugas, Florida, on May 21, and continued more or less common until June 4, 1899.

### TURRITOPSIS, McCrady, 1857.

#### *Turritopsis nutricula*, McCrady.

*Turritopsis nutricula*, McCrady, J., 1857, *Gymn. Charleston Harbor*, p. 25, Pls. IV., V., VIII. Fig. 1.

*Modeeria multitentacula*, Fewkes, J. W., 1881, *Bull. Mus. Comp. Zool. Harvard Coll.*, Vol. VIII. p. 149, Pl. III. Figs. 7-9.

This medusa was well described by McCrady in 1856 and 1857. Fewkes, 1881, however, redescribed it as a new species under the name "*Modeeria multitentacula*." To add to the confusion respecting this species, a medusa that has since been identified by Martha Bunting, 1894, as *Podocoryne carnea*, was described by A. Agassiz, 1862, 1865, under the name of "*Turritopsis nutricula*." The latter author was deceived by the close resemblance of the young of *Podocoryne carnea* to the young medusa of *T. nutricula*, McCrady, 1857, into the belief that the two were identical. The mature medusæ, however, are easily distinguished one from the other, and the hydroid stocks differ widely from each other.

*Specific Characters.* — Mature medusa. The bell is pear-shaped with thin walls, and is 4 mm. in height. There are 40-50 marginal tentacles that are capable of much contraction and extension. There is a single brown, ectodermal, pigment spot upon the centripetal side of each tentacle near the point of its junction with the tentacle bulb. The velum is well developed. There are 4 straight, narrow, radial canals. The proboscis is wide and fills about half of the cavity of the bell. The upper portion of the proboscis consists of highly vacuolated cells, or chambers, through the midst of which run the 4 radial canals. The mouth opening of the proboscis is found at the end of a short, narrow, cylindrical neck, and is surrounded by 4 radially arranged nematocyst-bearing knobs. The gonads are situated within the proboscis. The entoderm of the proboscis is dull yellow, streaked with brownish orange. The ocelli of the tentacle bulbs are orange, or brown in color.

This medusa is extremely abundant from the coast of Cuba to Newport, Rhode Island. It is not found north of Cape Cod, Massachusetts. It is very common in Charleston Harbor, South Carolina, where it is infested by the young of *Cunoctantha octonaria*. This medusa is one of the few that appears to develop from the hydroid stock both at the Tortugas and at Newport, Rhode Island. For while medusæ indigenous to the Tortugas are often driven into Newport Harbor by southerly winds, very few of these southern visitors establish themselves permanently in the northern waters.

The hydroid stock of this species was found by Brooks, 1886, at Morehead City, North Carolina. It is a Tubularian belonging to the genus *Dendroclava*. Brooks gives a number of good figures of it in his paper in the *Memoirs of the Boston Society of Natural History*, Vol. III., 1886.

### CYTAEIS, ESCHSCHOLTZ, 1829.

#### *Cytaeis gracilis*, nov. sp.

**Figs. 122-124, Plate 36.**

*Specific Characters.* — Mature medusa; Figure 122. The bell is dome-shaped and a little broader than it is high, and the aboral apex terminates in a slight projection. The animal is 3 mm. in diameter. The gelatinous substance of the bell is of only moderate thickness. There are 8 quite stiff curled tentacles; 4 radial and 4 interradial. The radial tentacles are about two thirds as long as the bell height, while the interradial ones attain only about one half this length. The basal bulbs of all of the tentacles are large and deeply pigmented. The velum is broad. There are 4 straight, narrow, radial canals, and a simple slender circular vessel. The proboscis is mounted upon a short, wide peduncle. The gastric portion of the proboscis is only about one half as long as the height of the bell cavity. The mouth is a simple, round opening, surrounded by 8 unbranched oral tentacles. 4 of these tentacles are radial and 4 interradial in position, and each one terminates in a knob-like end formed of spindle-shaped

nematocyst cells. Medusa buds arise from the sides of the gastric portion of the proboscis. When set free each medusa possesses 4 short equally developed tentacles. The entoderm of the proboscis is usually red in color, although sometimes the inner core is red or pink and the outer annulus is green. Each tentacle bulb is provided with a dense mass of red entodermal pigment, which in the case of the radial tentacles extends for a considerable distance up the course of the radial canals.

*Young Medusæ.* — The youngest medusa found free in the water was 1.5 mm. in height (Figure 124), and the bell was about twice as high as it was broad. The gelatinous substance was quite thin. There were only 4 marginal tentacles and these were radial in position. The distal tips of these tentacles were slightly knobbed and their entoderm was tinged with green. There were 8 simple oral tentacles, and the proboscis lacked a peduncle. In an older individual, which was 2.5 mm. in height, the bell was pyriform. The proboscis possessed a peduncle, and there were 8 marginal tentacles, 4 radial and 4 interradial. There were no traces of medusa buds upon the proboscis.

This medusa was quite common at the Tortugas, Florida, about the middle of June, 1899.

### DYSMORPHOSA, PHILIPPI, 1842.

#### *Dysmorphosa dubia*, nov. sp.

Figs. 64-66, Plate 22.

*Specific Characters.* — The bell is egg-shaped and 1.5 mm. in height. The bell walls are thin and flexible. There are 8 quite stiff tentacles (Figure 66) that are carried curled slightly upward. The distal ends of these tentacles are thickly covered with netting cells. A very large black ocellus is situated in the ectoderm of the under side of each tentacle bulb. The velum is well developed. There are 4 straight, narrow, radial tubes; and a slender circular canal. The proboscis is pear-shaped, and there is a slightly developed peduncle. 4 radially situated oral tentaculæ surround the mouth. Each one of these terminates in a knob-like cluster of nematocysts (Figure 65). 4 small, rudimentary gonads? appear to be developed at points midway along the lengths of the 4 radial canals. The entoderm of the proboscis, tentacle bulbs, and gonads? is of a delicate yellow. One specimen was found at the Tortugas, Florida, on July 20, 1898.

The presence of what appear to be gonads? upon the radial tubes is certainly remarkable; it should be remembered, however, that such appearances are not unknown among genera of Tubularian medusæ that normally bear their gonads upon the proboscis. In the case of *Dipurena halterata* bodies that are very similar in general appearance to rudimentary gonads are found upon the radial canals. (See Forbes, E., 1848, *British Naked-Eyed Medusæ*, p. 53, Plate VI, Figures 1, b, c, d. Also Browne, E. T., 1898, *Proc. Zoöl. Soc. London*, p. 816, Plate 49, Figure 2.)

**Dysmorphosa minuta**, nov. sp.

Fig. 42, Plate 18.

*Specific Characters.* — The medusa is extremely minute, the bell being only 0.3 mm. in height. It is pear-shaped and the walls are quite thick. The gelatinous substance is remarkably delicate, and the medusa soon contracts into a shapeless mass in captivity. There are 8 marginal tentacles, with well-developed basal bulbs. The velum is small. There are 4 straight, slender radial canals and a narrow circular vessel. The proboscis possesses a distinct peduncle. The gastric portion as well as the peduncle is 4-sided in cross-section. 4 well-developed oral tentacles surround the mouth, one being situated at each radial corner. Each of these tentacles terminates in a knob-shaped distal end, which is thickly covered with nematocysts. The entodermal cells of the oral tentacles are disk-shaped and highly vacuolated. Several medusa buds in various stages of development are found upon the upper interradial regions of the gastric portion of the proboscis. In some specimens the entoderm of the proboscis and tentacle bulbs is turquoise blue, and in others lilac. The medusa was common at the Tortugas, Florida, in the middle of July, 1898. It is the smallest hydromedusa known. Its color is also very different from *D. fulgurans*, A. Agassiz, of Newport Harbor.

**BOUGAINVILLIA**, LESSON, 1836.**Bougainvillia frondosa**, nov. sp.

Fig. 5, Plate 3.

*Specific Characters.* — The bell is dome-shaped and about 2 mm. in height. There are 4 bunches of marginal tentacles, which are situated at the bases of the 4 radial canals. Each tentacle bulb gives rise to but 2 tentacles, thus making 8 in all. There are no ocelli at the bases of the tentacles. The velum is small. There are 4 straight, simple, radial tubes. The proboscis is short, thick, and flask-shaped, and extends only about one half of the distance from the inner apex of the bell cavity to the velar opening. There are 4 radially situated oral tentacles, each of which branches dichotomously two or three times. The mature gonads are found in 4 radially situated swollen regions upon the ectoderm of the proboscis, above the origins of the oral tentacles. There are a number of flask-shaped bodies with narrow necks protruding from the surface of the proboscis in the region of the gonads. Each of these flask-shaped capsules is filled with yellow-colored cells. Although it is possible that these may be developing planulæ, we incline to the opinion that they are parasitic zoöxanthellæ. We are led to this opinion on account of the decided yellow-green color of these cells, and also because we have found similar capsules scattered irregularly over the surface of the sub-umbrella of *Laodicea*

ulothrix at the Tortugas. The entoderm of the proboscis and tentacle bulbs is cream-colored, and the tips of the tentacles are turquoise. A single specimen of this medusa was found at the Tortugas, Florida, on June 11, 1897, and another in June, 1899.

### *Bougainvillia niobe*, MAYER.

*Bougainvillia niobe*, Mayer, A. G., 1894, Bull. Mus. Comp. Zool. at Harvard Coll., Vol. XXV. p. 236, Pl. I. Fig. 2.

*Specific Characters.*—The bell is 6.75 mm. in height and 4.8 mm. broad. The bell walls are thick and gelatinous. The marginal tentacles arise from 4 radially situated bulbous swellings, each one of which gives rise to 6–8 tentacles. At the base of each tentacle, upon the inner or centripetal side, there is a dark-colored pigment spot, or ocellus. This is an ectodermal structure, and it projects slightly from the surface of the tentacle. The tentacles are not very flexible and are about as long as the bell height. The velum is well developed. There are 4 straight, narrow, radial tubes. The proboscis is wide, but not very long, extending only about half the distance from the apex of the bell cavity to the velar opening. There is a small peduncle. There are 4 large, radially arranged bunches of oral tentacles. These arise as 4 main stems, each of which branches dichotomously 4 times, thus giving rise to 16 tentacle tips from each quadrant of the proboscis. These terminal tentacle tips are slightly knobbed, and are composed chiefly of nematocyst cells. The tentacles of the proboscis are very flexible and may be observed waving gracefully to and fro within the cavity of the bell.

The most remarkable characteristic of this species is the presence of numerous medusa buds that arise from the gastric region of the proboscis. These budding medusæ are found in 8 radially arranged clusters situated near to and on both sides of the places where the 4 radial tubes enter the gastric portion of the proboscis. A study of sections of the proboscis of medusæ killed in Flemming's Chrome-Osmic-Acetic, and stained in Kleinenberg's 70% Alcoholic Hæmatoxylin, has shown that *the proliferating medusæ are formed entirely from the ectoderm*, the entoderm taking no part whatsoever in their formation. There is a very well-defined lamella between the ectoderm and the entoderm of the proboscis of the parent medusa, and the membrane of this lamella is never broken during the time of the formation of the medusa bud from the ectoderm of the proboscis. Indeed, the gastro-vascular cavity of the budding medusa is never connected with that of the parent. The medusa buds develop very much as has been demonstrated by Chun (1895; Bibliotheca Zoologica, Heft 19, Lfg. 1, p. 1–51, Taf. I., II.) in *Rathkea octopunctata*, and *Lizzia Claperèdei*; excepting that while in the forms studied by Chun the gastro-vascular cavity of the bud finally acquires a connection with that of the parent, in *Bougainvillia niobe* no such connection is ever formed. Chun concluded that medusa buds which are derived entirely from ectoderm cannot be homologous with those that are

formed from both ectoderm and entoderm in the manner commonly observed in Hydroids, and in the medusa of *Sarsia*; for it is necessary, if organs be homologous, that they have a similar origin. It has occurred to us, however, that Chun may be mistaken in this conclusion, and that his statement may be more a matter of definition than of fact; for it may well be that, in the course of phylogeny, the entoderm has come to take less and less part in the formation of medusa buds, until finally, as in the case of *Bougainvillia niobe*, it has abandoned all share in their formation. Considered from the physiological standpoint it may be that in *B. niobe* the ectoderm of the parent proboscis being very thick, there is an abundance of cells from which to form the bud without having resource to those of the deep-lying and somewhat inaccessible entoderm. When set free the young medusa possesses 4 radial tentacles. The bell of the medusa is transparent, and the entoderm of the proboscis and tentacle bulbs is rosin-yellow.

Found in Nassau Harbor, New Providence Island, Bahamas, in March, 1893.

It is interesting to notice that Hartlaub (1897; *Hydromedusen Helgolands*) has shown that the sex cells of *Bougainvillia superciliaris* are first found in the entoderm of the young medusa, and that as development proceeds they pass into the ectoderm, where they become mature. It is possible that the cells which give rise to the medusa buds of *Bougainvillia niobe* are similarly derived from the entoderm of the young medusa. We have not seen the young and immature medusa of *B. niobe*, and in the mature animal the supporting lamella between the ectoderm and entoderm of the proboscis is very distinct and unbroken, and we have never succeeded in discovering any cells which were passing through it.

### *Margelis carolinensis*, AGASSIZ, L.

*Hippocrene carolinensis*, McCrady, J., 1857, *Gymn. Charleston Harbor*, p. 62, Pl. 10, Figs. 8-10.

*Margelis carolinensis*, Agassiz, L., 1862, *Cont. Nat. Hist. U. S.*, Vol. IV. p. 344.

In the Tortugas and Charleston Harbor examples of this species, the entoderm of the tentacle bulbs and of the proboscis is of a delicate sage-green color; while the gonads are cream-colored, and the tentacular ocelli dark-brown or black. In northern examples of this medusa, found at Newport, Rhode Island, and Naushon, Massachusetts, A. Agassiz describes the color of the tentacle bulbs as brilliant red surrounded by a green edge bordered with light yellow; and the digestive cavity as brick-red, or green. No such brilliant coloration has been seen in the southern specimens. The medusa is not very common at the Tortugas, being met with only occasionally during the summer months. In Charleston Harbor, South Carolina, however, it is extremely abundant.

**LIZZIA, FORBES, 1846.*****Lizzia elegans*, nov. sp.****Fig. 127, Plate 38.**

*Specific Characters.* — The bell is 3-7 mm. in height, and the gelatinous substance is of moderate and nearly uniform thickness. The sides of the bell are almost straight and vertical, and the top is dome-shaped. There are eight groups of marginal tentacles, 4 radial and 4 interradial. Each radial group is composed of 4, and each interradial of 3 tentacles. The tentacles are quite stiff and curve upward, and are only about one-half as long as the bell height. There is a small dark-brown ectodermal ocellus upon the under (oral) side of each tentacle near the basal bulb. The velum is wide and provided with strong muscles. There are 4 straight, narrow, radial canals, and a simple circular vessel. There is a well-developed conical peduncle to the proboscis, down which the radial canals lead in their course to the gastric sac. The gastric part of the proboscis is cruciform in cross-section and pear-shaped in general longitudinal contour. The mouth is a simple round opening without prominent lips. The oral tentacles arise from the four radial sides of the proboscis at a short distance above the mouth. Each tentacle branches dichotomously 3 times and then each tip terminates in three small branches which are covered with nematocysts. The entodermal cells of the oral tentacles are chordate. The genital products are situated upon the 4 radial sides of the gastric portion of the proboscis. The entoderm of the tentacle bulbs and radial canals is of an intense opaque pearly-white color, often displaying a tinge of pink. The entoderm of the gastric portion of the proboscis is of an intense green, and the oral tentacles are pearly-pink. The intense opaque color of the radial canals contrasting with the hyaline transparency of the bell renders this medusa one of the most beautiful to be found at the Tortugas, Florida.

Several specimens were captured early in July, 1899.

**DISSONEMA, HAECKEL, 1879.*****Dissonema turrida*, nov. sp.****Figs. 3, 4, Plate 2.**

*Specific Characters.* — Adult medusa; Figure 3. The bell is about 4 mm. in height. It is blunt and cone-shaped, and there is a prominent apical projection, which is hollow. There are 2 large hollow tentacles, which when expanded are 3-4 times as long as the bell height. In addition to these, there are 14 small solid tentacles, or marginal cirri. There are 16 ocelli, one at the base of each tentacle. These ocelli are situated within the ectoderm of the outer

(centrifugal) side of the tentacles. The proboscis is pyriform, and the lips project beyond the velar opening. The walls of the proboscis are very thin, and the lips are crenulated. The 4 radial canals are broad, and the 4 gonads occupy their proximal halves. In the female each gonad contains about six large ova, which stand out prominently over the surface of the organ. The entoderm of the proboscis and tentacles is of a delicate shade of green. The genital organs and circular canal are tinged with pink.

*Young Medusa.* — Figure 4, Plate 2, represents a young medusa of this species in which the genital organs have not yet made their appearance. There are but 4 tentacles, and 8 ocelli; and it is remarkable that the long tentacles are as yet solid, although they become hollow throughout their length in the adult medusa. This species is common throughout the summer at the Tortugas, Florida.

### NETOCERTOIDES, nov. gen.

#### *Netocertoides brachiatum*, nov. sp.

Figs. 43, 44, Plate 18.

*Generic Characters.* — Cannotidæ with 8 bifurcating, radial canals. 16 canals reach the circular vessel. There are neither marginal sense-organs nor cirri.

*Specific Characters.* — The bell is mitre-shaped and 3 mm. in height. There are 32 marginal tentacles. 16 of these are well developed, and are situated at the bases of the 16 radial canals; and the others are smaller, and alternate with the large tentacles in position. The large tentacles are only about one quarter as long as the bell height, and the others are much smaller. There are no marginal sense-organs. The velum is well developed. The proboscis has the shape of an 8-rayed star, each ray of which bifurcates, thus giving rise to 16 radial canals which reach the circular vessel. The gastric portion of the proboscis is wide, but flat, and the mouth extends but a short distance down into the bell cavity. The gonads appear to be situated upon the 8 rays of the stomach. Two specimens were found at the Tortugas, Florida, on July 10, 1898.

As it floats in the water this medusa bears a wonderfully close resemblance to the little pelagic Alga (*Trichodesmium*), which is very abundant at the Tortugas.

## STAURODISCUS, HAECKEL, 1879.

*Staurodiscus tetrastaurus*, HAECKEL.

Figs. 47-49, Plates 18, 19.

*Staurodiscus tetrastaurus*, Haeckel, E., 1879, Syst. der Medusen, p. 145, Taf. IX.  
Figs. 1-3.

*Specific Characters.* — The bell is 4.5 mm. in diameter, and about twice as wide as it is high. In adult medusæ there are 8 long flexible tentacles with hollow basal bulbs. In some specimens there are 24, and in others 16 sensory clubs upon the bell margin. There are always 32 black entodermal ocelli, one at the base of each tentacle bulb and sensory club. The velum is well developed. Only 4 radial canals reach the circular vessel. Each of these canals gives rise to a pair of side branches that end blindly. The gonads are situated upon these side branches and upon the distal portion of each radial canal. The proboscis bears 4 prominent lips. The color of the entoderm of this medusa is green or yellow.

In the youngest specimen observed, the bell was 1 mm. in diameter and about as high as it was broad. There were 4 well-developed tentacles, 4 rudimentary tentacle bulbs, and 8 marginal clubs (see Figure 47, Plate 18). The medusa was very common at the Tortugas, Florida, in July and August, 1898. Haeckel, 1879, found this species in the Canary Islands, at Lanzerote.

## TETRACANNOTA, nov. gen.

*Tetracannota collapsa*, nov. sp.

Figs. 14-16, Plates 7, 8.

*Generic Characters.* — *Tetracannota* is closely allied to *Cannota* and *Berenice*. It may be defined as having 16 radial canals, which in the adult become arranged in 4 groups, each group consisting of 4 canals. Gonads 16 in number, and situated upon the distal regions of the radial canals. An entodermal pigment spot at the base of each tentacle. No otcysts. Tentacles numerous.

*Specific Characters.* — Adult medusa; Figure 14. The bell is 7 mm. in diameter, and about as high as it is broad. The top is dome-shaped, and the side walls are vertical. There are 16 well-developed tentacles that are carried tightly coiled in close helices. In addition to these there are 112 very small, rudimentary tentacles. Dark-brown entodermal pigment is found at the base of each tentacle. There are 16 radial canals, arranged in 4 groups of 4 each. The gonads are found in the proximal portions of the 16 radial canals very near to the point where they branch off from the proboscis. The peduncle of the proboscis is wide and prominent. The proboscis possesses 8 slightly crenu-

lated lips. The entoderm of the proboscis in some specimens is green, in others pearly-white or yellowish. The entodermal pigment spots at the bases of the tentacles are dark brown.

*Stages in Development.*—The youngest medusa observed possessed a bell 1.5 mm. in diameter (see Figure 15). It had 4 simple radial canals, and 32 tentacles, 4 well developed and 28 rudimentary. The velum was prominent. There were 4 lips to the proboscis, and as yet no peduncle. There was no trace of the genital organs. In the next older stage (Figure 16), we find 16 radial canals, and 8 lips to the proboscis. As yet there is no peduncle and no trace of the gonads, nor have the radial tubes grouped themselves into four bundles as in the adult.

This medusa was very common at the Tortugas in June, and ample opportunity for observing its transformation was afforded. It possesses the curious habit of collapsing into an almost shapeless mass, in which condition it may remain for several hours and then "straighten out" and swim about in excellent condition.

Fewkes, 1883 ("On a Few Medusæ from the Bermudas," Bull. Mus. Comp. Zoöl., Vol. XI., No. 3, Figures 7, 7<sup>a</sup>) has evidently figured the young of this species under the name of "Larva of an unknown Tubularian."

## DYSCANNOTA, HÆCKEL, 1879.

### *Dyscannota gemmifera.*

#### Fig. 17, Plate 8.

*Willia ornata?* Brooks, W. K., 1880, American Naturalist, Vol. XIV. p. 670.

*Willia ornata*, Brooks, W. K., 1881, Studies Johns Hopkins Univ. Marine Lab., Vol. II. p. 144.

*Willia gemmifera*, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. IX. p. 300, Fig. 24, Pl. I.

*Specific Characters.*—The bell is hemispherical, with a slight apical projection, and is 4 mm. in diameter. There are 12 long tentacles with well-developed basal bulbs. Each tentacle arises from the point of juncture of a radial tube with the circular vessel. The velum is well developed. 4 radial vessels arise from the proboscis, and each of these gives rise to two side branches, so that 12 radial tubes reach the circular vessel. In addition to these 12, very slender tubes branch off at right angles to the circular vessel and end blindly in the gelatinous substance of the bell. These tubes alternate with the 12 radial tubes and tentacles. Each one terminates under a cluster of nematocysts upon the outer surface of the bell. The proboscis is long and slender, and reaches about three quarters of the distance from the apex of the bell cavity to the velar opening. It is provided with 4 slightly recurved and fimbriated lips. This species is remarkable in that a stolon arises from each

of the 4 main radial canals near to their point of juncture with the proboscis. Each of these stolons gives rise to a number of medusa buds. The medusæ become free and thus the species is perpetuated. The proboscis is of a decided sage-green, and the entoderm of the basal bulbs of the tentacles is brown. A number of specimens of this medusa were found at the Tortugas, Florida, in June. A single specimen was found by Brooks at Beaufort, North Carolina. Brooks considered it to be an asexual form of *Willetta ornata*, and this explanation may prove to be correct; we have not found the sexual form of *W. ornata*, however, at the Tortugas, and incline to regard it as a distinct species.

The species differs from the common *Willia ornata*, A. Agassiz, of Buzzard's Bay and Newport Harbor, in that the proboscis is far more slender, the narrow tubes branching off from the circular vessel end each in a single cluster of nematocysts, instead of several clusters as in *Willetta ornata*; and above all, the possession of stolons bearing medusa buds separates this form from all other known Atlantic species of *Willetta*. It is interesting to notice that Huxley (1891, *Anatomy Invert. Anim.*, p. 120, Figure 17) took a species of *Willsia* (*Willetta*) in the north Pacific, in which medusa-bearing stolons were developed at the point of bifurcation of each of the four main radial canals.

### LAODICEA, LESSON, 1843.

#### *Laodicea neptuna*, nov. sp.

Figs. 50-52, Plate 20.

*Specific Characters.*—The bell is a little more than a hemisphere, and is 2.5 mm. in diameter. There are 8 short tentacles with large basal bulbs, and 8 small rudimentary tentacle bulbs. The tentacles are thickly covered with nematocysts and are usually carried coiled in a contracted bunch. A single, large, black ocellus is found at the base of each tentacle. There are numerous small nematocyst-bearing cirri upon the bell margin between the tentacles. The velum is well developed. There are four straight radial tubes, the upper regions of which, adjacent to the proboscis, are occupied by the gonads. The proboscis reaches slightly beyond the velar opening, and the lips are surrounded by 4 prominent clusters of nematocyst cells. The color of the entoderm of the proboscis, tentacle bulbs, and circular and radial tubes is pearly-white. The entodermal lamella of the bell is of a delicate shade of green. This medusa was occasionally found at the Tortugas, Florida, during July and August, 1898.

*Laodicea ulothrix*, HÆCKEL.

*Laodicea ulothrix*, Haeckel, E., 1879, Syst. der Medusen, p. 133, Taf. VIII, Figs. 5-7.

*Specific Characters.* — The bell is about 20 mm. in diameter and is about twice as broad as it is high. (Haeckel, 1879, p. 133, says "etwa doppelt so hoch als breit.") This is doubtless a misprint. There are 70-100 long, slender, stiff tentacles, the distal ends of which are coiled in a close helix. The basal bulbs of these tentacles are large and hollow, and there is a well-developed ectodermal ocellus upon the inner (centripetal) side of each bulb. In addition to these ocelli one often sees small spur-like projections upon the outer (centrifugal) sides of the tentacle bulbs. Not all of the tentacles possess these spurs. Sensory clubs and cirri are scattered somewhat irregularly between the tentacles. The sensory clubs are almost as numerous as the tentacles. They are flask-shaped, and their entodermal cores are in direct connection with the entoderm of the circular tube. There are no otoliths. The cirri are usually less numerous than the tentacles. They are coiled in a helix, and their distal ends are covered with large spindle-shaped nematocyst-capsules. The velum is well developed. There are 4 straight, narrow, radial tubes, the proximal halves of which, adjacent to the proboscis, are occupied by the gonads. The proboscis is short, and there are 4 recurved lips. The entoderm of the proboscis, gonads, and tentacle bulbs is brownish-white, or greenish-white in color. This medusa is one of the commonest at the Tortugas, Florida. Haeckel found it at the Canaries, and Brooks describes it from the Bahama Islands. The distribution of the sensory clubs is usually more irregular than is described by Brooks.

## TIAROPSIS, AGASSIZ, L., 1849.

*Tiaropsis punctata*, nov. sp.

Figs. 60-63, Plate 22.

*Tiaropsis diademata*, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl., Vol. IX, p. 277, Pl. VII. Figs. 13-14.

*Specific Characters.* — The bell is bluntly cone-shaped and is 4 mm. in diameter. There are 4 well-developed, radially placed tentacles, the distal ends of which are usually coiled in a close helix. In addition to these there are 4 rudimentary tentacle bulbs. The 8 marginal sense-organs are situated midway between the 8 tentacles. Each of these organs consists of a pocket-like fold of the velum containing 8-13 otoliths. Immediately above the otocyst there is a well-developed, deeply pigmented eye (see Linko, A., 1899; Travaux Soc. Imp.

des Nat. de St. Pétersbourg, T. XXIX. p. 155, Plate I. Figure 5). The velum is very well developed. There are 4 straight, narrow, radial tubes, upon the upper regions of which the gonads are situated. The proboscis is wide and flask-shaped, and the mouth is provided with four prominent, crenulated lips. The color of the entoderm of the proboscis and tentacle bulbs is ochre-yellow, or reddish-brown. Several specimens were found at the Tortugas, Florida, late in June and early in July, 1898, and in June, 1899.

It is evident that this species has been noticed by Fewkes, 1882, under the name of "*Tiaropsis diademata*." The species is quite distinct from *T. diademata*, however, for it is smaller, possesses fewer tentacles, and is of a different color; moreover the bell of the young medusa is very much flatter than is that of *T. diademata* in a corresponding stage of development. The Tortugas form is closely allied to *T. roseæ* of the Fiji Islands; and it also bears some resemblance to *T. mediterranea*, Metschnikoff (1886; *Arbeit Zool. Inst. Wien. Bd. VI. p. 239, Taf. I. Figs. 6-8*).

## OCEANIA, PERON and LESUEUR, 1809.

### Oceania McCradyi.

**Figs. 56-59, Plate 21.**

*Epenthesi* McCradyi, Brooks, W. K., 1888, *Studies Johns Hopkins Univ. Biol. Lab.*, Vol. IV. pp. 147-162, Pls. 13-15.

We present some colored figures of this remarkable medusa which develops hydroid-blastostyles upon its gonads. It has been found by Brooks among the Bahama Islands, and by Bigelow off the Florida Coast. We found it at the Tortugas, Florida, in July, 1898. Brooks, 1888, claims to have found the hydroid of this species.

### *Oceania magnifica*, nov. sp.

**Figs. 18, 18a, Plate 9.**

*Specific Characters.*—The bell is thin and flat and 14 mm. in diameter. There are 32 slender tentacles of short length. There are 64 otocysts, 2 between each successive pair of tentacles. Each otocyst contains a single, spherical otolith. The velum is small. There are 4 straight, narrow, radial tubes. The gonads are developed upon the distal portion of these tubes near to the circular canal. The proboscis is short, and there are 4 sharply curled lips. The color of the entoderm of the proboscis and tentacle bulbs is intense green, while the ectoderm of the proboscis and of the genital organs is usually rich purple.

Several specimens were found at the Tortugas, Florida, in June, 1897, and a large number during the summers of 1898 and 1899.

*Oceania globosa*, nov. sp.Figs. 19, 19<sup>a</sup>, Plate 9.

*Specific Characters.*—The bell is globular in form, 14 mm. in diameter. The cavity of the bell is shallow so that the gelatinous substance is very thick. There are 32 large tentacles and 32 rudimentary ones. There are 64 otcysts alternating with the tentacles. Each otcyst contains 3–5 spherical otoliths (Figure 19<sup>a</sup>). There are 4 straight, narrow, radial canals. The 4 gonads are situated upon the distal portions of the canals. The proboscis is very short and there are 4 prominent lips. The color of the entoderm of the proboscis and tentacle bulbs is light drab.

Single specimen found at Tortugas, June 16, 1897.

*Oceania gelatinosa*, nov. sp.Figs. 20, 20<sup>a</sup>, Plate 10.

*Specific Characters.*—The bell is 7 mm. high and 3.3 mm. in diameter. The gelatinous substance of the upper portion of the bell is very thick. There are 16 well-developed tentacles and 16 rudimentary ones that may develop later. There are 32 otcysts alternating with the tentacles. Each of these otcysts contains 3–5 spherical otoliths (Figure 20<sup>a</sup>). The velum is prominent. There are 4 radial canals, in the upper or proximal portion of which the gonads are developed. The proboscis is long and slender and there are 4 prominent lips. The color of the entoderm of the proboscis and tentacle bulbs is light drab, or opaque white.

A specimen was found at the Tortugas, Florida, on June 14, 1897, and several others during the summer of 1899.

*Oceania discoida*, nov. sp.

Figs. 53–55, Plate 20.

*Specific Characters.*—The bell is quite flat, with conically sloping sides, and is 4 mm. in diameter. There are 16 short marginal tentacles with large basal bulbs. There are usually 3 otcysts between each successive pair of tentacles (see Figure 55). The velum is well developed. There are 4 straight radial tubes, upon the greater portion of the length of which the gonads are situated. In the case of the female the eggs are very large and prominent. The proboscis is urn-shaped and there are 4 recurved lips. The proboscis, gonads, and tentacle bulbs are yellow, or yellow-green. The entodermal supporting lamella of the bell is often of a delicate shade of green. The medusa is easily distinguished from the other species of *Oceania* at the Tortugas by the circumstance that it is very small in size, the bell is conical in shape, and the gonads are large and prominent. It is quite common throughout the summer.

*Obelia*, sp.

*Eucepe*, sp. Agassiz, A., 1881, Bull. Mus. Comp. Zool. at Harvard Coll., Vol. IX. p. 149.

A very few specimens of the medusa of an *Obelia* were found at the Tortugas, Florida, late in June, 1898. The bell was disk-shaped and about 3 mm. in diameter. There were 96 tentacles and 8 otocysts. The gonads were large and spherical, and much distended with ova. The bell was colorless. Not having seen the hydroid stock we are unable to determine whether or not this *Obelia* is identical with any of the forms found at Newport, R. I.

**EPENTHESIS**, McCrady, 1857.***Epenthesis folleata***, McCrady.

**Fig. 139, Plate 41.**

*Epenthesis folleata*, McCrady, J., 1857, Gymn. Charleston Harbor, p. 89.  
*Oceania folleata*, Agassiz, A., 1865, North Amer. Acal., p. 70.

*Specific Characters.*—Adult medusa. The bell is usually flatter than a hemisphere, and is about 5 mm. in diameter. Its cavity is shallow, and the bell walls diminish in thickness very gradually from the summit towards the margin. There are 16 slender tentacles with well-developed basal bulbs. 16 otocysts alternate in position with the tentacles. Each otocyst contains a single spherical otolith. The velum is well developed. There are 4 slender, straight, radial canals and a narrow ring-canal. The proboscis is short and simple and there are 4 slightly recurved lips. The 4 gonads are short and linear and are developed upon the 4 radial canals near the circular canal. In the young medusa they are found higher up upon the radial canals, but they migrate centrifugally as development proceeds. The entoderm of the proboscis, tentacle bulbs, and gonads is of a decided green color. This medusa is very common at the Tortugas, Florida, during the spring months, but becomes rare after the first of June. We have found it abundant in the Bahamas during the winter months. It is rare at Charleston, South Carolina, but Brooks found both hydroid and medusa at Beaufort, North Carolina.

**EUCOPIUM**, Haeckel, 1879.***Eucopium parvigastrum***, nov. sp.

**Fig. 140, Plate 42.**

*Specific Characters.*—The bell is half egg-shaped and is 1 mm. in height. There is a very small apical projection. There are 4 very small radially

situated tentacles, which are hardly more than mere tentacle bulbs. There are 8 otocysts, 2 in each quadrant. Each otocyst contains a single spherical otolith. The velum is well developed. There are 4 straight, narrow, radial canals, and a slender circular vessel. The proboscis is very small, and is a mere tube, cruciform in cross-section and provided with 4 simple lips. The gonads occupy 4 linear swollen regions near the mid-regions of the 4 radial canals. The entoderm of the tentacle bulbs, gonads, and proboscis is of a decided brown color. This medusa was quite common at the Tortugas, Florida, late in June, 1899.

The very small proboscis and marginal tentacles as well as the remarkable swollen condition of the gonads in this medusa foreshadow the condition of *Agastra mira* (Hartlaub, 1897; Wissen. Meeresuntersuch. Biol. Anstalt Helgoland, Neue Folge, Bd. II. p. 504, Taf. XII. Fig. 10), where there is no trace either of proboscis or tentacles.

### PSEUDOCLYTIA, nov. gen.

#### *Pseudoclytia pentata*, nov. sp.

**Figs. 24-26, Plate 12; Figs. 35, 35<sup>a</sup>, Plate 15; Figs. 131, 132, Plate 39.**

*Generic Characters.*—*Pseudoclytia*. Eucopidæ with numerous simple tentacles (20 in this species). Otocysts alternating with the equally numerous tentacles. 5 simple radial canals, 72° apart. 5 gonads situated upon the 5 radial canals. The proboscis lacks a peduncle and is provided with 5 simple lips.

*Specific Characters.*—Adult medusa. The bell is flatter than a hemisphere and is 8-13 mm. in diameter. There are 20 simple tentacles with well-developed basal bulbs. Each of these tentacles is a little less than half as long as the bell height. There are no lateral or marginal cirri. There are 20 otocysts which alternate in position with the 20 tentacles. Each otocyst contains a single spherical otolith (Figure 26). The velum is well developed. There are 5 straight, narrow, radial canals 72° apart. The 5 gonads are situated upon the radial canals at points midway between the proboscis and the bell margin (Figures 35, 131). In the female the ova are large and prominent, and when immature are seen to have a well-defined nucleus and nucleolus (Figures 35<sup>a</sup>, 131). The proboscis is flask-shaped and there are 5 simple recurved lips. The entoderm of the proboscis, gonads, and tentacle bulbs is usually slightly milky in color, with a few scattered cinnamon-colored granules. Occasionally an individual is met with in which these cinnamon-colored granules are developed to such an extent that the medusa displays a brick-red color (Figure 35). In most individuals, however, the colored granules are so faint as to be almost imperceptible. In some individuals there is a more or less decided green spot in the entoderm of each tentacle bulb (Figures 131, 132).

This medusa is very common throughout the summer months at the Tortugas, Florida. On July 22, 1898, a great swarm of them appeared, and were so abundant that one could not dip up a bucketful of sea-water without capturing several specimens; and two such swarms came in the summer of 1899.

This is the only Hydromedusa known which is normally formed upon the plan of five (pentamerous). It seems very probable that it has arisen, phylogenetically, as a sport from some species of *Epenthesis* or *Oceania*, some individuals of which made their appearance with 5 radial canals instead of 4; and these abnormal individuals succeeded in perpetuating a new species. Bateson (1894; *Materials for the Study of Variation*, p. 425) calls attention to an abnormal specimen of *Sarsia mirabilis* having five complete segments, and says that "there is perhaps in the whole range of natural history no more striking case of the Discontinuity and perfection of Meristic Variation. In the case of *Eucope* (*Obelia*) it has been shown by Agassiz and Woodworth (1896; *Bull. Mus. Comp. Zool. at Harvard Coll.*, Vol. XXX. p. 121-150, 9 Plates) that among 3,917 medusæ 9 had three radial canals, 20 had five, and 3 had six radial canals. It thus appears that in *Obelia* the tendency to produce sports having 5 radial canals is about twice as great as that to produce individuals with any other number of canals. Yet sports of *Obelia* with 5 radial canals have not succeeded in perpetuating a new species.

I have made careful observations of 1000 individuals of *Pseudoclytia pentata*, and find that 70.3% are normal (*i. e.* have 5 canals 72° apart, 5 gonads, and 5 lips to the proboscis). The remaining 29.7% are abnormal in some respects, and a large number of the abnormalities tend toward the ancestral condition of 4 canals and 4 lips. The medusa is very much more variable than the 4-rayed *Epenthesis folleata* at the Tortugas, and its greater variability may be due to the fact that being a new form it displays a greater tendency toward variability in various directions. This question will, however, be made the subject of a special paper.

### MULTIORALIS, nov. gen.

#### *Multioralis ovalis*, nov. sp.

Figs. 129, 130, Plate 39.

*Generic Characters.*—*Multioralis*. Leptomedusæ having a circular canal, and a single, simple chymiferous canal which extends across the sub-umbrella. A number of separate manubria are situated upon the chymiferous canal.

*Specific Characters.*—Adult medusa. The bell is quite flat, and is elliptical in outline, the major axis being 4 mm. and the minor 2.4 mm. The gelatinous substance is not very thick and is quite flexible. There are 20-25 short, simple, coiled tentacles with well-developed basal bulbs. These tentacles are only about one half as long as the minor axis of the bell. There are no lateral or marginal cirri. The otocysts are slightly more numerous than the tenta-

cles; usually one, but occasionally two, being found between each successive pair of tentacles. Each otcyst contains a single spherical otolith. The velum is simple and quite broad. There is a slender circular vessel, and a single straight chymiferous canal extends along the major axis of the bell. In the oldest medusæ observed there were 4 manubria. Two equally developed large manubria were situated on either side of the centre of the sub-umbrella, upon the chymiferous canal; while two small manubria were found upon the same canal centrifugally away from the larger manubria. There was thus no manubrium at the centre of the sub-umbrella. There were two small gonads upon the chymiferous canal immediately centrifugal from the small manubria. The entoderm of the manubria and of the basal bulbs of the tentacles is of an opaque glistening white. The supporting lamella of the bell is of a delicate green.

*Young Medusa.*—In the youngest medusa observed, there were but 2 manubria situated upon the chymiferous canal on either side of the centre of the disk. The major axis of the bell was 2.5 mm. and there was no trace of gonads. About a dozen specimens of this medusa were captured at the Tortugas, Florida, from June 30–July 2, 1899.

It seems possible that the bell of the large medusæ may divide by transverse fission, for one individual was found in which there was a decided notch in the bell-margin extending inward in the plane passing through the centre of the sub-umbrella perpendicular to the main chymiferous tube. This notch appeared, however, upon only one side of the bell and may have been due to an accident. The main chymiferous canal is of course equivalent, morphologically, to two diametrically opposed radial canals.

### EUCHEILOTA, McCrady, 1857.

#### *Eucheilota ventricularis*, McCrady.

Fig. 128, Plate 38.

