TAXONOMIC STUDIES ON THE HYDRAS OF NORTH AMERICA

I. General Remarks and Description of Hydra americana, New Species.

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Up to 1917 the identification of the species of Hydra was a matter of great difficulty and uncertainty owing to the lack of exact descriptions of these animals. In the year in question, Paul Schulze published his invaluable monograph of the hydras of Europe. This monograph did not come to my attention until two or three years ago. I had in the meantime been studying and cultivating the hydras of the Chicago region chiefly for experimental and class purposes. Comparison of the local hydras with the descriptions in Schulze's monograph revealed the presence in the Chicago region of two species which do not correspond with any of the forms described by Schulze. One of these species has long been erroneously designated as *Hydra vulgaris*, while the other is apparently new to the literature.

No adequate descriptions of North American hydras have ever been published owing probably to the circumstance that these animals have served chiefly for experimental purposes. Experimental zoologists working with hydras have been content to attach to them the names of European species which the American forms most nearly resembled, using color as the chief criterion. This habit of applying indiscriminately European names to American animals superficially resembling them has resulted in vast confusion and much error. The present paper attempts to rectify one of the errors in the naming of species of Hydra.

Downing ('04, and '09) has given some valuable if incomplete information concerning the American hydras, particularly those of the Chicago region. Unfortunately he fell into considerable error through the misidentification of *Hydra fusca (Pelmatohydra oligactis)* which he considered a new species, naming it *Hydra dioecia.* Smith in Ward and Whipple's *Fresh Water Biology* attempted the first synopsis of the American species, using Downing's data and the publications of Brauer ('08, '09), a German authority on the subject. Schulze's monograph was unfortunately not available at the time of publication of *Fresh Water Biology.* Owing to the unsatisfactory state of the taxonomy of the hydras previous to the appearance of Schulze's work, Professor Smith could scarcely be expected to furnish us with a correct evaluation of the American species and indeed he states that his key must be regarded as tentative.

The taxonomic history of the European hydras has been so adequately discussed by Schulze ('17) that only a few of the more important points need be mentioned here. Linnaeus in 1758 had placed all hydras under one

specific name, *Hydra polypus*. Pallas (1766) first gave definite specific names to the species of Hydra whose characters had already been clearly defined by Trembley (1744), namely *viridissima*, *vulgaris*, and *oligactis;* and added a fourth species, *attenuata*, from Rosel's description (1755). In the following year, 1767, Linnaeus recognized Pallas' descriptions but quite unjustifiably changed the names to *viridis*, *grisea*, *fusca*, and *pallens*, respectively. It is quite clear, as first pointed out by Brauer, that Linnaeus' names are wholly invalid, Pallas' names having indisputable priority. *Hydra attenuata* Pallas was generally believed to be synonymous with *H. vulgaris* and the name disappeared from the literature until Toppe (1910) believed that he had rediscovered the species. But Schulze has pointed out that Toppe's form is a new species, not identical with *H. attenuata* Pallas. Schulze also emphasized that *H. attenuata* is a valid species distinct from *vulgaris* and that in fact most of the experimental work purporting to deal with *vulgaris* really concerns *attenuata* which is the more common of the two species. Species additional to the four recognized by Pallas are also described by Schulze in his monograph.

Schulze has further split up the hydras into three genera: Chlorohydra, distinguished by the presence of symbiotic green algae in the entoderm cells; Pelmatohydra, characterized by the differentiation of the column into a slender basal stalk region and a stout body region; and Hydra, including all species with neither symbiotic algae nor a stalk. These generic distinctions seem a little questionable to me. The presence of symbiotic algae has not generally been regarded in other groups as constituting a generic character. The differentiation of a stalk is perfectly evident and unmistakable in some species of hydra, as *oligactis*, but study of several species has convinced me that in all of them the proximal part of the column is more or less different from the distal part and that various gradations towards the stalked condition exist. It thus becomes difficult to decide in some cases whether the animal should be placed in the genus Hydra or Pelmatohydra. Decision as to whether the proximal part of the column shall be regarded as a stalk or not in any given case becomes an arbitrary matter. On the other hand I am in entire agreement with Schulze as to what characteristics of hydra are sufficiently distinctive to serve for taxonomic purposes. It cannot be too greatly emphasized that the usual sort of description which limits itself to color, form, and size is practically worthless, since these characters are subject to wide variation.