*Eucheilota ventricularis*, McCrady, J., 1857, *Gymn. Charleston Harbor*, p. 85, Pl. 11, Figs. 1, 2; Pl. 12, Figs. 1–3.

This medusa is quite rare at the Tortugas, Florida, and not more than a dozen specimens were obtained. They were remarkable in that the entoderm of the tentacle bulbs and proboscis was of a decided green color. Each otcyst contained 2–4 spherical otoliths. In specimens 2 mm. in diameter there were as yet no gonads upon the radial canals.

***Eucheilota bermudensis.***

*Oceanopsis bermudensis*, Fewkes, J. W., 1883, Bull. Mus. Comp. Zoöl., Vol. XI. p. 86, Pl. I. Figs. 8-10.

*Specific Characters.* — Adult medusa. The bell is not quite hemispherical, the sides being relatively straight and sloping and the top quite flat. It is about 6 mm. in diameter. There are 8 tentacles, 4 radial and 4 interradial. These tentacles are only about one third as long as the bell diameter, and are thickly covered with nematocysts. Their basal bulbs are large, and are each flanked by a pair of short, coiled, nematocyst-bearing cirri. In addition to these there are normally about 8 other cirri in each quadrant, and scattered between them are 8 otocysts. Thus the medusa has 32 otocysts and 48 cirri. Each otocyst is of small size and contains a single spherical otolith. The velum is well developed. There are 4 straight, narrow, radial canals, and a simple circular vessel. The proboscis is short, but wide, and there are 4 cruciform, slightly recurved lips. There is no peduncle. The 4 gonads are found upon the 4 radial canals near the proboscis. These are visible in young medusæ about 1.5 mm. in diameter; and in the adult they become quite large and swollen, the ova being distinctly seen lying along the side of the canal. The entoderm of the proboscis gonads and tentacle bulbs is grass green, and the supporting lamella of the bell is tinged with the same color. This medusa was quite common at the Tortugas, Florida, from June 17-25, 1899.

*Young Medusa.* — The youngest medusa was about 2 mm. in height and 1.5 mm. in diameter. It was very much in the condition described by Fewkes, 1883. There were 4 simple radially situated tentacles and 4 interradial tentacle bulbs. The interradial tentacle bulbs were flanked by lateral cirri, while the radial tentacle bulbs lacked these appendages. There were 4 otocysts, one upon the side of each of the interradial tentacle bulbs. Each otocyst contained a single spherical otolith. The gonads were already quite large, and lay along the 4 radial canals near the sides of the proboscis. The proboscis was short, and there were 4 simple lips.

***Eucheilota paradoxica*, nov. sp.**

**Figs. 134-136, Plate 40.**

*Specific Characters.* — Adult medusa: the bell is somewhat fuller than a hemisphere and is 4 mm. in diameter. The gelatinous substance is of moderate thickness, and there is a very slight, blunt, aboral projection. There are 4 equally developed, radially situated tentacles. These tentacles are about as long as the bell height, but are usually carried coiled in a close helix. Their basal bulbs are elongate, and are hollow. The shafts of these tentacles are thickly covered with nematocysts. A pair of tightly coiled lateral cirri arise from the sides of each tentacle bulb. In addition to these well-developed tentacles there

are 4 interradial, rudimentary tentacle bulbs which are flanked by lateral cirri. There are 8 otocysts, 2 in each quadrant. Each otocyst contains a single spherical otolith. The velum is well developed. There is a narrow circular vessel, and 4 straight simple radial canals. The proboscis is flask-shaped, and there is no peduncle. There are 4 simple cruciform lips. Medusa buds in various stages of development are found upon the 4 gonads, which are situated at the middle points of the 4 radial canals. These medusa buds first develop 2 diametrically opposed tentacles (Figure 135), but when about to be set free they have 4 equally developed tentacles as in the adult. They have, however, no trace of gonads, and the interradial tentacle bulbs are not provided with lateral cirri. Usually from 2-5 medusa buds in several stages are found upon each gonad. The entoderm of the proboscis gonads and tentacle bulbs is of a milky-green color.

This medusa was common at the Tortugas, Florida, in June, 1899.

This is the first and only Leptomedusa which has been observed to give rise to free medusa buds.

### EUTIMA, McCrady, 1857.

#### *Eutima mira*, McCrady.

*Eutima mira*, McCrady, J., 1857, *Gymn.* Charleston Harbor, p. 88, Pl. XI. Figs. 8, 9.

This medusa is common throughout the summer at the Tortugas, Florida. It is also abundant at Charleston, South Carolina, and at Beaufort, North Carolina. Damaged specimens are occasionally drifted into Newport Harbor, Rhode Island, by the southerly winds, late in the summer.

### EUTIMALPHES, Hæckel, 1879.

#### *Eutimalphes cœrulea*.

Figs. 22, 22<sup>a</sup>, Plate 11.

*Eirene cœrulea*, Agassiz, L., 1862, *Cont. Nat. Hist. U. S.*, Vol. IV., p. 362.

*Irene cœrulea*, Hæckel, E., 1879, *Syst. der Medusen*, p. 203.

*Specific Characters.* — The bell is 10 mm. in diameter and a little broader than it is high. The gelatinous substance at the apex of the bell is quite thick, but becomes progressively thinner as one approaches the margin. There are about 32 short, slender, marginal tentacles, each one of which is furnished with small lateral cirri. In addition to the well-developed tentacles there are about 96 rudimentary tentacular swellings upon the bell margin. There are usually about three of these swellings between each successive pair of tentacles. (Figure 22<sup>a</sup>.) There are 8 otocysts, 2 in each quadrant, and each one of them contains 3-5 spherical otoliths. There are 4 radial tubes. The

velum is well developed. There are 4 linear, slightly convoluted gonads. They begin about halfway between the circular vessel and the peduncle, and extend to a point close to the proboscis. The peduncle is well developed and reaches slightly beyond the velar opening. The gastric portion of the proboscis is short and is furnished with 4 slightly fimbriated lips. The proboscis, gonads, and tentacle bulbs are opaque white. Common at the Bahamas and Tortugas in the spring and winter months.

### EUTIMIUM, HAECKEL, 1879.

#### *Eutimium serpentinum*, nov. sp.

**Figs. 69-72, Plate 23.**

*Specific Characters.*—The bell is 10 mm. in diameter, and about  $2\frac{1}{2}$  times as broad as it is high. There are 4 radially situated tentacles; each being about as long as the bell diameter. There are no lateral or marginal cirri. The 8 otocysts are situated near to and on both sides of the radial tentacles. (Figure 70.) Each otocyst contains 4-8 spherical otoliths. The velum is well developed. There are 4 straight narrow radial tubes and a narrow circular vessel. The proboscis possesses a very long peduncle, which is about 3 times as long as the bell diameter. The upper region of the peduncle is conical in shape; then follows a long slender cylindrical region leading to the gastric part of the proboscis, which is urn-shaped with 4 slightly recurved lips. (Figure 71.) The 4 gonads are situated upon the long cylindrical portion of the peduncle, where they lie upon the radial canals. (Figure 72.) The proboscis, gonads, and tentacles are opaque bluish-white. Half a dozen specimens of this medusa were found at the Tortugas, Florida, late in July, 1898. It is closely allied to *Eutimium elephas*, Haeckel (1879; *Syst. der Medusen*, p. 190, Taf. XII. Figures 10-12), of the German Ocean.

### PHORTIS, McCrady, 1857.

#### *Phortis lactea*, nov. sp.

**Fig. 133, Plate 40.**

*Specific Characters.*—The bell is 5 mm. in diameter and the sides flange slightly outward at the margin. The gelatinous substance is of moderate thickness at the aboral pole, but becomes thin at the margin of the bell. There are about 18-22 short simple tentacles, the basal bulbs of which are large and swollen. These tentacles are only about one fifth as long as the bell diameter. There are no lateral or marginal cirri. The otocysts are slightly more numerous than the tentacles, there being at least one, and occasionally two, of these structures between each successive pair of tentacles. Each otocyst contains a

single spherical otolith. The velum is well developed. There are 4 straight slender radial canals, which extend down the peduncle to the gastric portion of the proboscis. The peduncle is wide at its base, but not so wide as in *Phortis pyramidalis*. It extends for a short distance beyond the velar opening of the bell. The gastric portion of the proboscis is cruciform in cross-section and there are 4 simple recurved lips. The 4 gonads are situated upon the 4 radial canals a short distance above their junction with the circular vessel. Each gonad is linear, and in the female the ova are quite conspicuous. The gonads and the gastric portion of the proboscis are milky in color, while the tentacle bulbs are cream-colored with greenish entodermal granules. Found at the Tortugas, Florida, in June.

### *Phortis pyramidalis*.

Figs. 21, 21<sup>a</sup>, Plate 10.

*Eutima pyramidalis*, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV., p. 363.

*Specific Characters*.—Adult medusa. The bell is slightly flatter than a hemisphere, and attains a diameter of about 35 mm. There are about 100 small slender tentacles, which lack lateral cirri. About 100 otocysts alternate with the equally numerous tentacles. Each otocyst contains a single spherical otolith. (Figure 21<sup>a</sup>.) There are 4 narrow radial canals. The proboscis is provided with a wide cone-shaped proboscis which fills most of the cavity of the bell, and projects outward for a considerable distance beyond the velar opening. The gastric portion of the proboscis is very small, and is provided with 4 delicately crenulated lips. The gonads are linear and are developed upon the centrifugal portions of the 4 radial canals near to the circular canal. The proboscis, tentacle bulbs, and gonads are of a delicate blue-green color. This medusa is very abundant among the Bahama and Tortugas Islands. At night, when disturbed, it glows with an intense blue-green phosphorescence which is far more brilliant than that of any other medusa that we have observed.

*Young Medusa*.—*Phortis pyramidalis*. In the youngest medusa observed the bell was higher than a hemisphere and 3 mm. in diameter. There was no peduncle to the proboscis, and the gelatinous substance of the bell was not very thick. There were 4 slender radial tubes and 16 tentacles, only 8 of which had attained to any length, the others being mere basal bulbs. There were about 8 otocysts, each containing a single spherical otolith. When the medusa is about 7 mm. in diameter, the bell is flatter than a hemisphere. The peduncle is well developed and extends beyond the velar opening. The gastric portion of the proboscis has grown very little and is relatively to size of the medusa much smaller than in the younger animal. There are 4 recurved lips. There are now about 32 tentacles and 16 otocysts.

## ZYGODACTYLA, BRANDT, 1835.

*Zygodactyla cubana*, nov. sp.

Figs. 84, 85, Plate 25.

*Specific Characters.* — Young medusa. The bell was quite flat and disk-shaped and 4.5 mm. in diameter. There were 8 long tentacles, 8 rudimentary, undeveloped tentacles, and 16 very small undeveloped tentacle bulbs, that probably develop later into tentacles. The tentacle bulbs possessed excretion papillæ and were further distinguished by the fact that there were two entodermal green pigment spots one on either side of the bulb (see Figure 85). These spots had the appearance of ocelli, but we do not venture to state that they are such. There were 32 otocysts, each containing one or two spherical otoliths. The velum was well developed. There were 16 radial canals, only 8 of which reached the circular vessel. The 8 others projected about half-way from the proboscis to the circular canal. The proboscis was wide and flask-shaped, and projected for a considerable distance beyond the velar opening. The 16 lips were recurved. The gonads were beginning to appear upon the radial canals. The entoderm of the proboscis and radial canals is sage-green. The entoderm of the tentacle bulbs was flesh-colored and the "ocelli" were green. Tortugas, Florida, July 25–29, 1898, and June, 1899.

*Zygodactyla cyanea*, AGASSIZ, L.Figs. 23, 23<sup>a</sup>, Pl. 11; Figs. 33, 34, Pl. 15.

*Zygodactyla cyanea*, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. p. 361.  
*Mesonema cyaneum*, Haeckel, E., 1879, Syst. der Medusen, p. 227.

*Specific Characters.* — Adult medusa. None of our figures were drawn from full-grown medusæ. The bell is flatter than a hemisphere and is about 45 mm. in diameter (22 mm. in Figure 33). The gelatinous substance of the central part of the bell is very thick and there is a well-developed peduncle which projects downward into the cavity of the stomach. The peripheral zone of the bell is quite thin and flexible. There are 90–100 well-developed tentacles with large conical basal bulbs. Each tentacle bulb is hollow and is provided with a conical excretion papilla which projects outward (centrifugally). See Figure 34, Plate 15. There are one or two (usually one) otocysts between each successive pair of tentacles. Each otocyst contains one or two spherical otoliths. The velum is well developed. There are 90–100 simple, straight radial tubes. The radial tubes do not extend down the peduncle of the proboscis, but empty into the stomach cavity at their highest point. The proboscis is wide and shallow, and does not protrude beyond the velar opening. The mouth is surrounded by numerous crenulated lips which are equal in number to the radial

canals. The stomach is about two thirds as wide as the bell diameter. The gonads are linear, and occupy almost the whole length of the radial canals. The entoderm of the gonads, tentacle bulbs, and proboscis is blue-green. The medusa is very common off the Florida Coast both in summer and winter.

### ÆQUOREA, PÉRON and LESUEUR, 1809.

#### *Æquorea floridana.*

*Rhematodes floridanus*, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. p. 361.

*Specific Characters.*—The bell is hemispherical and 25 mm. in diameter. The gelatinous substance of the bell is thick and of a tough consistency. There are 16 radial tubes and 64 well-developed marginal tentacles. The tentacle bulbs are large and hollow, and are provided each with one or two excretion papillæ, which project outward from the side of the bell. There are about 192 otocysts, three between each successive pair of tentacles. Each otocyst contains 2 spherical otoliths. The velum is well developed. The 16 gonads are developed upon the distal halves of the 16 radial canals. The surface of the mature gonads is slightly convoluted. The proboscis is wide and very shallow, and there are 16 slightly fimbriated lips. The gonads and the edge of the bell are milky-white. Common at the Tortugas and Bahamas in the spring months.

### RHACOSTOMA, AGASSIZ, L., 1862.

#### *Rhacostoma dispar*, nov. sp.

**Figs. 27-29, Pl. 13.**

*Specific Characters.*—The bell is leus-shaped, and about 40 mm. broad and 20 mm. high. The cavity of the bell is remarkably small and shallow, so that the gelatinous substance is very thick. The velar opening of the bell is only about 5 mm. in diameter. There are about 8 very small rudimentary tentacles. There are 30-40 otocysts scattered between the tentacles. Each otocyst contains 3-5 oval-shaped otoliths (see Figure 29). There are no excretion papillæ. The velum is well developed. There are about 80 radial tubes, fully half of which end blindly without reaching the circular tube. The gonads are situated upon all of the radial tubes. They are linear, and their surfaces are slightly convoluted. They do not extend quite to the periphery of the stomach, nor do they reach the circular canal. The proboscis is very wide, and may at times be protruded beyond the velar opening. There are about 80 small crenulated lips, which are apparently as numerous as the radial canals. The bell has a faint steel-blue tinge, and the genital organs are pink. A single specimen

was found at the Tortugas, Florida, in June, 1897. This remarkable species is extremely inactive. Owing to the small size of the velum, it is of but little service in swimming, and the medusa makes use of the contractions of its widely open mouth in order to propel itself through the water.

### GONIONEMUS, AGASSIZ, A., 1865.

#### *Gonionemus aphrodite*.

*Cubaia aphrodite*, Mayer, A. G., 1894, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXV. p. 237, Pl. II. Figs. 1-3.

This medusa is occasionally met with at the Tortugas, Florida, and an examination of mature individuals has convinced me that it belongs to the genus *Gonionemus*. The gonads consist of a series of finger-shaped, or papilliform, processes that are crowded alternately to one side and the other of the radial canal very much as in the species of *Gonionemus* found at Woods Holl, Massachusetts.

### GONIONEMOIDES, nov. gen.

#### *Gonionemoides geophila*, nov. sp.

Figs. 6-11, Plates 3-5.

*Generic Characters.* — This genus is closely related to *Gonionemus*, but differs from it in that the marginal tentacles are of two distinct kinds, and arise at slightly different levels from the bell margin. One of these sets of tentacles is provided with netting cells, and the other is furnished with adhesive suckers, as in *Gonionemus*. There are 4 radial canals, and the circular vessel is simple without centripetal canals. The gonads are papilliform and are situated upon the radial canals. There are numerous otocysts upon the bell margin.

*Specific Characters.* — Adult medusa, Figures 6-9. The bell is quite flat and disk-shaped, and is about 9.5 mm. in diameter. There are 64 marginal tentacles. 16 of these bear, each one, a suctorial disk upon the aboral sides near their distal extremities. The extreme distal ends of the tentacles are cone-shaped, and are bent sharply at a right angle to the main shaft of the tentacle, very much as is the case in *Gonionemus vertens*, A. Agassiz. These sucker-bearing tentacles arise at a level, a little above the bell margin. The remaining 48 tentacles all arise from the bell margin, at a lower level than do the sucker-bearing ones. They possess no suctorial disks, but instead are armed with rings of nematocyst capsules (Figure 6). These nematocyst-bearing tentacles are far more flexible than are the sucker-bearing ones.

There are 12 otocysts upon the bell margin, each one of which contains a single otolith situated within an elongate, oval cavity (see Figure 7). The

velum is well developed. There are 4 straight radial tubes. The gonads occupy the distal halves of the radial tubes, but do not quite extend to the circular vessel. They present the appearance of a series of papilliform, or finger-shaped, processes that are crowded alternately to one side and the other of the radial tube, very much as is the case in *Gonionemus vertens*. The proboscis is a simple tube with 4 prominent lips. There are 4 radially situated green-colored spots upon the proboscis close to its junction with the 4 radial canals.

*Young Medusa.* — Figures 10, 11, Plate 5. The youngest medusa observed was 1.7 mm. in diameter. The bell was high and quite thick, and its aboral surface was covered with nematocyst capsules. The 16 sucker-bearing tentacles were already present, although the suctorial disk was visible upon only 8 of them. Figure 11 is a side view of the end of one of these young tentacles showing the beginning of the formation of the suctorial disk. There were 7 otocysts present. The velum was very prominent. There were no traces of genital organs present. The proboscis possessed a distinct peduncle. The color of the genital organs, bell margin, and proboscis of this medusa is pearly white. The entoderm of the tentacle bulbs and of the radial tubes in the region of the gonads is green. The ocelli? of the proboscis are green.

The adult medusa would frequently lie flat upon the bottom of the aquarium with its oral surface upward (Figure 9, Plate 4). In this position the sucker-bearing tentacles would be stretched far out and the suckers would anchor the medusa to the bottom. The nematocystic tentacles, on the other hand, would wave freely upward apparently in position for the capture of prey. When disturbed the medusa would swim actively about for a few moments, and then reassume its characteristic position of rest.

This medusa was common at Key West from May 27–June 10, 1897.

## HALICALYX, FEWKES, 1882.

### *Halicalyx tenuis*, FEWKES.

Figs. 12, 13, Plates 5, 6.

*Halicalyx tenuis*, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl. Harvard Coll., Vol. IX. p. 277, Pl. VII. Fig. 15.

*Generic Characters.* — This genus is closely allied to *Gonionemoides*, but differs from it in that none of the tentacles bear suctorial disks. The tentacles are of two distinct kinds and arise at different levels from the bell margin. The circular vessel gives off blind centripetal branches. There are otocysts at the bases of the tentacles. Tentacles numerous.

*Specific Characters.* — The bell is 25 mm. in diameter and is hemispherical. It is quite thick at the aboral pole, but becomes constantly thinner as one approaches the margin. The gelatinous substance is of very rigid consistency.

There are about 50 tentacles, and 64 short, blunt papillæ upon the bell margin. 32 of the tentacles arise from the side of the bell at a little distance above the margin. They are short and stiff and stand out sharply at right angles to the bell (see Figure 3). These tentacles are sprinkled over with wart-like protuberances of a deep purple color. A pair of otocysts, each containing a single otolith, are situated at the base of each of these stiff tentacles. Thus the medusa possesses 64 otocysts. In addition to the stiff tentacles there are about 20 others that are long and flexible, and arise from the bell margin. They are covered with rings of nematocyst cells closely coiled in a helical manner (see Figure 12). These tentacles are very flexible and are constantly being expanded to a length of 4-5 times the diameter of the bell and then contracted with a sudden jerk. The velum is small. There are 4 straight, narrow, radial tubes. The circular vessel is peculiar in that it gives off blindly ending, centripetal branches or diverticulæ, that penetrate inward into the substance of the bell. There are in all 28 side branches. 4 of these are each about half as long as the radial tube. 8 others are only one quarter as long as this, and the 16 remaining ones are still shorter. These diverticulæ are situated immediately above the short, stiff tentacles (see Figure 13). The gonads are found occupying the distal half of the radial canals, but do not reach quite to the bell margin. They hang downward into the bell cavity as a complex system of finger-shaped papillæ. The proboscis is very slender and the lips prominent. It extends for about three quarters of the distance of the height of the bell cavity. The gelatinous substance of the bell is slightly greenish in color. The entoderm of the proboscis, genital organs, circular tube, and tentacles is opaque yellow-green and reddish purple. There are 4 reddish-purple spots upon the proboscis just between the radial canals.

This medusa was common at Key West from May 27-June 10, 1897. It was extremely active in all of its movements and wonderfully hardy in captivity. One specimen lived for more than a week in a small glass bowl, the water of which was not changed. It seems probable that both this species and *Gonionemoides geophila* prefer the muddy and impure waters of the Florida Coast, for while they were both common at Key West, they were not seen at the Tortugas either in 1897, 1898, or 1899.

#### LIRIOPE, LESSON, 1843.

#### *Liriope scutigera*, McCrady.

*Liriope scutigera*, McCrady, J., 1857, *Gymn. Charleston Harbor*, p. 106.

*Xanthea scutigera*, Haeckel, E., 1864, *Geryoniden*, p. 24.

*Liriantha scutigera*, Haeckel, E., 1879, *Syst. der Medusen*, p. 287.

This medusa is not very common at the Tortugas, Florida. It is quite abundant at Charleston, South Carolina, and we have taken it at various places among the Bahama Islands, and off the Cuban Coast, during the winter months.

## GLOSSOCODON, HÆCKEL, 1864.

*Glossocodon tenuirostris*, FEWKES.

Figs. 75-78, Plate 24.

*Liriope tenuirostris*, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. p. 365.*Glossocodon tenuirostris*, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. IX. p. 278, Pl. VII. Figs. 1-9.*Liriope cerasiformis*? Maas, O., 1893, Ergeb. der Plankton Exped., Bd. II. K. C., p. 35, Taf. II. Fig. 5. 6.

This medusa is common at the Tortugas, Florida; as indeed it is also among the Bahama Islands and along the Cuban Coast. It is met with in considerable numbers in Charleston Harbor, South Carolina; and occasionally a damaged individual is drifted into Newport Harbor, Rhode Island, by the southerly winds late in the summer months.

## AGLAURA, PÉRON and LESUEUR, 1809.

*Aglaura hemistoma*, PÉRON and LESUEUR.

Figs. 79, 80, Plate 25.

*Aglaura hemistoma*, Péron, F., et Lesueur, C. A., 1809, Tableau des Méduses, p. 351, No. 73.*Aglaura Péronii*, Leuckart, R., 1856, Archiv für Naturges. Jahrg. 22, p. 10, Taf. I. Figs 5-7.

This medusa is occasionally met with in June at the Tortugas, Florida. It is found also in the Mediterranean and is widely distributed throughout the tropical regions of the Atlantic (see Maas, O., 1893, Die Craspedoten Medusen der Plankton Expedition, Taf. VII.). A very closely allied species is found in the Tropical Pacific (see Agassiz and Mayer, 1898; Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXXII. p. 166). One figure is drawn from a specimen obtained at the Tortugas, Florida.

*Aglaura hemistoma*, var. *Nausicaa*, HÆCKEL.*Aglaura Nausicaa*, Hæckel, E., 1879, Syst. der Medusen, p. 274, Taf. XVI. Fig. 1.*Aglaura vitrea*, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. IX. p. 277, Pl. VII. Fig. 10.*Aglaura hemistoma*, var. *Nausicaa*, Maas, O., 1892, Die Craspedoten Medusen der Plankton Expedition, Bd. II. K. C., p. 26.

This variety is occasionally met with at the Tortugas, Florida.

## CUNOCTANTHA, HAECKEL, 1879.

*Cunoctantha incisa*, nov. sp.

Figs. 145, 146, Plate 44.

*Specific Characters.* — The bell is slightly flatter than a hemisphere and is about 5 mm. in diameter. There is a slight apical projection, which is solid. 8 stiff tentacles arise from the sides of the bell, about halfway between the margin and the apex. These tentacles are provided with well-developed conical insertions, and their entodermal cells are disk-shaped and highly vacuolated. There is a well-developed peronium beneath each tentacle. The tentacles are all of equal length, and are about three quarters as long as the bell diameter. The ex-umbrella extends outwards in 8 lobes, which are held together in a web formed of the ascending velum. These are 24 pear-shaped marginal sense-organs, each containing a crystalline otolith and surrounded by a sensory pad bearing delicate bristles. The lower velum is well developed. The proboscis is flat and the stomach cavity is small. The mouth is a simple opening without prominent lips. The stomach gives rise to 8 pouches which extend outward in the radii of the 8 tentacles. The incisions between these pouches are deeper than in *Cunoctantha octonaria* of Charleston Harbor. The entoderm of the tentacles, and sometimes of the stomach, is green. Two specimens of this medusa were found at the Tortugas, Florida, late in May, 1899.

## ÆGINELLA, HAECKEL, 1879.

*Æginella dissonema*, HAECKEL.

Figs. 30-32, Plate 14.

*Æginella dissonema*, Haeckel, E., 1879, Syst. der Medusen, p. 340, Taf. XX, Fig. 16  
*Æginella dissonema*, Agassiz, A., and Mayer, A. G., 1899, Bull. Mus. Comp. Zool.  
 at Harvard Coll., Vol. XXXII, p. 166.

*Specific Characters.* — The bell is 3 mm. in diameter, and has the form of a frustum of a cone with rounded apex. It is a little wider than it is high. There are two long tentacles that arise from the sides of the bell at about  $\frac{3}{4}$  of the distance from the margin to the apex. These tentacles are quite stiff and incapable of contraction. They are carried trailing behind the medusa in two straight parallel lines, and are about 3 times as long as the bell height. The entodermal core of each tentacle consists in a row of disk-shaped, highly vacuolated cells. (See Figure 31.) In addition to the long tentacles there are two very small protuberances (t. Figure 30) that arise from the bell margin, at the foot of the pair of peronial tubes that are situated 90° from the large tentacles. Haeckel, 1879, does not mention or figure these protuberances, and it

seems probable that they may be absent in some individuals, for we did not observe them in specimens of *Æginella dissonema* from the Fiji Islands. In addition to the above-mentioned protuberances there are 4 small interradial swellings situated upon the bell margin. There are 8 sensory clubs, 2 in each quadrant (see Figure 32), each one of which contains a single spherical otolith. The velum is large and powerful and is constantly contracting and expanding with great rapidity. There are 4 peronial double canals, each canal being divided into two by means of a longitudinal septum. The proboscis is small and flat, and the mouth is a simple circular opening. There are 8 interradial pouches that extend outward from the stomach into the substance of the bell. The gonads are developed upon these pouches and in the specimen here figured they contained immature ova. The color of the entoderm of the proboscis and of portions of the entodermal core of the tentacles is intense golden-green. The gonads in the specimens described by Haeckel were rose-red; in ours they were colorless.

A single specimen was found at the Tortugas, Florida, June 19, 1897. This medusa appears to be very widely distributed. Haeckel found it at the Canary Islands, and we found it in Suva Harbor, Fiji Islands, in January, 1898.

## II. SCYPHOMEDUSÆ.

### NAUSITHOË, KÖLLIKER, 1853.

#### *Nausithoë punctata*, KÖLLIKER.

**Figs. 67, 68, Plate 23; Figs. 87, 88, Plate 26.**

*Nausithoë punctata*, Kölliker, A., 1853, Zeit für Wissen. Zoöl., Bd. IV. p. 323.

*Nausithoë punctata* (*Marginata albida*), Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. pp. 122, 167.

*Nausithoë albida*, Carus, V., 1857, Icones Zoötom., Taf. II., Figs. 17, 22, 23.

*Specific Characters.*—Adult medusa. The umbrella is quite flat and is about 9 mm. in diameter. There are 8 stiff tentacles, each one of which is about  $\frac{3}{4}$  as long as the bell diameter. The main portion of the entodermal core of each tentacle is solid, but as Vanhöffen, 1892, has shown, the basal bulbs of the tentacles are hollow and connected with the adjacent lappet-pouches. There are 8 marginal sense-organs that alternate with the 8 tentacles. As the Hertwigs (1878, Sinnesorgan der Medusen, Figure 2, Plate 9) and Claus (1883, Organ. Entwickl. Medusen, Figure 47, Plate 7) have shown, each sense-organ consists of an ectodermal eye, provided with a lens and with nerve fibres; and also of an entodermal otocyst containing a number of otoliths. (See Figure 68, Plate 23.) The 16 marginal lappets are long and flexible, and it is by means of their movements that the medusa is enabled

to swim through the water with great rapidity. 16 diverticulæ or pouches from the stomach enter the 16 lappets. Each of these pouches is simple, and does not give rise to any system of canals ramifying through the lappets. The mouth is a simple cruciform opening and there are no oral appendages, or palps. The gastro-vascular cavity is a wide space occupying the whole centre of the umbrella and extending outward into the lappets to form the 16 lappet-pouches. There are 4 groups of gastric cirri, situated in such manner that the 2 diameters passing through them are  $45^\circ$  apart from the 2 diameters passing through the cross formed by the lips of the mouth. All 4 of these diameters pass through the marginal sense-organs. There are about 6 tentaculæ in each group of gastric cirri, thus making in all about 24 gastric tentaculæ. The 8 gonads are of entodermal formation, and are found in the 8 tentacular radii. As Claus, 1883, has shown, each one is formed from a pocket-like fold of the entoderm. A band of circular muscles is found in the ectoderm of the sub-umbrella, and radial muscle fibres run out from this band into the 16 marginal lappets. The color of this medusa is quite variable. The gelatinous substance of the bell is usually bluish white or brownish. The gonads are brownish red or, in the case of the males, bright yellow rosin-colored pigment spots are found in the ectoderm of the ex-umbrella, especially upon the lappets. These rosin-colored spots are due to small crystals (see Claus, 1883; Figure 44, Taf. VI.).

A young ephyra of this species (see Figures 67, 68; Plate 23) was found by us near Flamingo Key, Bahama Islands, Feb. 9, 1893. It was 2 mm. in diameter. There were as yet no marginal tentacles. The otocysts each contained 5-6 oval otoliths. There were only 4 gastric cirri. A slightly older ephyra has been figured by Claus, 1883; Figure 48, Taf. VII.

This medusa is common in the Mediterranean, and is also found among the Bahama and Tortugas Islands. It was described by Vanhöffen, 1893, from near the mouth of the Amazon River. A *very* closely allied species was found by us in the Fiji Islands, Pacific Ocean.

### LINERGES, HAECKEL, 1880.

#### *Linerges mercurius*, HAECKEL.

*Linerges mercurius*, Haeckel, E., 1880, Syst. der Medusen, p. 495, Taf. XXIX.  
Figs. 4-6.

*Linerges pegasus*? Haeckel, E., 1880, Syst. der Medusen, p. 495.

Vast numbers of ephyrae of this medusa are found among the Bahama Islands and along the Florida Coast in March; and the mature medusæ are very abundant in June. At times these creatures appear in such numbers that hundreds are captured in every haul of the tow net. They congregate in great windrows, remain abundant for a few days, and then disappear for an indefinite period.

## DACTYLOMETRA, AGASSIZ, L., 1862.

*Dactylometra lactea*, L. AGASSIZ.

*Chrysaora lactea*, Eschscholtz, F., 1829, Syst. der Acalephen, p. 81, Taf. VII. Fig. 3.  
*Dactylometra lactea*, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. pp. 125, 126, 166.

*Dactylometra lactea*, Agassiz, A., and Mayer, A. G., 1898, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXXII. p. 7, Pls. XII, XIII., and Fig. 10, Pl. VII.

This medusa is extremely common in Havana Harbor, Cuba, in February, where it swims upon the surface during the afternoon hours. It has been described by Eschscholtz from the Bay of Rio Janeiro, Brazil. It is occasionally found at the Tortugas, Florida.

## AURELIA, PÉRON and LESUEUR, 1809.

*Aurelia habanensis*, nov. sp.

Figs. 73, 74, Plate 24; Fig. 86, Plate 26.

*Specific Characters.*—Adult medusa. The bell is 240 mm. in diameter. It is disk-shaped, and the gelatinous substance is quite thick. There are 8 simple marginal lappets, which bear upon their dorsal surfaces, at a slight distance above the bell margin, a row of numerous short tentacles. There are 8 marginal sense-organs that are deeply set within niches situated between the marginal lappets. The radiating chymiferous tubes are very similar to those of *Aurelia flavidula*, Péron and Lesueur. The mouth-arms, or palps, are long and narrow and extend almost to the bell margin. Their free edges are not lined with a fringe of tentacles as in *Aurelia flavidula*, but instead are covered with wart-like clusters of nematocyst cells (see Figures 73, 74, Plate 24). This, indeed, constitutes the principal difference between this species and *Aurelia flavidula*. The 4 gonads are horseshoe-shaped and there are 4 subgenital pits. Both the gonads and subgenital pits are smaller than in *Aurelia flavidula*. The gelatinous substance of the bell is bluish white in color. The genital organs of the males are pink, and of the females white in color. The basal bulbs of the marginal tentacles are often pink.

This medusa is extremely abundant in Havana Harbor, Cuba, in February. It makes its appearance at the Tortugas in August, but we do not know whether it is found also at Havana at that time or not.

While in Havana Harbor in February, 1893, we had the opportunity of observing the curious habits of this medusa. During the morning hours not one was to be seen, but at about four o'clock in the afternoon they began to appear in great numbers, and continued to be seen until long after nightfall.

This species is quite distinct from *Aurelia marginalis*, L. Agassiz (1862;

p. 86). In *Aurelia marginalis* the gonads are very large and occupy at least one half of the whole diameter of the disk, so that the distance from the peripheral outline of these organs to the margin of the disk is as great, if not greater, than that to the centre of the disk. The mouth-arms, on the contrary, are comparatively small. In *Aurelia habanensis* the gonads never occupy more than one third of the diameter of the disk, and the mouth-arms are long and slender.

### CHARYBDEA, PÉRON and LESUEUR, 1809.

#### *Charybdea aurifera*, nov. sp.

Figs. 81-83, Plate 25.

*Specific Characters.* — Young medusa. Only one specimen of this medusa was found at the Tortugas, Florida, August 6, 1898. The bell was 2 mm. in height and a little higher than it was broad. The external surface of the bell was covered irregularly with numerous wart-like clusters of nematocyst cells. The 4 interradial tentacles were evidently very immature, and consisted of small knob-like protuberances from the bell margin. They were hollow and were in communication with the general gastro-vascular cavities of the bell. The 4 sense-organs, or rhopalia, arose from 4 radially situated niches, found upon the sides of the bell at a little distance above the margin. It should be noted, however, that although the rhopalia appear to arise at some distance above the bell margin, they are morphologically homologous with appendages of the bell margin. Each rhopalium arises from a niche in the side of the bell, and consists in a stalk-shaped body, bearing upon its distal end a knob-shaped portion which, in turn, contains the otolith and eye-spots. There are 5 eyes in each rhopalium; one of these is large and median, and the other 4 are smaller and paired (see Figures 82, 83). They are so situated that they may look inward towards the bell cavity. These eyes are ectodermal structures, and possess a lens and a layer of pigment cells. The otolith, on the other hand, is entodermal in origin and consists in a mass of glistening white granules. The velarium is well developed, and is supported by means of 4 partitions, or frenulæ (*f*, Figure 81), that suspend it from the sub-umbrella. The proboscis is wide and flask-shaped, and there are 4 quadratic lips. 4 long gastric cirri, one in each interradius, extend downwards into the stomach cavity. A highly refractive band of muscle fibres? (*m s*, Figure 81) extend down the middle line of each radius of the bell to the rhopalia. The gelatinous substance of the bell possesses a bluish tinge. The nematocyst cells of the ex-umbrella, and also the proboscis, rhopalia, and tentacles are of a decided amber color.

Although careful search was made for them, no velar canals were observed. It is probable that these may develop at a later stage.

**Charybdea punctata.**

*Tamoya punctata*, Fewkes, J. W., 1883, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XI. p. 84, Figs. 4-6, Pl. I.

A single young medusa of this species was found at the Tortugas, Florida, on May 24, 1899. It was very nearly in the same state of development as the medusæ described by Fewkes, 1883, from the Bermuda Islands. The adult medusa has not been found.

**CASSIOPEA, PÉRON and LESUEUR, 1809.****Cassiopea frondosa, LAMARCK.**

*Medusa frondosa*, Pallas, P. S., 1774, Spicilegia Zoölog., Fasc. X. pp. 29, 30, Pl. 2, Figs. 1-3.

*Cassiopea frondosa*, Lamarck, J. de, 1817, Hist. Nat. Anim. sans Vert., Tom. II. p. 512.

*Cassiopea pallasii*, Péron, F., et Lesueur, C. A., 1809, Tableau des Meduses, p. 357, Nr. 85.

*Polyclonia frondosa*, Agassiz, L., 1860, Cont. Nat. Hist. U. S., Vol. III. Pls. 13, 13a.

This medusa is very abundant at the Tortugas and along the Florida Reefs early in the spring, but is not seen during the summer months.

**III. SIPHONOPHORÆ.****VELELLA, Bosc, 1802.****Velella mutica, Bosc.**

*Medusa velella*, Linné, 1767, Systema Naturæ, Ed. XII. p. 1098.

*Velella mutica*, Bosc, L. A. G., 1802, Hist. Nat. d. Vers., Tom. II. p. 158.

*Velella mutica*, Agassiz, A., 1883, Mem. Mus. Comp. Zoöl. at Harvard Coll., Vol. VIII. No. 2, p. 2, Pls. I.-VI. 91 Figures.

*Armenista mutica*, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl. Vol. XXVIII. p. 84.

This Siphonophore appears occasionally in great numbers at the Tortugas, Florida, especially when southerly breezes drive the surface waters of the Gulf Stream upon the Florida Reefs. It is common among the Bahama Islands and along the Cuban coast, and isolated individuals are often carried far to the northward by the Gulf Stream, specimens having been taken in Newport Harbor, Rhode Island.

**PORPITA**, LAMARCK, 1816.**Porpita Linnæana**, LESSON.

*Porpita Linnæana*, Lesson, R. P., 1843, Hist. Nat. des Zoöph. Acal., p. 588.

This Siphonophore is met with occasionally at the Tortugas, Florida. It often occurs in vast swarms, which appear at irregular intervals, all along the coast of the United States from the Tortugas to North Carolina. A single specimen was found by A. Agassiz, in Newport Harbor, Rhode Island, in 1875.

**RHIZOPHYSA**, PÉRON and LESUEUR, 1809.**Rhizophysa Murrayana**, CHUN.

*Rhizophysa filiformis*? Gegenbaur, C., 1854, Zeit. für Wissen. Zoöl., Bd. V. p. 324, Taf. XVIII. Figs. 5-11.

*Cannophysa Murrayana*, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. p. 324, Pl. XXIV. Figs. 1-9.

*Cannophysa Eysenhardtii*, Mayer, A. G., 1894, Bull. Mus. Comp. Zoöl. Harvard Coll., Vol. XXV. p. 239, Pl. III. Figs. 1, 2, 4.

*Rhizophysa Murrayana*, Chun, C., 1897, Siphonophoren der Plankton Expedition, p. 84.

This Siphonophore has been found by us among the Bahama Islands and off the Cuban coast, and a single damaged specimen was obtained at the Tortugas, Florida. It has been obtained by Haeckel, 1888, at the Canaries, and by Chun, 1897, in the Tropical Atlantic. The Mediterranean species *R. filiformis* of Gegenbaur, 1854, is certainly very closely allied, if not identical with the Atlantic form.

**Rhizophysa Eysenhardtii**, GEGENBAUR.

*Rhizophysa filiformis*, Huxley, T. H., 1859, Oceanic Hydrozoa, p. 90, Pl. VIII. Figs. 13-20.

*Rhizophysa Eysenhardtii*, Gegenbaur, C., 1859, Nova Acta Acad. Nat. Curios., Tom. 27, p. 408, Taf. 31, Fig. 46-49.

*Nectophysa Wyvillei*, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. p. 327, Pl. XXIII. Figs. 1-8.

This Siphonophore is found occasionally at the Tortugas, Florida. It has been obtained by Haeckel in the Canary Islands, by the Plankton Expedition in the Sargasso Sea, and by Fewkes in the Bermudas.

**Rhizophysa clavigera**, CHUN.

*Cannophysa filiformis*, Mayer, A. G., 1894, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXV. p. 241, Pl. III. Fig. 3.

*Rhizophysa clavigera*, Chun, C., 1897, Siphonophoren der Plankton Expedition, p. 104.