Characters of Taxonomic Value

The characteristics which can properly be utilized for the identification and description of species of hydra are the following: the shape, size and internal structure of the nematocysts, the shape of the testes, the form of the embryonic theca (spiny shell formed around the egg after it is fer-

tilized), the separation or non-separation of the sexes and the manner of origin of the tentacles on buds. The general shape and form of the column both contracted and expanded, the relative length of tentacles and column, and the characteristic attitudes assumed are of value when determined on healthy laboratory-cultured animals; but usually cannot be correctly ascertained on freshly collected specimens as these are commonly in a state of depression. Color should not be depended upon. These characters will now be discussed in more detail.

1. The Nematocysts. It has commonly been believed by zoologists that all or most hydras have three kinds of nematocysts. It was first pointed out by Toppe (1910) that all species of hydra possess four kinds of nematocysts and this fact anyone can verify. Schulze has named the four kinds as follows: penetrants, stereoline glutinants, streptoline glutinants, and volvents. The penetrants are the large barbed nematocysts whose complicated structure has been described by Schulze ('17, '22) and other German workers to whom reference will be found in Schulze's papers. The "neck piece" of the penetrants bears three large spines and three spiral rows of small thorns. The penetrants are similar in shape and structure in most species but differ in size, the range of size being constant for each species and constituting a specific character. In the unexploded state, the appearance of the spines (called by Schulze the stilette) and the windings of the thread differ with species and probably furnish specific characters.

The glutinants are the cylindrical nematocysts, usually considerably smaller than the penetrants. There are two kinds of glutinants in all species, one being generally larger than the other. The larger or streptoline glutinants are usually cylindrical or narrowly oval, but in some species pyriform, pointed at the end to which the thread is attached. The discharged thread is provided with a spiral row of minute thorns and tends to coil, hence the name streptoline. In the undischarged state the manner in which the thread is coiled in the interior of the capsule is very characteristic for each species and furnishes the best diagnostic character in the absence of sex organs. The smaller or streptoline glutinants are oval and discharge a straight, unarmed thread, the name streptoline being derived from the straightness of the thread.

The volvents are the small, broadly pyriform, almost spherical nematocysts, containing a thick unarmed thread which makes a single loop in the interior of the nematocyst. Upon explosion, this thread twists into a tight little coil of several turns. The volvents are similar in structure but may differ in size in the different species.

It is stated by several German authors (see Schulze, '17 for a complete account) that the penetrants serve to pierce smooth surfaces of prey, the volvents coil around the bristles and hairs of prey, while the glutinants are not employed in the capture of food but for adhesion in locomotion

by the sommersault method. By proper staining, an adhesive substance discharged from all types of nematocysts may be seen wound around the nematocyst threads in spiral strands.

For the identification of species of Hydra, particularly in the absence of sexual material, it is emphatically necessary that the nematocysts be examined, in the living state or in a macerating fluid which does not distort them, with an oil immersion lens and the absolute and relative sizee of the four kinds, their shape and internal structure, and particularly the manner of coiling of the thread in undischarged sfreptoline glutinants bs determined accurately.

2. Sex organs. The shape of the testes and the spination of the egg shell are differentin different species and furnish good diagnostic characters. Unfortunately it is not always possible to obtain sexual material. I have found, however, that many species tend to become sexual if cultivated for some time in the laboratory, although without any apparent cause. It is my impression that specimens collected near the time when they would become sexual in nature tend to develop sex organs in the laboratory at about the expected time. Some species can be caused to become sexual by lowering the temperature, others by raising it.