A single specimen of this Siphonophore was found floating within ten metres of the surface in the Gulf Stream between Havana and Key West.

## PHYSALIA, Bosc, 1802.

*Physalia pelagica*, Bosc.

*Salacia phisalus*, Linné, 1756, *Systema Naturæ*, p. 158.

*Holothuria physalis*, Linné, 1767, *Syst. Naturæ*, Ed. XII. p. 1090.

*Medusa caravella*, Müller, O. F., 1776, *Besch. Berlin Gesell. Natur. Freunde*, Bd. II. p. 290, Taf. IX. Fig. 1.

*Arethusa crista subrubella venosa*, Browne, P., 1789, *Nat. Hist. Jamaica*, p. 386.

*Physalia pelagica*, Bosc, L. A. G., 1802, *Hist. Nat. d. Vers.*, Tom. II. p. 168.

*Physalis arethusa*, Tilesius, W. G., 1812, *Krusenst. Reise*, p. 91, Pl. XXIII. Figs. 1-6.

*Physalia caravella*, Eschscholtz, F., 1829, *Syst. der Acalephen*, p. 160, Taf. XIV.

*Physalia aurigera*, McCrady, J., 1857, *Gymn. Charleston Harbor*, p. 74.

*Physalia Olfersii*, Quatrefages, A. de, 1854; *Ann. des Sci. Nat.*, Ser. 4, Zoöl., Tom. II. p. 112, Pl. III. Figs. 1-9; Pl. IV. Figs. 1, 2.

*Caravella maxima*, Haeckel, E., 1888, *Siphonophoræ*, *Challenger Report*, Zoöl., Vol. XXVIII. pp. 313, 338, 352, Pl. XXVI. Fig. 8.

*Physalia maxima*, Goto, S., 1897, *Journ. Coll. Sci. Imperial Univ.*, Tōkyō, Japan, Vol. X. Part II. p. 175, Taf. XV. Figs. 1-12.

This large Siphonophore is frequently seen throughout the year floating past the Islands of the Tortugas, Florida, and a southerly breeze is almost sure to strand large numbers of them upon the beaches. The animal is found all over the Tropical and Subtropical Atlantic. It is carried by the Gulf Stream to the shore of Europe, and is often found in the Mediterranean near the Straits of Gibraltar. It appears, however, not to be permanently established in the Mediterranean. During the latter part of the summer this Siphonophore is quite common along the southern coast of New England, and individuals have been found as far north as the Bay of Fundy.

## SPHÆRONECTES, HUNLEY, 1859.

*Sphæronectes gracilis*, HAECKEL.

Fig. 89, Plate 27.

*Monophyes gracilis*, Claus, C., 1874, *Schrift. Zoöl. Inst. Wien*, II. Die Gattung *Monophyes*, p. 29, Taf. IV. Figs. 8-14.

*Sphæronectes inermis*, Fewkes, J. W., 1880, *Bull. Mus. Comp. Zoöl. at Harvard Coll.*, Vol. VI. p. 143, Pl. II. Fig. 6.

This Siphonophore is abundant in the Mediterranean and Tropical Atlantic. It was found throughout the winter by Chun in the Canary Islands, and several specimens were found by us at the Tortugas, Florida, in July, 1898. A

single specimen of its sexual generation (*Diplophysa inermis*) was found by Fewkes (1881; Bull. Mus. Comp. Zoöl., Vol. VIII. p. 166, Plate VI. Figure 12), in Newport Harbor, Rhode Island.

The Atlantic species of *Sphæronectes* is closely allied to, if not identical with, *S. Köllikeri* of the Tropical Pacific. Chun (1892, Abhandl. Senck. Gesell., Bd. 18, p. 86) says that in *S. Köllikeri* the distal portion of the phyllocyst curves downward toward the edge of the swimming-bell, while in *S. gracilis* it bends upwards. Our observations on *S. Köllikeri* from the Fiji Islands do not support this view (see Agassiz and Mayer, 1899 Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXXII. p. 177, Plate 16, Figure 51), for there appears to be much individual variability in respect to the curvature of the phyllocyst in the Pacific species. All of the specimens of *S. gracilis* observed in the Tortugas, Florida, were colorless, whereas *S. Köllikeri* is often quite highly colored; the entoderm of the feeding-polypites being bright yellow, and the nematocyst batteries of the tentacles orange.

{ *DIPHYES*, CUVIER, 1817.  
 { *EUDOXIA*, ESCHSCHOLTZ, 1825.

{ *Diphyes bipartita*, COSTA.  
 { *Eudoxia campanula*, LEUCKART.

Figs. 114, 114<sup>a</sup>, Plate 34.

|                           |   |   |
|---------------------------|---|---|
| Polygastric<br>Generation | { | <i>Diphyes bipartita</i> , Costa, O. G., 1840, Genere <i>Diphya</i> , p. 4, Taf. IV.                        |
|                           |   | <i>Diphyes acuminata</i> , Leuckart, R., 1853; Die Siphonophoren, p. 61, Taf. III. Figs. 11-19.             |
|                           |   | <i>Diphyes gracilis</i> , Gegenbaur, C., 1854, Zeit. für Wissen. Zoöl., Bd. V. p. 309, Taf. XVI. Figs. 5-7. |
|                           |   | <i>Diphyes Sieboldii</i> , Kölliker, A., 1853, Die Schwimmpolypen der Messina, p. 36, Taf. XI. Figs. 1-8.   |

This species is very abundant all over the Tropical Atlantic and in the Mediterranean; and specimens are often found at Newport, Rhode Island, late in the summer.

{ *DIPHYOPSIS*, HÆCKEL, 1888.  
 { *ERSÆA*, ESCHSCHOLTZ, 1829.

*Diphyopsis campanulifera*, CHUN.

Figs. 93-95, Plate 28.

- Polygastric  
 Generation { *Diphyes* —, Quoy, J. R. C., and Gaimard, P., 1827, Ann. des Sci.  
 Nat., Tom. 10, Pl. I. Fig. 7.  
*Diphyes campanulifera*, Eschscholtz, F., 1829, Syst. der Acalephen,  
 p. 137.  
*Diphyes Bory*, Quoy, J. R. C., and Gaimard, P., 1833, Voyage de  
 l'Astrolabe, Tom. IV. Zoöphytes, p. 83, Pl. IV. Figs. 1-6.  
*Diphyopsis campanulifera*, Chun, C., 1888, Sitzungsber. Akad.  
 Wissen. Zoöl., Bd. XLIV. p. 1159.  
*Diphyopsis compressa*, Haeckel, E., 1888, Siphonophoræ., Challen-  
 ger Report, Zoöl., Vol. XXVIII. p. 153, Plates 33, 34, 18 Figs.

*Ersæa Lessonii*, CHUN.

Figs. 96, 97, Plate 28.

- Free Sexual  
 Generation { *Ersæa Gaimardi*, Eschscholtz, F., 1829, Syst. der Acalephen, p.  
 128, Taf. XII. Fig. 4.  
*Eudoxia Lessonii*, Huxley, T. H., 1859, Oceanic Hydrozoa, p. 57,  
 Pl. III. Fig. 6.  
*Ersæa compressa*, Haeckel, E., 1888, Siphonophoræ., Challenger  
 Report, Zoöl., Vol. XXVIII. p. 123, Pl. XXXIV. Figs. 9-18.

This Siphonophore is common all over the Tropical and Subtropical Atlantic. A few individuals are drifted into Newport Harbor every summer by the southerly winds, and are probably blown northward from the waters of the Gulf Stream.

*Diphyopsis picta*.

- Polygastric  
 Generation { *Doramasia picta*, Chun, C., 1888, Sitzungsber. Akad. Wissen.  
 Berlin, Bd. XLIV. p. 1154.  
*Doramasia picta*, Chun, C., 1892, Abhandl. Senckenberg Gesell.,  
 Bd. XVIII. p. 91, Taf. VIII. Fig. 3; Taf. IX. Figs. 5-9.

*Ersæa picta*, CHUN.

Fig. 118, Plate 34.

- Free Sexual  
 Generation { *Ersæa picta*, Chun, C., 1888, Sitzungsber. Akad. Wissen. Berlin,  
 Bd. XLIV. p. 1154.

This form has been found by Chun in the Canary Islands, and it is also common at the Tortugas, Florida. We present a figure of the free sexual generation.

{ *Diphyopsis hispaniana*,<sup>1</sup> nov. sp.  
 { *Ersæa hispaniana*, nov. sp.

Figs. 98-99, Plate 29.

Polygastric generation = *Diphyopsis hispaniana*.

Monogastric, sexual generation = *Ersæa hispaniana*.

*Specific Characters.* — *Diphyopsis hispaniana*. Figures 98, 99. The animal is 12 mm. in length. The cavity of the anterior swimming-bell is very voluminous, so that the bell walls are remarkably thin. They are, however, quite rigid, so that swimming is accomplished almost entirely by the movements of the powerful velum. There is a well-developed hydræcium upon the ventral side of the anterior swimming-bell, and a long spindle-shaped phyllocyst arises from its inner apex, and extends upwards along the side of the bell cavity. The siphosome arises from the inner apex of the hydræcium, immediately under the point of origin of the phyllocyst. The first appendage of the siphosome is the large posterior swimming-bell that is almost as large as the anterior. It is provided with 4 radial canals, and a circular vessel, and these are placed in connection with the gastro-vascular space of the siphosome by means of a long slender duct. The posterior swimming-bell possesses a well-developed velum, the contractions of which acting simultaneously with those of the velum of the anterior swimming-bell, cause the animal to dart through the water at a very rapid rate. The posterior swimming-bell is provided with two large lateral wings having serrated edges. The siphosome extends downward through the groove between these wings. The order of development of the various organs upon the siphosome is as follows: — First the feeding-polypites, then the tentacles, then the gonads and swimming-bells, and lastly the covering scales. The feeding-polypites are spindle-shaped, and quite contractile. The outer surface of their proximal portions displays a number of wart-like swellings. The entodermal cells of these swellings are of a decided ochre-yellow color, and it seems not improbable that their function may be similar to that of the "liver cells" of the feeding-polypites of *Agalma*. The tentacles arise from the sides of the feeding-polypites very near their point of origin from the siphosome. They give rise to a number of lateral branches that are studded with sharply projecting nematocyst cells. (See Figure 99.) These lateral branches terminate in swollen nematocyst batteries. The covering scales are spathiform and possess a deep ventral groove. A single gonad and a swimming-bell bud out side by side, very close together, from the base of each feeding-polypite.

When sufficiently developed, each unit, consisting in a feeding-polypite, tentacle, gonophore, swimming-bell and covering scale, is set free from the siphosome of *Diphyopsis hispaniana*, and becomes the free-swimming, monogastric, sexual generation known as *Ersæa hispaniana*.

<sup>1</sup> Called "hispaniana" on account of its red and yellow coloration. The entoderm of the feeding-polypites being ochre-yellow, and the tentacular nematocyst-batteries port-wine-red.

*Ersæa hispaniana*, nov. sp.

Fig. 100, Plate 29.

*Specific Characters.*—*Ersæa hispaniana*. The mature animal is 7 mm. in length. The covering scale is hood-shaped without a sharp apex. Its lower portion is sharp-edged, and overlaps the large swimming-bell. The phyllocyst is short and blunt, and contains a highly refractive "oil" globule. The large swimming-bell is provided with 4 longitudinal, serrated ridges that give it a rectangular appearance in cross-section. There are 4 radial tubes, a circular vessel, and a well-developed velum. Two or more gonophores are seen budding out from the side of the feeding-polypite near its base. These gonophores (*g*, Figure 100) are medusiform and are provided with 4 radial tubes, a circular vessel, and a velum. The genital products are found within the manubrium. In Figure 100 a single large, oval egg is seen occupying this position.

Both *Diphyopsis hispaniana* and *Ersæa hispaniana* were common at the Tortugas, Florida, in July, 1898, but were not seen during the summer of 1899.

{ *ABYLA*, QUOY and GAIMARD, 1827.  
 { *AGLAISMA*, ESCHSCHOLTZ, 1829.

*Abyla pentagona*, ESCHSCHOLTZ.Figs. 101, 101<sup>a</sup>-103, Plate 30.

Polygastric  
 Generation { *Abyla pentagona*, Eschscholtz, F., 1829, Syst. der Acalephen, p. 132.  
*Calpe pentagona*, Quoy, J. R. C., and Gaimard, P., 1827, Ann. der Sci. Nat., Tom. X. p. 11, Pl. 2 A. Figs. 1-7.  
*Abyla trigona*, Vogt, C., 1854, Mém. de l'Institut Nat. Génevois, Tom. I. p. 121, Pl. XX. Figs. 4-7; Pl. XXI. Figs. 3-6, 10-13.  
*Calpe Gegenbauri*, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. p. 164, Pl. XXXIX. Figs. 1-12.  
*Abylopsis pentagona*, Chun, C., 1897, Siphonophoren der Plankton Expedition, Bd. II. K. b. p. 30.

*Aglaisma cuboides*, CHUN.

Fig. 104, Plate 30.

Free Sexual  
 Generation { *Eudoxia cuboides*, Leuckart, R., 1853, Siphonophoren, p. 59, Taf. III. Figs. 7, 8, 10.  
*Einzelthiere der Abyla pentagona*, Gegenbaur, C., 1854, Zeit. für Wissen. Zool., Bd. V. p. 295, Taf. XVI. Figs. 1, 2.  
*Aglaisma Gegenbauri*, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. p. 119, Plate XL. Figs. 13-20.  
*Aglaisma cuboides*, Chun, C., 1897, Siphonophoren der Plankton Expedition, p. 30.

This form is quite common at the Tortugas, Florida, as indeed it is all over the Tropical and Subtropical Atlantic. It is found in Charleston Harbor, South Carolina, but has not yet been taken north of the Carolina coast.

### *Abyla quincunx*, CHUN.

**Figs. 115-117, Plate 34.**

|                           |   |  |
|---------------------------|---|--|
| Polygastric<br>Generation | { | Abyla pentagona, Huxley, T. H., 1859, Oceanic Hydrozoa, p. 40,<br>Pl. II. Figs. 2-2 <sup>c</sup> . |
|                           |   | Abylopsis quincunx, Chun, C., 1888, Sitzungsber. Akad. Wissen.<br>Berlin, Bd. XLIV. p. 1160.       |

### *Aglaisma quincunx*.

|                           |   |  |
|---------------------------|---|--|
| Free Sexual<br>Generation | { | Aglaismoides Eschscholtzii, Chun, C., 1888, Sitzungsber. Akad.<br>Wissen. Berlin, Bd. XLIV. p. 1160. |
|                           |   | Aglaismoides quincunx, Chun, C., 1897, Siphonophoren der Plank-<br>ton Expedition, p. 29.            |

Chun found this Siphonophore in the Canary Islands, and it was taken by the Plankton Expedition in the Gulf Stream and Sargasso Sea. Huxley, 1859, found it in the tropical regions of the Atlantic, Pacific, and Indian Oceans. It has been taken by Agassiz and Mayer (1899; Bull. Mus. Com. Zoöl., Vol. XXXII. p. 180) in the Fiji Islands. These South Pacific specimens are, however, slightly different from those of the Atlantic in that their tentacular nematocyst-batteries are usually colorless instead of more or less orange, as in the Atlantic form.

### *Chunia capillaria*, nov. gen. et sp.

**Figure 90, Plate 27.**

*Generic Characters.* — *Chunia*, novum genus. This genus belongs to the family Diphyidiæ, Eschscholtz, and to the subfamily Abylinæ, L. Agassiz. It possesses a pentagonal, prismatic, anterior swimming-bell and a larger five-sided, posterior swimming-bell. The siphosome bears a long, slightly curved, sharp-pointed, hair-like bristle. The covering scales, or bracts, are leaf-shaped. The monogastric sexual generation is unknown.

*Specific Characters.* — The animal is about 10 mm. in length. The anterior swimming-bell is prismatic, and possesses one oblique, five-sided face and 5 lateral faces. Four of these are plane, but the fifth is sharply concave. The cavity of the swimming-bell opens upon this concave face. The bell cavity is long and spindle-shaped, and is provided with 4 radial tubes and a velum. There is a large spherical phyllocyst that gives rise to an apical cæcum containing a highly refractive "oil" globule. The hydræcium of the anterior

swimming-bell is long and tube-like, and its axis is parallel to that of the bell cavity. Indeed, it is quite similar in form to the hydræcium of *Abyla quincunx* (see Figure 115, Plate 34). The first appendage of the siphosome is the posterior swimming-bell. This is somewhat larger than the anterior and is five-sided, the sides being bounded by prominent, angular, serrated ridges. There is a single median dorsal ridge and two pairs of lateral ridges. The ventral-most pair of lateral ridges are wing-like, and enclose a trough-like groove through which the siphosome extends. The bell cavity of the posterior swimming-bell is spindle-shaped and is provided with 4 radial tubes and a circular vessel. These are placed in communication with the general gastro-vascular cavity of the siphosome by means of a long slender duct. The posterior swimming-bell is furnished with a powerful velum, by the contractions of which the animal is enabled to shoot through the water. The siphosome is not very long and rarely extends beyond the posterior extremity of the trough-like groove in which it lies. The first organs to be developed upon it are the feeding-polypites; the tentacles soon arise as buds from the sides of the polypites, each feeding-polypite being provided with a single tentacle. The tentacles give rise to lateral branches each one of which terminates in a swollen cylinder-shaped nematocyst battery.

A long, slightly curved, bristle-like spine arises from the siphosome at a short distance below its origin, and extends outward to a considerable distance beyond the distal end of the posterior swimming-bell. It seems probable that this structure may be morphologically equivalent to a bract, that has become thus modified for defensive purposes. Other covering scales or bracts were observed upon the siphosome, but these were leaf-shaped (see *cs*, Figure 90, Plate 27). No gonophores or sexual organs were observed, and the sexual generation is unknown.

This rare form is found among the Bahama Islands during the winter months. The specimen from which we have obtained our figure was captured in Nassau Harbor, New Providence Island. We also obtained a specimen at Watlings Island (San Salvador) on January 15, 1893.

### AGALMA, ESCHSCHOLTZ, 1825.

#### *Agalma Pourtalesii*, AGASSIZ and MAYER.

Figures 106-113, Plates 31-33.

*Agalma Pourtalesii*, Agassiz, A., and Mayer, A. G., 1899; *Aculephs* from the Fiji Islands, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXXII. p. 180.

*Specific Characters.*—The entire animal (Plate 32) is about 25 mm. in length. The feeding-polypites, dactylozoids, tentacles, and gonostyles, all arise from the ventral side of the siphosome. The float, or pneumatophore, is of small size, and its apical pore is surrounded by radially arranged streaks of dark

red pigment. The swimming-bells (Figures 109, 110, Plate 33) are dovetailed alternately, one above another, so that their velar openings are situated on two diametrically opposite sides of the nectosome (see Figure 108).

The siphosome is densely covered upon all sides with thick prismatic bracts, or covering scales. One of these bracts detached from the animal is shown in Figure 112. The angular edges of the older bracts are usually smooth, but in the younger ones they frequently display a row of regularly arranged nematocyst-bearing papillæ (see Figure 113). A single, long, slender canal runs through the substance of each bract.

The feeding-polypites are somewhat stouter in shape than the dactylozooids, but in other respects are quite similar to them in appearance. They are quite contractile, and their mouths may be expanded, at will, so as to assume a funnel shape.

The tentacles arise from the bases of the dactylozooids and feeding-polypites. Each tentacle gives off a number of lateral branches, each one of which terminates in a coiled nematocyst-battery, an ampulla, and two paired finger-like processes (see Figure 111, Plate 33).

Both male and female gonostyles spring from the siphosome of the same individual. They arise from the ventral side of the siphosome between the dactylozooids and feeding-polypites (see Figure 108). The gonophores arise from the sides of the gonostyles. The male gonophores are long and slender, while the female are short and stout. Both resemble medusa buds and are provided with 4 radial tubes, a circular vessel, and a velum. The genital products occupy the manubrium. The gonophores are borne upon long slender filaments attached to the sides of the gonostyle. These filaments are highly contractile.

The color of the entoderm of the stem, swimming-bells, feeding-polypites, and dactylozooids is rose-pink. The nematocyst batteries upon the terminal portions of the tentacles are port-wine-red. The gonads and bracts are colorless.

This species was found by us at the Tortugas Islands in June, 1897. We also met with it in Suva Harbor, Fiji Islands, in December, 1898.

### *Agalma virida*, nov. sp.

Figs. 119-121, Plate 35.

A single immature individual of this beautiful species was obtained on June 6, 1899, at the Tortugas.

*Specific Characters.*—The animal is 3 mm. in length. The float is spherical and almost egg-shaped, and is covered by one of the larval bracts. The pore is a simple round opening at the aboral pole of the float, and is surrounded by large, polygonal pigment cells. There is a single large axial feeding-polypite which is capable of much expansion and contraction. The gastric cells of this polypite are large and oval. Six to eight mouthless

cystons arise from the side of the feeding-polypite. These are stiff and slender, and their distal extremities are armed each with several oval nematocyst cells of large size. The entoderm of the cystons display large, highly refractive oval cells quite similar to the digestive cells of the feeding-polypite. About half a dozen branched tentacles arise from between the cystons. Each branch terminates in a complexly formed coiled nematocyst battery which is enclosed within the substance of the terminal knob. The knob ends distally in a bladder-shaped ampulla and a pair of long curved finger-shaped processes, the latter being lined on their convex sides with a row of hair-cells (see Figure 120). Several small hernia-like protuberances, which probably consist of young swimming-bells, arise from the side of the main axis immediately below the level of the float. The bracts are three-cornered, and their sharp distal ends are armed with large nematocyst cells. The free edges of the primitive larval bract are lined with a row of small nematocyst cells. Each bract is provided with a long slender, unbranched canal. The pigment cells of the float are rich brown in color. The entoderm of the feeding-polypite and cystons is of a decided pink, and the coiled nematocyst batteries in the tentacle knobs are of a more decided reddish color. The entoderm of the float and the ectoderm of the terminal knobs of the tentacles are yellow, and the canals of the bracts are grass-green in color.

#### IV. CTENOPHORÆ.

##### OCYRÖE, RANG, 1826.

##### *Ocyroë crystallina*, RANG.

Fig. 105, Plate 31.

*Ocyroë crystallina*, Rang, S., 1828, Mem. Soc. Nat. Paris, Tom. IV. p. 172, Pl. XX.  
Fig. 4.

This Ctenophore is quite often met with at the Tortugas, Florida, from April until July. It makes its appearance at the surface when the ocean is perfectly flat and calm, and even a slight ripple is sufficient to induce it to sink into the depths. The species appears to be widely distributed over the Tropical Atlantic.

##### BOLINA, MERTENS, 1833.

##### *Bolina vitrea*, L. AGASSIZ.

Figs. 91, 92, Plate 27.

*Bolina vitrea*, Agassiz, L., 1860, Cont. Nat. Hist. U. S., Vol. III. pp. 269, 289,  
Fig. 93.

*Bolina littoralis*? McCrady, J., 1858, Proc. Elliott Soc., Charleston, p. 1, Pl. 14.

Large numbers of this Ctenophore may be seen floating in the water on almost any calm day throughout the summer at the Tortugas, Florida. It is also common among the Florida Reefs, and probably extends as far up the coast as Charleston, South Carolina.

**HORMIPHORA**, AGASSIZ, L., 1860.

**Hormiphora plumosa?** CHUN.

Cydippe hormiphora, Gegenbaur, C., 1856; Archiv für Naturges., p. 200, Taf. VIII. Fig. 10.

Hormiphora plumosa, Chun, C., 1880, Die Ctenophoren des Golfes von Neapel, p. 281, Taf. I. Figs. 5, 6; Taf. II. Figs. 2, 3; Taf. III. Figs. 8, 9.

Numerous fragments of a Hormiphora, that may be specifically identical with the common *H. plumosa* of the Mediterranean, were found during the summer of 1898 at the Tortugas, Florida.

Unfortunately no perfect specimens were captured, and we must remain in doubt concerning the specific identity of this animal with *H. plumosa*.

**EUCHARIS**, ESCHSCHOLTZ, 1825.

**Eucharis multicornis?** ESCHSCHOLTZ.

*Eucharis multicornis*, Eschscholtz, F., 1829, Syst. der Acalephen, p. 31.

A species of *Eucharis* believed to be specifically identical with *E. multicornis* of the Mediterranean is found at Key West and the Tortugas, Florida.

**BERÖE**, BROWNE, 1789.

**Beroë Clarkii.**

Beroë, Browne, P., 1789, The Civil and Nat. Hist. of Jamaica, p. 384, Table 43, Fig. 2. *Idyiopsis Clarkii*, Agassiz, L., 1860, Cont. Nat. Hist. U. S., Vol. III. pp. 288, 296; Figs. 101, 102.

This Ctenophore is very abundant among the Bahama, Tortugas, and Florida Reefs; and it extends as far northward as Charleston Harbor, South Carolina.



PLATE 1.

- Fig. 1. *Pandea violacea*, Agassiz and Mayer.  
Fig. 2. *Stomotoca australis*, nov. sp.

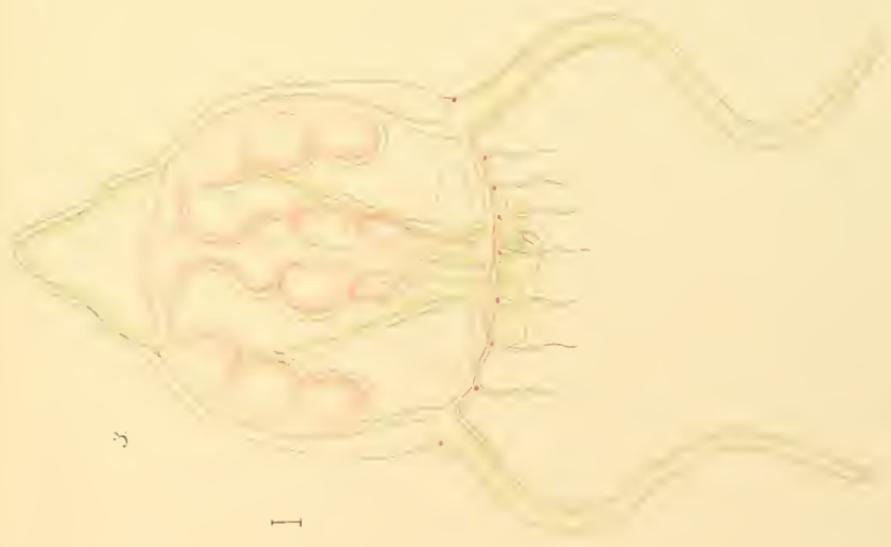






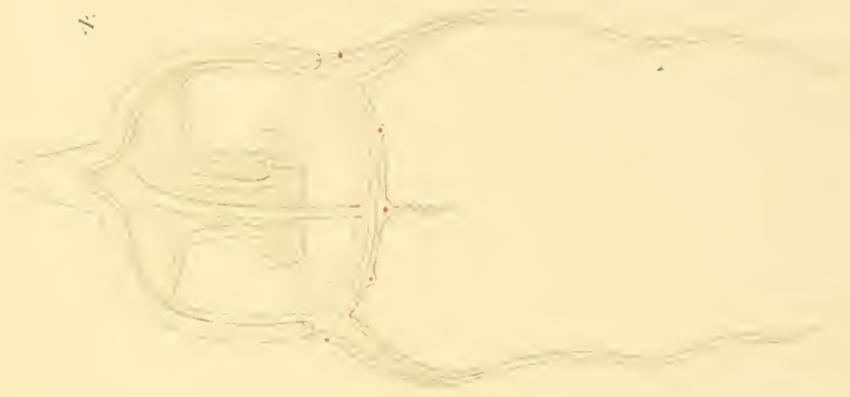
PLATE 2.

- Fig. 3. *Dissonema turrida*, nov. sp. Adult medusa.  
Fig. 4. " " " Young medusa.



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PLATE 3.

- Fig. 5. *Bougainvillia frondosa*, nov. sp.  
Fig. 6. *Gonionemoides geophila*, nov. gen. et sp. Portion of bell margin showing sucker-bearing and nematocyst-bearing tentacles.  
Fig. 7. *Gonionemoides geophila*, otocyst.

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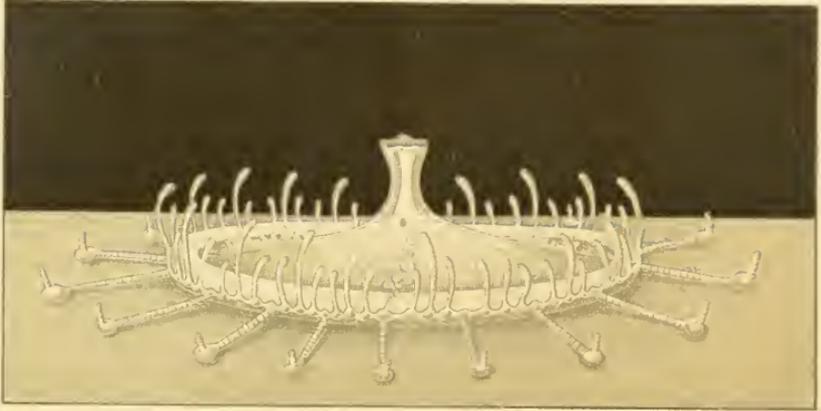




PLATE 4.

- Fig. 8 *Gonionemoides geophila*, nov. gen. et sp. Side view of adult medusa.  
Fig. 9.       "       "       "       Medusa with oral surface upward, and holding  
fast to the bottom of the aquarium by means of the adhesive suckers  
upon its tentacles.

9.



8.



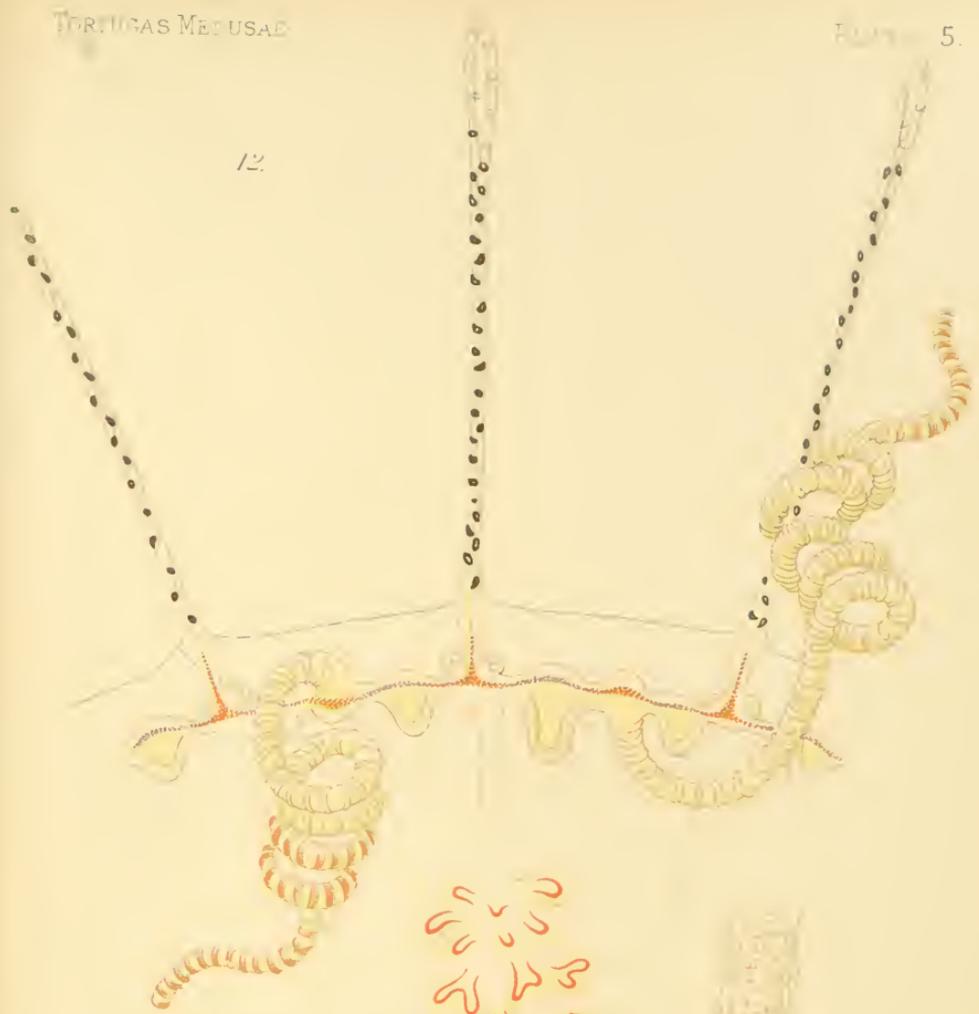




PLATE 5.

- Fig. 10. *Gonionemoides geophila*, nov. sp. Young medusa.  
Fig. 11. *Gonionemoides geophila*, nov. sp. Distal end of tentacle showing the beginning of the formation of the suctorial disk.  
Fig. 12. *Halicalyx tenuis*, Fewkes. Portion of bell margin.

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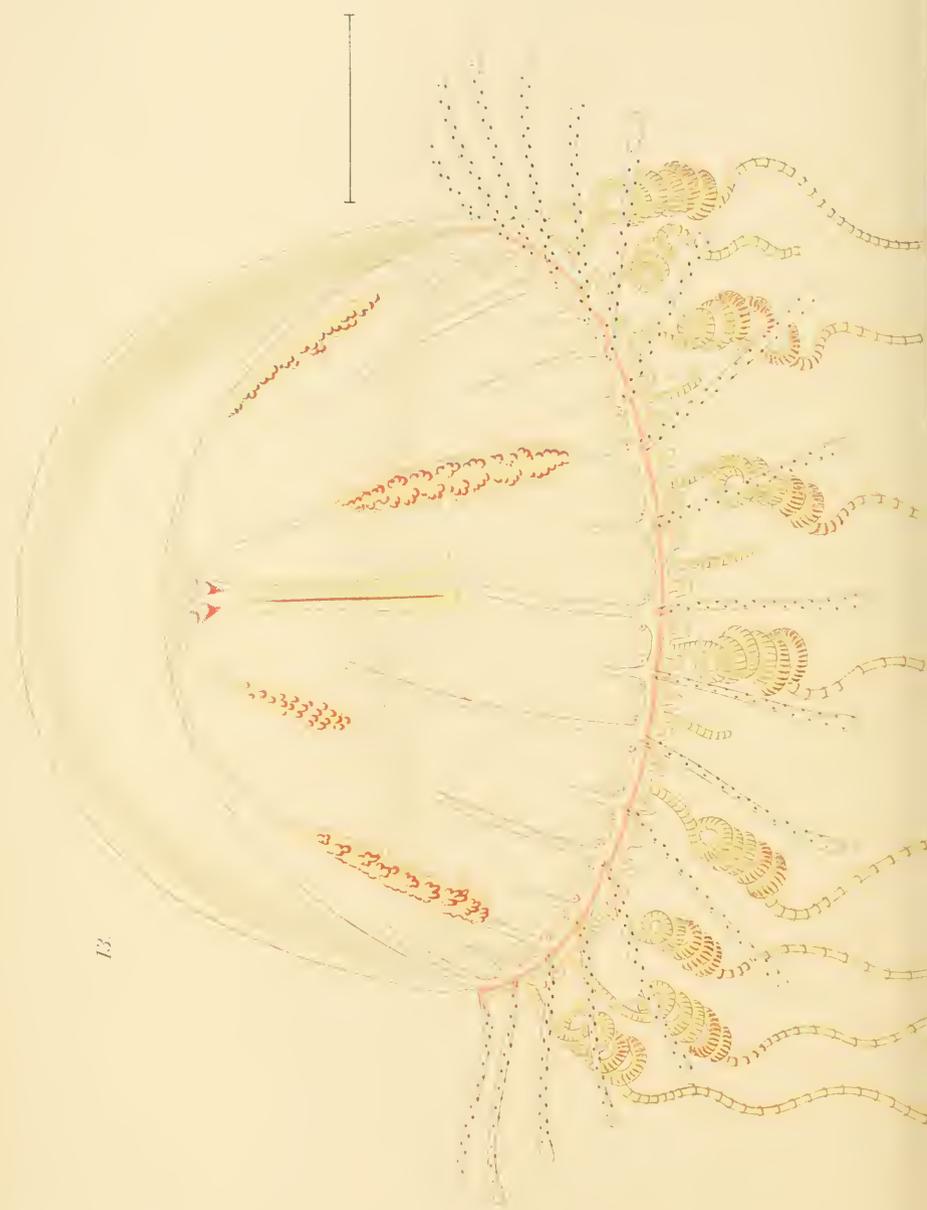




PLATE 6.

Fig. 13. *Halicalyx tenuis*, Fewkes. Side view of mature medusa.





13







PLATE 7.

- Fig. 14. *Tetracannota collapsa*, nov. gen. et sp. Adult medusa.  
Fig. 15. " " " " Very young medusa

15.



14.







PLATE 8.

- Fig. 16. *Tetracannota collapsa*, nov. gen. et sp. Half-grown medusa.  
Fig. 17. *Dyscannota gemmifera* = *Willia gemmifera*, Fewkes.

16.



17.







PLATE 9.

- Fig. 18. *Oceania magnifica*, nov. sp.  
Fig. 18<sup>a</sup>.       “       “       Portion of bell margin, showing otocysts.  
Fig. 19. *Oceania globosa*, nov. sp.  
Fig. 19<sup>a</sup>.       “       “       Portion of bell margin.



18



18<sup>a</sup>

19<sup>a</sup>



19





PLATE 10.

- Fig. 20. *Oceania gelatinosa*, nov. sp.  
Fig. 20<sup>a</sup>. “ “ Otocyst.  
Fig. 21. *Phortis pyramidalis* = *Eutima pyramidalis*, L. Agassiz.  
Fig. 21<sup>a</sup>. “ “ Portion of bell margin.

20<sup>a</sup>

20.



21.



21<sup>b</sup>





PLATE 11.

- Fig. 22. *Eutimalphes cœrulea* = *Eirene cœrulea*, L. Agassiz.  
Fig. 22<sup>a</sup>. " " Portion of bell margin.  
Fig. 23. *Zygodactyla cyanea*, L. Agassiz. Young medusa.  
Fig. 23<sup>a</sup> " " Otocysts.

22<sup>a</sup>

22

23

23<sup>a</sup>

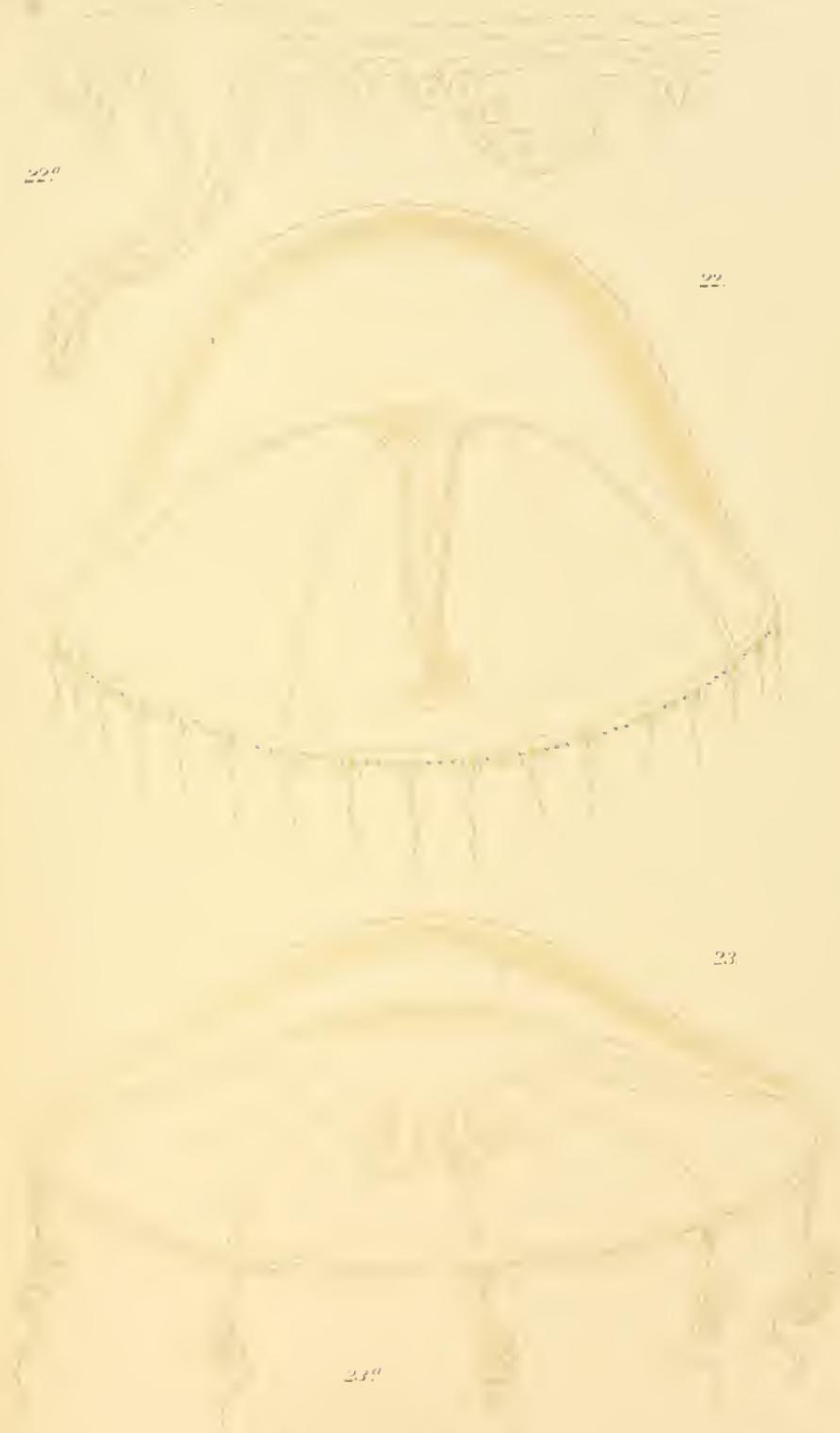






PLATE 12.