The testes may be rounded, or conical, or almost cylindrical. They may or may not be provided with nipples. Zoologists seem to be generally under the impression that the testes of hydra are always provided with nipples for the escape of the sperm but in some species, as *Pelmatohydra oligactis,* nipples are entirely absent and in others they are not well developed. In hermaphroditic species the testes tend to be distal in location but in dioecious species they cover thickly the entire column from hypostome to the budding zone. They do not occur on the stalk of stalked forms nor in the immediate vicinity of the foot. The shape of the testes and the presence or absence of a nipple constitute specific characters.

The ovaries offer no distinctive specific differences. They tend to be proximal in location but may spread towards the hypostome, particularly in dioecious species, where their distribution on the column is similar to that of the testes. When the egg is mature, it bursts through the ectoderm, which then withdraws around the base of the egg, forming a calyx to which the egg adheres for a few days. The egg must be fertilized shortly after extrusion; otherwise it dies and disintegrates. As soon as the egg is fertilized, there appears on its surface a membrane, apparently chitinous, which thickens and develops spines upon its outer surface. This egg shell or embryonic theca furnishes a valuable diagnostic aid, since the form and length of the spines is constant for each species. The theca is generally spherical but in some species is flattened on the attached surface.

Zoologists appear to be under the impression that all hydras are hermaphroditic. However, certain species as *Pelmatohydra oligactis* are undoubt-

edly strictly dioecious. Others seem to simulate dioeciousness or perhaps are evolving in that direction, for they are commonly either male or female and only prolonged observation or cultivation reveals the occasional occurrence of hermaphroditic individuals. Protandry does not account for these conditions since I have observed over long periods in one species male and female specimens which certainly never developed gonads of the opposite sex; but within the same species hermaphroditic individuals bearing ripe ovaries and testes simultaneously occasionally appeared. Protandry, however, certainly does occur in some species, as the green hydra. Some protandrous species seem to be in process of becoming dioecious. In one species which came under my observation, fully developed males with mature testes never gave rise to ovaries; but specimens destined to develop into females first produced small abortive testes, probably sterile. It is thus evident that only prolonged observation and cultivation of a species will enable one to determine its sexual behavior.

3. Tentacle formation on buds. According to Schulze, Haacke ('80) was the first observer to notice that in *P. oligactis,* the order of tentacle formation on buds is very characteristic for the species. The tentacles in this species never arise simultaneously. Two, opposite each other, invariably appear first; the third tentacle develops opposite these two, which in the meantime have shifted nearer together; and the subsequent ones come between those already present in an alternating manner. Details will be found in Schulze's work. In consequence of their manner of appearance, the tentacles on buds of *P. oligactis* are always of very unequal lengths and the species can be recognized in doubtful cases by this characteristic alone. In other species, the tentacles of the bud sprout simultaneously or nearly so and are of equal length on advanced buds. Other species present still other modes of tentacle development, which thus constitutes a character of diagnostic value.

4. Shape. Undoubtedly each species presents a characteristic shape but this is evidenced only by healthy, well-fed specimens. Freshly collected material is not dependable in this regard as it frequently undergoes depression, a state in which column and tentacles are more or less contracted and reduced. It is desirable that the general form, attitude, relative lengths of column and tentacles, etc., be studied in specimens cultivated in the laboratory. In some species the tentacles are shorter than the column and are held in an erect attitude. Others possess long tentacles, often two or three times longer than the column, and such commonly droop or may be extended horizontally. The column may be slender and of equal diameter throughout or stout with a narrower basal region or markedly divided into a stout distal body and slender proximal stalk. All such features are of diagnostic value when carefully observed on a number of healthy specimens.

5. Color. Color is the most unreliable of the characteristics commonly utilized in descriptions of hydras since it is largely dependent upon the nature of ingested food. It is true that some species are rather constant as to color, for instance, *P. oligactis,* which is commonly reddish-brown. But even in this species, color cannot be relied upon since young, starved or sickly specimens are frequently of a pale tint. In other cases, the color in nature has been found to alter upon laboratory cultivation. Abundant food commonly deepens the color of pale species to tan or orange or brown hues. In one species common around Chicago on the under surface of stones in certain localities, all of the specimens on some stones are orange-pink in color while those on adjacent stones may be decidedly greenish. Greenish specimens of *P. oligactis* have been reported by German zoologists (Goetsch, '21) as resulting from the ingestion of algae. These examples will suffice to illustrate the unreliability of color as a specific character.

General Remarks on the American Species

In comparing the American with the European hydras with the aid of Schulze's descriptions of the latter, it becomes evident that there is only one species which is certainly common to the two continents. This is the brown hydra which according to Schulze's terminology is designated as *Pelmatohydra oligactis* (=*Hydra oligactis* Pallas, *Hydra fusca* Linnaeus, *Hydra dioecia* Downing). I have seen and reared hundreds, even thousands, of specimens of this species, and observed repeatedly sexual individuals; and I can state unreservedly that the American form is identical in all respects with the *Pelmatohydra oligactis* of Europe. The species appears to be widely distributed throughout the eastern United States and typical specimens have been purchased from a commercial firm in Lincoln, Nebraska. Whether it occurs west of the Great Plains region cannot be stated owing to a lack of trustworthy records. The characteristics of this species have been fully treated by Schulze but as his account may not be available to many American zoologists, I shall later describe the form with illustrations.

In the case of the green hydra, no definite conclusions can be reached at present. Schulze has not as yet published any description of the green species of Europe, although he some time ago stated his intention to do so. By green hydras, of course, one means only those bearing symbiotic algae in their entoderm cells. If there be but one such species in Europe, its name in Schulze's terminology is *Chlorohydra viridissima* (=*Hydra viridissima* Pallas, *Hydra viridis* Linnaeus). But as Schulze remarked in his 1917 publication, it is not certain that all of the green hydras of Europe belong to one and the same species., The same uncertainty exists concerning the American forms. Green hydras are undoubtedly common throughout the

entire United States but without careful study of specimens from widely separated localities it cannot be stated that they belong to one species nor if so that this species is identical with a European species, the latter having not yet been adequately characterized.

As to the American species of the genus Hydra, using this generic name in the restricted sense proposed by Schulze, a chaotic situation exists. It has long been customary with American zoologists to lump all hydras that were neither brown nor green into one category, labelled *Hydra vulgaris* (=*Hydra grisea* Linnaeus). Study of American hydras has lead me to doubt very strongly whether *Hydra vulgaris* occurs in this country at all. The species which has commonly been designated by that name does not at all correspond to Schulze's description of *Hydra vulgaris* and is obviously an unnamed species. In addition to this form there are probably in the United States several other species assignable to the genus Hydra and not identical with any European forms. Some of them, however, are close to *Hydra attenuata* Pallas and may constitute additional varieties of this widespread and variable species.

From Downing's 1904 paper, it appears that another species of *Pelmatohydra* besides ***oligactis*** must occur in the Chicago region. Downing described, erroneously as *Hydra fusca,* a brown hydra which presumably must closely resemble *P. oligactis* (=*fusca*), judging from Downing's error in the identification, but differs from this species in that it is hermaphroditic and the egg shell is flattened, not spherical. Whether this species of Downing is identical with *Pelmotohydra braueri* of Europe, also hermaphroditic and with flattened eggs, is considered doubtful by Schulze. Unfortunately I have not as yet been able to rediscover this species despite repeated collections from the same habitat mentioned by Downing, namely, the Jackson Park lagoon, Chicago. Downing also records this form as occurring in New York.