- Fig. 24. *Pseudoclytia pentata*, nov. gen. et sp. Side view.  
Fig. 25. " " Oral view of medusa.  
Fig. 26. " " Side view of otocyst.

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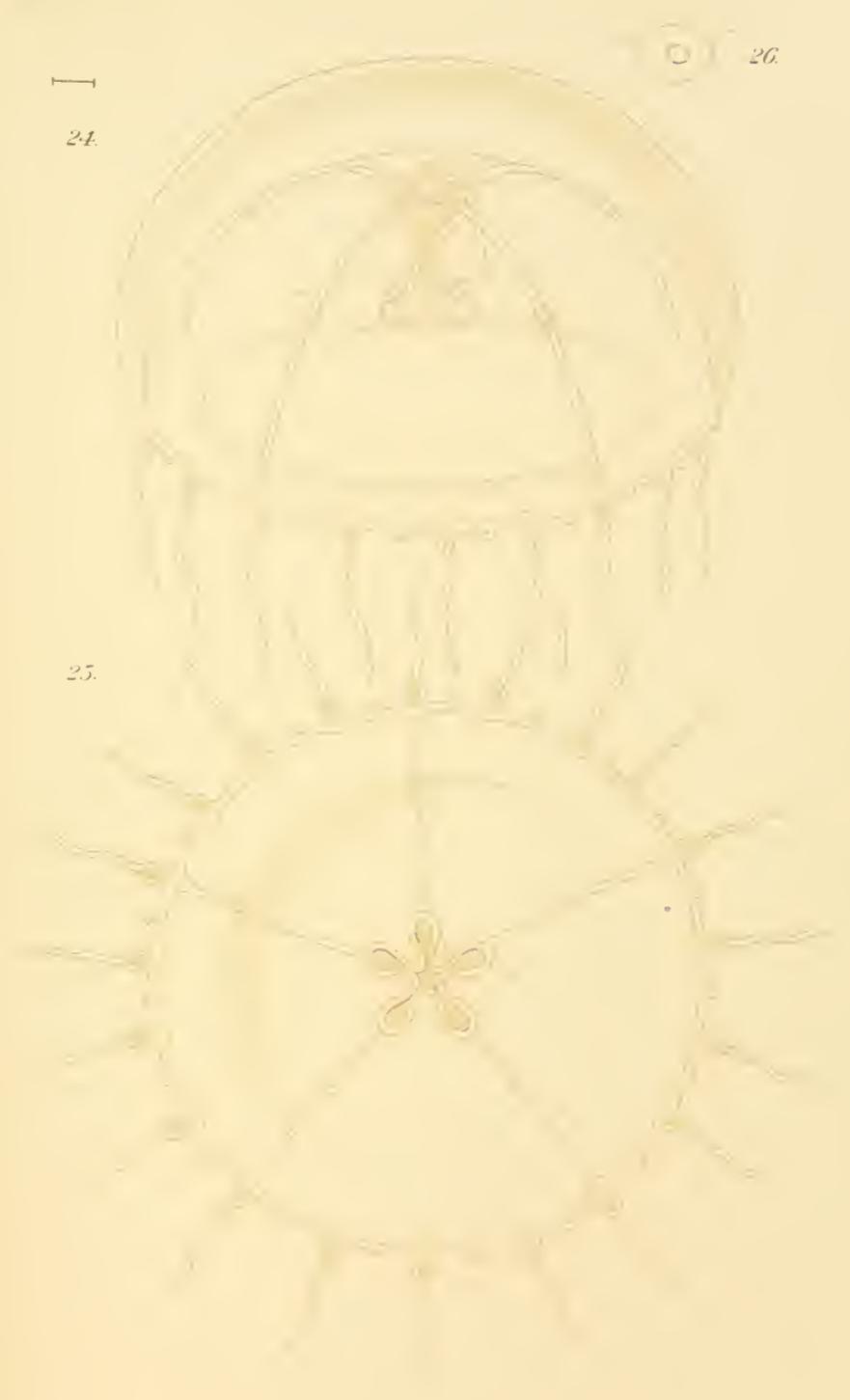






PLATE 13.

- Fig. 27. *Rhacostoma dispar*, nov. sp. Side view of medusa.  
Fig. 28. " " Oral view of medusa.  
Fig. 29. " " Otocyst.

27.

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PLATE 14.

- Fig. 30. *Æginella dissonema*, Haeckel. Side view of medusa.  
Fig. 31. “ “ Longitudinal section of tentacle.  
Fig. 32. “ “ Marginal sense-organ.

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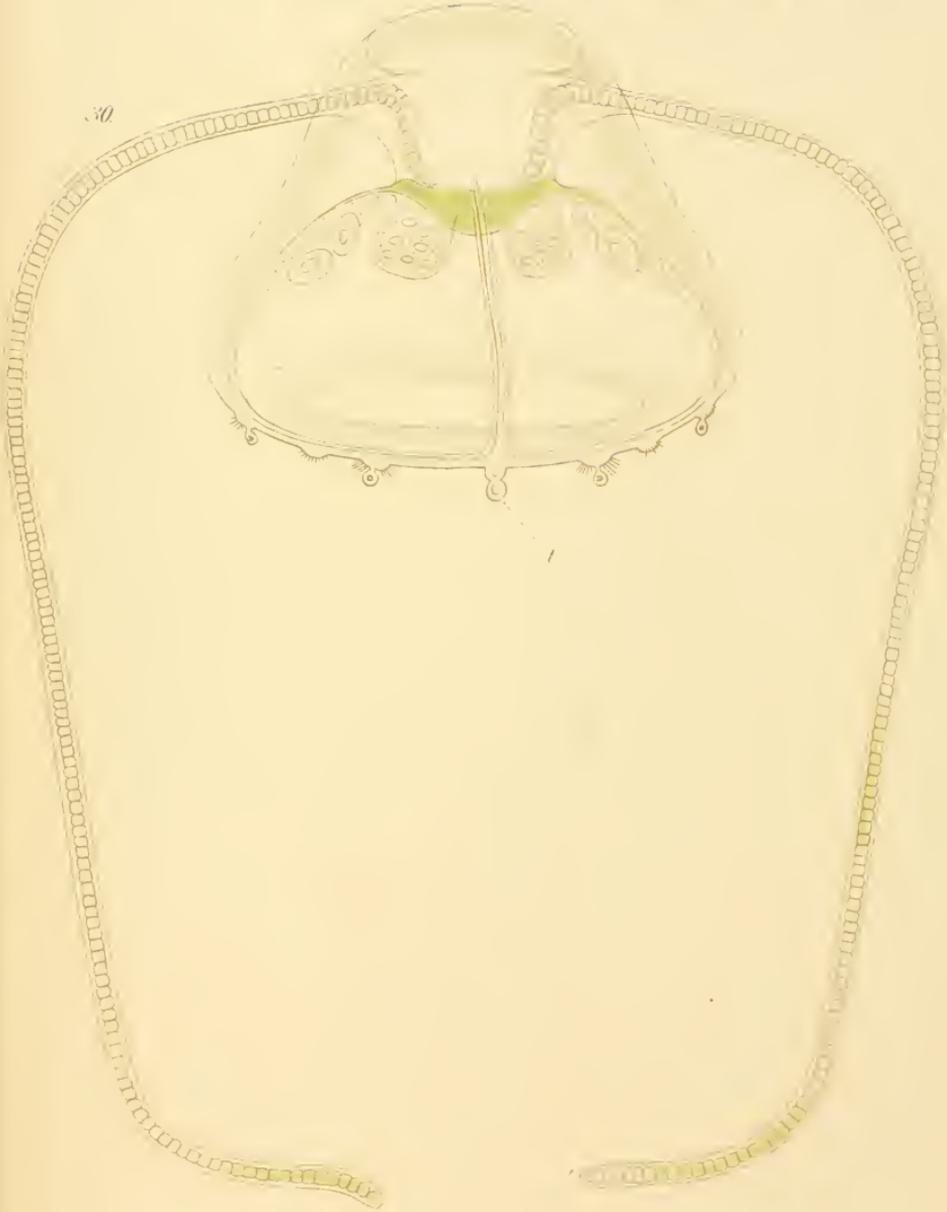


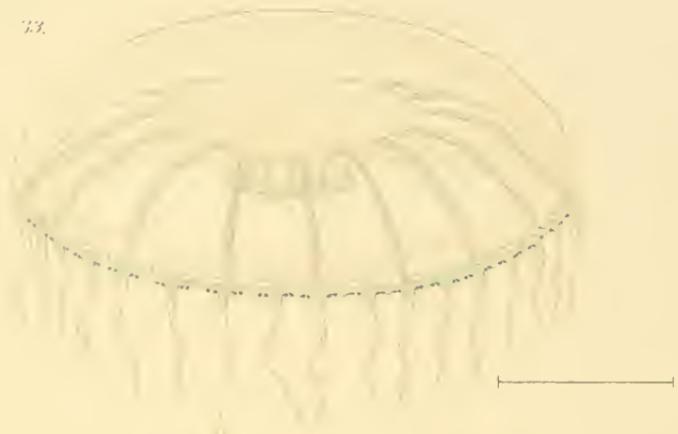




PLATE 15.

- Fig. 33. *Zygodactyla cyanea*, L. Agassiz. Medusa with 16 radial tubes.  
Fig. 34. " " " Portion of bell margin.  
Fig. 35. *Pseudoclytia pentata*, nov. gen. et sp., red variety.  
Fig. 35<sup>a</sup>. " " " View of ovary.

33.



35''

34.



35.







PLATE 16.

- Fig. 36. *Steenstrupia gracilis*, Brooks. Mature medusa ♂.  
Fig. 37. “ “ “ Young medusa.  
Fig. 38. *Ectopleura minerva*, nov. sp.  
Fig. 39. *Tiara superba*, nov. sp.

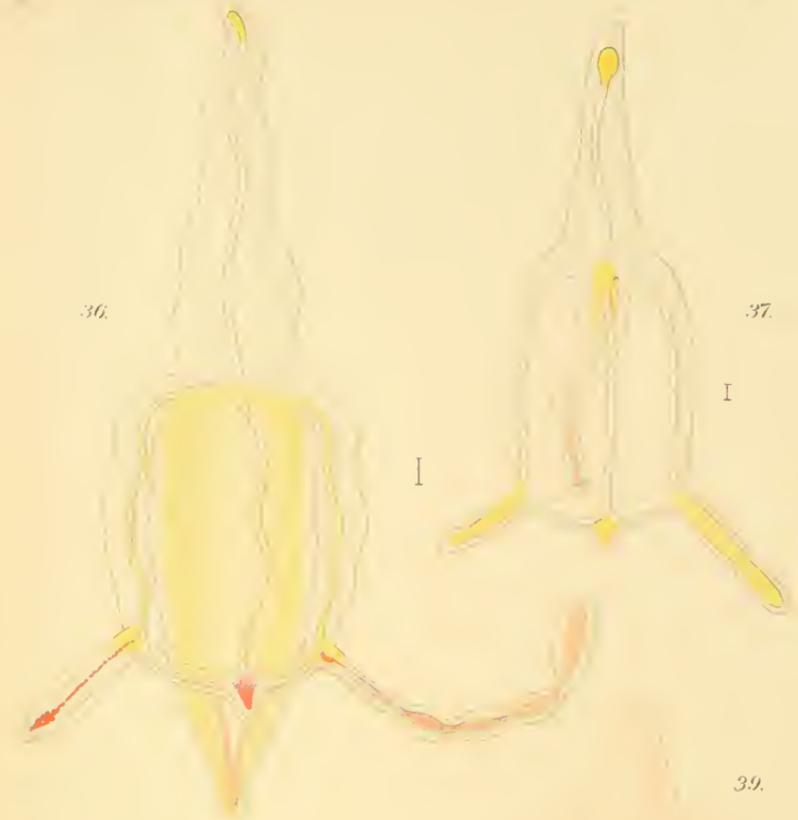




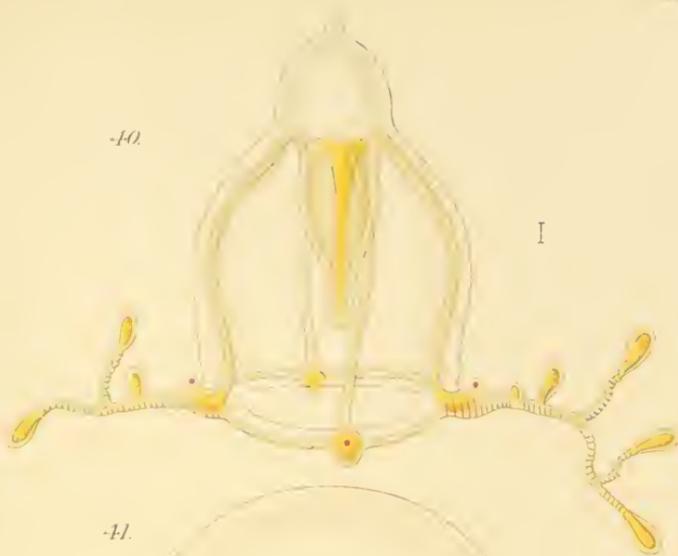


PLATE 17.

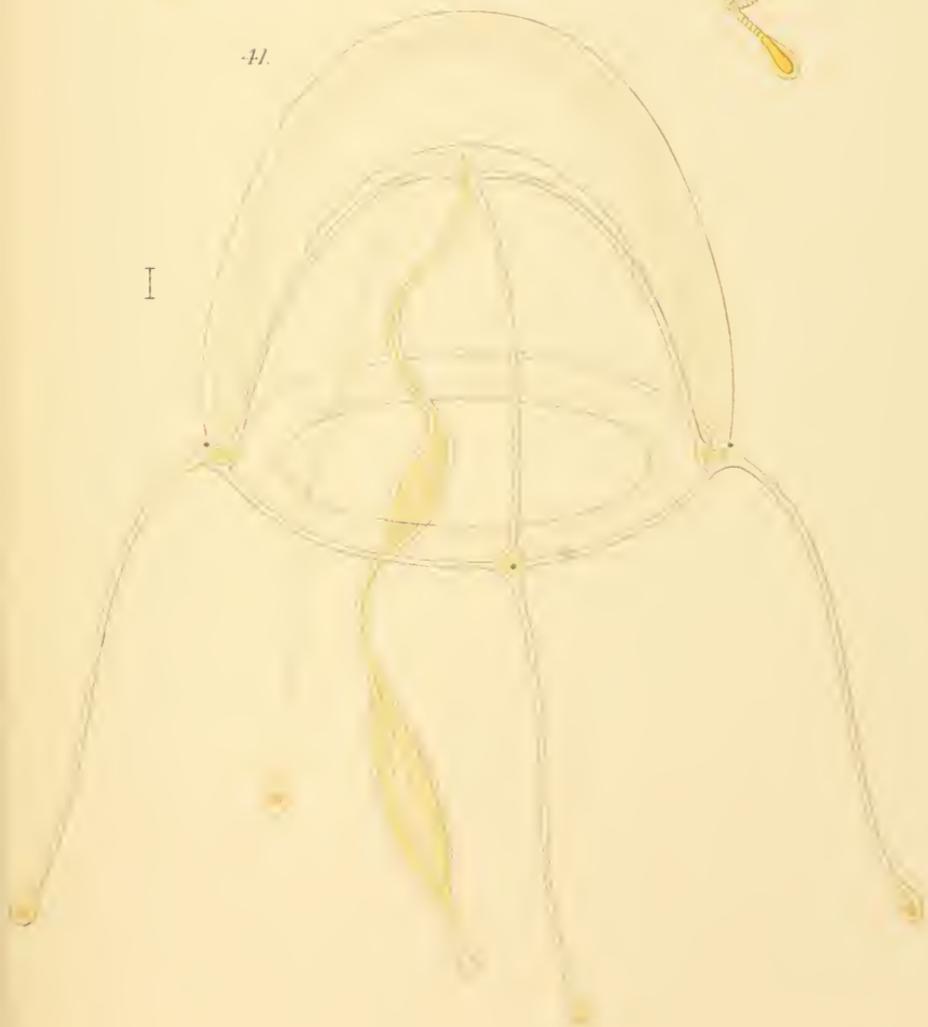
Fig. 40. *Gemmaria dichotoma*, nov. sp.

Fig. 41. *Dipurena fragilis*, nov. sp.

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PLATE 18.

- Fig. 42. *Dysmorphosa minuta*, nov. sp.  
Fig. 43. *Netocertoides brachiatum*, nov. gen. et sp. Side view.  
Fig. 44. " " Aboral view.  
Fig. 45. *Dipurena picta*, nov. sp.  
Fig. 46. " " Terminal portion of tentacle.  
Fig. 47. *Staurodiscus tetrastaurus*, Haeckel. Young medusa.

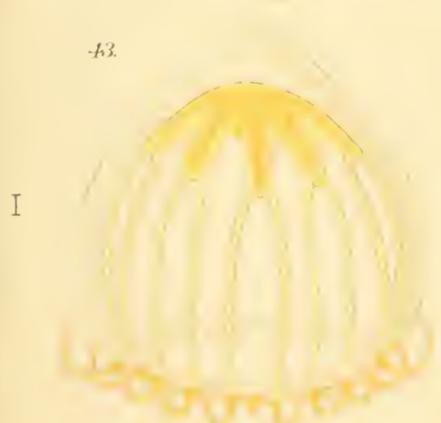
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PLATE 19.

- Fig. 48. *Staurodiscus tetrastaurus*, Haeckel. Oral view of mature medusa.  
Fig. 49. " " Side view of mature medusa.

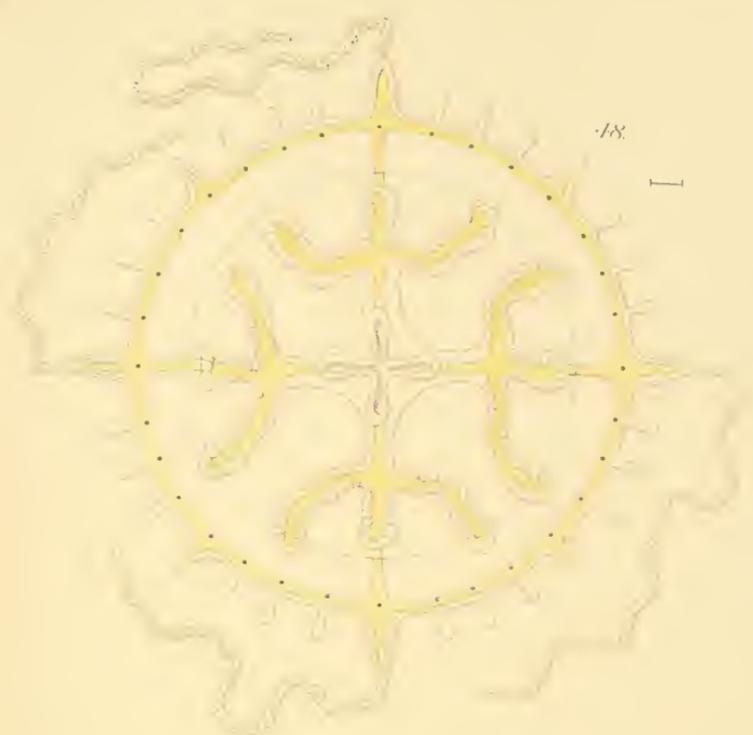






PLATE 20.

- Fig. 50. *Laodicea neptuna*, nov. sp. View of tentacle and ocellus.  
Fig. 51. " " Side view of mature medusa.  
Fig. 52. " " Oral view of mature medusa.  
Fig. 53. *Oceania discoida*, nov. sp. Side view of mature medusa.  
Fig. 54. " " Side view of young medusa.  
Fig. 55. " " Oral view of bell margin of a young medusa.

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PLATE 21.

- Fig. 56. Oceania McCradyi, Brooks. Side view of mature medusa.  
Fig. 57. Oceania McCradyi, Brooks. View of one of the hydroid blastostyles that  
are produced upon the gonads.  
Fig. 58. Oceania McCradyi, Brooks. Young blastostyle.  
Fig. 59. " " " Oral view of mature medusa.

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PLATE 22.

- Fig. 60. *Tiaropsis punctata*, nov. sp. Young medusa.  
Fig. 61. " " Medusa older than Fig. 60.  
Fig. 62. " " Otocyst of young medusa.  
Fig. 63. " " Otocyst of medusa drawn in Fig. 61.  
Fig. 64. *Dysmorphosa dubia*, nov. sp. Side view.  
Fig. 65. " " Oral region of the proboscis.  
Fig. 66. " " Tentacle and ocellus.

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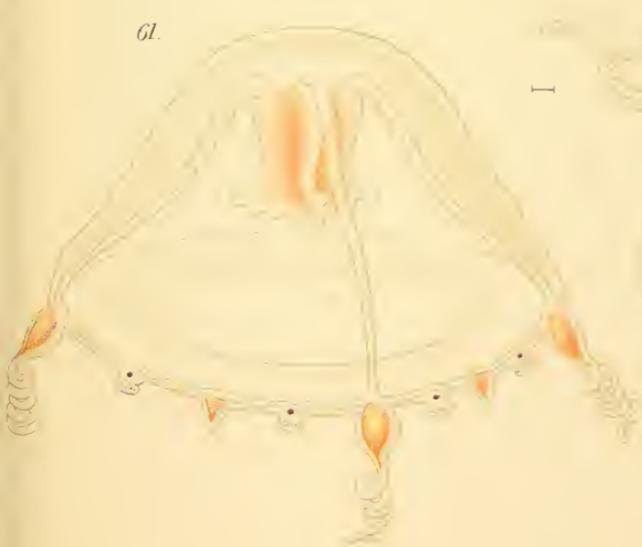






PLATE 23.

- Fig. 67. *Nausithoë punctata*, Kölliker. Oral view of young ephyra.  
Fig. 68. " " Oral view of sense-organ of young ephyra.  
Fig. 69. *Eutimium serpentinum*, nov. sp. Mature medusa.  
Fig. 70. " " View of bell margin, and tentacle.  
Fig. 71. " " Gastric portion of the proboscis.  
Fig. 72. " " Proximal portion of the peduncle.

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PLATE 24.

- Fig. 73. *Aurelia habanensis*, nov. sp. View of the edge of the mouth-arms, or palps, showing the wart-like clusters of nematocyst cells.
- Fig. 74. *Aurelia habanensis*, nov. sp. One of the wart-like clusters of nematocyst cells from the edge of the palps.
- Fig. 75. *Glossocodon tenuirostris*, Fewkes. Mature medusa.
- Fig. 76. " " View of mouth.
- Fig. 77. " " View of ovary.
- Fig. 78. " " View of tentacle and otocyst.

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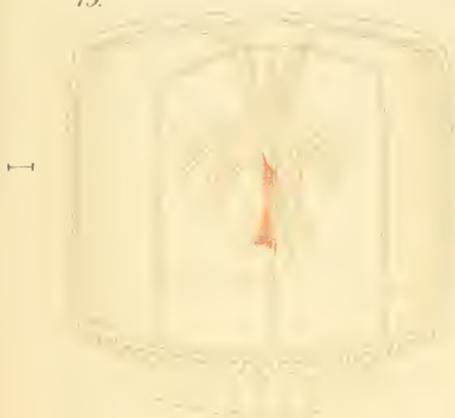




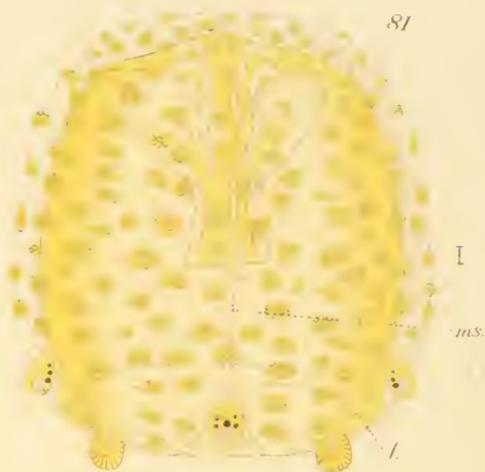
PLATE 25.

- Fig. 79. *Aglaura hemistoma*, Péron and Lesueur. Mature medusa.  
Fig. 80. " " Otocyst.  
Fig. 81. *Charybdea aurifera*, nov. sp. (*f*), frenula; (*ms*) muscle strands?  
Fig. 82. " " Side view of rhopalium.  
Fig. 83. " " View of rhopalium from without the bell.  
Fig. 84. *Zygodactyla cubana*, nov. sp.  
Fig. 85. " " View of bell margin.

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84.







PLATE 26.

- Fig. 86. *Aurelia habanensis*, nov. sp. Oral view of mature medusa.  
Fig. 87. *Nausithoë punctata*, Kölliker. Oral view of mature medusa.  
Fig. 88. " " " Otocyst and ocellus.







PLATE 27.

- Fig. 89. *Sphæronectes gracilis*, Haeckel. (*c*) connecting canal, (*f*) phyllocyst, (*p*) feeding-polypite, (*t*) tentacle.
- Fig. 90. *Chunia capillaria*, nov. gen. et sp.
- Fig. 91. *Bolina vitrea*, L. Agassiz. Mature animal.\*
- Fig. 92. *Bolina vitrea*, L. Agassiz. View of apical sense-organ. (*c*) gastric cilia; (*f*) funnel; (*mu*) "muscle" fibres.

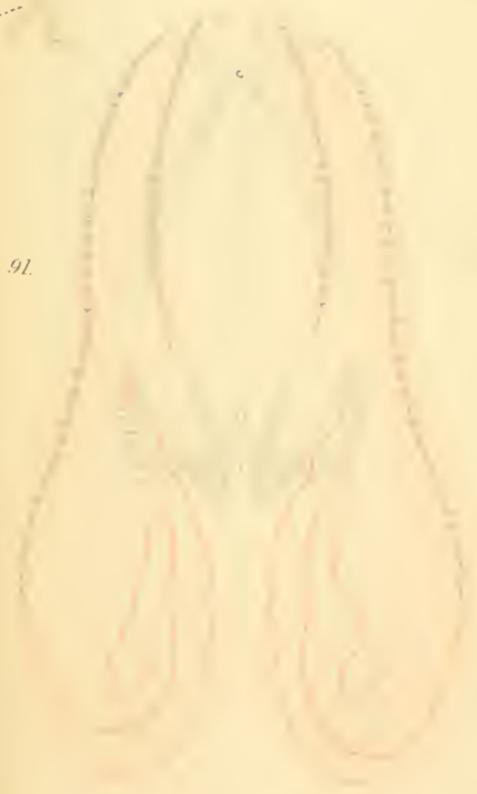
89.



90.



91.



92.







PLATE 28.

- Fig. 93. *Diphyopsis campanulifera*, Chun. Side view of mature animal. The posterior swimming-bell has been lost through accident.
- Fig. 94. *Diphyopsis campanulifera*. Enlarged view of the proximal portion of the siphosome. (*ps*) place of origin of the large posterior swimming-bell that has been lost through accident; (*as*) small "reserve" swimming-bell; (*p*) feeding-polypite; (*t*) tentacle; (*cs*) covering scale, or bract; (*b*) immature swimming-bell (shown mature in Fig. 96, *b*).
- Fig. 95. *Diphyopsis campanulifera*. Tentacular nematocyst battery.
- Fig. 96. *Ersæa Lessonii*, Chun. The monogastric, sexual generation of *D. campanulifera*. (*b*) swimming-bell; (*cs*) apical bract, or covering scale; (*g*) gonophore.
- Fig. 97. *Ersæa Lessonii*. Young ♀ gonophore containing two ova.



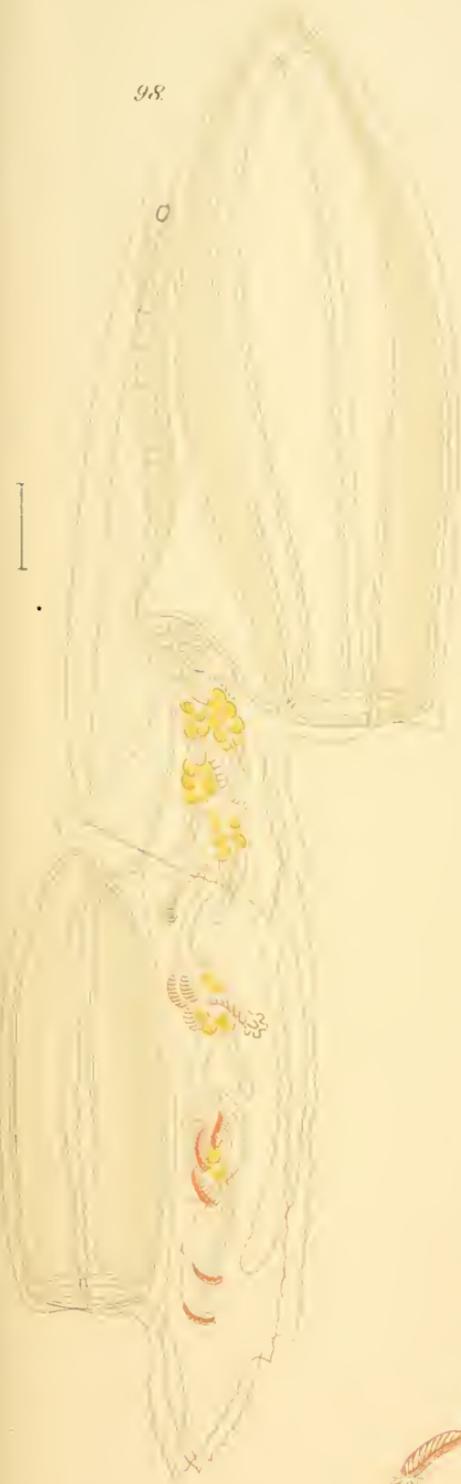




PLATE 29.

- Fig. 98. *Diphyopsis hispaniana*, nov. sp.  
Fig. 99. " " Portion of the siphosome.  
Fig. 100. *Ersæa hispaniana*, nov. sp. The monogastric, sexual generation of  
*Diphyopsis hispaniana*. (*g*) gonophore.

98.



100.



99.







PLATE 30.

- Fig. 101. *Abyla pentagona*, Eschscholtz.  
Fig. 101<sup>a</sup>. “ “ Usual form of the phyllocyst.  
Fig. 102. “ “ Enlarged view of the siphosome. (*as*) small “re-  
serve” swimming-bell; (*es*) bract, or covering scale; (*d*) duct of the  
large posterior swimming-bell; (*gs*) medusiform gonophore.  
Fig. 103. *Abyla pentagona*. Tentacular nematocyst battery.  
Fig. 104. *Aglaisma cuboides*, Chun. The monogastric, sexual generation of *Abyla*  
*pentagona*. (*cs*) bract, or covering scale; (*gs*) medusiform gonophore  
that functions also as a swimming-bell.

101A.



101



102



101c



103.







PLATE 31.

- Fig. 105. *Ocyroë crystallina*, Rang. Figure  $1\frac{1}{4}$  times the natural size. (*w*) wart-like protuberances upon the surface of the Ctenophore; (*au*) auricle.  
Fig. 106. *Agalma Pourtalesii*, Agassiz and Mayer. Female gonads.  
Fig. 107. " " Male gonad.

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♂







PLATE 32.

- Fig. 108. *Agalma Pourtalesii*, Agassiz and Mayer. Side view of the entire animal.  
From a specimen obtained at the Tortugas, Florida.







PLATE 33.

- Fig. 109. *Agalma Pourtalesii*, Agassiz and Mayer. Swimming-bell seen from above.
- Fig. 110. *Agalma Pourtalesii*. Swimming-bell seen from the side.
- Fig. 111. " " Terminal portion of tentacle.
- Fig. 112. " " View of a detached bract.
- Fig. 113. " " Nematocyst-bearing papillæ sometimes seen on young and immature bracts.

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112



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PLATE 34.

- Fig. 114. *Diphyes bipartita*, Costa.  
Fig. 114\*. " " One of the units of the siphosome. (*g*) medusiform gonad, (*h*) siphosome, (*p*) feeding-polypite, (*t*) tentacle, (*cs*) covering scale or bract.  
Fig. 115. *Abyla quincunx* = *Abylopsis quincunx*, Chun.  
Fig. 116. " " Tentacular nematocyst battery.  
Fig. 117. " " Small "reserve" swimming-bell.  
Fig. 118. *Ersaa picta*, Chun.

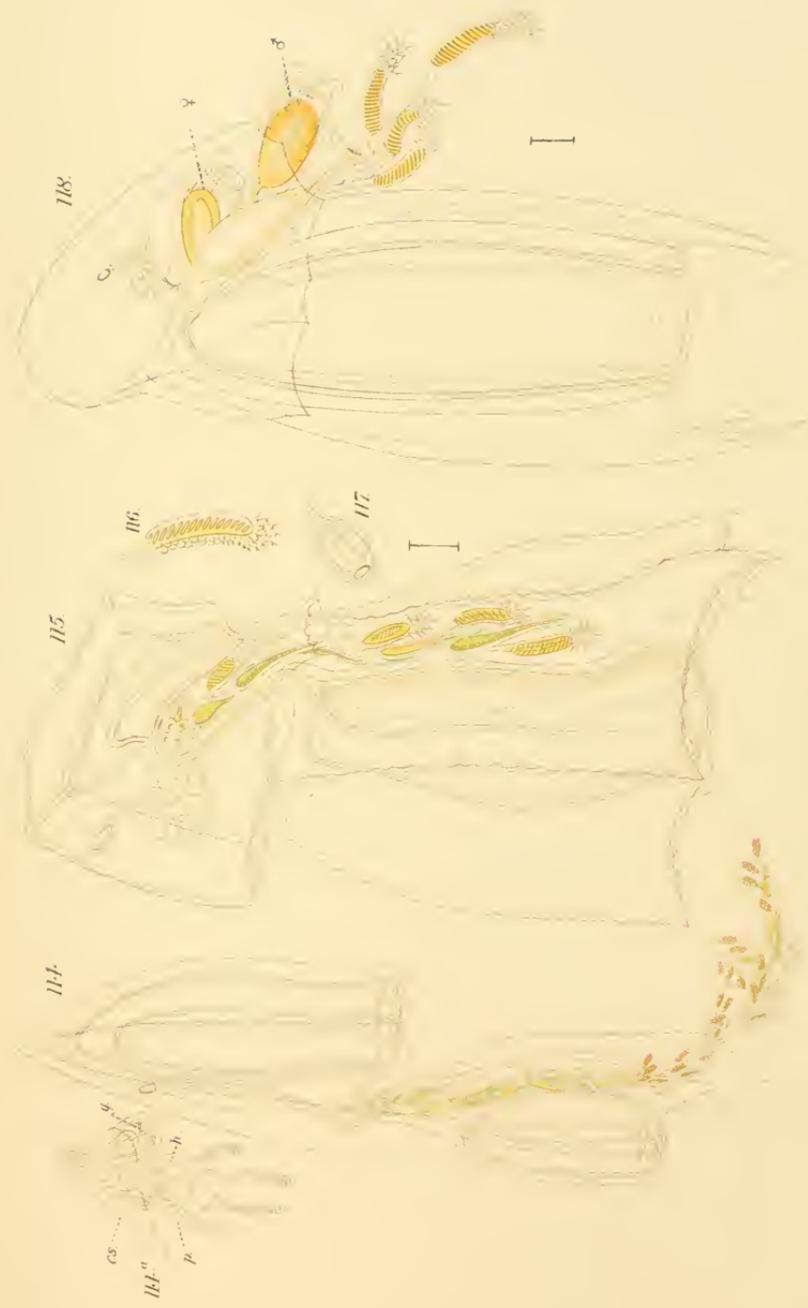






PLATE 35.

- Fig. 119. *Agalma virida*, nov. sp. Immature individual.  
Fig. 120. “ “ Terminal knob of the tentacles.  
Fig. 121. “ “ Polygonal pigment cells of the float.

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121

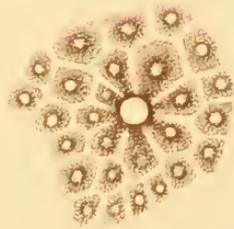






PLATE 36.

- Fig. 122. *Cytaeis gracilis*, nov. sp. Mature medusa.  
Fig. 123. “ “ Young medusa.  
Fig. 124. “ “ Very young medusa.

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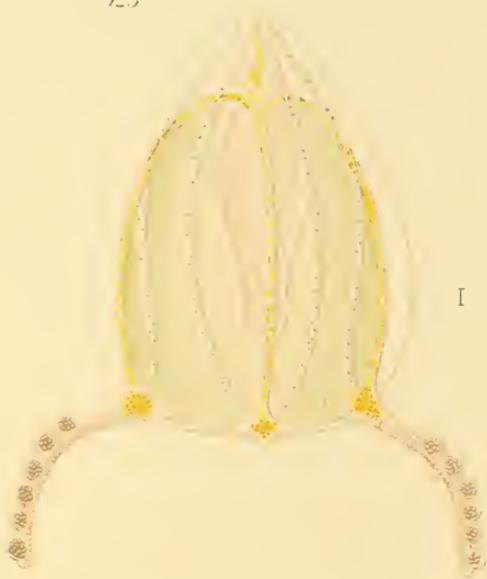




PLATE 37.

- Fig. 125. *Ectopleura minerva*, nov. sp.  
Fig. 126. *Dinema jeffersoni*, nov. sp.

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PLATE 38.

Fig. 127. *Lizzia elegans*, nov. sp.

Fig. 128. *Eucheilota ventricularis*, McCrady.







PLATE 39.

Figs. 129, 130. *Multioralis ovalis*, nov. gen. et sp.

Fig. 131. *Pseudoclytia pentata*, nov. gen. et sp. Side view of mature medusa ♀.

Fig. 132. " " Tentacle-bulb showing green entodermal pigment.



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- Fig. 133. *Phortis lactea*, nov. sp.  
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Fig. 135.       "       "       A young medusa bud.  
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                  parent.

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PLATE 41.

- Fig. 137. *Zanlea gemmosa*, McCrady. Young medusa of *Gemmaria gemmosa*.  
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PLATE 42.

- Fig. 140. *Eucopium parvigastrum*, nov. sp. Adult medusa.  
Fig. 141. *Niobia dendrotentacula*, nov. gen. et sp. Side view of an adult medusa.  
Fig. 142. *Niobia dendrotentacula*. A young medusa recently separated from the adult individual.  
Fig. 143. *Niobia dendrotentacula*. The proboscis and ova of a mature medusa after the cessation of the medusa-forming process.

143.

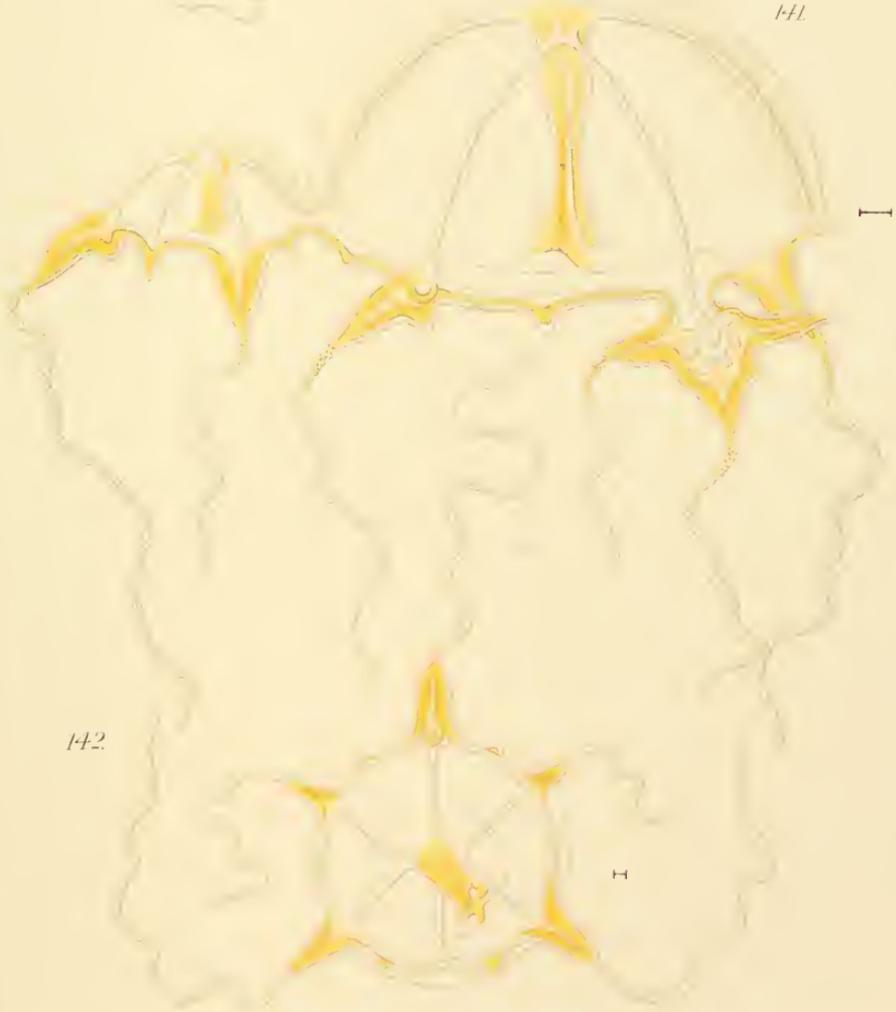


140.



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141.



I

142.



H





PLATE 43.

- Fig. 144. *Niobia dendrotentacula*, nov. gen. et sp. Oral view of an adult medusa, showing stages in the formation of new medusæ from the tentacle bulbs of the parent form.

1-4.

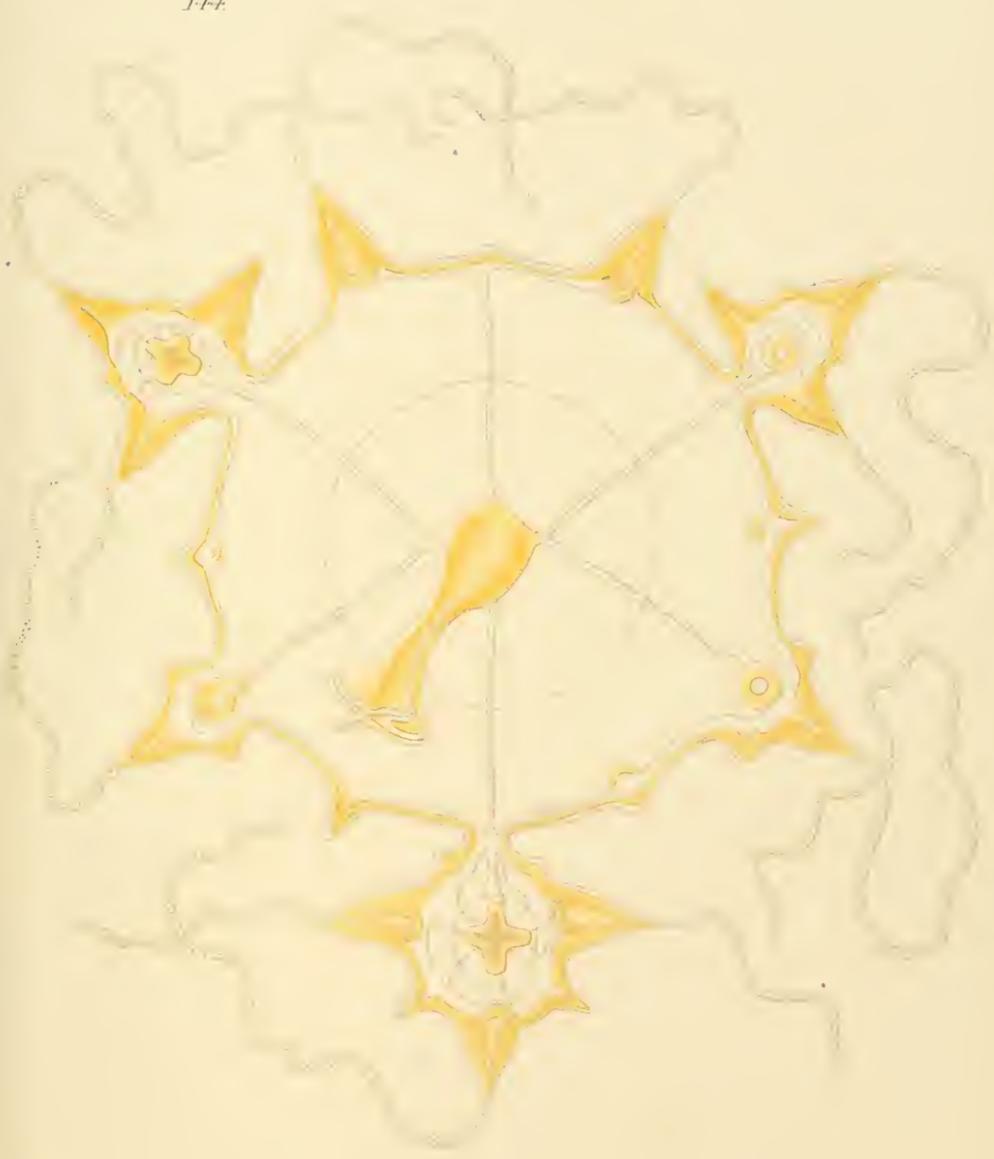


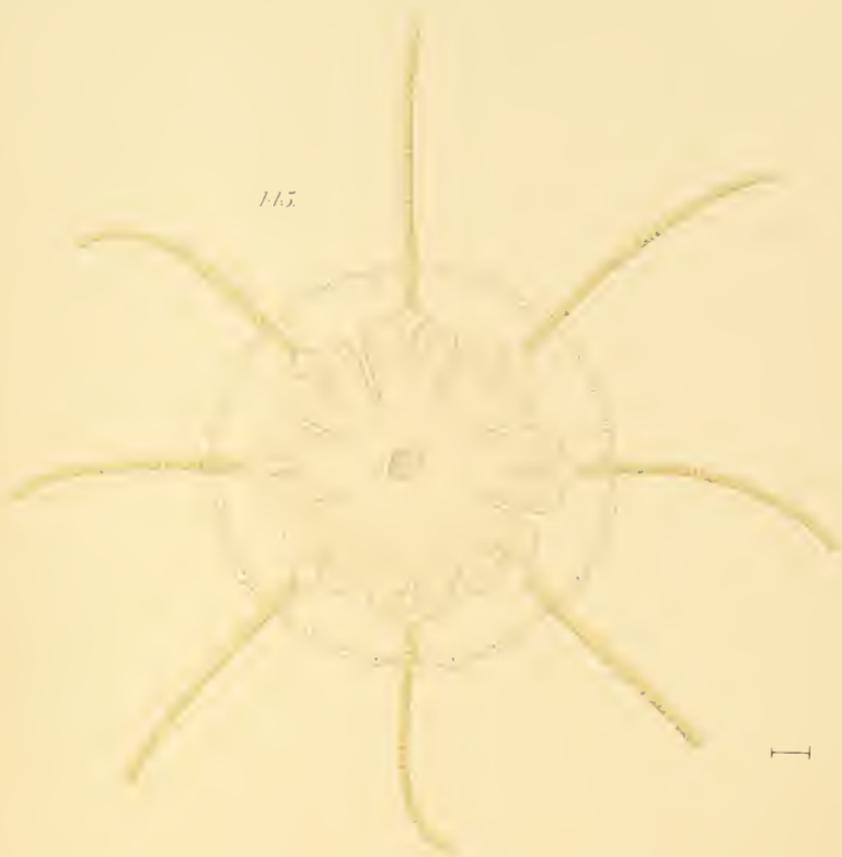




PLATE 44.

- Fig. 145. *Cunoctantha incisa*, nov. sp. Oral view.  
Fig. 146. “ “ “ Side view.

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The following Publications of the Museum of Comparative Zoölogy  
are in preparation:—

Reports on the Results of Dredging Operations in 1877, 1878, 1879, and 1880, in charge of ALEXANDER AGASSIZ, by the U. S. Coast Survey Steamer "Blake," as follows:—

- E. EHLERS. The Annelids of the "Blake."  
C. HARTLAUB. The Comatulæ of the "Blake," with 15 Plates.  
H. LUDWIG. The Genus *Pentacrinus*.  
A. E. VERRILL. The Aleyonaria of the "Blake."

Illustrations of North American MARINE INVERTEBRATES, from Drawings by BURKHARDT, SONREL, and A. AGASSIZ, prepared under the direction of L. AGASSIZ.

- A. AGASSIZ. The Islands and Coral Reefs of the South Seas. "Albatross" Expedition of 1899-1900.  
LOUIS CABOT. Immature State of the Odonata, Part IV.  
E. L. MARK. Studies on *Lepidosteus*, continued.  
" On *Arachnactis*.  
R. T. HILL. On the Geology of the Windward Islands.  
W. McM. WOODWORTH. On the Bololo or Palolo of Fiji and Samoa.  
A. AGASSIZ and A. G. MAYER. The Acalephs of the East Coast of the United States.  
A. G. MAYER. Some Acalephs from the South Pacific.  
A. G. MAYER. Acalephs from the Tortugas, Florida.  
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Reports on the Results of the Expedition of 1891 of the U. S. Fish Commission Steamer "Albatross," Lieutenant Commander Z. L. TANNER, U. S. N., Commanding, in charge of ALEXANDER AGASSIZ, as follows:—

- |   |  |
|---|--|
| A. AGASSIZ. The Pelagic Fauna.                          | J. P. McMURRICH. The Actinarians.                  |
| " The Echini.   | E. L. MARK. Brauchiocerianthus.                    |
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| G. VON KOCH. The Deep-Sea Corals.                       |  |
| C. A. KOFOID. Solenogaster.                             |  |
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THE REGENERATING NERVOUS SYSTEM OF LUMBRICIDÆ  
AND THE CENTROSOME OF ITS NERVE CELLS.

BY HERBERT W. RAND.

WITH EIGHT PLATES.

CAMBRIDGE, MASS., U. S. A. :  
PRINTED FOR THE MUSEUM.  
SEPTEMBER, 1901.



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No. 3. — *Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. MARK, No. 126.*

THE REGENERATING NERVOUS SYSTEM OF LUMBRICIDÆ AND THE CENTROSOME OF ITS NERVE CELLS. By HERBERT W. RAND.

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## I. Introduction.

For several years after the description by van Beneden, in 1883, of the mitotic polar structures to which he gave the names, "sphères attractives" and "corpuscules polaires," such structures were observed only in cells undergoing mitosis, and were believed to be visibly present only during the mitotic process, although it was suggested by van Beneden himself that they might be preformed in the cell, becoming evident only during mitosis. It was therefore a matter of some interest when, in 1891, Flemming described structures in certain resting cells of the salamander similar to those found at the poles of the mitotic figure. Flemming was the first to describe these structures minutely, although the observations of Solger ('89) and Rabl ('89) had been made previously.

This discovery led to the search for the centrosome in the resting cells of various tissues, and interest in the question culminated with the announcement by von Lenhossék, in 1895, of the discovery of a centrosome and sphere in the nerve cells of the frog. Von Lenhossék was quickly followed by other authors who described similar structures in the nerve cells of other animals, and at the present time the "centrosome" is known to exist in the nerve cells of many vertebrates and invertebrates.

It is a matter of some importance, as has been pointed out by several authors, to determine whether or not the "centrosomes," "spheres," and radiations seen in the cytoplasm of fully differentiated and presumably functional nerve cells are related to the polar structures of past or future mitotic divisions of the cell. Accepting the general belief that functional nerve cells do not divide, we are limited to proving either that the centrosome and its accompanying structures of the last mitosis of the embryonic nerve cell persist as the centrosome and radiating system of the differentiated nerve cell, or that, on the contrary, they do not persist, and that we have to do in the differentiated nerve cell with structures which have arisen in the cytoplasm independently of the last mitosis of the cell. That certain parts of the radiating system of the resting cell could have been left over from the last division, and other parts not, is, of course, a possibility to be considered.

The following work was undertaken at the suggestion of Professor E. L. Mark, with the purpose of throwing some light upon the origin of the so-called centrosome of the nerve cell. The work was carried on

at Harvard University under the direction of Professor Mark and Doctor W. E. Castle, from whom have been received much valuable assistance and many helpful suggestions as to the proper interpretation of the results obtained.

## II. Historical.

### 1. THE CENTROSOME IN NERVE CELLS.

Previous to von Lenhossék's discovery, in 1895, of the centrosome in the nerve cell, we find in the literature a few references to a fibrillar structure of the cytoplasm of nerve cells and a concentric arrangement about the nucleus.

Remak ('44, p. 469) described in the nerve cells of *Astacus* "sehr zarte granulirte, den Kern umkreisende Fasern." In the nerve cells of *Raja* he ('53) mentions two systems of fibrillæ, — peripheral ones extending into the axis cylinder, and deeper ones concentric to the nucleus.

Walter ('63), Leydig ('64, p. 84), Arnold ('67), and Schwalbe ('68) found a fibrillar structure concentric to the nucleus in nerve cells of vertebrates and invertebrates.

Arnold ('65, '67), Courvoisier ('66), Sigmund Mayer ('72), Eimer ('77), and other authors speak of fine fibres extending out from the nucleus, or even from the nucleolus, in vertebrate nerve cells, but from the descriptions and figures given it is impossible that these structures could have been identical with the exceedingly delicate radiations recently observed in connection with the centrosome.

Max Schultze ('71) found fibrillæ concentric to the nucleus in certain brain cells of *Torpedo*, as well as fibrillæ which enter the cell from the processes.

Hans Schultze ('79) described fibrillæ concentric to the nucleus in nerve cells of vertebrates.

Flemming ('82, '82<sup>a</sup>) mentioned a "streifige Structur" concentric to the nucleus in the central nerve cells of the pig. In the cells of the spinal ganglion of various mammals he found a fibrillar structure, but it exhibited no concentric or radial arrangement.

Von Lenhossék ('86) figured and described, in the spinal-ganglion cells of the frog, an arrangement of fibrillæ generally, but not always, concentric to the nucleus. In some of his figures the nuclei are very excentrically placed and are flattened or even slightly concave on the side nearest the centre of the cell, agreeing in this respect with the con-

ditions found in his later work on the same material, in which the centrosome and sphere were discovered.

Heidenhain ('94) declared that the presence of a centrosome was least to be expected in nerve cells. Nevertheless, he pointed out that the evidences of radial and concentric arrangement which have been described in such cells demand that a careful search for the centrosome be made.

Flemming ('95) mentioned the frequent occurrence of the concentric arrangement in the nerve cells of many animals investigated by him. He says (p. 25): "Die Anordnung ist nicht im vollen Sinne concentrisch, sondern scheint von der Polstelle in zwei opponirten Strahlungen an der Peripherie der Zelle zu verlaufen, so dass der Kern etwa die Mitte zwischen beiden bildet."

Von Lenhossék ('95), after the demonstration by Flemming and Heidenhain of the centrosome in resting cells, returned to the study of the nerve cells in which the excentric and flattened nuclei had been observed, and by methods other than those used in his previous work demonstrated the presence of a centrosome and sphere. The conditions which he finds in some of the spinal-ganglion cells of the frog are briefly as follows.

The nucleus is in a very excentric position and generally flattened, or even concave, on the side nearest the cell centre. The centrosome and sphere lie at the centre of the cytoplasmic mass, *exclusive of the nucleus*; for, as a result of planimetric measurements, von Lenhossék declares that "das Centrosom ist also in den Spinalganglien des Frosches wohl ein Centralgebilde in Bezug auf das Zellprotoplasma mit Abzug des Kerns, nicht aber in Bezug auf die kernhaltige Gesamtzelle" (p. 367). Heidenhain had found that in leucocytes the "Microcentrum" occupied the geometrical centre of the entire cell, except when displaced by a nucleus greater than one-half the diameter of the cell.

The centrosome of von Lenhossék is about  $0.5\mu$  in diameter, and is composed of never fewer than twelve granules imbedded in a feebly staining matrix, which he compares to the "achromatische Substanzmasse" by which Heidenhain's "Centralkörper" were connected. Surrounding this group of granules is the sphere, which appears in sections as a sharply defined, homogeneous, circular area from  $4\mu$  to  $6\mu$  in diameter. Its sharp boundary is not due to a layer of microsomes, but is marked only by the contrast between the substance of the sphere and the surrounding cytoplasm. This contrast is often emphasized by a narrow clear area about the sphere.

The cytoplasm is arranged concentrically around the sphere, showing a differentiation into an endoplasm and an exoplasm. The endoplasm is finely granular, the granules being more concentrated toward the centre. The exoplasm gives up its stain more readily than the endoplasm, remaining diffusely stained and appearing less granular than the endoplasm.

The conditions described were found in only the smaller cells of the ganglia. No centrosome was found in the spinal-ganglion cells of the dog or cat, but a concentric arrangement of the cytoplasm about the nucleus, which in those animals was found generally at the cell centre, was observed, leading von Lenhossék to suggest (p. 368) that "das dynamische oder vielleicht auch morphologische Aequivalent des Centrosoms hier in den Kern verlagert ist." No radiations were seen by von Lenhossék. All of his figures are from preparations fixed in sublimate and stained by Heidenhain's bordeaux-iron-hæmatoxylin method.

Bühler ('95), working simultaneously with von Lenhossék, announced the discovery of "Centralkörper" in the cortex of the fore-brain of the lizard, and also in nerve cells of the human brain. Bühler used warm corrosive sublimate and Flemming's fluid as fixing agents, and stained in various aniline dyes. His best demonstration of the "Centralkörper," however, resulted from the use of Heidenhain's iron-hæmatoxylin with bordeaux, safranin, or rubin.

Bühler found the nuclei to lie generally nearer the end of the cell from which the process came off, frequently so close to the surface "dass er stellenweise die Zellgrenze zu bilden scheint" (p. 17). On the side of the nucleus toward the greatest cytoplasmic mass, and therefore opposite the nerve process where that is to be seen, appear from one to three small, intensely stained granules, lying close together, and sometimes connected by a "Substanzbrücke." About this granule or group of granules is a clearer area of cytoplasm, and there may be one or several more or less complete dark circles concentric about the central granules. Radial fibres often appear extending out from the central granules, sometimes only to the inner of the surrounding circles, and sometimes quite to the periphery of the cell. Each of these concentric circles is due to a series of varicosities on the radial fibres, at equal distances from the central granules. In some preparations, however, the radial fibres are not conspicuous, and the circles appear to be made up of rows of granules.

Other systems of fibres run more or less parallel to the cell surface,

or concentric to the nucleus, and are traceable out into the processes. These fibres, which Bühler believes to be limited to the surface of the cell, also bear varicosities and appear to intersect the radial fibres, the points of intersection being marked by "kleine Knötchen." The central granules Bühler believes to correspond to the "Centralkörper" of Heidenhain, and the radial fibres to Heidenhain's "organische Radien."

As to the function of the centrosome in the resting cell, Bühler says (p. 37): "Wo, wie in reifen Ganglienzellen ihre Beziehung zur Zellteilung nicht nachgewiesen werden kann, da tritt ihre zweite Function in ihre Rechte: Sie sind in der ruhenden Zelle die Insertionsmittelpunkte für das centrirte Fibrillensystem." Bühler states (p. 38) his belief that "nicht nur das dynamische Centrum der Zellteilung in Gestalt der Centralkörper, sondern das gesammte System der organische Radien einschliesslich der Attractionssphäre dauernd in ruhenden Zellen sich erhält."

Dehler ('95) described structures in the sympathetic-ganglion cells of the frog very similar to those described by von Lenhossék for the spinal-ganglion cells of the same animal. Dehler, like von Lenhossék, obtained his best results with sublimate fixation and Heidenhain's staining methods. He found the nuclei excentric and lying at the end of the cell opposite the nerve process. They are generally flattened or concave on the side toward the cell centre. The cytoplasm contains "Schollen die sich concentrisch im Zelleib zu einander reihen." The centre about which the "Schollen" are arranged is approximately the centre of the cell. They are generally larger toward the periphery of the cell. The central region of the cell is more often quite free from them, and they are less marked, or even absent, in the smaller cells.

At the centre of the cell lies the "Centralkörpergruppe," composed of several deeply staining granules. About them the section of the cell exhibits a well-defined circular clear area from  $5\mu$  to  $7\mu$  in diameter. It is very finely granular and is bounded by neither a membrane nor a row of granules. In some of Dehler's figures there is about the central clear area a considerable zone free from the coarse "Schollen." In other cases the "Schollen" extend quite to the boundary of the clear area, which corresponds to von Lenhossék's "Sphäre." Dehler found no radiations from the region of the centrosome.

Flemming ('95\*) described a concentric arrangement of granules about the nucleus of the spinal-ganglion cells of mammals, but he found no structures similar to the centrosome and sphere which then had been recently described by von Lenhossék in the frog.

Schaffer ('96) described centrosomes in certain cartilage cells of *Myxine glutinosa* and also in nerve cells of the cranial ganglia of *Petromyzon planeri* 15.5 cm. long. His material was fixed in picro-sublimate and stained in hæmalum-eosin. Schaffer found cells with the nuclei excentric. The cytoplasm was very finely granular, and in it was commonly found a structure forming "eine Art von Gegengewicht im Protoplasma gegenüber dem Kern" (p. 26). These cytoplasmic structures appeared in some cases as merely small areas of irregular shape and varying size, staining red in contrast to the surrounding blue. Often two such areas of unlike form and size lay near together. In some cases a small clear space surrounded the darker area. In still other cells a circular clear area contained a small central granule, and at one side of the clear area lay an irregularly shaped red-staining mass similar to those found where no clear area and granule were present. Schaffer interprets the granule, clear area, and red-staining mass as centrosome, sphere, and archoplasm, respectively. He attributes the failure to find all three of the structures in so many cells to unfavorable planes of cutting, or to other causes. No radial arrangement of the cytoplasm was seen. He suggests that the structures described may be concerned in nuclear divisions of the ganglion cells, since he has often seen in *Petromyzon* ganglion cells with two nuclei.

McClure ('96, '97) described centrosomes and spheres in the nerve cells of *Helix* and thinks they may exist in *Limulus*. In *Astacus*, *Cambarus*, *Homarus*, *Lumbricus*, *Arion*, and *Limax* he failed to find these structures. In unipolar ganglion cells of *Helix* with a transverse diameter between  $17\mu$  and  $22\mu$  he finds excentric nuclei often flattened, or more frequently kidney-shaped. His figures show the nuclei lying at the end of the cell opposite the nerve process, and the flattened or concave side of the nucleus is never "directed exactly opposite to the base of the axis-cylinder process, but always to a point on one side of it." "In the body of the cell, directly opposite the invagination [of the nucleus], a disc-shaped structure was found." The disc is finely granular, but shows no radial arrangement. "Within these discs and at about their centre, two or three small granular bodies were present which stained much deeper than the surrounding granules and which I have taken for centrosomes." A zone of cytoplasm immediately surrounding the disc stains darker than the disc, because of a concentration of small chromophilous granules, but no radial arrangement among these granules is to be seen. The centrosome and sphere were best seen in material fixed in Flemming's fluid and stained in iron-

hæmatoxylin. Sublimate preparations with the same stain gave confirmatory results. In some cases, large spherical pigment granules were found arranged in a circle just outside the disc and close to its boundary.

Miss Lewis ('96, '98) described the presence of a centrosome and sphere in the giant nerve cells of *Clymene producta*. She demonstrated the presence of these structures by the use of vom Rath's picric-osmic-acetic-platinic chloride mixture, not followed by a stain. Sublimate fixation followed by Heidenhain's iron-hæmatoxylin gave confirmatory results.

The nucleus of these giant cells is excentric and flattened or concave on the side toward the cell centre. The sphere is a more or less sharply defined region lying near the cell centre and has a diameter about one-third that of the cell. It consists of an outer "broad zone of coarsely granular protoplasm; within this a smaller area of more nearly homogeneous protoplasm; and in the centre of this a very small highly refractive body, or occasionally two or three such bodies." The central bodies sometimes have the form of short rods. From the central granule, or granules, radiations "traverse both the inner, more homogeneous zone and the outer, coarsely granular zone. Sometimes the radiations pass even beyond this into the surrounding, finely granular protoplasm of the cell" ('96, p. 296). The radiations are composed of minute granules arranged in radiating lines.

Dahlgren ('97) examined spinal-ganglion cells of the dog and found appearances which resembled centrosomes and "centrospheres," but which he believed to be artifacts due to the crystallization of corrosive sublimate. The questionable structure, always found between the pigment mass and the nucleus, appeared in the section as a disc free from granules and having at its centre a black spot. Focussing revealed a radial arrangement of the disc, and the surrounding cytoplasm showed a "distinct concentric arrangement."

In some twenty-five cells, before the sublimate had been dissolved out by means of iodine, Dahlgren observed radiating crystals of the sublimate occupying the region where, in the same cells after staining, the supposed artifacts were seen.

That the crystals should always be found at the same region of the cell, Dahlgren says, "would indicate some difference in the constitution of the cell at this point."

Dogiel ('97, p. 108) mentions that, in methylen-blue preparations of the spinal-ganglion cells of certain mammals, "in einer gewissen Ent-

fernung vom Kerne ein runder oder ovaler heller Fleck mit einem kleinen, von Methylenblau stark gefärbten Körnchen im Centrum zu bemerken war." This is probably, he thinks, the centrosome and sphere described by von Lenhossék.

Heidenhain und Cohn ('97) find the "Microcentrum" in the cells of most of the tissues of bird embryos. In the cylindrical cells of the neural tube the microcentres lie at the extreme outer ends of the cells. In a surface view of a group of these cells their outlines form a polygonal network, "dessen Maschen die übrigens nicht regelmässig central gestellten Microcentren, je eines in einem Zellenterritorium, einschliessen. . . . Findet man in einem bestimmten Zellenfelde das Microcentrum nicht vor, so ist man häufig in der Lage zu konstatiren, dass in dem zugehörigen Zellenkörper eine Theilungsfigur enthalten ist, dass somit die Centalkörper zum Zwecke der Mitose in die Tiefe der Epithelzelle eingerückt sind" (p. 205).

Bühler ('98) finds excentric nuclei in cells of the spinal ganglia of *Bufo vulgaris*. In the cytoplasm chromophilous flakes, which are larger toward the periphery of the cell and smaller toward the centre, are arranged in concentric order about a point lying near the cell centre. Certain fibres also participate in this concentric arrangement. Close to the nucleus and on the side toward the cell centre lie two minute granules staining deeply in hæmatoxylin and connected by a dark band. About these as a centre are one or two rows of similar but less conspicuous granules arranged in arcs of circles. Extremely fine radiations pass outward from the central granules; they intercept in their courses the granules of the concentric arcs and are sometimes capable of being followed quite to the cell periphery. Granules staining in hæmatoxylin occur at rather regular intervals along the course of a fibril. *The concentric arrangement is about the approximate cell centre and not about the granules at the centre of the radiating system.* The latter centre lies in the line passing through the centre of the nucleus and the centre of the cell as a whole, — the principal axis, as determined by Heidenhain, — but toward the nucleus end of the cell from the cell centre. The "Microcentrum" described by Heidenhain for leucocytes lay at the cell centre. Bühler says (p. 49): "Bei mehreren Centalkörpern gelang es mir fast immer, eine Verbindung in Gestalt eines dunklen Bandes, die primäre Centrodosome Heidenhain's zu sehen." The system described by Bühler corresponds, therefore, to the "Microcentrum" and "organische Radien" of Heidenhain.

The results, then, of the work of von Lenhossék and Bühler upon

the same material, the spinal-ganglion cells of the frog, are at considerable variance. They agree in showing a concentric structure in the cell body, but von Lenhossék finds the centrosome at the centre of the concentric structure, while Bühler finds his "Centralkörper" near the nucleus and remote from the centre of the concentric arrangement. Von Lenhossék's centrosome is composed of a large number of granules; Bühler finds generally only two granules composing his "Centralkörper." In the toad and other vertebrates, including mammals, Bühler finds radiations from the "Centralkörper;" von Lenhossék described no radial structures. Bühler, in the paper referred to ('98), compares critically his results with those of von Lenhossék and other authors.

Bühler states that structures similar to those described by him ('95) in the brain of the lizard he has seen also in some of von Kölliker's Weigert preparations of pyramid cells from the human brain, and likewise in Cohn's preparations of nerve cells from an adult mouse.

Hunter ('98) noticed that van Beneden et Julin ('84), in a work on the central nervous system of ascidians, represented excentric invaginated nuclei in the nerve cells of *Molgula*. He consequently was led to investigate the cells of the central nervous system of *Cynthia partita*, and found the nuclei always excentric and generally at the end of the cell opposite the process. The form of the nuclei varied from spherical to cup-shaped. Occupying the centre of the cell was a structure which he considered homologous to the centrosome and sphere of von Lenhossék. At the centre of a "clearly staining area, homogeneous or finely granular," were one or several "black deep-staining granules, the centrosome or central bodies of authors." Surrounding the clear area was a coarsely granular zone of varying diameter. In some cells were "well developed astral rays, presenting the appearance found in leucocytes."

There were many modifications of the structure. In some cells all the parts mentioned were found, while in others only a central deeply staining granule was found with no definite cytoplasmic arrangement about it. In very young animals killed shortly after metamorphosis a larger proportion of cells showed the structure than in the adults. In these young cells the sphere and radiations were generally lacking, or at most only a very narrow clear area with a slight condensation about it was found. There were generally two central granules. In the cells of the young *Cynthia* the nuclei were excentric but rarely invaginated, and the centrosomes seemed to have no fixed position in the cell body, often being found "laterally between the nucleus and the cell membrane." Speaking of the absence of sphere and radiations in the young cells, and the

varying position of the centrosomes, Hunter says: "These facts can only be explained on the supposition that the centrosome does not exert any decided mechanical influence on the cell protoplasm."

Hunter found individual variation as to the frequency of the presence of the centrosome in the nerve cells of different animals killed at the same time, the preparations being subjected to exactly the same treatment throughout.

Rohde ('98) finds that certain "Nebennucleolen" wander out from the nuclei into the cytoplasm of nerve cells of the frog, and come to resemble closely the sphere described by Dehler. In the cytoplasm of the nerve cells of the dog he found bodies of nucleolar origin.

In nerve cells of the frog, Rohde commonly finds structures that resemble a "centrosphere." They consist of a central dark body in a clear area, which lies within a sphere exhibiting a radial arrangement. The whole structure suggests the centrosome and sphere described by von Lenhossék. Rohde, however, maintains the existence of such structures in all the cells of the ganglia,—not merely in cells of a certain size, as described by von Lenhossék,—and in any region of the cell whatever, even within the nucleus, or immediately outside the cell body. Moreover, as many as eight of them may occur in one cell. They were not found in the cells of mammals. Rohde thinks they are not artifacts. As regards the existence of the centrosome in the nerve cells of either invertebrates or vertebrates, he says, "Centrosomen kommen also bei Ganglienzellen nicht vor."

Hamaker ('98) found structures in the nerve cells of *Nereis* which he considered to be comparable to the centrosomes described for nerve cells by other authors. Often two or three of these structures and sometimes as many as ten were found in a single cell. Each one consisted of a deeply stained granule in a clear space enclosed within a hollow sphere of coarse granules. No radiations were seen. The nuclei were excentric and often flattened. The "centrosomes" lay at the centre of the cell body.

Holmgren ('99) occasionally finds sections of cells which exhibit a central structure very similar to the sphere of von Lenhossék. He describes a system of fibres which sweep in from the periphery of the cell to form a "Spiralfigur." Similar conditions are described by Bühler ('98). Among the generally hyaline fibres of this system are some more deeply staining fibres. Holmgren thinks certain favorable sections through this spiral system give the appearances interpreted by von Lenhossék as a sphere, his "centrosomes" being simply sections

of some of the deeply stained fibres that happened to lie at the centre of the spiral figure.

Kolster ('00) gives a brief preliminary account of centrosomes in the nerve cells of *Cottus scorpius*. The only two figures given represent one or two deeply stained granules surrounded by a small clear area and lying near the cell centre, the nuclei being excentric and concave on the side toward the cell centre.

## 2. THE CENTROSOME IN OTHER RESTING CELLS.

Leaving nerve cells and turning now to the question of the centrosome in other resting cells, and especially in tissue cells, a considerable literature on this subject is found to have grown up during the last ten years. Previous to 1889 no accurate description had been given of a centrosome and sphere in resting tissue cells, but doubtless many of the descriptions of "Nebenkerne" and "Centralmassen" refer to structures that would now be recognized as centrosomes or spheres.

Van Beneden et Neyt ('87, p. 279) found that the attraction sphere persisted during the resting periods of the early cleavages of *Ascaris*. "Nous sommes donc autorisés à penser que la sphère attractive avec son corpuscule central constitue un organe permanent, non seulement pour les premiers blastomères, mais pour toute cellule; qu'elle constitue un organe de la cellule au même titre que le noyau lui-même; que tout corpuscule central dérive d'un corpuscule antérieur; que toute sphère procède d'une sphère antérieure, et que la division de la sphère précède celle du noyau cellulaire."

Boveri ('88) showed the continuity of the centrosome in the cleavage of *Ascaris*, and set forth his conception of a specific "archoplasm," which is strewn through the cell in granular form during the resting period, and, in mitosis, collects about the centrosomes to give rise to the radiating systems.

Rabl ('89) observed that the resting nuclei of epithelial cells in Triton were indented upon one side, while in the cytoplasm, in the region of the indentation, was a highly refractive homogeneous mass which, he suggested, was due to the presence of the "Polkörperchen" or the "Attractionssphäre."

Solger ('89, '90) found a radiating structure in the pigment cells of some teleosts. The cells frequently have two nuclei which are situated at the cell centre, and between them is a small clear area, from which proceed radiating lines of granules toward the periphery. The central

area Solger suggests to be "das Centralkörperchen oder die Sphère attractive im Ganzen oder ein Theil derselben."

Kölliker ('89) found the attraction sphere in cleavage cells of Sire-don while the nucleus was in the resting condition.

Bürger ('91) found an attraction sphere with centrosome and radiations in the cells of the body fluid of nemertines.

Flemming ('91, '91<sup>a</sup>, '91<sup>b</sup>) described "die strahligen Sphären und ihre Centralkörper" in resting leucocytes of the salamander. In the amitotic divisions of the nuclei of these cells the sphere does not divide, but Flemming believes that it exerts some influence over the amitotic process, since "bei den Abschnürungen die Sphäre eben nicht einer beliebigen Stelle der Kernmasse benachbart liegt, sondern grade an den Abschnürungsbrücken" ('91<sup>a</sup> p. 285). The centrosome was also found in the resting cells of the lung epithelium and in the flat connective-tissue cells and endothelial cells of the peritoneum of the salamander larva, but in these fixed cells no radiations could be seen. The "Centralkörper" generally consisted of two minute granules lying close together in the cytoplasm very near the nuclear membrane. Often a dark band could be seen connecting the two granules. When the nucleus was approaching the spireme condition the centrosomes were farther apart and this dark band was more conspicuous. Flemming therefore believed it to be "die erste Bildungsanlage der Spindel."

Flemming's discovery, made on leucocytes of the salamander, was corroborated by Heidenhain ('91), who also found the centrosome and sphere in the cells of the bone-marrow of young rabbits, as well as in pathological epithelium from human lungs and in some leucocytes from the same human material.

Henne-guy ('91) showed the continuity of the attraction spheres in the developing trout egg.

Hermann ('91) found an "Archoplasmastrahlung" in resting spermatogonia of the frog, and resting spermatocytes of *Helix pomatia*. In resting spermatocytes of *Proteus* he describes an archoplasm with a conspicuous central granule.

Meves ('91) described amitosis in the spermatogonia of the salamander. During the dividing of the nucleus the "attraction sphere" took the form of a ring about the region of constriction.

Solger ('91) described an attraction sphere in resting chromatophores of teleosts.

Heidenhain ('92) observed, in two cases of leucocytes with two nuclei, two spheres present, with a well-developed spindle formed between them.

Generally the leucocytes had a single sphere, even though more than one nucleus may have been present.

Vom Rath ('92) found amitotic conditions in the "Stützzellen" of the testis of *Gryllotalpa*. He says, "Es gelang mir mehrfach in unmittelbarer Nähe der Kerne zwei winzige Centrosomen zu erkennen und ebenso constatirte ich in seltenen Fällen bei eingeschnürten Kernen eine deutliche Strahlung um die beiden Centrosomen, die offenbar als Attractionssphäre bezeichnet werden muss" (p. 115).

Van der Stricht ('92) showed the continuity of the attraction spheres in the cleavage of Triton. He also showed that the centrosomes of mitosis in cartilage cells of various vertebrates persist in the resting cell.

Brauer ('93, '93<sup>a</sup>) discovered the centrosome *within* the resting nucleus of spermatocytes of *Ascaris megalocephala univalens*. Preceding a division of the cell, the centrosome divided while inside the nucleus and the two resulting centrosomes migrated into the cytoplasm.

Moore ('93) described an archoplasm with a "central body," "medullary zone" and radiations in resting cells of the undifferentiated genital ridge of the larval salamander. The archoplasm gave rise to the spindle of mitosis. In leucocytes of the larval salamander a similar structure was found, instead of the simpler conditions described by Flemming ('91).

Vom Rath ('93) described attraction spheres and centrosomes in various resting cells of Amphibia and studied the behavior of these structures during amitosis of the sexual cells. The structures were found also in the sexual cells of *Astacus*.

Watasé ('93, p. 442) concludes that "the *centrosome* is not a unique organ of the cell, but is identical with the *microsome* which exists everywhere in the cytoplasm."

Zimmermann ('93) described what he considered to be a modified attraction sphere in pigment cells of teleosts. There is a very much elongated "Centralstab," comparable to a centrosome, imbedded in a correspondingly elongated "Archiplasm," whence proceed radiations. In certain very large cells the radiations proceed from a "Centralnetz" instead of from a "Centralstab." In the smaller cells a spherical "Archiplasm" with radiations and a minute centrosome were present.

Heidenhain ('94) investigated, in great detail, the conditions in leucocytes and other cells of vertebrates. The "Microcentrum," which he finds generally present, consists of two or three granules imbedded in an

achromatic "Centrodesmose," which he believes gives rise to the spindle. The microcentre is the point of insertion of a system of radiating fibres, which extend to the periphery of the cell. These fibres, according to Heidenhain, are contractile and in a state of tension, which is a source of energy displayed in the mitotic processes. The microcentre lies at the centre of an astrosphere, which is bounded by a layer of microsomes occurring on the radial fibres at equal distances from the centre. The astrosphere is not an organ of the cell, but only a region which takes a characteristic stain because of the concentration of the radial fibres.

In the giant cells of bone-marrow, which have polymorphic nuclei, mitosis occurs without a division of the cell body. In these cells several groups of "Centralkörper" were found, each group containing many granules.

Heidenhain predicted that the microcentre with its radiating system would be found in most resting cells.

Reinke ('94) found the centrosome and sphere in leucocytes of the salamander. Leucocytes of amœboid form differed from those of resting form in having coarser radiations of unequal thickness and thickenings of the fibres arranged in arcs concentric about the centrosome.

Dehler ('95<sup>a</sup>) described a microcentre (Heidenhain), without radiations, in the red blood corpuscles of the chick embryo. He believed the microcentres to be derived from the centrosomes of mitosis.

Drüner ('95) observed centrosomes in the resting sperm cells of the salamander and in resting cells of the gastrula of *Triton alpestris*. He gives an extended criticism of Heidenhain's mechanical theory of the centred system and sets forth an opposed theory. Drüner believes that the radiations of the resting cell disappear before a mitosis and that new radiations arise from the centrosomes. He divides the mitotic process into two periods, the first ending with the division of the chromosomes in the equatorial plate. "Die erste Periode ist die der Expansion, die zweite die der Kontraktion des gesammten Strahlensystems" (p. 333).

Niessing ('95) found the centrosome with sphere and radiations in the liver and spleen cells of the salamander and in the liver of the human embryo.

Vom Rath ('95<sup>a</sup>) described a centrosome and sphere in the large gland cells of the head of *Anilocra mediterranea*; also in the hepatopancreas cells of *Porcellio scaber* and in spleen cells of a young dog. In amitotically dividing leucocytes and sperm cells there are sometimes one and sometimes two centrosomes and spheres. Vom Rath

concludes "dass eine Theilung der Attractionssphäre bei der Amitose stattfinden kann . . . ; ob sie aber immer stattfinden muss, ist unwahrscheinlich" (p. 61).

Von Erlanger ('96) observed the centrosome in resting epithelial cells of salamander larvæ. There were always two, connected by a band of substance. In mitosis these centrosomes moved apart and the spindle formed between them. In another paper ('96<sup>a</sup>) he describes a "Nebenkern" in resting sperm cells of the earthworm. In rare cases a central granule and weak radiations were present. He believed the structure to be archoplasm and centrosome.

Meves ('96), in the spermatogonia of the salamander, found the spheres of adjacent cells connected by bands of substance which are probably remnants of the spindle.