The descriptions of *Hydra corala* Elrod and Ricker 1902 and of *H. pallida* Beardsley 1902 are so meager that the validity of these supposed species cannot be decided without further evidence. It is practically certain that both are *P. oligactis.*

The remainder of the paper will be devoted to a description of the common white hydra of the United States, commonly but erroneously known as *Hydra vulgaris,* from which species it is, however, unquestionably distinct. For some time I thought this form coincided with *Hydra stellata* Schulze of Europe but further study has convinced me that it is an undescribed species. I propose for it the name *Hydra americana.*

Hydra americana, n. sp.

1919 *Hydra* ***vulgaris,*** Child and Hyman, Biol. Bull. 36
1928 ***Hydra stellata,*** Hyman, Biol. Bull. **54**

It is highly probable that this is the species which appears repeatedly in the American literature on regeneration and grafting in hydra as *Hydra vulgaris*, or *Hydra grisea*. It has been known by these names at Chicago for many years. After consulting Schulze's monograph, I perceived that the identification was erroneous and I decided that our form corresponded with *Hydra stellata* Schulze. I came to this conclusion from the pyriform shape of the streptoline glutinants of both species. Consequently in a paper of mine dealing with reproduction and budding in hydra (Hyman,'28) I designated the form as *Hydra stellata*. Further study of the species has convinced me that this identification was also erroneous and that the species does not correspond to any of those given by Schulze. I therefore consider it as new.

1. Shape and size. The form is slender, the column being of about the same diameter from hypostome to budding zone except for a slight narrowing just below the hypostome. Below the budding zone the column is a little more slender (fig. 1). There is no differentiation of the column into distal body and proximal stalk. Hence the species clearly belongs to the genus Hydra, as defined in the strict sense by Schulze. The animal is of moderate size, measuring at most 10 to 12mm. from foot to tip of the extended tentacles. The tentacles are always shorter than the column, varying in length from 1/4 to 3/5 of the length of the column, depending upon the size of the animal. They seem to be proportionately longer in large, well-fed specimens than in the smaller individuals. The tentacles are always held erect, either spreading widely as in fig. 1 and fig. 7 or converging in an arched manner, as in fig. 8 The former attitude is characteristic of those fastened to the bottom or dependent from the surface film; the latter of those attached to the sides of the vessel. The number of tentacles is six or seven, generally six, occasionally 5 or 8. Of 29 specimens in which tentacle number was counted, 20 possessed 6 tentacles, 7, 7 tentacles, and one each 5 and 8 tentacles.

The form in the fully contracted state is illustrated in fig. 2. A flower-like pattern is assumed, quite unlike the star-shaped form stated to be characteristic of *Hydra stellata* when contracted. This difference in the contracted shape is one reason for deciding that one species under consideration is distinct from *stellata*.

The tentacle outgrowths on young buds arise nearly but not quite simultaneously as shown in fig. 3. This slight difference at the start does not persist and in the later buds, the tentacles are of practically equal length.

2. Color. The color is commonly white. In very well-fed specimens, a tan hue develops in the entoderm.

3. Nematocysts. The species possesses the usual four kinds of nematocysts which are illustrated in figure 4, drawn to scale. The penetrants or large barbed nematocysts are remarkably variable in size in this species and some

of them attain an unusually large size. Measurements of many penetrants from a number of different individcals have given a size range of 13 to 21 micra, taken along the longest axis, from the flattened pole where the thread is attached to the opposite rounded pole. Fig. 4a and b give in outline the size range drawn to scale, a the minimum and b themaximumsize.

The large or streptoline glutinants, illustrated in figures 4c, and 9a, b, and c, constitute the most characteristic feature of the species and the one of the greatest taxonomic value. They are decidedly pyriform, while those of most hydras are cylindrical. The pointed end is slightly beak-like and the thread which extends inwards from this makes three or four coils, usually three, in a transverse or oblique direction. Below these coils the thread is wound in a tangled mass. The length of the streptoline glutinants, measured along the long axis, was found to vary from 7.5 to 10 micra, averaging 9 micra. Since no other American species of hydra possesses pear-shaped streptoline glutinants, this character may be considered diagnostic of the species.