Ballowitz ('97<sup>a</sup>) demonstrated the centrosome and sphere in the cells of the pharyngeal and cloacal epithelium of *Salpa*, without the use of stains. The material was fixed in either weak or strong Flemming's fluid, sublimate, or acetic-sublimate, and examined in water. The nuclei are sickle-shaped, and in the concavity of each could be seen the large sphere which Ballowitz had previously described ('97). A detailed study of the epithelial cells of *Salpa* appeared in a later paper ('98<sup>a</sup>). The centrosomes were best seen in the unstained Flemming's preparations. At the centre of the sphere were generally two, but sometimes three or four, very highly refractive bodies. They often appeared to be irregularly shaped or elongated, instead of spherical granules. Ballowitz concludes "dass es zum Nachweise der Centrosomen nicht immer einer specifischen Färbung bedarf, dass diese wichtigen Zellbestandtheile vielmehr auch in ungefärbtem Zustande in Folge ihres charakteristischen starken Lichtbrechungsvermögens so scharf begrenzt hervortreten, dass sie leicht und sicher in der Sphäre erkannt und unterschieden werden können" (p. 358).

Ballowitz believes the sphere and centrosomes to be present also in the epidermal cells of *Amphioxus* larvæ ('98). These cells have nuclei varying in form from those that are deeply invaginated to those that are sickle-shaped or complete rings.

Eisen ('97) described a new element found by him in the blood of some amphibians, reptiles, and man. To this element he gave the name of "plasmocyte." He attempts to show that the plasmocytes "are composed of the centrosomes and archoplasm (with part of the cytoplasm) of the nucleated erythrocytes, . . . surviving in the blood serum as free and independent elements capable of growth through

assimilation of food, and taking their place as blood elements, equal in importance to the erythrocytes and leucocytes" (p. 13).

Von Lenhossék ('98), in studying the development of the spermatozoa of the rat, found the flagellum to be a product of the centrosome. In another paper ('98<sup>a</sup>) he described the centrosomes and "Basalkörperchen" in the cells of ciliated epithelium. In cells that did not bear cilia, the microcentre was present, lying at the extreme outer end of the columnar cell. In the ciliated cells no microcentres were found, but there was a layer of granules just beneath the ciliated surface of the cell, the number of granules corresponding closely with the number of cilia. Von Lenhossék gives the name of "Basalkörperchen" to these granules, and thinks they are homologous with the microcentre of the non-ciliated cells.

Zimmermann ('98) discusses the centrosome in epithelial and gland cells of mammals, including man. He points out that, as in mitosis the centrosome is the centre of motor processes, so in resting cells the centrosome is always located at the centre of activity. If there is an equal degree of activity throughout the cell, the centrosome is at the centre of the cell, unless displaced by a large nucleus (leucocytes, pigment cells, non-striated muscle cells). In gland cells, it is at the centre of secretory activity. In ciliated cells and epithelial cells with pseudopodial processes, the microcentre is close to the outer end of the cell. Where there is a single flagellum, as in the spermatozoön, the centrosome is at the point where the flagellum enters the cell. He says (p. 697): "Ich glaube . . . dass, ganz allgemein gesprochen, das Mikrocentrum das motorische Centrum, also das 'Kinocentrum' der Zelle sei (gegenüber dem Kern als 'Chemocentrum')."

Von Lenhossék ('99) describes a microcentre, in the sense of Heidenhain, in the non-striated muscle cells of the cat. As non-striated muscle cells are known to divide by mitosis in cases of regeneration, we should expect to find the microcentre in the resting cell.

Among other authors who have described centrosomes in resting cells may be mentioned Hansemann ('91, '93; cells of human brain tumor, cancer cells, human leucocytes, mesenterial connective tissue of young cats and rabbits); Guignard ('91, '97; plant cells); Eismond ('94; cleavage cells of Triton tæniatus and Siredon); Zimmermann ('94; human epithelium, stroma cells of cat ovary); de Bruyne ('95; connective-tissue cells); Meves ('95; spermatogonia of salamander; '95<sup>a</sup>; sesamoid cartilage cells in the tendon achilles of the frog); Moore ('95; sperm cells of elasmobranchs); Rawitz ('95; sperm cells of sala-

mander); Gulland ('96; leucocytes); Spuler ('96; connective-tissue cells); Child ('97; ovarian stroma cells of mammals); Heidenhain ('97; red blood corpuscles of duck embryo); Rawitz ('98; sperm cells of *Scyllium canicula*); Niessing ('99; lymphocytes).

Reviews of the centrosome question, with lists of literature, have been given from time to time by various authors, among them Flemming ('93), Moore ('93), Häcker ('94), Heidenhain ('94), vom Rath ('95), Henneguy ('96), von Erlanger ('97), Heidenhain ('97), Kostanecki und Siedlecki ('97), Bühler ('98; centrosome in nerve cells), and Meves ('98).

### III. Methods of Investigation.

The identity of the so-called centrosome of nerve cells with the centrosome of mitosis can be established by a series of observations showing that the centrosome of the last mitosis of the embryonic nerve cell persists through the development of the nerve cell and becomes the structure seen in the resting cell; or, if the cells can be induced to divide by mitosis, it may be possible to show that the centrosome of the resting cell gives rise to the centrosomes of the mitotic figure. The problem, then, is open to attack from two directions. Given, material in which the presence of a centrosome in the differentiated nerve cells can be demonstrated, — as it has been in many vertebrates and invertebrates, — and in which the centrosome is also to be found in the embryonic neural tissues, — as Heidenhain und Cohn ('97) have found it in the neural epithelium of bird embryos, — then we may seek to establish the genetic relationship of the organ in the embryonic cell with that of the differentiated cell.

A second method of investigation is offered by the process of regeneration. If any cells of adult nervous structures are capable of undergoing mitotic division, regeneration would seem to offer the most favorable opportunity for the exercise of such power. If, however, the regenerated nerve cells do not arise from old nervous tissues, the development of the new nerve cells from other tissues would still offer opportunities for determining whether the "centrosome," if present in the regenerated cells, had persisted from the last mitosis in the history of the cell.

The question arises as to whether processes which take place in the *embryonic* origin of nerve cells will be repeated in the *regenerative* development of similar cells. To show that a centrosome in a regen-

erated nerve cell is one of the centrosomes of the mitosis of the mother cell, does not necessarily prove that the centrosome of a nerve cell which has arisen by the natural embryonic process of development is also identical with a centrosome of the mitosis of its parent cell. Yet, if the regenerated nerve cells arise from ectodermal tissues, we should certainly expect the processes of regenerative development to resemble very closely those of embryonic development, especially in so fundamental a thing as the fate of mitotic organs. Many investigations have shown the similarity of regenerative and embryonic processes. If it is shown that the "centrosome" of a regenerated nerve cell is a true centrosome, — that is, the organ concerned in mitosis, — it must be admitted as highly probable that the similar organ in the naturally developed cell is likewise a true centrosome.

In an investigation upon any one kind of material, the regenerative process has an advantage over the embryonic, for it affords not only the opportunity for the study of the development of nerve cells, but also the possibility of observing whether the structures under consideration in the already differentiated nerve cells have anything to do with the formation of new cells.

The observations about to be described have been made upon tissues in process of regeneration, the object being twofold, — to determine, first, the behavior of elements in old nervous structures in the presence of the necessity for regeneration; and, secondly, the source and method of development of the new nervous parts.

### 1. MATERIAL.

Two qualities were demanded of material intended for this work. The fully differentiated nerve cells must contain some such structure as has been called a centrosome by various authors, and the animal must have the ability to regenerate excised parts of the nervous system. It was at first proposed to work upon the annelid, *Axiothea* (*Clymenella*) *torquata*. In the giant cells of a nearly allied form, *Clymene producta*, Miss Lewis ('96, '98) found the centrosome and sphere to be present. I found some evidence of a centrosome in the giant cells of *Axiothea*, but nothing as definite as Miss Lewis demonstrated for *Clymene*. *Axiothea* was found to regenerate segments very readily at either the anterior or posterior end. I obtained regeneration in a large number of the worms during the summer of 1898, at the laboratory of the United States Fish Commission at Wood's Hole. A number of seg-

ments having been cut from either or both ends, the worms were placed in glass vessels partly filled with clean sand over which ran sea water. In the course of two to four weeks a considerable regeneration was found to have taken place at the cut ends. Two facts caused this material to be abandoned. The centrosome in the giant cells was too indefinite a structure to deal with satisfactorily, while the very limited number of giant cells in a segment made the prospect of obtaining a comprehensive series of conditions in the regenerative development of these cells anything but encouraging.

Hamaker ('98) demonstrated some centrosome-like structures in the nerve cells of *Nereis*. I made preparations of *Nereis* and found some very decided evidence of the presence of the centrosome in the cells of the ventral ganglia (page 115). At the same time I examined nerve cells of the earthworm, obtaining results which inspired further investigation of that material. This fact, together with the well-known regenerative power of the earthworm and the greater ease of conducting regeneration experiments upon the land annelid, determined its use for this work in preference to *Nereis*. It is, therefore, mainly with the earthworm that the following work has to do.

## 2. REGENERATION METHODS.

The worms, *Allolobophora* (*terrestris* Savigny?) and *Lumbricus agricola* Hoffmeister, were easily obtained near the laboratory in Cambridge. From five to ten segments were removed from the anterior end, and the beheaded worms were placed in large earthen jars filled with the soil in which the worms were found. The soil was first carefully examined and all other worms removed. Most of the regeneration was obtained during the winter or early spring months. The jars were kept in the vivarium at a temperature of about 16° C. The earth was moistened from time to time so that it never became dry at the surface. Many of the beheaded worms burrowed a short distance below the surface, but many others refused to burrow and persisted, if buried under a little earth, in returning to the surface. To protect them from the light and from drying, sheets of moistened filter paper were spread over the surface of the earth and the jars were covered with glass plates.

The cutting of the anterior end prevented feeding. In the course of a few days the intestine of the worm was entirely free from earthy material. The smaller worm, *Allolobophora*, generally burrowed beneath the surface and coiled itself into an intricate close knot, remaining in that

condition, unless disturbed, as long as it was kept, — five or six weeks. The larger earthworm, *Lumbricus*, which generally remained on the surface, was always found stretched out when the earth was exposed for moistening.

An attempt was made to keep some worms during regeneration in glass vessels containing moist filter paper, instead of in earth; but the method was more troublesome and possessed no advantages over the other. Unless the paper was changed every day or two, the worms were likely to die, while of those kept in the earth only about ten per cent died during regeneration.

Worms were killed after from seven to forty days subsequent to the operation. In *Allolobophora*, the light-colored conical bud that marked the regenerated segments was usually to be seen in two or three weeks after the operation of cutting. *Lumbricus* regenerated much more slowly. All of the preparations which I shall discuss are from individuals of *Allolobophora*.

Regeneration of posterior ends was also obtained, but little was done upon that material. The anterior ends have the advantage that the regeneration of both the brain and ventral nerve-cord can be observed.

When the desired period of regeneration had elapsed, the worms were dropped into fresh water for a moment to remove the clinging earth. The anterior end, including some six to twelve of the old segments, was clipped off with scissors and the fragment bearing the regenerated part was at once dropped into the fixing fluid. Stupefaction, where such small fragments were to be fixed, was found to be of no advantage.

In the less advanced stages of regeneration the inability to feed made unnecessary the cleaning out of the intestine before fixing. In some of the more advanced stages feeding had been resumed and the worms had to be kept upon moist linen for a day or two until the anterior part of the intestine had become clean.

### 3. FIXING FLUIDS.

The best fixing fluid for general purposes was found to be Fleming's stronger chromic-osmic-acetic mixture. This fluid not only gave the best fixation of the old ganglion cells, but also gave by far the most satisfactory fixation of mitotic cells. Some of the best demonstrations of the exceedingly fine radiating fibrillæ in the ganglion cells were obtained by this method, and the achromatic fibres of the mitotic figure were very sharply brought out.

Material was left in the fixing fluid for from five to forty-eight hours. A longer or shorter time within these limits gave no appreciable difference in results. The objects were then washed in distilled water for about twenty-four hours, then passed through ascending grades of alcohol, cleared in cedar oil and imbedded in paraffin.

Hermann's acetic-osmic-platinic chloride mixture was used with good results, although it seemed to be in no way superior to the Flemming mixture. The Flemming preparations gave a rather better quality of stain with Heidenhain's iron-hæmatoxylin. The method of treatment with Hermann's fluid was similar to that just described for Flemming's fluid.

Vom Rath's picric-osmic-acetic-platinic chloride gave no results of value. The after treatment with crude pyroligneous acid was used as described by vom Rath ('95). In some cases a two per cent solution of pyrogallic acid was substituted for the pyroligneous, with similar results. The length of time of the after-treatment, during which the reduction of the platinic chloride takes place, was varied, but in all cases the cytoplasm was blackened to such an extent that it became too opaque for the observation of the exceedingly delicate structures revealed by other methods. In some preparations mitotic figures were brought out with remarkable clearness by this method, especially as to the sharpness of spindle fibres, but, for the observation of polar and cytoplasmic structures, fixation in Flemming's or Hermann's fluid followed by a regressive stain gave results far superior to those obtained by a method which depends upon the deposition of a metallic salt in the cell structures.\*

Corrosive sublimate in a saturated aqueous solution containing one per cent of acetic acid was used with results which corroborated those obtained by the Flemming and Hermann fluids as to cytoplasmic structures in the ganglion cells, but the demonstration of these structures was far inferior to that obtained by the other methods. The sublimate failed to bring out the finer structure of the cytoplasm as clearly as the osmic mixtures. Radiating fibres were very indistinctly shown. The sublimate gave decidedly inferior results in the demonstration of mitotic figures. My preparations lead me to believe that the sublimate effects violent mechanical injuries in delicate tissues. In such solid tissues as the epidermis or intestinal epithelium there were no evidences of injurious effects; but among the very loosely aggregated masses of cells that constitute some of the regenerated parts, there were signs of serious damage. In the epidermis, for example, spindle figures occur imbedded in a dense cytoplasmic mass. These figures were faithfully

preserved by the sublimate. In the regenerating brains and ganglia, the mitotic figures more often occur in cells the remaining contents of which appear to have become entirely fluid. Such figures, unsupported by a dense cytoplasm and completely exposed to the action of the fixing fluid, were very seriously distorted in the sublimate preparations. In all cases spindle fibres were very poorly shown in the sublimate preparations.

As for the superiority of Flemming's fluid for the demonstration of the centrosome, my experience agrees with that of Ballowitz ('97, p. 358) who demonstrated centrosomes in epithelial cells of *Salpa* without the use of stains. He succeeded in doing this with sublimate, but Flemming's fluid gave by far the best results. He says, "Ich behaupte auf Grund meiner Erfahrungen an meinem Untersuchungsobject, dass es mit grösserer Sicherheit und mehr Constanz gelingt, die Centrosomen an dem mit Flemming'scher Lösung fixirten, ungefärbten Material zu erkennen, als durch spezifische Tinction an den mit Sublimat behandelten Objecten sichtbar zu machen."

My Flemming preparations were all stained with iron-hæmatoxylin, but they were decolorized to such an extent that, examined by a low power, the cell bodies appeared scarcely darker than in the unstained preparation. But examination with high power revealed the fact that the cell granules had retained the stain. It was in such preparations that central granules were most clearly seen, because of their deep stain in contrast to the unstained ground substance of the cytoplasm. Hermann's fluid gives substantially the same results in this respect. I have examined unstained Hermann's fluid preparations and have been able to distinguish fairly well the granules and fibrillæ of the cytoplasm. In stained sublimate preparations there is apt to be present in the cytoplasm a large amount of deeply staining material scattered about in irregular masses, obscuring finer details of structure. If the decolorizing is carried so far as to clear out these masses, the granules and fibrillæ are left much less distinct than in the decolorized osmic acid preparations.

All the material was cleared in cedar oil and imbedded in paraffin. Sections were cut generally  $6\frac{2}{3}\mu$  thick. A few series were cut at  $3\frac{1}{2}\mu$ .

#### 4. STAINS.

Heidenhain's iron-hæmatoxylin proved to be by far the most useful stain. Sections were treated with a two per cent solution of iron-alum from three-quarters of an hour to three hours and stained about the

same length of time in a one-half per cent solution of hæmatoxylin. Decolorization was effected by the two per cent mordant, the process being controlled under the microscope.

This stain gave the best results both for the structure of the nerve cells and for mitotic figures in the regenerating tissues. No advantage was found to be gained by using safranin in combination with the hæmatoxylin. From what has been said, then, it follows that fixation in Flemming's mixture, followed by the iron-hæmatoxylin stain, proved to be the best combination.

Gentian violet was used to obtain sharp selection of kinetic chromatin, but it was useless for finer cytoplasmic structure. Kernschwartz gave results similar to those obtained by the iron-hæmatoxylin, but inferior in clearness. One sublimate series was stained in Kernschwartz and safranin with fairly good results, especially as to some cells of the regenerated epidermis (Figures 44 and 45).

Whatever the stain used, the best demonstration of the "centrosome" and cytoplasmic fibrillæ was obtained when the stain had been well extracted from the cytoplasm. In heavily stained cells the finer structures were made out with much greater difficulty.

## 5. DRAWINGS.

The preparations were studied with a Zeiss  $\frac{1}{8}$  oil immersion and Zeiss achromatic oculars 3 and 4. The drawings were made with the aid of an Abbé camera. Attention is called to the fact that all the drawings of cells and mitotic figures are to the same scale, a magnification of 2000 diameters. The outlines of cells, nuclei, and nucleoli were traced with the aid of the camera. Generally the "centrosome" and prominent granules could also be located, but only in rare cases could the radiations represented in the figures be seen with the camera in place. The figures are reproduced from pencil drawings.

A diagrammatic treatment of the drawings was avoided as far as possible, and it was attempted rather to reproduce, as accurately as could be, the appearances seen in the preparations. The drawings were reproduced by the heliotype (gelatine) process because by it a more accurate reproduction of the relative conspicuousness of the structures represented in the drawings may be obtained than by the lithographic process. It must be understood, however, that in the figures of nerve cells the conspicuousness of the radiating systems is slightly exaggerated. These lines catch the eye more readily in the printed figures

than they do in the preparations. In most cases it required the most careful focussing and varying of illumination to bring out the less distinct radiating fibrillæ.

#### IV. Observations.

##### 1. THE NERVE CELLS OF LUMBRICIDÆ.

My first study to ascertain the condition of the nerve cells of the earthworm was made upon normal unregenerated material fixed in sublimate and stained in iron-hæmatoxylin. Some evidences of concentric and radial cytoplasmic structure were found, suggesting the presence of structures which might be brought out more clearly by better methods.

In transverse sections of the ventral ganglia the greater number of ganglion cells are cut in planes parallel to their long axes. The cells are situated ventrally and laterally in the cord. They are unipolar and pear-shaped, the larger ends being peripheral, while the processes extend dorsally and centrally. The nuclei, with extremely rare exceptions, are situated in the process end of the cell, often so far toward that end that the nuclear membrane is tangent to the tapering sides of the cell. The diameter of the nuclei varies from  $6\ \mu$  to  $16\ \mu$ . The cells are from  $22\ \mu$  to  $60\ \mu$  in length, and from  $10\ \mu$  to  $28\ \mu$  in transverse diameter.

The nuclei are always nearly or quite spherical and *never invaginated*. In the resting nerve cells of many animals where the centrosome has been found the nucleus has been described as invaginated, the centrosome occurring in the cytoplasm on the invaginated side of the nucleus. The position of the nuclei in the nerve cells of the earthworm is such as to leave by far the greater mass of cytoplasm on that side of the nucleus opposite the nerve process.

Early in my study of these cells I was impressed with the fact that, in a large number of them, more or less irregular small masses of deeply stained material occurred near the nucleus and on the side of it toward the centre of the cell. If a line through the centre of the nucleus and the centre of the cell be called the axis of the cell, these masses occurred in or near the cell axis. Occasionally faint radiations could be detected coming from the region of the central masses just mentioned and extending toward the periphery of the cell.

A more careful study of later and more favorable preparations

demonstrated the common occurrence, in the cells of the brain and ventral ganglia, of such cytoplasmic structures as are represented in Figures 1-9.

Figures 1, 2, and 3 represent cells from the subœsophageal ganglion of a normal worm, — that is, one that had not undergone regeneration. These cells are from a preparation which was fixed in strong Flemming's fluid for forty-eight hours and stained in iron-hæmatoxylin. The cells are typical unipolar nerve cells, lying in the ventral anterior region of the ganglion, with their processes extending dorsally. Figure 4 represents a cell from the dorsal posterior border of the brain of the same animal.

#### *a. The Nuclei.*

The nucleus of the nerve cell has a characteristic appearance. In osmic acid preparations it is nearly always spherical, or departs only slightly from that form, as in Figures 2 and 4. In sublimate preparations, however, there are often irregularities in form, as seen in Figure 5. From a general comparison of my osmic-acid preparations with those fixed in sublimate, I am inclined to believe that the nuclei often suffer distortion in sublimate, and that the spherical form represents a more faithful fixation. The excentric nuclei are never flattened nor invaginated, except in a few cases in which I have observed that one side of a nucleus was indented in such a way as to suggest mechanical distortion due to fixation. So fluid are the contents of the nuclei that it is not strange that such distortions should sometimes occur. These indentations, which are probably artificial, had no regularity in form or in position.

The nuclei must contain a very large proportion of fluid material which is not coagulated by the fixing agent. In both stained and unstained preparations the nuclei are much clearer than the surrounding cytoplasm. They contain a very small amount of matter that takes stain.

With very rare exceptions, there is but one nucleolus. It is always excentric, often very near the nuclear membrane, and generally departs little from the spherical form. In osmic-acid preparations the nucleolus is always sharply outlined and never exhibits anything but a perfectly homogeneous structure. It takes a quality of stain different from that of the chromatin, being somewhat brownish instead of dark blue or black. This is doubtless due to the fact that it does not take or hold the stain as strongly as the chromatin, the brown color being due to the osmic acid.

The chromatic substance is scattered about in the form of small granules, approximately spherical in shape but more or less irregular. They are often not sharply outlined and appear as if imbedded in some achromatic substance. The chromatic granules are mostly collected about the periphery of the nucleus where, with the achromatic substance, they form a very loose, irregular network. Many of the chromatic masses appear to lie directly upon the nuclear membrane. The central region of the nucleus is often quite free from chromatic material. The occurrence of small sharply stained chromatic granules close about the nucleolus, or lying directly upon its surface, is a very common condition. Figures 1, 2, and 3 show these well.

Rather coarse strands of achromatic material form more or less of a network between the chromatic masses. There is often a tendency toward a radial arrangement of this network about the nucleolus, which appears supported within the nucleus by that means (Figures 3 and 4). The nuclear membrane is always very sharply outlined, being emphasized at the median plane of focussing by the occurrence of chromatic masses upon it.

#### *b. The Cytoplasm.*

Very little can be said as to the finer structure of the cell protoplasm. The most careful examination fails to reveal its precise nature. It varies in degree of homogeneity somewhat according to the size of the cell. In the smaller cells (Figures 4, 7, 8, and 9) it usually appears compact and fairly homogeneous. In larger cells (Figures 2 and 3) it is much less homogeneous, and there is a tendency toward the formation of large vacuolar spaces, as seen at the process end of the cell in Figure 2.

The substance of the fixed cytoplasm, as it appears to the eye, may be said to be of four kinds. There is (1) a perfectly homogeneous "ground," represented by the lightest areas in the figures; (2) material which gives the impression of being very finely granular; in the smaller cells this material is quite evenly distributed, while in the larger cells it tends to concentrate in regions, giving the cytoplasm a blotchy appearance; (3) rather conspicuous granules or masses staining fairly deeply and often surrounded by an area within which the material of the second class is less dense, as best seen in Figures 2 and 3; (4) fine fibres irregularly distributed throughout the cell body, but often appearing to be associated with the more conspicuous granules and sometimes occurring about granules as centres of radiation, as can perhaps be recognized

in some places in Figures 2 and 3. It is possible that the granules of the third class may be due simply to concentration of the finely granular material of the second class.

To what extent these appearances in the fixed cell correspond to structure in the living cell cannot be said. The occurrence of the larger granules or masses within clearer areas suggests coagulation effects, the substance of the clearer area having been massed at the centre of it by the action of the fixing fluid. It is quite likely, however, that there may be some structural basis for this effect. The occurrence of fibres radiating from these larger granules suggests that they may mark the more important centres of a cytoplasmic network.

In some cells, especially in certain ones of the brain, a system of fibres could be detected lying at the periphery of the cell and extending out into the nerve process.

In the larger cells no definite, sharply outlined cell membrane is ever seen. The cells appear to be enclosed by fine connective-tissue fibres, which form more or less of a capsule about them. Small nuclei, doubtless of non-nervous nature, often occur about the nerve cells, as seen in the regenerated cell of Figure 11 (Plate 2).

### *c. The Centred System.*

Evidences of concentric and radial structure are commonly seen, but the exact nature of this structure would be overlooked except in the most careful study, with the aid of oil immersion lenses.

*Cells of the first type.* — The conditions represented in Figure 1 may be considered typical for a large number of cells. This cell is from a section  $6\frac{2}{3}\mu$  thick. In focussing up and down upon the section the eye is caught by a granule which is conspicuous by its size, sharpness of outline, and depth of stain. If it were a matter of a few cells or a single one, this might be a chance condition, but when a similar condition is commonly found in the observation of a large number of cells, we must conclude that we have not to do with an accidental granule. Moreover, when such a conspicuous body is found to occupy a definite and constant position in relation to other parts of the cell, and when it is found to be the centre of a system of radiating fibres, it is evident that the whole structure is one of importance. In speaking of the centre of this structure as a "conspicuous granule," it is not meant that it is the first thing that catches the eye in a casual glance at the cell. Many of the granules or masses, which have been described

as forming the third class of constituents of the fixed cell, may be more prominent because of their greater size and their frequent occurrence within a clear area. But these larger masses differ from the central granule in being less deeply stained and less sharply outlined. The central granule is conspicuous as compared with any bodies in the finely granular cell substance. When once found, it is generally very easy to distinguish it from other elements contained in the cell body.

The position of the central granule is characteristic. It always lies in the part of the cell opposite the nerve process, and very nearly in the long axis of the cell. It is generally very near the nucleus, as in Figures 2 and 3; but it may be farther away, as in Figure 4, especially if much the greater bulk of the cytoplasm is on that side of the nucleus.

The central body of Figure 1 is a single minute granule, and is spherical, as nearly as could be determined for a thing so small. It lies at the centre of a very small spherical space which appears in the section as a narrow clear area about the granule. The clear area is not sharply outlined.

Several extremely delicate radiating fibres extend outward from the central granule into the surrounding cytoplasm. Those represented in the figure all lay in a plane parallel to the surface of the section. It was rarely possible to detect a fibre if it was so oblique that it did not come into the focal plane all at once. Generally not more than six or eight of these fibres could be detected. In all of the first nine figures can be seen fibres which extend well out toward the periphery of the cell. Many of the radiations, however, could not be traced so far. So fine are these radiations that it is only with the greatest difficulty that anything as to their nature can be made out. The more conspicuous radiations appeared to be made up of minute granules arranged in line. The finer radiations show no evidence of granules, appearing rather as most delicate hyaline threads. However, radiations were found exhibiting both characters at different parts of their course. It is therefore probable that these radiations consist of achromatic fibrils bearing more or fewer granules along their courses. The granules may be so thickly set that the radiation appears as a line of granules, or they may be absent, when only the achromatic fibril can be seen.

If a distinct radiation be carefully traced, it will be seen that at intervals there occur some fairly conspicuous granules, which are more easily seen because of a surrounding clear space. Figures 1, 2, and 3 show this to some extent, but the fact is much more clearly brought out in some of the regenerated cells to be described later (Plate 2, Figures 10-13).

Very often these granules, which occur along the course of a radiation, mark the point of divergence of secondary fibrils. In Figure 1, if the radiation which is most nearly in the axis of the cell be followed for one-third its length from the centre, a granule will be seen from which two fibrils proceed on toward the periphery of the cell. Figure 2 shows similar conditions, but the regenerated cells (Plate 2, Figures 10-13) exhibit this arrangement more clearly.

Figure 2 represents a cell of the same type as that of Figure 1; but the central body is much nearer the nucleus, and is either elongated or else consists of two granules very close together. The central clear space is confluent with the clear spaces around two granules that lie in the courses of radiations from the central body.

Figures 5 and 6 are from acetic-sublimate preparations stained in iron-hæmatoxylin. They represent cells very similar to those just described. The attempt has been made to show something of the difference between the appearance of an osmic-acid and a sublimate preparation. The nuclear structures are fairly well brought out by the sublimate, but not so clearly as by the osmic acid. The structure of the cytoplasm is much less definite, but as far as it could be made out, it agrees with the description given for osmic preparations. Both cells show some evidence of an arrangement in the cytoplasm concentric about the centre of the radiating system. This is especially well marked in Figure 6.

*Cells of the Second Type.*—Figure 3 represents a cell in which a further complication of the radial system is introduced. The central body in this case appeared very large and of irregular form, but careful focussing resolved it into three granules of different sizes. They are surrounded, not by a clear space, but by a region which appears dense and very finely granular. The limit of this region is emphasized, in the section, by the occurrence of a number of stained granules which are arranged in the arc of a circle about the central granules. The radiations from the centre can be seen to include in their courses certain conspicuous granules lying in this arc. This finely granular region is evidently comparable to the "sphere" described by many authors. Figure 3 is strikingly similar to some of the figures in Bühler's paper of 1895.

Figures 7, 8, and 9 (Plate 2) represent small cells of this type from the brain. In Figure 7 the body of the sphere differs in no visible way from the surrounding cytoplasm, but a number of granules form a complete circle about the central granule. In Figure 8 the entire radiating system is very faint, but there are evidences of two concentric cir-

cles. The structure in Figure 9 is very similar to that in Figure 3. The central body may consist of two granules, but they could not be clearly separated.

Figure 4 (Plate 1) represents a condition frequently met with. There is, in the cell drawn, a condensation of finely granular cytoplasm extending halfway from the centre to the periphery of the cell. This is probably in no way comparable to such a sphere as is shown in Figures 3 and 9. It is not sharply outlined, and it lacks the bounding layer of granules. The body at the centre of this finely granular region is surrounded by a clear space; and radiations, lacking, however, any conspicuous granules, extend toward the cell periphery. Cells of this character may best be considered as belonging to the first type (Figure 1), as far as the structure of the radiating system is concerned.

## 2. THE NERVE CELLS OF NEREIS.

In the ventral ganglia of *Nereis* are certain large cells situated near the median plane and having their nuclei in their dorsal or process ends. The nuclei are often flattened or invaginated on the side toward the cell centre. In one very large cell with an invaginated nucleus an intensely stained granule was seen lying in the concavity of the nucleus, and around the granule were several fine radiations. The cytoplasm was completely decolorized, the granule mentioned being the only stained object in it. This appeared to be a good case of the "centrosome." *Nereis* was not studied sufficiently to determine whether such structures are commonly present.

## 3. OUTLINE OF THE PROCESS OF REGENERATION OF THE BRAIN AND ANTERIOR GANGLIA.

The regeneration of the anterior ends of the worms (*Allolobophora*) took place substantially in the manner described by Hescheler ('98). I have made no preparations at periods of regeneration earlier than seven days.

Figure 14 (Plate 3) represents a parasagittal section of the anterior end of a worm after seven days' regeneration. The limit of the old tissues is easily distinguishable in all such early stages, and, in fact, there is no difficulty, up to a comparatively late period, in distinguishing old tissues from those that are being regenerated. In Figure 14 the old epidermis ends at points designated by the asterisks. The new

epidermis, between these points, is considerably thinner than the old. Underlying the new epidermis is a solid cicatricial mass of considerable thickness. The circular and longitudinal muscle layers are seen to end abruptly against the inner surface of the cicatricial mass. The anterior end of the alimentary canal is closed by the cicatrix and may remain closed for several weeks. The nerve cord also ends abruptly against the cicatricial mass. Even after the regenerating part of the cord is well established, the limit of the old cord is sharply indicated by the end of the old sheath, the inner homogeneous layer of which generally curls outward and backward a little at its cut end. In the preparation from which Figure 14 is taken, a more or less lens-shaped mass of newly formed cells lay near the end of the old cord. This is better seen in Figure 18 (Plate 4), which shows the end of the cord drawn to a larger scale, — 160 diameters. Two mitotic cells (Figure 18, *cl. mit.*) are seen in the lens-shaped mass. The origin and nature of them will be discussed later (page 121).

Figure 15 represents a parasagittal section through the anterior end of a worm after sixteen days' regeneration. The regenerated parts are, as in the younger stage, included between two asterisks. The regenerated epidermis remains thinner than the old epidermis. A thin layer of circular (*mu. crc.*) and of longitudinal muscle fibres (*mu. lg.*) has been laid down in the conical regenerated end. The end of the old nerve cord is sharply marked by the extent of the sheath (*tu.*) and the abrupt termination of the mass of ganglion cells. Extending forward from the end of the old cord is a fibre tract, which runs out to the apex of the cone, lying ventral to the alimentary canal. The fibres become less distinct anteriorly, and are lost in a mass of cells underlying the epidermis. Along the ventral border of this fibre bundle is a thin layer of cells (*gn. nov.*) whence are to be derived the cells of the regenerated ganglia.

Figure 16 is from a parasagittal section of a worm after twenty-four days' regeneration. The regenerated parts are included between two asterisks. There is much variation as to the relative times of appearance of the regenerated organs. In Figure 15 (16 days) the regenerated muscle layers are well established. In Figure 16 (24 days) only a few longitudinal muscle fibres in the ventral part of the regenerated cone are to be seen.

In the sixteen-day preparation (Figure 15) the alimentary canal does not open to the exterior. In Figure 16 (24 days) the breaking through of the alimentary canal to the exterior is nearly, if not quite, accom-

plished. According to Hescheler the alimentary canal grows forward to meet a stomodæum or invagination of the epidermis, and the opening to the exterior is effected by a rupturing of the epithelial and epidermal layers, the epidermal invagination becoming the mouth cavity and the region posterior to the point of rupture becoming the pharynx. In the preparation from which Figure 16 is taken, the epidermal invagination has progressed to meet the alimentary epithelium. In some sections a delicate layer of the epithelium was found still closing the end of the canal (see Figure 16). In other sections this layer was broken away, probably accidentally.

As to the nervous system, Figure 16 represents a much more advanced stage of regeneration than Figure 15. In this advanced stage the end of the old cord is as sharply marked as ever. The new fibre tract has extended forward to encircle the alimentary canal, the two branches uniting in a small mass of cells (*gn. su'oes.*) above the stomodeal invagination. This mass of cells constitutes a well-defined brain fundament.

After the condition of Figure 16 has been reached, we have to do only with growth and segmentation of the parts already laid down. I made no preparations of material regenerated more than forty days. There is much individual variation as to the rapidity of the process. In one animal after thirty-four days' regeneration the brain was scarcely smaller than in the normal worm and had come to occupy its position in the third segment. The number of segments regenerated in this case could not be determined. The brain and anterior end of the ventral cord in this animal could hardly be distinguished from those of a normal worm except for the occurrence of numerous dividing cells at the anterior tip of the cord and in the posterior dorsal region of the brain. The sheaths enclosing the new nervous parts were well developed. But in most of the worms, after thirty-five to forty days' regeneration, the regeneration of the nervous parts had not reached so advanced a stage.

The foregoing statements are sufficient to give a general outline of the process of regeneration. Hescheler ('98) has described the process in more detail; as far as my observations go, my results agree with his. I now propose to discuss the origin of the new nervous parts more minutely.

## 4. ORIGIN OF THE CELLS OF THE NERVOUS FUNDAMENTS.

According to Hescheler the cells which give rise to the regenerated brain and ventral ganglia are derived chiefly from the epidermis. The cicatrix is at first composed of lymph cells and spindle-shaped cells of doubtful origin. Later appear cells with nuclei like those of the epidermis. These he believes to be derived chiefly from the epidermis, but some may come from the alimentary epithelium and some from certain large nuclei found in the muscle layers. In addition to these sources there is mitosis within the old nerve cord which doubtless gives rise to cells that assist in the regeneration.

From my own preparations similar conclusions as to the origin of the regenerated nervous elements must be drawn, except that only in rare cases is there any evidence that cells of the old cord assist in the regeneration.

In the preparation from which Figure 14 is taken, the cicatrix (*cic.*) is a solid mass composed mainly of greatly elongated spindle-shaped cells with small oval or elongated nuclei. Figure 17 represents a number of these cells more highly magnified. The nuclei are totally unlike epidermal nuclei, being much smaller, of different shape, and lacking a prominent nucleolus. Epidermal nuclei drawn to the same scale as Figure 17 may be seen in Figures 43-45 (Plate 6). There are also present in the cicatricial mass some very small spherical nuclei. These are doubtless nuclei of lymph cells, for they present exactly the appearance of the nuclei of the lymph cells commonly found in the body cavity. These lymph cells, in some preparations, are much more numerous in the regenerating region than elsewhere, often occurring in almost solid masses.

There is individual variation as to the character of the cicatrix. In most of my preparations of early stages (7 to 11 days) the cicatrix was composed chiefly of the spindle-shaped cells. In one eleven-day preparation, however, there was only a small mass of cells underlying the regenerated epidermis, and this mass was composed mainly of cells with large nuclei having all the characters of epidermal nuclei. These cells were actively dividing. Figure 57 (Plate 8) shows a group of these nuclei.

According to Hescheler the spindle cells give rise to the new muscle layers. In my preparations of later stages, too, these spindle cells are seen to be taking the direction of the fibres of the two muscle layers in

such a way as to leave no doubt as to their fate. After the first week or two the spindle cells form a smaller proportion of the cicatricial mass at the regenerated end, this fact generally being due to the accumulation of these cells into the new muscle layers. The remaining scattered elements are either lymph cells or cells with large nuclei of the epidermal type. The latter cells tend to collect in the region into which the regenerating cord is extending.

The forward growth of the fibre bundle precedes the accumulation of cells about it ventrally and laterally in the position of the ganglionic masses.

Of the three kinds of nuclei to be met with among the incompletely differentiated cells of the regenerating region, there is no evidence that either the lymph nuclei or the nuclei of the spindle cells give rise to new nervous elements. The nuclei of these two types are totally unlike the nuclei which are first found associated with the new nervous parts, and there is no evidence of a transformation of one kind into the other. Granting this, the origin of the new nervous elements must be referred to the larger nuclei, those of the epidermal type. That these large nuclei are derived from the epidermis, there is good evidence in the preparations.

The formation of a new epidermis over the cicatrix offers some interesting problems, which, however, require a study of earlier stages of regeneration than any I have worked with. After seven days there is always found over the cut end of the worm a continuous thin layer of more or less flattened epidermal cells, and a thin layer of cuticula also is already formed. In rare cases I have found mitosis in the epidermis at this early stage. At later stages there is abundant mitosis in the new epidermis, and in one case numerous dividing cells were found among the basal or subepidermal cells back through several uninjured segments. Some signs of *amitosis* were found in the regenerated epidermis, but not conclusive evidence. Nuclei were found with two nucleoli, and several columnar epidermal cells were found containing two nuclei pressed so closely together that their contiguous surfaces were quite flat, suggesting that there had been a direct division and that the two nuclei had not yet moved apart. In one case four nuclei in a common cytoplasmic mass were found so closely pressed together that the group presented the appearance of the four-cell cleavage stage of an egg. No nuclei in process of constriction were observed.

The new epidermis having once been established, there is little room for doubt that its later increase is effected by the mitotic division of its

own cells. It is after the first week that we find evidence that not all the cells produced by the epidermis are destined to remain epidermal cells.

The normal epidermis consists of a single layer of columnar cells with some basal cells of irregular form wedged in among their deep ends. The nuclei of these basal cells are unlike those of the columnar cells. They are smaller, often lack a prominent nucleolus, and generally present a darker appearance, due to a greater proportion of chromatic material. In the regenerated epidermis places are often found where certain cells, with nuclei of the kind characteristic of the columnar cells, tend to form a second layer. Single cells are found so placed as to suggest that they are being pushed down below the surface layer. Others, apparently, have been quite displaced from their superficial position and lie free underneath the epidermis. There may frequently be found small masses of cells with nuclei precisely like those of the epidermis, lying close to the deep surface of the epidermis, and so far removed from any other tissue containing similar nuclei that their epidermal origin is beyond doubt.

The surface of the regenerated end is often very uneven in the early stages. The new epidermis is thrown into folds or marked by elevations and pits. At an inner angle of a sharply invaginated region of epidermis may sometimes be seen evidences of an inward proliferation of the epidermal cells. There is also some evidence, as Hescheler finds, that not only single cells, but also considerable masses of cells, may be pushed in and separated from the surface layer. Small local invaginations are sometimes found which are nearly closed over, and in one or two places I have seen small cavities completely enclosed by epidermal cells, as if small invaginations had become closed over and had sunk beneath the surface.

In one animal of twenty-four days' regeneration the new nerve cord was already well established. The region of the epidermis nearest the anterior end of the regenerating cord consisted of loosely aggregated cells. Between this region and the end of the cord were numerous scattered cells with nuclei like those of the epidermis and also like those of the cells already definitely associated with the new cord. The scant cytoplasm of these scattered cells was more or less drawn out to spindle shape, and most of the cells were placed with their long axes extending in the direction of the nerve cord. Similar conditions were found in other animals. The appearance indicates a separation of cells from the epidermis and the migration of these cells in toward the regenerating cord.

All the facts taken together justify the belief, as Hescheler concludes, that the epidermis is an important source of cells that take part in regeneration, and especially of cells that go to the regenerating cord.

There are other possible sources of the nuclei which resemble those found in the regenerating cord. The alimentary epithelium contains such nuclei, and it is not impossible that it may furnish cells for the regeneration of other organs, but there is no good evidence for believing that it does so to an important extent in the case of the nervous system. There are scattered nuclei among the muscle fibres, and elsewhere, which resemble the epidermal nuclei, and these may also take part in regeneration.

Three facts justify the conclusion that the cells of the new brain and ganglia are mainly of epidermal origin. (1) In the early stages of regeneration the nerve cord is in more intimate relation with the epidermis than with any other tissue. (2) The new nervous parts are laid down in a region whose cells (with the exception of the lymph cells and the spindle cells) are doubtless derived mainly from the epidermis. (3) There is an apparent inward shifting of cells from the epidermis to the new cord.

One possibility remains to be considered. Hescheler finds, in regenerating worms, abundant mitosis in the ganglia of the old cord back through some fifteen segments, and concludes that the old cord furnishes some material toward regeneration. This increase of cells in the old cord has not been commonly found in my preparations. In most of the series that have been carefully studied there was no evidence whatever of mitosis or increase of cells in the old cord. In one or two animals a condition was found similar to that described by Hescheler. In one worm of ten days' regeneration were found several masses of cells presenting an appearance unlike anything to be found in a normal ganglion and containing so many mitotic cells as to indicate a rapid increase. The preparation included nine segments back of the injured segment. The most posterior mass of proliferating cells was in the eighth segment. Several similar masses occurred in ganglia of more anterior segments and occasionally isolated dividing cells were found.

In the worm from which Figure 14 (Plate 3) is taken, the mass of cells which has already been mentioned (page 116) as lying at the anterior end of the old cord is doubtless of the same nature as those found farther back in the other animal. This preparation included only five segments and no similar masses were found in other segments. In appearance the cells of this mass (Plate 4, Figure 18) are precisely like

those of the more posterior groups of the other worm, and unlike any found in the near-by cicatrix. These facts, and the position of the mass well within the limit of the old cord, make it scarcely to be doubted that the mass owes its origin to the increase of cells of the old cord, rather than to any cells which may have wandered in from the cicatrix.

It is the occurrence of masses of actively dividing cells, rather than the character of the individual cells or nuclei, that distinguishes this from the condition found in the cord of a normal worm. The nuclei of these cells differ in no marked way from nuclei which may be found in the ganglia of uninjured worms. They are smaller than the nuclei of the large nerve cells, but they show the same structure as to chromatic material and the presence of a single large nucleolus. Figure 57 (Plate 8) shows some cicatricial cells of the epidermal type, but the same drawing would represent equally faithfully a group of cells from one of these masses in the old cord. The nuclei differ from any found in the normal cord mainly in being more or less elongated. In Figure 18 it can be seen that the nuclei in the thin posterior end of the mass are more elongated than those in the thicker anterior part of it. This condition suggests a mechanical deformation of the nuclei as a result of the rapidly growing mass pushing its way back into the tissue of the cord. There was scant cytoplasm about these nuclei and no definite cell outlines, as is also the case in the nuclei of Figure 57.

The absence of this cell increase in the old cord of many animals shows that it is not a necessary feature of the regenerative process. The presence of one of these masses of cells exactly at the region of injury, as in Figure 18, makes it probable that it provides material for regeneration. It can hardly be supposed that an increase of cells in ganglia situated five or ten segments back of the region of injury has anything to do with the actual regeneration of new ganglia anterior to the old cord.

##### 5. HISTOLOGY OF THE NERVOUS FUNDAMENTS.

Having considered the origin of the cells which constitute the fundaments of the brain and new ganglia, I now propose to consider certain questions pertaining to the development of the nerve cells from the cells of these fundaments. The main purpose at this point is to determine if any polar structures of a mitotic cell pass into the resting cell, persisting through all the stages of growth and differentiation to become, or give rise to, the centred system of the mature nerve cell. It is therefore necessary to examine the mitosis, and especially the later stages of it,

in the cells of the fundamentals, and to find, if possible, a series of cells which shall represent successive stages in the development of nerve cells.

Preparations from the later stages of regeneration were found most favorable for this purpose. In worms of from thirty to forty days' regeneration the new brain and ganglia were represented by large masses of cells, among which dividing cells were very abundant. In the same animals the differentiation of nerve cells was in progress, and frequently a single section contained not only dividing cells with scant cytoplasm, but also large, apparently fully developed nerve cells, and perhaps many intervening stages.

In the earlier stages of regeneration, cells in a solid mass, showing no signs of segmentation, are found lying laterally and ventrally about the fibre bundle which has previously marked out the position of the nerve cord. In the brain fundament a similar mass of cells lies about the neuropile, chiefly on its dorsal and posterior border, as seen in Figure 16 (Plate 3). This position of the cells is characteristic. These cells have a very small amount of cytoplasm, so that the fundamentals look like masses of solidly packed nuclei. There are no distinct cell outlines, but where the nuclei are less solidly aggregated an irregular mass of cytoplasm may be found collected about each one. At sufficiently early stages the nuclei are all alike, ellipsoidal or spherical in form, and generally have a single large spherical nucleolus. Nuclei without a nucleolus are often found. They may belong to cells which have recently divided. The absence of the nucleolus is often associated with a condition of the chromatin which indicates a recent or approaching division of the nucleus.

At later stages of regeneration many of the nuclei lying deeper in the mass become larger and more nearly spherical and accumulate a considerable body of cytoplasm about them. *Cells which assume this character have ceased dividing and are in process of development into nerve cells.* The nuclei on the outer borders of the fundamentals retain their embryonic character and continue actively dividing.

The more advanced the stage of regeneration, the more nearly have the deeper cells attained the character of typical nerve cells.

Figure 20 (Plate 4) represents a parasagittal section through the brain of a worm after thirty-four days' regeneration. The regenerated brain is smaller than the normal brain. (Compare Figure 20 with Figure 19, a similar section from the corresponding region of the brain of a normal animal.) The cells occupy the posterior and dorsal border of the neuropile. This relation of cells and fibre mass is found at the earliest

stages in the fundament (Figure 16) and persists through all the later development. It is characteristic also of the normal brain. (Compare Figure 19.) In the deeper part of the cell mass (Figure 20) may be seen a number of pear-shaped cells with their processes directed toward the centre of the neuropile. These cells are, to all appearance, fully differentiated nerve cells, like those occupying similar positions in the normal brain. Between these cells and the periphery are smaller cells, some of them pear-shaped and with processes, others in which no processes could be found. About the extreme posterior border is a mass of nuclei with indefinitely assignable cytoplasm and exhibiting abundant mitoses, — exactly the condition which the entire cell mass of the fundament presents at earlier stages.

It is evident, then, that the deeper cells are the first to become differentiated into nerve cells, while the cells on the periphery of the mass long retain their embryonic character and continue dividing to give rise to new elements.

In the normal brain (Figure 19) the large typical nerve cells occupy a deep position. About the posterior border of the brain are smaller cells, some pear-shaped and with processes, others apparently lacking processes. There are also nuclei like those of the smaller pear-shaped cells, but having very scant cytoplasm, or there may be several of them lying near together in what is, to all appearance, a common cytoplasmic mass. Such nuclei, or groups of nuclei, differ in no visible way from the actively dividing nuclei which constitute the early fundaments. They resemble likewise the peripheral layer of nuclei present at so late a stage of regeneration as is seen in Figure 20. If it could be assumed that the embryonic development of the normal brain is similar to the regenerative development, there would be little reason for doubting that the small cells and "indifferent" nuclei of the posterior border of the normal brain represent the mass of embryonic cells which have given rise to the differentiated nerve cells. There is little or no reason for regarding them as neuroglia cells. The nuclei which, beyond question, belong to the neuroglia are of an entirely different character.

Conditions in the regenerating cord are similar to those in the brain. The deeper cells are first differentiated into nerve cells, while the cells along the ventral border and at the anterior tip of the ganglionic mass continue dividing long after the deeper cells have attained the size and form of typical nerve cells.

## 6. MITOSIS IN THE NERVOUS FUNDAMENTS.

Figures 21 to 30 are taken from the actively dividing cell masses in the regenerating brain and cord of animals after about five weeks' regeneration. As already mentioned, these cells have very little cytoplasm and there are no definite cell outlines. Often the nuclei are packed so closely together as to appear imbedded in a common cytoplasmic mass. In the resting cells of this character I have been unable to discover any structure which could, beyond doubt, be taken for a centrosome. If present, it must be an extremely minute body, and all the conditions are most unfavorable for its discovery. It is not until the cell has passed into the earlier stages of mitosis that an unquestionable centrosome is to be observed.

Cells in the early prophase are numerous and generally present the appearance of the cell at the right in Figure 21. Such cells are conspicuous objects because of their sharply defined spherical outlines and the clear area surrounding the chromatic elements. The sharp outline is due to the presence of a distinct membrane, and, for reasons to be given later, this membrane must be considered to be a cell membrane and not an expanded nuclear membrane. At some time during the formation of the chromosomes the nuclear membrane disappears.

The appearance of the cells at this stage indicates a condition of turgescence. The entire cell contents, cytoplasmic as well as nuclear, with the exception of the chromatin, are in a highly fluid condition, judging by the absence of stained substance (except the chromatin) in the preparations. That there is a swelling of the cell during the beginning of mitosis is proved by such conditions as are seen in Figure 21. Here are two dividing cells close together. The one at the right is in the prophase, while the one at the left is in the metaphase. (The axis of the spindle in the latter cell is oblique to the plane of the section, and one pole has been cut away. The remainder of the cell was easily identified in the next section.) The two mitotic cells have increased in volume; and the large nucleus of another cell, caught between them, has been pressed out of shape by the combined pressures from the two swelling cells.

The smallness of these cells and the large number of chromatic elements make it difficult to determine the exact manner of formation of the chromosomes. One or two nuclei have been found which gave some evidence of a spireme condition of the chromatin, but, aside from these,

the earliest condition of the chromosomes was that seen in Figure 21, where the chromatin is in the form of large, nearly spherical granules. The number of chromosomes could not be accurately determined.

The presence of a centrosome was not observed until the spindle had been well formed. The two granules lying at the edge of the chromatic mass in Figure 21 (cell at the right) may be the centrosomes which have not yet taken their position at opposite poles. Cells were found where the two poles of the spindle had been established, and the chromosomes were not yet aggregated into an equatorial plate. Sometimes an extremely minute centrosome could be distinguished at the poles of the spindle at this stage. When the cell is in the metaphase the centrosomes are generally conspicuous objects, although there is much variation as to their size. The half spindle in Figure 21 (cell at the left) shows a centrosome. In Figure 22 the centrosomes are unusually large for cells at that stage. The average size of the centrosomes is perhaps fairly indicated by Figure 24.

In the metaphase the cell membrane is still present. The loss of a perfectly spherical form may mean a decreased internal pressure. Particular attention is directed to the fact that there is very little stained material outside the limits of the spindle. Figure 23 represents a very typical metaphase. Except for a slight cloudiness near the poles, the cell body is quite clear. The spindle is very sharply outlined, and at its poles are minute deeply stained centrosomes. No polar radiations are visible. In Figure 22, except for a few indefinite irregular masses of unstained material, the body of the cell is clear. In this case, however, a few very indefinite polar rays could be seen. In Figure 24 there is an unusually large amount of material, apparently finely granular, in the region of the two poles, and into this material extend some well defined polar radiations. The half spindle of Figure 21 shows an extreme case of the presence of solid substance outside the spindle.

In the metaphase, then, the body of the cell is generally clear. If solid material be present outside the limits of the spindle, it tends to be accumulated about the poles and may be associated with polar radiations.

The division of the chromosomes must take place at a very early stage of the equatorial plate, for in most of the cells in the metaphase the chromosomes are in a double layer.

The region occupied by the spindle always presents a compact and homogeneous appearance, although not deeply stained. A limited number of conspicuous fibres may be seen lying upon the surface of the

spindle. These are quite likely "mantle fibres" attached to the chromosomes. They exhibited a finely granular structure.

The anaphase must be a period of very short duration, for figures in which the chromosomes were just separating, or had traversed less than half the distance toward the poles, were rarely found. The few that were found exhibited no unusual features.

Figure 25 represents a cell in which the chromosomes have nearly completed their migration toward the poles. At the right pole the chromosomes are aggregated into a nearly solid mass. At the left pole they are still somewhat scattered. The sharp cell outline is still preserved, indicating the presence of the cell membrane. There is a very slight equatorial constriction of the cell. The body of the cell, outside the spindle figure, is perfectly clear except for a slight trace of indefinite material on one side of the spindle. The interzonal filaments occupy a barrel-shaped region. This shape of the figure is characteristic for this phase, and cells in this condition were very abundant. The barrel-shaped figure lies sharply outlined in the surrounding clear space. The interzonal filaments are of granular appearance, and some irregular dark masses occur upon them.

The presence of a centrosome at the left pole of the figure is doubtful. The black granule which appears to occupy the position of the centrosome is much larger than the centrosome usually is at this stage. It is possibly an aberrant chromosome. The axis of the figure is oblique to the plane of the section, the left end being higher. This position favors the obscuring of a centrosome. Although the chromosomes at the right pole are in a nearly compact mass, something of the form of individual chromosomes is still to be distinguished. The centrosome is unmistakable, lying at the apex of the old spindle. The chromatic mass is more smoothly outlined on the polar side, being concave toward the centrosome. This condition is characteristic and is seen to better advantage in the cell represented in the next figure.

Figure 26 is a somewhat later stage than Figure 25, as is shown by the complete consolidation of the chromosomes and the deeper equatorial constriction of the cell. The cell membrane is still distinctly present, although at some regions it appears fainter and less clearly defined. The cell body, outside the region of the spindle, is still nearly clear. The figure itself is barrel-shaped, as before, but the interzonal filaments are more sharply bent at the equator. Each group of daughter chromosomes appears to have fused to a solid mass. In the mass at the right pole the position of a lagging chromosome is indicated by a chromatic process extending toward the equator.

The important feature at this stage, in its relation to later stages, is the condition on the polar side of the chromatic mass. Each chromatic mass is concave on the side toward the centrosome and convex on the opposite side. The polar and equatorial surfaces of the chromatin lie in the surfaces of two spheres whose common centre is marked by the centrosome. These conditions point to the centrosome as the centre of the forces by which the chromosomes have been moved toward and grouped around the poles.

Between the centrosome and the polar surface of the chromatin is a region otherwise bounded by a conical surface extending from the centrosome, as apex, to the nearer outer edge of the chromatic mass. This is the region originally occupied by the end of the spindle, but at this stage it is impossible to detect any fibres extending from the centrosome toward the chromatin. This polar region is stained sufficiently to be sharply outlined against the outer clear space of the cell, and yet it is so much lighter than the chromatin as to be clearly distinguished from the chromatic mass. It appears perfectly homogeneous, exhibiting neither fibres nor granules.

This condition of chromatin and polar structures persists for some time while certain equatorial changes occur. These changes include the formation of a membrane between the daughter cells (Plate 5, Figure 27). The figure meanwhile loses its barrel shape, assuming the form of two cones with apices together at the plane of the new membrane. The axis of the entire figure may become bent at the meeting of the two cones. The axis of the left daughter cell in Figure 27 is almost parallel to the plane of the section. The chromatic mass is of characteristic appearance, but the centrosome was not clearly to be made out. The axis of the right daughter cell extends obliquely upward, so that the centrosome is obscured, and the observer looks down into the concavity of the chromatic mass. The interzonal filaments are not sharply constricted at the equator. The fact that varying degrees of equatorial constriction of these filaments may be found, supports the view that the fibres are carried inward toward the axis of the figure by an ingrowing membrane. However, in most cells at this stage may be found traces of fibres still occupying the region formerly filled by the barrel-shaped figure. Such fibres are to be seen in Figures 27-29.

Two facts of importance are to be noted at the stage of Figure 27. The original cell membrane is in process of degeneration, the clear space about the mitotic figure being no longer sharply outlined. It is of irregular form, as if being encroached upon by the cytoplasm of near-by

cells. The second fact is the presence of considerable loosely aggregated, rather granular material outside the limits of the constricted figure. As the volume of the constricted figure is much less than that of the barrel-shaped figure which precedes it, and as the material in question is mainly in the region formerly occupied by the barrel-shaped figure, it is reasonable to conclude that this material is some of that originally contained within the limits of the larger figure.

In Figure 28 one chromatic mass has been cut away. The centrosome of the other pole is not visible, probably because of the obliquity of the axis. Something of the lightly stained polar region can be seen. The old cell membrane has degenerated to a less extent than in Figure 27. A distinct equatorial membrane is present, and the interzonal filaments are sharply constricted. Outside the constricted figure is some loose material, as in Figure 27, and a few fibres from the chromatic mass mark the outlines of the former barrel-shaped figure.

Figure 29 is a reconstruction. The left chromatic mass was cut away from the rest of the figure, being found in an adjacent section. The old cell membrane is indistinct. The equatorial membrane is clearly present. The interzonal filaments are sharply constricted, and there is a suggestion of a "Zwischenkörper." There are some traces of fibres outside the constricted figure, but, except for these, *the space outside the figure is almost clear*. The chromatin appears enclosed in a membrane, and the daughter chromatic masses show considerable increase in size. The chromatin is in the form of large granules. At the polar side of the left chromatic mass (nucleus?), the lightly stained region and the centrosome are to be seen. These could not be seen in the other daughter cell, perhaps because of the position of the axis. The condition of the chromatin in this case is much more advanced than ordinarily when the interzonal fibres are still present.

In Figure 30 the chromatic masses are in much the same condition as in Figure 27. Owing to the obliquity of the axis of the right daughter cell, the centrosome is not to be seen. The old cell membrane is fairly distinct in some regions, but quite lacking in others. The interzonal filaments are sharply constricted. There is, again, a suggestion of a Zwischenkörper, although the concentration of the fibres may account for the darkness at their equatorial region. The important points to be noticed are, first, that the daughter-cell bodies outside the limits of the constricted figure are practically clear, and, secondly, that there is no trace of an equatorial membrane. The constriction of the old cell outlines and the constriction of the interzonal filaments would indicate that the equatorial membrane had been formed and has disappeared.

## 7. DEVELOPMENT OF THE NERVE CELLS.

The significance of these facts concerning the cell membranes will best be understood after a description of Figures 31-36 (Plate 5), which represent further stages in the progress of recently divided cells toward a resting condition. That such objects as are seen in these figures are what I have taken them to be admits, I believe, of no doubt. They occur with about the same frequency as the later stages of mitosis. Moreover, there are no other objects present which could possibly be taken for recently divided cells. They are found in pairs oftener than would occur by chance. That they seem not always to occur in pairs may be explained, in part, at least, by two facts. It is frequently observed that two sister nuclei may progress toward the resting condition with very unequal degrees of rapidity. There is much evidence that this is so in the case of these cells. Figures 32 *a* and 32 *b* represent two objects which lay so close together as to leave no doubt as to their being sister cells, but there is a marked difference in the size and compactness of the chromatic masses. It must be that one of two sister cells may so far outstrip the other in regaining the resting condition as to leave the slower cell apparently without a mate. Secondly, when two sister cells lie in different sections, having found one, it is difficult to identify the other, especially if they are not alike in appearance.

It often happens that two very similar young nuclei are found, not so very far apart, but yet farther apart than they could have been at the end of mitosis. In some regions of the fundaments of the nervous parts the cells are very loosely aggregated, the spaces doubtless being filled with fluid in the living animal. It seems probable that there may be a mechanical shifting of the less securely supported cells, merely as a result of the muscular activities of the animal. In this way young sister cells may become separated from each other.

Figure 31 represents a young cell from the ventral posterior border of the regenerating brain, together with three nuclei of adjacent resting cells. A similar object was found in the next section, but at a distance considerably greater than could have intervened between the two at the end of a mitosis. If the darkly stained object in Figure 31 be compared with the chromatic masses and their accompanying polar structures in Figures 26-30, it will readily be seen that the disappearance in the latter of that part of the spindle which lies between the two chromatic masses, and the assuming of a more nearly spherical form by the chro-

matic masses would result in two objects like the one seen in Figure 31. Figures 32 *a* and 32 *b* represent two young sister cells with several of the surrounding nuclei. They lay in two adjacent sections, and by means of camera drawings their centres were found to be exactly superposable.

The interpretation of Figure 31 is obvious. The heavily stained compact mass, concave upon one side, otherwise spherical, is one of two daughter chromatic masses resulting from the fusion of a group of daughter chromosomes. On the concave side of the chromatin is an area distinguished by a stain distinctly lighter than that of the chromatin, but yet sufficiently heavy to outline it sharply against the outer clear space. On the mid-border of this lightly stained region is a dark granule. This granule is the centrosome, and the lightly stained region corresponds to the polar region of the old spindle. The chromatic mass and its accompanying polar structures lie in an irregular, indefinitely outlined, clear space. This clear space is the region formerly limited by the old cell membrane, which has completely disappeared. In the later stages of mitosis represented in Figures 27-30 various stages in the degeneration of the cell membrane of the mother-cell are to be seen. The dark masses (Figure 31) lying in the clear space, on the apolar side of the chromatic mass, may be remnants of the old spindle.

In Figure 32 *a* is a similar condition of the chromatic mass with the lightly stained polar region on its concave side. No distinct centrosome was visible in this case. The surrounding clear space marks the region formerly bounded by the daughter-cell membrane. In Figure 32 *b* a more advanced condition of the chromatin is seen. The volume of the chromatic mass has increased, and this increase is attended by the separation of the chromatin into a number of large granules, between which the mass has a lighter appearance. The concavity on the polar side of the chromatin is still marked. The lightly stained polar region is sharply outlined. It has increased in volume and lost its conical form. The centrosome no longer lies at its border, but well in toward the concavity of the chromatic mass. There are some faint lines extending from the centrosome to the periphery of the lightly stained region. Chromatic mass and polar structure lie in a clear space.

Figure 33 shows two pairs of sister cells. *a* and *β* are to be regarded as the chromatic masses of one pair. The chromatic masses of the other pair lie one over the other. *γ* is the upper of the two masses, and the outline of the lower is indicated by *δ*. In *a* and *β* the condition of the chromatin is much as in Figure 32 *b*. *a* shows the concavity of the chromatic mass, the lightly stained polar region, and the centrosome at

its apex.  $\beta$  is in an unfavorable position for the observation of the polar structures.  $a$  and  $\beta$  lie in a common clear space, which shows a constriction in the region between the two chromatic masses. This common clear space is that formerly bounded by the mother-cell membrane. The equatorial membrane, separating the two daughter cells, has disappeared.  $\gamma$  and  $\delta$  are unfavorably situated for study.

Figures 34 and 35 represent two young cells whose sister cells could not be identified. The chromatic masses are in the same condition, both showing the polar concavity and the loosening of the chromatin into large indistinctly separable granules. In both cases the lightly stained polar region and its centrosome are present, and in both cases a thin layer of lightly stained material extends from the polar region along one side of the chromatic mass to its opposite end. In Figure 35 a slightly clearer area bounded by a darker ring surrounds the centrosome. In both figures a clear space surrounds the ellipsoidal body, which is composed of the chromatic mass plus its polar structures.

Figure 36 shows a group of cells from the posterior ventral border of a regenerating brain. At the centre of the group is a young cell. The chromatic mass is composed of indistinctly separated granules. On one side of it is the lightly stained polar region within which lies a dark granule, doubtless the centrosome. On the border of the lightly stained region are two dark places, but focussing shows that they are not distinct granules. There is no marked polar concavity of the chromatic mass. The surrounding clear space belonging to the daughter cell is well defined.

Above the dividing cell in Figure 29 is a young cell which shows the swelling chromatic mass, the polar region, centrosome, and the clear space about the entire stained object.

Figures 37 and (Plate 6) 38 show later stages in the condition of the chromatic masses; it is not until such stages as these are reached that answers can be confidently given to the questions, which already must have suggested themselves. How much is nucleus and where is the cytoplasm in Figures 31-36? Unless one is prejudiced by holding the belief that the centrosome must lie outside the nucleus, there are two possible interpretations of the object shown in Figure 32 *b*. It may be that the nucleus is identical with the chromatic mass, or it may be that the new nuclear membrane is represented by the elliptical outline which encloses the chromatic mass together with the lighter region at its pole. Upon careless observation with a dry objective, one would hardly hesitate in saying that the elliptical outline is that of the nuclear membrane.

According to this interpretation, the centrosome would lie within the nuclear membrane.

When the condition of Figures 37 and 38 is reached, it becomes evident that *the lightly stained polar region is not included within the nuclear membrane.*

Figure 38 shows a group of cells from the anterior end of a regenerating cord. At the centre of the group is a large nucleus slightly irregular in form. It contains a single nucleolus and is denser in chromatin than most resting nuclei. On one side of the nucleus is a lightly stained region, appearing crescent-shaped in the section, and sharply outlined against the clear space which surrounds it and the nucleus. At the mid-periphery of the light region is a dark granule. A comparison of Figure 38 with Figures 31-36 leads to the conclusion that *the chromatic masses of Figures 31-36 are the daughter nuclei, and the lightly stained polar regions including the centrosome are not contained within the nuclear membrane, but represent cytoplasmic structures.*

Figure 37 shows a cell from a regenerating brain. The nucleus, containing a large proportion of chromatin, still exhibits the polar concavity seen in the earlier "chromatic masses." No nucleolus is yet visible. In this case the lightly stained region on the concave side of the nucleus is of much greater volume in proportion to the nucleus than in Figure 38. Near the mid-border of it is a small deeply stained granule surrounded by a slightly clearer space. Some weak radiations proceed from the granule. In Figure 37, then, we have a nucleus, upon the concave or polar side of which is a considerable mass of cytoplasm containing a centrosome and radiations. But what of the clear space surrounding the nucleus and its polar mass of stained cytoplasm? In all the stages represented in Figures 31-38, this clear space is present. It can be interpreted only as the space originally bounded by the mother-cell membrane, which has now degenerated. In such a case as Figure 37, is the clear space to be regarded as a part of the cell territory belonging to the nucleus which lies within it, or is the entire daughter cell at this stage to be considered as included within the outline which encloses the nucleus and the dense, cytoplasmic mass lying on its concave side? I hold the latter to be the correct interpretation. In all of Figures 31-38, *the lightly stained polar region containing the centrosome constitutes the fundament of the cytoplasm.* This cytoplasmic fundament increases in volume along with the nucleus, occupying more and more of the space originally bounded by the old cell membrane.

At all stages it must be said that all the *living parts*, at least, of

the daughter cell are included within the limits of the nucleus and its polar cytoplasmic fundament. It may be that the surrounding clear space contains fluid material derived from the degenerated parts of the mother cell, and that the growing cytoplasm of the daughter cell utilizes some of this material. In that sense only can the clear space be regarded as actually a part of the young cell.

Figure 39 shows two cells from a regenerating subœsophageal ganglion. The nucleus at the left is in a typical resting condition, having a chromatic network and large nucleolus. Its cytoplasm is massed at one end of it and contains the centrosome surrounded by a dark ring. The nucleus at the right shows no nucleolus. The cytoplasm is massed at one end of the nucleus and contains a clear space at the centre of which is a dark granule with some weak radiations. The young cells of Figures 34 and 35 may readily be imagined to become such cells as are seen in Figure 39.

Figures 40 and 41 represent cells from the brain after five weeks' regeneration. The nuclei have the form and structure typical for those of nerve cells. The cytoplasm in both cases is collected upon one side of the nucleus and contains an unmistakable centrosome and radiations, constituting a centred system like that which has been described in nerve cells of the normal worm. No nerve processes from these cells could be seen. Cells like these may be derived from cells like those in Figures 37 and 39 simply by the increase in volume of nucleus and cytoplasm. By this growth the space originally bounded by the old cell membrane becomes entirely filled, and there is no longer a clear space about the growing cell.

In Figure 36 the large nucleus at the extreme left possesses a considerable cytoplasmic mass, which contains evidence of a centred system, although no distinct centrosome could be seen. The nucleus is peculiar in lacking a nucleolus. The cell at the extreme right has a pear-shaped form, and there is some evidence of a process at the smaller end. On the side of the nucleus toward the larger end of the cell is a region of denser cytoplasm with a lighter centre, but no centrosome or radiations can be seen.

Figure 42 shows a group of three cells from a subœsophageal ganglion of thirty-four days' regeneration. The three nuclei lie at different levels, the smallest one being lowest. A centrosome and radiations may be seen close to each of the two larger nuclei, and on the side toward the greatest cytoplasmic mass.

### 8. THE CENTROSOME IN THE MATURE REGENERATED NERVE CELLS.

Evidences of the presence of the centred system are to be found in cells of all sizes from those represented in Figures 40-42 (Plate 6) to the fully differentiated nerve cells such as are shown in Figures 10-13 (Plate 2), which are from a brain of thirty-four days' regeneration. The cells shown in Figures 10-12 lay side by side in a single section of the brain. Figure 10 represents a cell whose centred system places it among cells of the "first type," as described (pages 112-114) for cells of the normal animal. The whole structure in this case was unusually distinct. The centrosome (for so it can now be called) lies in the axis of the cell and so close to the nucleus that the small clear space about the centrosome is tangent to the nuclear membrane. Four distinct radiations extend nearly or quite to the periphery of the cell. They appear finely granular. The presence upon the radiations of conspicuous granules surrounded by small clear spaces can be seen. The two radiations nearest the axis of the cell appear connected by a cross fibre, which extends between two of the larger granules mentioned.

In Figure 11 there is a distinct centred system with its centrosome in the axis of the cell and near the nucleus. About the centrosome is an imperfectly described circle of granules, four of which lie on the paths of radiations from the centre. In this respect, the system is one of the "second type" (page 114), but the region bounded by the circle of granules is rather lighter than the surrounding cytoplasm, instead of denser, as in Figure 3. A small neuroglia nucleus lies close upon one side of the cell.

Figure 12 shows a clear circle tangent to the nucleus and in the cell axis. At the centre of the clear circle are three indistinctly defined granules, from which several faint radiations extend into the cytoplasm.

Figure 13 exhibits a remarkable complexity of the centred system. The cytoplasm in this case was practically unstained, yet its fibres stood out with much clearness. This cell shows to advantage the presence of secondary centres. The primary centre, or centrosome, is easily distinguished as lying in the cell axis and in being the point from which proceed several radiations which extend in straight lines almost to the periphery of the cell. Upon these radiations are conspicuous granules from which extend secondary radiations. The secondary radiations some-

times appear to connect certain larger granules on two different primary radiations. This cell is one of the first type, lacking anything that could be called a "sphere."

## V. General Conclusions,

### 1. MITOSIS IN THE NERVOUS FUNDAMENTS.

To summarize briefly the process of mitosis as seen in the cells of the ganglionic fundaments :

The prophase is accompanied by a turgescence of the cell ; a distinct cell membrane is formed ; the nuclear membrane disappears ; the chromatin takes the form of nearly spherical chromosomes ; the region between the chromosomes and the cell membrane is nearly or quite clear ; a spindle appears with its centrosomes very minute, if visible at all.

In the metaphase a distinct cell membrane is still present ; the spindle with its equatorial plate of chromosomes lies sharply outlined in the cell body, which is otherwise nearly or quite free from any solid material ; generally the centrosomes are clearly to be seen at the spindle poles and often they become fairly conspicuous objects.

In the later phases the chromosomes separate and move toward the poles, each daughter group fusing into a compact mass, which is concave on its polar side ; the centrosome remains visible at the apex of the old spindle, the end of which forms a lightly staining region between the centrosome and the concave surface of the chromatic mass ; the interzonal filaments occupy a barrel-shaped region ; an equatorial constriction of the cell membrane appears. The ingrowth or differentiation of an equatorial membrane between the two daughter cells follows, accompanied by the constriction of the barrel-shaped figure to the form of two cones with apices together at the plane of the equatorial membrane. As a result of this decrease in the volume of the figure, some of the substance of the barrel-shaped figure, including a few of its filaments, is left outside the limits of the constricted figure. This substance disappears later.

During the forming of the equatorial membrane, the old cell membrane (now become the daughter-cell membranes) undergoes degeneration, and finally the new equatorial membrane also disappears. At this period, then, the constricted figure lies sharply outlined in an irregular clear space which is not definitely outlined, not enclosed in a

membrane, and not divided by an equatorial membrane (Fig. 30). The interzonal filaments degenerate, leaving the two daughter chromatic masses and their accompanying polar structures lying in a common clear space (Fig. 33,  $\alpha$  and  $\beta$ ). The chromatic mass is the nucleus; the lightly stained conical polar region with the centrosome at its apex is the fundament of the cytoplasm.

The chromatic mass, enclosed within its new nuclear membrane, breaks up into granules, which become the chromatic parts of the resting nuclear network. The polar concavity persists during the earlier growth of the nucleus.

The polar cytoplasmic fundament increases in volume along with the nucleus, the centrosome persisting through all the growth of the cytoplasm, and becoming the centre of the radiating system of the resting cell.

That the spherical membrane seen in the prophase (Fig. 21) is a cell membrane and not an expanded nuclear membrane admits of no doubt when its fate is considered. It is identical with the membrane which encloses the clear space surrounding the figure in the metaphase (Figs. 22-24), and it is this membrane which constricts during the later phases, in connection with the formation of the equatorial membrane. Moreover, the centrosome in the daughter cell lies outside the nucleus. During the prophase, therefore, we should not expect to find it within the nuclear membrane.

The peculiar feature in the reconstitution of the daughter cells is the complete degeneration, during the telophase, of all parts of the mother cell outside the limits of the spindle figure, together with the newly formed equatorial membrane. Still later, the interzonal filaments having disappeared, there comes a period when all the living parts of each daughter cell consist of the compact chromatic mass (nucleus) and its polar region (cytoplasmic fundament), including the centrosome.

## 2. DEVELOPMENT OF THE NERVE CELLS.

In the progress of the nucleus toward the resting condition there is little, if any, increase in the volume of the chromatin. The growth of the nucleus is due to the increase in its fluid contents. As nearly as can be judged, the total volume of the scant chromatin in the large resting nucleus is about the same as the volume of the compact chromatic mass immediately after mitosis.

The growth of the cytoplasmic fundament involves the assimilation

of outside material and its transformation into a dense protoplasm. As already stated, the cytoplasm in the smaller cells is denser, more finely granular and homogeneous than in the larger cells. It seems highly probable that the fluid material resulting from the degeneration of parts of the mother cell is utilized by the growing cytoplasm of the daughter cells, which finally come to occupy the territory originally filled by the mother cell. It is commonly the case that the cytoplasm becomes more or less fluid during the earlier phases of mitosis, having a clear appearance in preparations; especially is this the case immediately about the nucleus or the spindle. But in the usual forms of mitosis, the cytoplasmic structure reappears throughout the body of each daughter cell during the later phases, and the daughter nucleus, during its reconstitution, lies in a cytoplasmic mass which is obviously half that of the mother cell. The mother cytoplasm undergoes only a temporary alteration in structure. In the mitosis of the cells of the ganglionic fundaments with which we are dealing, there is, on the contrary, nothing which suggests the reappearance of the old cytoplasmic structure throughout the bodies of the daughter cells, but a growth of new cytoplasm takes place progressively outward from the polar region of the nucleus. *The end of the old spindle lying between the centrosome and the daughter chromatic mass (nucleus), together with the centrosome, contains the substance which effects the regeneration of the cytoplasm.*

This regeneration of the cytoplasm of newly divided cells takes place only among the cells of the nervous fundaments. It is found in none of the other regenerating tissues. In all of the preparations from which my figures have been taken, mitosis of the ordinary type may be found in other regenerating tissues. In the dividing cells of the cicatrix there is at all phases a more or less dense mass of cytoplasm about the spindle figure. The mother cytoplasm in these cases is divided in the usual way, one half persisting, without degeneration, about each daughter nucleus. In cells of the epidermis, of the alimentary epithelium, and in nuclei lying in the muscle layers, the mitosis is accompanied by no sign of degeneration and subsequent regeneration of the cytoplasm. In cells of the brain sheath itself, or in cells lying immediately outside it, the telophase shows some dense cytoplasm about each daughter nucleus, whereas, in the same preparations, telophases within the brain fundament exhibit the conditions which have been described, — the absence of structure outside the spindle figure itself. Moreover, in the nervous fundaments, at least in their later stages, all of the mitoses are of the type described. No dividing cells whatever were found pre-

senting conditions other than these. At what period of regeneration mitosis of this type appears, I am unable to say. My preparations have not as yet yielded stages favorable for determining conditions in the very earliest fundamentals. In some preparations otherwise favorable, mitosis in the fundamentals is rare or absent, indicating that the animal was killed during an interval between periods of cell increase. All of the mitoses described are from preparations in which the fundamentals are well established, containing, in their deeper parts, cells which have ceased dividing and assumed the appearance characteristic of nerve cells.

It is not certain that all the products of division, in fundamentals at this stage, immediately acquire a large cytoplasmic mass and become differentiated into nerve cells. It is evident that, at some earlier period of the fundament, this could not possibly be so, else the supply of undifferentiated cells would be exhausted before the needful number of nerve cells had been produced. It must be that up to a certain period one or both of two sister nuclei acquire only scant cytoplasm after a division, retaining their embryonic character for the purpose of further division. After a sufficient number of nuclei have been produced, it may be that both of two sister nuclei give rise to nerve cells, while some of the embryonic cells cease dividing without undergoing differentiation into nerve cells, remaining as the small embryonic cells seen about the posterior border of the full-grown brain. Or it may be that one of two sister nuclei gives rise to a nerve cell, the other ceasing to divide and remaining as an undifferentiated cell.

Little can be said as to the origin of the neuroglia of the regenerated brain and cord. As the new nerve cells become differentiated, there also appear among them small nuclei similar in character to nuclei — doubtless of non-nervous nature — found in the normal brain and cord. It is not improbable that cells of the early fundamentals give rise to the neuroglia as well as to the nervous nuclei, — a differentiation from the indifferent cicatricial cells in two directions. It is also possible, however, that the neuroglia may be derived from cells having a common origin with those that give rise to the sheath.

### 3. PERSISTENCE OF THE CENTROSOME.

A definite centrosome is first to be seen at the time of the formation of the spindle in the prophase. It is an extremely minute body at that time, but during the later phases it increases in size, appearing as a

single, very dark, spherical granule lying at the pole of the spindle. At the close of mitosis it increases considerably in size, and sometimes appears less intensely stained. In Figures 31-35 (Plate 5) the centrosome is seen to be much larger than at any stage of the mitotic figure. In Figure 34 it is not a spherical granule, but is somewhat elongated. In cells showing a greater development of the cytoplasm (Figures 36-38) there is generally present a large dark granule near the centre of the cytoplasmic mass. In as early conditions as those seen in Figures 32 *b*, 35, 37, and 38, the differentiation of a clear space, or a darker circle, about the centrosome, or some evidence of radiations can sometimes be seen. The centrosome is largest immediately after mitosis. As the cytoplasm increases in volume the centrosome becomes somewhat smaller. In cells like those of Figure 39, where the nucleus is in typical resting condition, the small cytoplasmic mass contains the centrosome, frequently with evidences of concentric and radiating structures about it. With further increase in the size of the cell and the volume of the cytoplasm (Figures 40-42) there is to be seen a centred system — centrosome, clear space and radiations — comparable in all respects to the system seen in the mature nerve cell.

In all stages of development between the last mitosis and the mature cell, the centrosome and its accompanying structures are so frequently met with that one is warranted in concluding that they are generally present.

It is evident, then, that the centrosome of mitosis is present during the earliest stages in the reconstitution of the daughter cells, that it persists during the growth of the cell, becoming associated with certain concentric structures and radiations, and becomes finally the central body of the complex system of radiating and intersecting fibres found in the fully differentiated nerve cell. This is true for the regenerated cells. That it will be found true in the case of nerve cells developed by the normal embryonic process is hardly to be doubted.

#### 4. THE CENTROSOME IN NERVE CELLS.

In transverse sections of a ganglion the cells are most likely to lie with their axes nearly parallel to the plane of cutting. In such sections evidences of the centred system are often to be found in the majority of the pear-shaped nerve cells. Thus the three cells of Figures 9-11 (Plate 2), from a regenerated brain, lay side by side in the same section.

A centred system is not to be made out, however, in every cell of a section. Even if the structure is one generally present, we should not expect to be able to see it in all cells, for only the most favorable conditions could bring it to view. If the axis of the cell is not approximately parallel to the plane of cutting, the cell is likely to be cut so that the centrosome is not in the same section with the nucleus, — a condition which increases the difficulty of identification. So delicate a structure may often be obscured by some of the darkly staining masses of the cytoplasm. Considering the difficulties of observation, then, the centred system can be made out in so large a proportion of cells as to justify the belief that it is a structure usually, if not always, present in the mature nerve cells.

The largest cells of the brain and subœsophageal ganglion were least satisfactory for showing the presence of this structure. It was found with greatest frequency in cells of medium size, like those shown in Figures 1-4.

The "centrosomes" and "spheres" described for nerve cells by various authors present such widely different conditions as to suggest that they are not all homologous structures. For example, the condition in the centred system as I have found it in the earthworm is in no way similar to the sharply outlined homogeneous sphere and its numerous central granules described by von Lenhossék for spinal ganglion cells of the frog. The structure in such a cell as is represented in my Figure 3 may suggest his "sphere," yet it differs in being bounded by a layer of granules which occur on the radial fibres. Von Lenhossék found no granules bounding his sphere, nor any radiations.

The structure described by Dehler resembles that of von Lenhossék, being equally unlike anything found in the earthworm.

It is not impossible that the centrosome of mitosis, persisting in the resting cell, may give rise to structures differing as widely as the centrosome and sphere of von Lenhossék and Dehler differ from the centred system which I have described. A fuller knowledge of the structures described by them is needful. As long as they can be interpreted as sections of a "spiral figure" (Holmgren), or as wandering nucleoli (Rohde), a detailed comparison of these with the centred system is hardly warranted.

The methods used by Schaffer were not specially adapted to the study of finer cytoplasmic structure. McClure examined *Lumbricus* and found no evidence of the centrosome. The centrosome and sphere described by him for the nerve cells of other invertebrates exhibited no radial struc-

ture comparable to the radiating system I have described. Hunter sometimes found in ascidians "well developed astral rays" proceeding from the central homogeneous sphere with its centrosomes. Such a cell as that shown in my Figure 3 presents somewhat similar conditions.

Miss Lewis found in *Clymene producta* a centred system, — central granules and fine radiations, — with the additional complication of a sphere having a diameter perhaps one-third that of the cell. The condensed central region of the cell in my Figure 4 resembles such a sphere.

The structures most nearly resembling the centred system seen in the earthworm are those described by Bühler ('95) for brain cells of the lizard and ('98) for nerve cells of amphibians and mammals. In the later paper Bühler finds in some cells a centred system with its one or two central granules lying close to the nucleus and fine radiations extending toward the cell periphery, and in the same cell he also finds a concentric arrangement about the centre of the cytoplasmic mass, strongly suggesting the sphere of von Lenhossék. In other cells he finds a "spiral figure" similar to that described by Holmgren. These conditions suggest that the spheres of von Lenhossék and Dehler may be structures in no way connected with a centred system of fibrils, and that both structures may be present in the same cells.

The theory of the structure of the centred system, as proposed by Bühler, is strongly supported by my results. Bühler believes that the centrosome is the insertion point of the stronger fibrils, which may extend to the periphery of the cell. Other fibrils may not insert in the centrosome, but in the granules of the microsome stratum which constitutes the boundary of the sphere, or in large granules borne upon the primary radiations. The cell granules are, in general, the insertion points of fibrils, and the granules are larger, the stronger and more numerous the fibrils that insert in them. Accordingly, the centre of the entire system — the centrosome — is the most conspicuous granule. The system of primary, secondary, and tertiary fibrils which I have described presents exactly these conditions. The fibrils lose in prominence the farther removed they are from the centre. Therefore the primary radiations are oftenest seen. The granules that give rise to secondary radiations may be called secondary centrosomes. We may thus have centrosomes of lower and lower degrees of importance until the limit is reached, — the ordinary microsome.

Reinke ('94) finds secondary and tertiary centrosomes. He advances the proposition that a centrosome is potentially present in any micro-

some of the cell, and that it is not an organ *sui generis*, like the nucleus. Centrosomes and microsomes, he believes, are mechanical centres. A centrosome may arise at any point when needed, by the aggregation of microsomes. Similar views were expressed by Watasé ('93). Mead ('98) shows that in the maturation of the egg of *Chætopterus* a large number of asters arise in the cytoplasm. They are finally reduced to two, which become the asters of the maturation spindle.

The presence of the secondary and tertiary centres in the nerve cell is not inconsistent with the belief that the primary centrosome is the centrosome left from the last mitosis. The continuity of the centrosome of mitosis with that of the resting cells has been established in many cells other than nerve cells. That a centrosome may in some cases arise *de novo* must be granted in view of the results obtained by Mead in *Chætopterus*. Where the centrosome is continuous it may be regarded as a permanently differentiated microsome of special functional importance. After a mitosis it persists in the resting cell and marks the starting-point of the centred system of the mature cell. As the cytoplasm of the growing cell increases, the primary centrosome becomes connected, by means of fibrils, with other granules of the new cytoplasm. With continued growth of the cytoplasm, the radiating network develops from the centre outwards, being composed of "centrosomes" and radiating fibrils of lower and lower degrees of importance according to their distance from the primary centre. This is substantially the centred system described by Heidenhain.

That the function of such a system is a mechanical one appears most probable. The centrosome is generally believed to possess an important rôle in connection with the motor activities of cells, whether of the cell as a whole (leucocytes), or of appendages of the cell (cilia; flagellum of the spermatozoön), or in the movements observed in mitosis. In the absence of known motor activities in mature nerve cells, the most likely function for the centred system is that of mechanical support.

I have found no evidence whatever that the primary centrosome of the nerve cell ever resumes its mitotic functions. In all of the regenerating worms examined, no typical nerve cells with processes were found showing any change that would suggest the possibility of their dividing.

As already mentioned (pp. 78-80), masses of dividing cells are found occasionally in the old ganglia of a regenerating worm, but no such cell proliferation is to be found in the cord of a normal worm. These cell masses probably arise from "indifferent" cells which, in the early

history of the cord, ceased dividing and failed to develop into nerve cells, retaining their embryonic character. Small cells, apparently without processes and having nuclei similar to those of the nerve cells, are to be found in the normal brain and cord. The injury to the nervous system is a stimulus which may set some of these cells to dividing. The purpose of cell increase in ganglia many segments back of the region of injury is not apparent. The stimulus of the injury is not restricted to the injured segment, and, in response to it, cell proliferation may occur where it is of no direct advantage in the regeneration of the new nervous parts.

In conclusion, it is to be observed that the centrosome and the nerve process in the earthworm occupy a definite position in relation to each other and the nucleus. They are always on opposite sides of the nucleus, the centrosome occupying the greater cytoplasmic mass. The point of origin of the process may therefore be considered to be determined at as early a period as the telophase of the last mitosis in the history of the cell. The chromatic mass is the nucleus. The polar region of the spindle occupies the position of the cytoplasmic fundament. The nerve process will be developed from the equatorial side of the nucleus. In the smallest cells that give evidence of any nerve process, the centrosome and process are on opposite sides of the nucleus.

## VI. The Centrosome in Cells of the Epidermis.

A study of the cells of both the old and the regenerated epidermis brings to light strong evidence for the presence of the centrosome in the resting cell of this derivative of the ectoderm. The cells of the old epidermis are less favorable for the detection of the centrosome than the regenerated cells. The old epidermis consists of much elongated columnar cells, whose contents are often coarsely granular. The cells of a recently formed epidermis are more flattened and their contents finely granular.

In Figure 43 (Plate 6) are shown two cells from the epidermis of the anterior end of a normal worm. In both of these there is a conspicuous deeply stained spherical granule, lying in a clear space directly at the deeper end of the much elongated nucleus. In the cell at the left in the figure this granule (*c'so.*) is the only prominent object in the cytoplasm. In the cell at the right, at the outer end of the nucleus, is a region in which are scattered a dozen or more deeply stained granules.

Two of them lying very close together occupy a slightly clearer space just at the outer end of the nucleus. The condition in the right cell, taken by itself, makes doubtful the interpretation of any of its granules as a centrosome. The large granule at the deeper end of the nucleus, or the pair in the small clear space at its outer end, or both, might pass for centrosomes. Or they might almost equally well be considered accidental granules of the kind which forms the group at the outer end of the nucleus. It must be noted, however, that the granule at the inner end is in some respects unique. It is larger than any of the others, its clear space is better defined, and the end of the nucleus is sharply invaginated at the region nearest the granule, the curvature of the invagination corresponding to the outline of the clear space. These facts, together with the fact that the next cell contains a similar granule, similarly located, and without the presence in the cell of any other like bodies, make it highly probable that the granule at the inner end of the nucleus of each cell is not an accidental thing.

These two cells well represent the conditions in the old epidermis. Very many, perhaps most, of the cells resemble the cell at the right in Figure 43. There are several, or very many, large granules in the cytoplasm, often at both ends of the nucleus. Frequently one of these granules lying near the inner end of the nucleus will appear slightly larger than the others, or it may lie in a clear space; yet it is not sufficiently peculiar to justify considering it anything but an accidental granule like others in the cytoplasm. The combined evidence from all such cells affords alone no conclusive argument for the presence of a centrosome. But very often there are found cells like the left one of the two in Figure 43, where there is a single conspicuous granule, which is generally situated not far from the inner end of the nucleus. In rare cases some weak radiations can be detected. It is not uncommon to find the nucleus invaginated at its inner end, as in the right cell. These granules are doubtless "centrosomes" in the sense that such bodies in resting cells are so called, without knowledge as to their history or function. The occurrence of cells with the single definitely located granule makes it likely that in cells whose cytoplasm is filled with large granules the centrosome is present, but its identity is rendered doubtful by the presence of other bodies of similar appearance.

Figures 44 and 45 represent cells from recently regenerated epidermis. A thin layer of cuticula is present. The nuclei are more nearly spherical than in the old epidermis, and the cells are more flattened. Often no distinct cell limits can be seen. These figures are from sublimate

preparations stained in Kernschwartz and safranin. In Figure 44 the middle nucleus has an irregular outline on the side toward the greater cytoplasmic mass. Two small granules lie close to the nuclear membrane, each one opposite a slight concavity of the nucleus. Each granule is surrounded by a clear space. From both granules radiations extend into the cytoplasm, some of them going in straight lines nearly to the cell periphery, others (those directly opposite the nucleus, in the middle region of the cell) showing an arrangement like that described in the nerve cells. The primary radiations from the centre meet granules from which go off secondary radiations, resulting in something of a radiating network of fibres with granules at their intersections. The radiations, like those of the nerve cell, appear either as hyaline fibrils, or as rows of granules. The presence of the two central granules in Figure 44 suggests preparation for mitosis.

In Figure 45 the larger nucleus has a sharp invagination at its deeper end. Opposite the invagination is a granule with a complex radiating system about it. Primary, secondary, and tertiary radiations may be detected.

#### VII. Mitosis in the Regenerating Epidermis.

Figures 46-52 (Plate 7) represent stages in the mitosis of cells in the regenerating epidermis of a single worm. Figure 46 shows a cell in the prophase. The chromatin has assumed the form of nearly spherical chromosomes. The nuclear membrane is still present, but indistinct or absent at the regions where the spindle comes into relation with the chromosomes. No distinct granules could be detected at the spindle poles. Well defined polar radiations are present. The cytoplasm is fairly dense throughout the cell, and there is a distinct cell membrane. The deformation of adjoining cells shows that the cell has increased in volume. This condition is followed by the total disappearance of the nuclear membrane, and the chromosomes are assembled into an equatorial plate. Figure 47 shows the daughter chromosomes on their way toward the poles. Indistinct interzonal filaments are present. The centrosomes are extremely minute, but definite granules. Numerous polar radiations extend to the periphery throughout the entire cell.

Figure 48 shows a cell seen from the surface of the epidermis, the axis of the nucleus being perpendicular to that of the cell. The nuclear figure is in the telophase with barrel-shaped interzonal region. The centrosomes could not be found. Figures 46-52 are, with the exception of Figure 48, all from a limited region of epidermis at the ventral edge

of the cut end of the worm. Figure 48 is from a mass of cells more dorsally placed, and so near the end of the alimentary tract that its epidermal origin is perhaps doubtful. No other cells in this phase could be found in the preparation.

Figures 49-51 show late telophases in the same group of cells from which Figures 46 and 47 are taken. All of these cells show a peculiar condition of the cell membrane. In Figure 49 the interzonal filaments are constricted at the equator, and there is a distinct "Zwischenkörper." An equatorial membrane has formed between the daughter cells. The triangular clearer region on the deep side of the two cells can best be interpreted as the space from which the mother-cell membrane has receded in its constricting. In the daughter cell at the right there is a narrow clearer space immediately about the interzonal filaments and the chromatic mass. On the deep side this space is so sharply outlined as to appear bounded by a membrane. In the cell at the left there is something which appears like a faint membrane (*mb.'*) lying just within the old cell membrane.

In Figure 50 there is a remarkable doubling of cell membranes, and in Figure 51 a well defined membrane (*mb.'*) in each daughter cell evidently corresponds to the membrane *mb.'* in Figure 50. Outside each of these membranes in Figure 51 is a region corresponding to the regions in Figure 50 enclosed by the membranes, *mb.* In Figure 51, however, these two regions are indefinitely outlined.

These conditions would force upon us the conclusion that a new cell membrane is formed within the old membrane of each daughter cell, and that the old membrane finally disappears. A search through the epidermis of this animal failed to reveal other stages which would throw any more light upon the question.

A centrosome may be seen in the concavity of the chromatic mass in the right daughter cell of Figure 50, and in the left daughter cell of Figure 51. In the latter figure a distinct nuclear membrane is formed about the chromatin. Figure 52 shows two sister cells from the same region. The section is somewhat oblique to the surface of the epidermis. The nuclei have increased in size, the concavity still persisting. In the cell at the right the concavity of the nucleus is filled by a dense, finely granular mass containing the centrosome with some faint radiations. The presence of the centrosome at so late a period in the history of the young cell is evidence that the central granule of the radiating system of the resting cells (Figs. 44 and 45) is a true centrosome, remaining from the last mitosis.

### VIII. Mitosis in the Subepidermal Cells of the Old Epidermis.

Figures 53-56 (Plate 8) represent subepidermal cells, or basal cells of the epidermis. These cells occur wedged in between the deep ends of the columnar epidermal cells. In one worm of seven days' regeneration, many dividing cells were found among the subepidermal cells in five or six segments back of the injured segment. However, no mitosis was found in the elongated columnar epidermal cells of the same animal.

Figure 53 represents a cell in which the division is complete. The new nuclear membranes have been formed. The nuclei are cup-shaped, and the greater mass of chromatin is collected on the concave side of the nucleus. At the concavity of the nucleus in the lower cell may be seen the conical spindle region with a minute centrosome at its apex. In the upper cell there is a slightly denser region immediately outside the concavity of the nucleus, and at the centre of this denser region is the centrosome. Several indistinct granules lie at the edge of the denser region. There are some weak radiations from both centrosomes. A dividing cell membrane is present. This membrane is represented as if the cell were seen as a transparent object. The lower of the lines,  $mb'$ , is the intersection of the membrane with the upper surface of the old cell membrane; the upper line,  $mb''$ , is its deeper intersection. On the dividing membrane and in the axis of the old spindle (whose former position is marked by a darker region extending between the two nuclei) is a small dark mass, perhaps a "Zwischenkörper."

Figure 54 shows two sister cells. In one the concavity of the deeply cup-shaped nucleus, as well as a considerable space immediately outside of it, is filled by a mass of dense cytoplasm. The centrosome, an intensely staining granule with weak radiations, lies just outside the concavity of the nucleus. The condition of the young nucleus is characteristic. The chromatin is massed in a nearly solid layer on the concave side of the nucleus, while more or less isolated masses of chromatin extend from this layer to the equatorial surface of the nucleus. The upper nucleus of Figure 54 is seen in the direction of its (spindle) axis. The mass of chromatin which lines the cavity is seen as a nearly complete circular band.

A young cell whose nucleus has increased in size and lost something of its concavity is shown in Figure 55. A finely granular region separated from the outer coarser cytoplasm by a narrow clear space,

and containing at its centre a prominent centrosome with some radiations, is seen at the polar concavity of the nucleus. The sister cell was immediately adjoining, but its axis was in an unfavorable position.

Figure 56 represents a cell in which the resting condition has been regained. There is still a slight flattening of the nucleus on one side, — the remains of the polar concavity. The centrosome, imbedded in a mass of cytoplasm denser and more finely granular than that of the rest of the cell, lies on the flattened side of the nucleus and directly opposite the flattened region. The sister cell was identified in the next section. It showed similar conditions as to the nucleus, slightly concave on one side, and the presence of a denser mass of cytoplasm at this region of the nucleus, but no definite centrosome could be seen.

A study of the earliest stages of regeneration may reveal that the new epidermis over the cicatrix owes its origin to the subepidermal cells rather than to the columnar cells of the old epidermis. The occurrence of mitosis in the subepidermal cells many segments back of the one injured recalls the fact of groups of actively dividing cells in ganglia remote from the cut end of the worm. The subepidermal cells may act as "Ersatzzellen," receiving an impulse toward mitosis even in segments remote from the injury.

### IX. Some Peculiar Mitoses.

I desire to call attention briefly to certain dividing cells in a worm of seven days' regeneration. Directly under the new epidermis was a small mass of cells with nuclei like those of the epidermis. Abundant mitoses were found among these cells. Figure 57 shows a group of the cells with a dividing cell in the metaphase. All stages of mitosis could be found, presenting a series of conditions exhibiting no unusual features. There were telophases with chromatin solidly massed at the poles and a barrel-shaped interzonal region, the whole figure being imbedded in a mass of dense cytoplasm. Later stages showed the formation of an equatorial membrane, the constricting of the interzonal filaments and some evidence of a *Zwischenkörper*. The old cell membrane and the equatorial membrane eventually disappear, but at all stages there is some dense cytoplasm collected about the daughter chromatic masses. The cytoplasm of the resting nuclei is indefinitely outlined; there are no cell membranes.

Among these cells a few cases were found which exhibit exceptional

conditions. These are shown in Figures 58-60. Figure 58 is the only cell of its kind which could be found. To describe it in terms of normal mitosis, there are two chromatic masses with some interzonal filaments extending in straight lines between them. Enclosing these straight fibres is a sharply defined membrane (*mb. nl.*) slightly constricted near the equatorial region. This membrane is less distinct in the neighborhood of the chromatic masses. It could not be determined whether the membrane enclosed the chromatin, or not. Outside the membrane several fibres could be seen curving from pole to pole. Figure 59 is, beyond all doubt, a later stage of the condition seen in Figure 58. The cell outlines are sharply defined, and the equatorial membrane has formed, dividing the cytoplasm. The membrane (*mb. nl.*) must be identical with the one similarly designated in Figure 58. It can now be seen to enclose the chromatin. It is deeply constricted at the equator, and some indistinct fibres extend, within this membrane, between the chromatic masses. Figure 60 is readily seen to be a stage following that of Figure 59. The division of the cytoplasm is complete, a clear space intervening between the two daughter cells. The membrane, *mb. nl.*, is very sharply constricted, and the two cells are still united by it. The chromatin is in the form of large granules. Between the two chromatic masses extend some fibres which become thicker and darker as they approach the chromatic masses.

A careful search through the series failed to reveal any other stages in this process of division, and nothing like it was seen in other worms. It can hardly be doubted that the membrane, *mb. nl.*, of Figure 60 is a nuclear membrane. The membrane, *mb. nl.*, of Figure 58 is therefore a nuclear membrane. Is it the old nuclear membrane, or a new one? The question cannot be answered with the evidence at hand. Early stages of mitosis are present in abundance, but none showed any sign of the persistence of the old nuclear membrane. However, divisions of this type are so rare that we may readily suppose its earlier stages to be absent in the preparation. If *mb. nl.* is the old nuclear membrane, we have here a case of indirect cell-division, during which the nuclear membrane persists and divides by constriction in amitotic fashion. In some Protozoa the nuclear membrane normally persists during mitosis. It has been maintained by some writers that, in ordinary mitosis, the nuclear outline persists and can be made visible by certain methods (Pfitzner, '83, '86; Waldeyer, '88).

The other alternative is that *mb. nl.* is a *new* nuclear membrane, formed about both chromatic masses during the early telophase and

secondarily dividing by constriction. Whatever the proper explanation, the condition is of sufficient interest to invite an effort toward obtaining additional stages in the process.

## X. Summary.

I. There is commonly present in the nerve cells of Lumbricidæ a centred system, consisting of centrosome and radiations.

1. The single centrosome (or rarely two, or even three, small granules lying close together) is found in the axis of the cell, on the side of the nucleus opposite the nerve process, and therefore on the side of the greatest cytoplasmic mass. It is generally not far from the nucleus and approximately at the centre of the cell as a whole.

2. Radiations consisting of fibrils bearing minute granules extend from the centrosome toward the periphery of the cell. Calling these "primary radiations," there may also be distinguished secondary radiations, which arise from certain of the larger granules in the course of the primary radiations. In rarer cases tertiary radiations may be found arising from granules in the secondary radiations. The centred system is therefore a complex one, consisting of a chief centre or centrosome, and numerous inferior centres situated throughout the cytoplasm, all with their corresponding sets of radiations, the whole system forming a radiating network whose complexity increases toward the periphery of the cell.

3. In most cases, no structure which could be called a centrosphere is present. The centrosome, as well as each of the inferior centres, is generally surrounded by a small clear space.

Sometimes the centrosome is surrounded by a narrow region of denser cytoplasm, and the primary radiations, where they intersect the periphery of this region, bear conspicuous granules. In other cases the centrosome lies in a central mass of slightly denser, more finely granular cytoplasm, of perhaps one-half the diameter of the cell, but not bounded by a layer of granules.

II. A centred system like that found in nerve cells of normal worms is found in regenerated nerve cells. Its chief centre, or centrosome, is the centrosome of the last mitosis in the history of the cell.

1. If the anterior five or ten segments of a worm be removed, the regeneration of a brain and a certain length of ventral cord (not yet segmented) takes place in the course of five weeks.

2. The epidermis is the chief source of cells which give rise to the new nervous parts.

3. In the old cord no evidence of mitosis is found among the large pear-shaped cells with processes.

4. In some cases, masses of actively dividing cells are found in ganglia many segments back of the region of injury. These masses probably owe their origin to certain small indifferent cells which have retained their embryonic character since the development of the cord.

These cell masses can take no part in the regeneration of ganglia anterior to the region of injury, except when such a mass arises at the place of injury.

The stimulus due to the injury is not restricted to the segment injured, but may cause mitosis among cells of embryonic character in ganglia remote from the region of injury.

5. The regeneration of ganglia is preceded by a forward growth of fibres from the cut end of the old cord. Cells of epidermal origin accumulate ventrally and laterally about this new fibre tract to form the fundament of the new ganglia.

The fibre bundle divides to encircle the alimentary canal. At a region dorsal to the canal, it becomes associated with a mass of cells lying dorsally and posteriorly to the fibre mass, and, together with these, constitutes the brain fundament.

6. The deeper cells of the nervous fundaments are the first to become differentiated into nerve cells. The more superficial cells long retain their embryonic character, continuing to divide actively after the deeper cells have become typical pear-shaped ganglion cells.

7. About the posterior dorsal surface of the normal brain there are some cells with scant cytoplasm, and lacking nerve processes. These are doubtless cells which, in the development of the brain, stopped dividing without becoming differentiated into nerve cells, retaining their embryonic character, perhaps for purposes of regeneration in case of injury.

8. In mitosis among cells of the nervous fundaments of about five weeks' regeneration, the following peculiarities are to be observed:—

*a.* Throughout the process of mitosis the body of the cell outside the limits of the spindle figure is practically homogeneous and clear.

*b.* A well defined cell membrane, formed during the prophase, becomes constricted in the telophase, and an equatorial membrane is formed between the daughter cells. During the later phases the old

cell membrane, as well as the newly formed equatorial membrane, degenerates and disappears, leaving the two daughter chromatic masses, connected by the equatorially constricted interzonal filaments, lying free in an indefinitely outlined clear space.

c. The daughter chromosomes, having completed their migration toward the poles, fuse to form solid chromatic masses, concave on their polar sides. *The chromatic mass represents the nucleus.*

d. In the concavity of each chromatic mass is a sharply outlined, lightly stained, conical region, — the region of the old spindle-end, — with the centrosome at its apex. *This conical polar region is the fundament of the cytoplasm of the young cell.*

e. The interzonal filaments disappear, leaving the two chromatic masses and their accompanying polar structures lying free in a common, irregularly defined, clear space formerly occupied by the mother cell. *All the living parts of each daughter cell are comprised within the chromatic mass and its polar region.*

f. The two young sister cells may become separated by the pushing in of adjacent tissue between them.

g. The transformation of the chromatic mass into a resting nucleus involves the swelling of the newly formed nuclear membrane, the increase in the volume of its contents probably being due to the absorption of fluid material. The solid mass of chromatin meanwhile gradually breaks up into small granules which, together with the achromatic substance, form the loose peripheral nuclear network of the resting nucleus. During this process a nucleolus appears.

h. Accompanying these changes in the nucleus, the polar cytoplasmic fundament increases in volume, remaining always sharply outlined in the surrounding clear space. For a considerable period the growing cytoplasm is massed upon the concave polar side of the nucleus. At length the nuclear concavity disappears and the increasing cytoplasm envelops the entire nucleus. By far the greater mass of cytoplasm, however, always remains on the polar side of the nucleus.

i. The size and form of the typical pear-shaped nerve cell are finally attained as a result of the continued swelling of the nucleus, the increase in volume of its large polar body of cytoplasm, and the development of a nerve process from the smaller mass of cytoplasm on the equatorial side of the nucleus.

j. Distinct centrosomes are to be seen at the poles of the mitotic figure at all stages.

After the disappearance of the interzonal filaments the centrosome is

found at the apex of the polar cytoplasmic fundament, attaining its greatest size at this period.

During the early growth of the cytoplasm the centrosome persists, generally being found not far from the centre of the cytoplasmic mass. At an early period evidences of concentric and radiating structure about the centrosome are seen.

With continued increase of the cytoplasm, the centrosome assumes its characteristic position in the axis of the cell near the nucleus, and becomes associated with a system of radiating fibres whose complexity increases until the conditions found in the mature cell (I. 2) are attained.

III. 1. Some resting cells of recently regenerated epidermis possess a centrosome and system of radiations similar to those of the nerve cells.

2. In the mitosis of cells in the regenerating epidermis the centrosome persists in the cytoplasm after the nucleus has regained the resting condition.

3. In the much elongated columnar cells of the epidermis of the normal worm, there is strong evidence for the presence of a centrosome. In these very attenuated cells, however, no radiating system could be detected.

4. The final stages of mitosis in some cells of the regenerating epidermis exhibit peculiar conditions of the cell membranes, pointing toward the conclusion that, after the division of the cytoplasm, a new cell membrane forms within the old cell membrane of each daughter cell, the original cell membrane disappearing.

IV. 1. The stimulus due to the injury may cause abundant mitosis among the subepidermal cells or basal cells of the epidermis, several segments back of the injured segment.

2. The centrosome of mitosis in these subepidermal cells persists in the cytoplasm after the cell has returned to the resting condition.

V. In certain cicatricial cells, evidently of epidermal origin, a few mitoses were found where, in the telophases, both daughter chromatic masses were enclosed within a common membrane of doubtful origin (a distinct outer cell membrane being also present). This membrane finally constricts and divides equatorially, becoming, apparently, the nuclear membrane of the two daughter nuclei.

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PLATE 1.

All the figures magnified 2000 diameters.

- Figs. 1-3. Cells from the subœsophageal ganglion of a normal worm. Iron-hæmatoxylin.
- Fig. 4. Cell from the brain of the same worm.
- Figs. 5, 6. Cells from a posterior ganglion of a normal worm. Acetic-sublimate, iron-hæmatoxylin.







PLATE 2.

All the figures magnified 2000 diameters.

- Figs. 7-9. Smaller cells from the posterior dorsal region of the brain of a normal worm. Iron-hæmatoxylin.
- Figs. 10-12. Cells from a regenerated brain after 34 days' regeneration. These three cells lay side by side in the same section. Iron-hæmatoxylin.
- Fig. 13. Cell from a brain of 34 days' regeneration. Iron-hæmatoxylin.

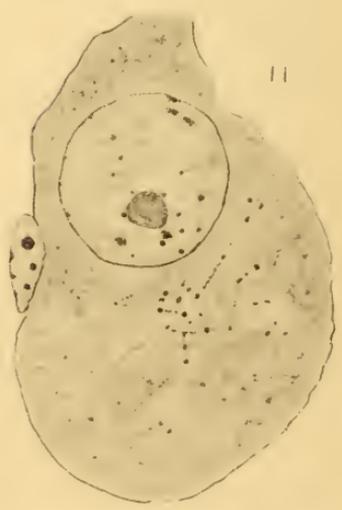
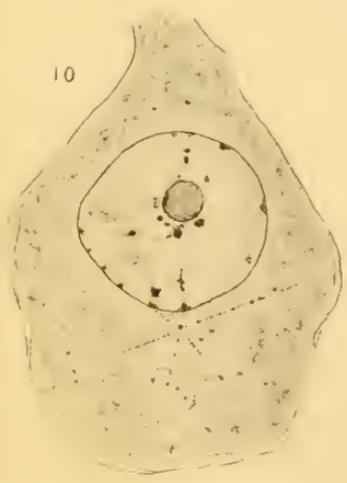
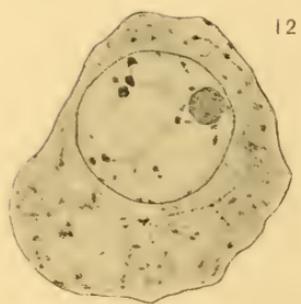






PLATE 3.

- Fig. 14. Parasagittal section through the anterior end of a worm after 7 days' regeneration.  $\times 25$ . Hermann's plat.-acet.-osm., iron-hæmatoxylin.
- Fig. 15. Parasagittal section through the anterior end of a worm after 16 days' regeneration.  $\times 25$ . Acetic-sublimate, iron-hæmatoxylin.
- Fig. 16. Parasagittal section through the anterior end of a worm after 24 days' regeneration.  $\times 25$ . Acetic-sublimate, iron-hæmatoxylin.
- Fig. 17. Spindle cells from the cicatrix of the worm from which Figure 14 is taken. (7 days' regeneration.)  $\times 2000$ .

14

te.  
can ali.



ec'drm.  
mu. cre.  
mu. lg.

cic.  
a  
ec'drm.  
tu.

cl. prf.

mu. cre.

mu. lg.

tu.

gn.

mu. cre.

mu. lg.

mu. cre.

15



mu. lg.  
mu. cre.  
ec'drm.  
gn. su'oes

mu. lg.  
mu. cre.

mu. cre.

tu.

mu. lg.

16



stmd.  
can. ali.  
trt. fbr.  
gn. nov.

mu. lg. tu.

mu. cre.

mu. lg.

17







PLATE 4.

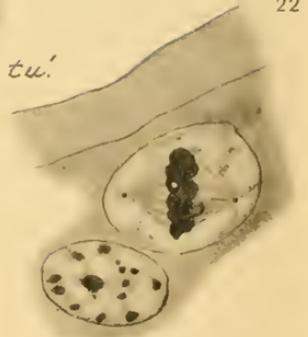
- Fig. 18. Anterior end of the nerve cord of Figure 14, showing a mass of newly formed cells. (7 days' regeneration.)  $\times 160$ .
- Fig. 19. Parasagittal section through the middle region of one lobe of the brain of a normal worm.  $\times 160$ .
- Fig. 20. Parasagittal section through the middle region of one lobe of a brain of 34 days' regeneration.  $\times 160$ .
- Fig. 21. A dividing cell in the prophase and one in the metaphase (one pole cut away) from a brain of 34 days' regeneration.  $\times 2000$ . Iron-hæmatoxylin.
- Fig. 22. Metaphase from a brain of 34 days' regeneration.  $\times 2000$ . Iron-hæmatoxylin.
- Fig. 23. Metaphase from the anterior end of a cord after 34 days' regeneration.  $\times 2000$ . Gentian violet.
- Fig. 24. Metaphase from a brain of 34 days' regeneration.  $\times 2000$ . Gentian violet.
- Fig. 25. Telophase from a brain of 34 days' regeneration.  $\times 2000$ . Gentian violet.
- Fig. 26. Telophase from the posterior dorsal region of a brain of 34 days' regeneration.  $\times 2000$ . Iron-hæmatoxylin.



*cic.*

22

*tu.*

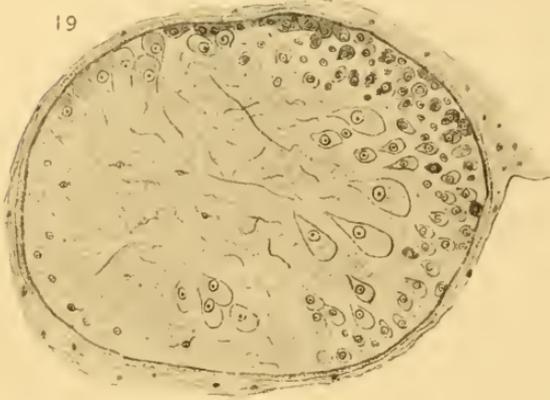


*cl. mit.*

*d.*

19

*a.*



23



20

*d.*

*a.*



24



25



*m.b.*

21

*m.b.*

26

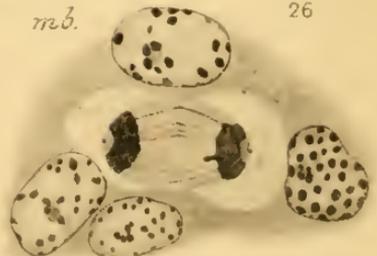






PLATE 5.

All the figures magnified 2000 diameters.

- Fig. 27. Telophase from a brain of 34 days' regeneration. Gentian violet.
- Fig. 28. Telophase from a brain of 34 days' regeneration. One chromatic mass cut away. Gentian violet.
- Fig. 29. Telophase from a brain of 34 days' regeneration. Reconstructed from two sections. Above it, a young cell. Iron-hæmatoxylin.
- Fig. 30. Telophase from the anterior end of a cord after 34 days' regeneration. Gentian violet.
- Fig. 31. Young cell (with several of the neighboring nuclei) from the posterior ventral region of a brain of 34 days' regeneration. Iron-hæmatoxylin.
- Figs. 32*a*, 32*b*. A pair of young sister cells from a brain of 34 days' regeneration. The cells are in successive sections. Iron-hæmatoxylin.
- Fig. 33. Two pairs of young sister cells from a brain of 34 days' regeneration.  $\alpha$  and  $\beta$  are one pair. The two cells of the other pair lie one over the other.  $\gamma$  is the upper of the two and the outline of the lower is indicated by  $\delta$ . Gentian violet.
- Figs. 34, 35. Young cells from the anterior end of a cord of 34 days' regeneration. Iron-hæmatoxylin.
- Fig. 36. A group of cells from the posterior ventral region of a brain of 34 days' regeneration. At the centre of the group is a young cell. Iron-hæmatoxylin.
- Fig. 37. Young cell from the dorsal region of a brain of 34 days' regeneration. Gentian violet.

27

*m.b.*



29



28



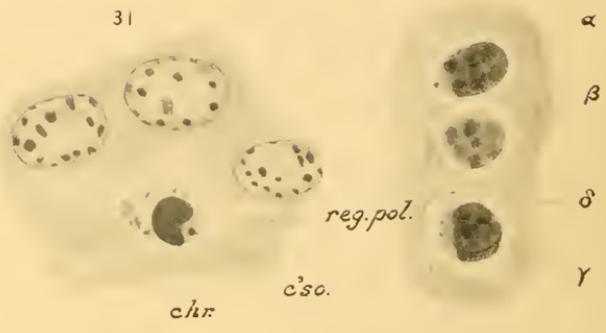
*chr.* 30

*reg.pol.*

*m.b.*

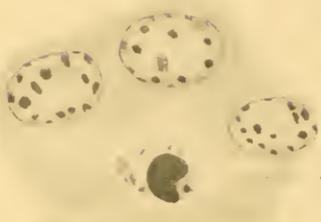


33



$\alpha$   
 $\beta$   
 $\delta$   
 $\gamma$

31



*reg.pol.*

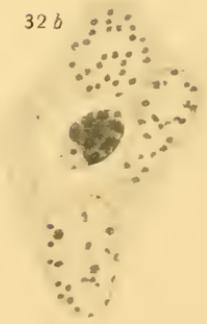
*c'so.*

*chr.*

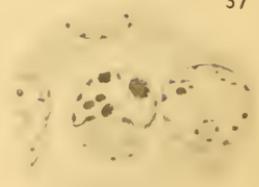
32 a



32 b



37



34



35



36

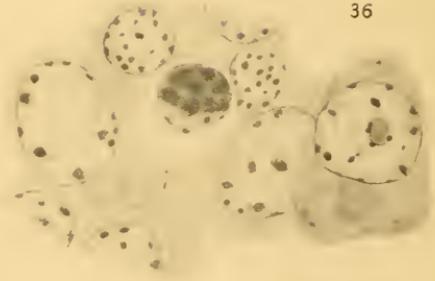




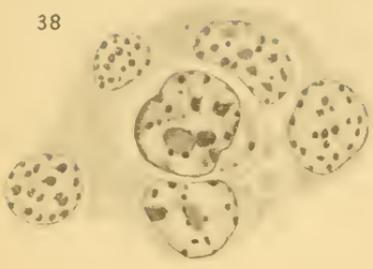


PLATE 6.

All the figures magnified 2000 diameters.

- Fig. 38. Young cell (with several of the neighboring nuclei) from the anterior end of a cord of 34 days' regeneration. Iron-hæmatoxylin.
- Fig. 39. Small cells with resting nuclei from the anterior end of a cord of 34 days' regeneration. Each of the two cells has a centrosome. Iron-hæmatoxylin.
- Fig. 40. Cell with a greater mass of cytoplasm than in the cells of Figure 39; centrosome and radiations. From a brain of 34 days' regeneration. Iron-hæmatoxylin.
- Fig. 41. Cell, similar to that of Figure 40, from a brain of 37 days' regeneration; centrosome and radiations. Iron-hæmatoxylin.
- Fig. 42. Three cells from the anterior end of a cord of 34 days' regeneration. A centrosome with radiations may be seen near each of the two larger nuclei, on the side toward the greatest cytoplasmic mass. Iron-hæmatoxylin.
- Fig. 43. Two cells from the epidermis of a normal worm. The centrosome is at the deeper end of each nucleus. Iron-hæmatoxylin.
- Figs. 44, 45. Cells from regenerated epidermis, showing centrosomes and radiations. 16 days' regeneration. Acetic-sublimate, Kernschwartz and safranin.

38



39



40



42



45

*cta.*



43

*cta.*



41



*eso.*

44

*cta.*







PLATE 7.

All the figures magnified 2000 diameters.

Figs. 46-52. Dividing or recently divided cells from the regenerated epidermis of a worm, after 11 days' regeneration. Hermann's plat.-acet.-osm., iron-hæmatoxylin. See pages 146-147 for a discussion of the membranes.

46

*cta.*



47

*cta.*



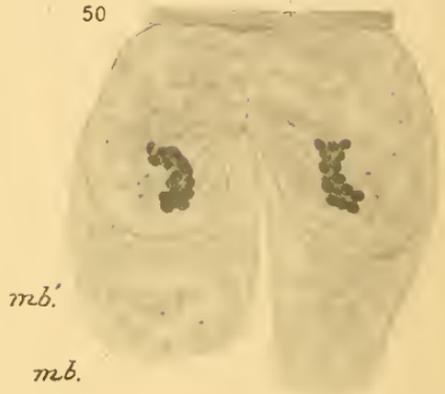
49

*cta.*



50

*cta.*



51

*cta.*



48



*cta.*

52







PLATE 8.

All the figures magnified 2000 diameters.

- Figs. 53-56. Recently divided subepidermal or basal cells of the old epidermis, from one to four segments back of the segment cut. The centrosome of mitosis persists in the resting cells. 7 days after the operation. Hermann's plat.-acet.-osm., iron-hæmatoxylin.
- Fig. 57. Group of cells, with nuclei of the epidermal type, from a thin layer of cells lying directly beneath the regenerated epidermis of a worm of 11 days' regeneration. Hermann's plat.-acet.-osm., iron-hæmatoxylin.
- Figs. 58-60. Dividing cells from the layer of cells mentioned in the explanation of Figure 57, showing peculiar conditions as to the presence of a nuclear membrane. See page 149.

53

*mb.*

*mb.*



54



55



56



58



*mb.*

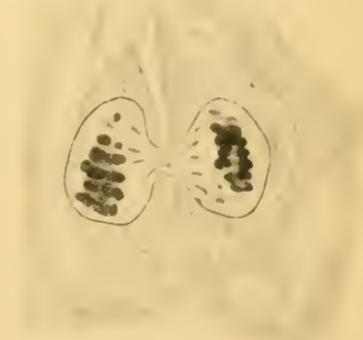
*mb.nl.*

57



60

*mb.nl.*



59

*mb.*

*mb.nl.*





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