The small or stereoline glutinants are cylindrical and decidedly smaller than the streptoline type. They range in length from 6.5 to **7.3** micra. The thread is wound inside in a figure 8 fashion. This type of nematocyst is illustrated in fig. 4d, and 9d.

The volvents or small spherical nematocysts present no particular feature (fig. 4e). They range from 8.3 to 9.5 micra in length, being slightly longer and much wider than the small glutinants.

4. Sex organs. Sexual maturity occurs in nature in the fall of the year, during the months of September and October, possibly later. Sexual specimens have, however, appeared in laboratory cultures at all seasons of the yea:, without apparent cause. The sexes are commonly separate but hermaphroditic specimens have occurred occasionally in laboratory cultures. In such specimens, testes and ovaries were ripe simultaneously. In male specimens the testes occur in moderate numbers distributed from the hypostome to the budding zone. A male specimen, drawn from a fixed and hence slightly contracted preparation is illustrated in fig. 5, and another male, drawn from life and fully extended, in fig. 10. The testes are seen to be conical in form in extended specimens, somewhat rounded in contracted specimens, and to be provided with definite, well-developed nipples. **A** profile view of a testis from a relaxed specimen is given in fig. 10 a, of a contracted testis in fig. 10b.

A female *Hydra, americana,* from a fixed preparation, is illustrated in fig. 11. The ovaries are proximal in location, near the budding zone. On the right side of the specimen is borne a fully developed ovary containing an amoeboid egg, whose pseudopodial processes are well preserved. On the left is an extruded fertilized egg inclosed in the spiny embryonic theca, and resting in the calyx formed by the withdrawal of the ectoderm at

the time of extrusion. An enlarged view of a portion of the theca is given in figure 12. It is seen that the theca is composed of rather long spines. The theca of *H. americana* resembles that of *H. vulgaris* but the spines on the latter are a little longer and more apt to branch. The resemblance between the eggs shells of these two species has contributed to the confusion in their identification.

An hermaphroditic specimen, drawn from a fixed preparation, is shown in fig. 6. Proximally three ovaries are present, the lowermost one about to discharge the ovum, and distally four testes. This individual was one of four hermaphrodites which appeared simultaneously in a laboratory culture, in which up to that time only males had occurred. In all four specimens, testes and ovaries were ripe synchronously and fertilized eggs were observed several times. Other hermaphroditic individuals have occasionally been seen in laboratory cultures since these first four. No cause for the appearance of hermaphroditism can be assigned.

5. Habitat and Distribution. The species lives in the sort of habitat frequented by hydras, —namely, attached to the vegetation in ponds and lagoons and old streams. It has been found, in company with the green hydra and *Pelmatohydra oligactis*, in a number of such bodies of water within a radius of fifty miles from Chicago. If we assume that it is the form previously identified as *Hydra vulgaris*, it must be widely distributed throughout the eastern United States. In the absence of exact information, however, Chicago and vicinity must be designated as the sole locality in which the species has been taken with certainty at the time of writing.

Type specimens will be deposited in the U.S. National Museum.

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PLATE XXIX

Fig. 1. *Hydra americana,* fully extended, from life

Fig. 2. *Hydra americana,* contracted, from life.

Fig. 3. Young bud of *Hydra americana,* showing inequality in time of origin of the tentacles; from life.

Fig. **4.** Nematocysts of H. *americana,* fromlife, drawn to scale. *a,* penetrant, minimum size; *b,* outline of maximum sized penetrant; *c,* streptoline glutinant; *d,* stereoline glutinant; *e,* volvent.

Fig. **5.** Male specimen of *H. americana,* from a whole mount.

Fig. *6.* Hermaphroditic specimen of *H. americana,* from a whole mount.

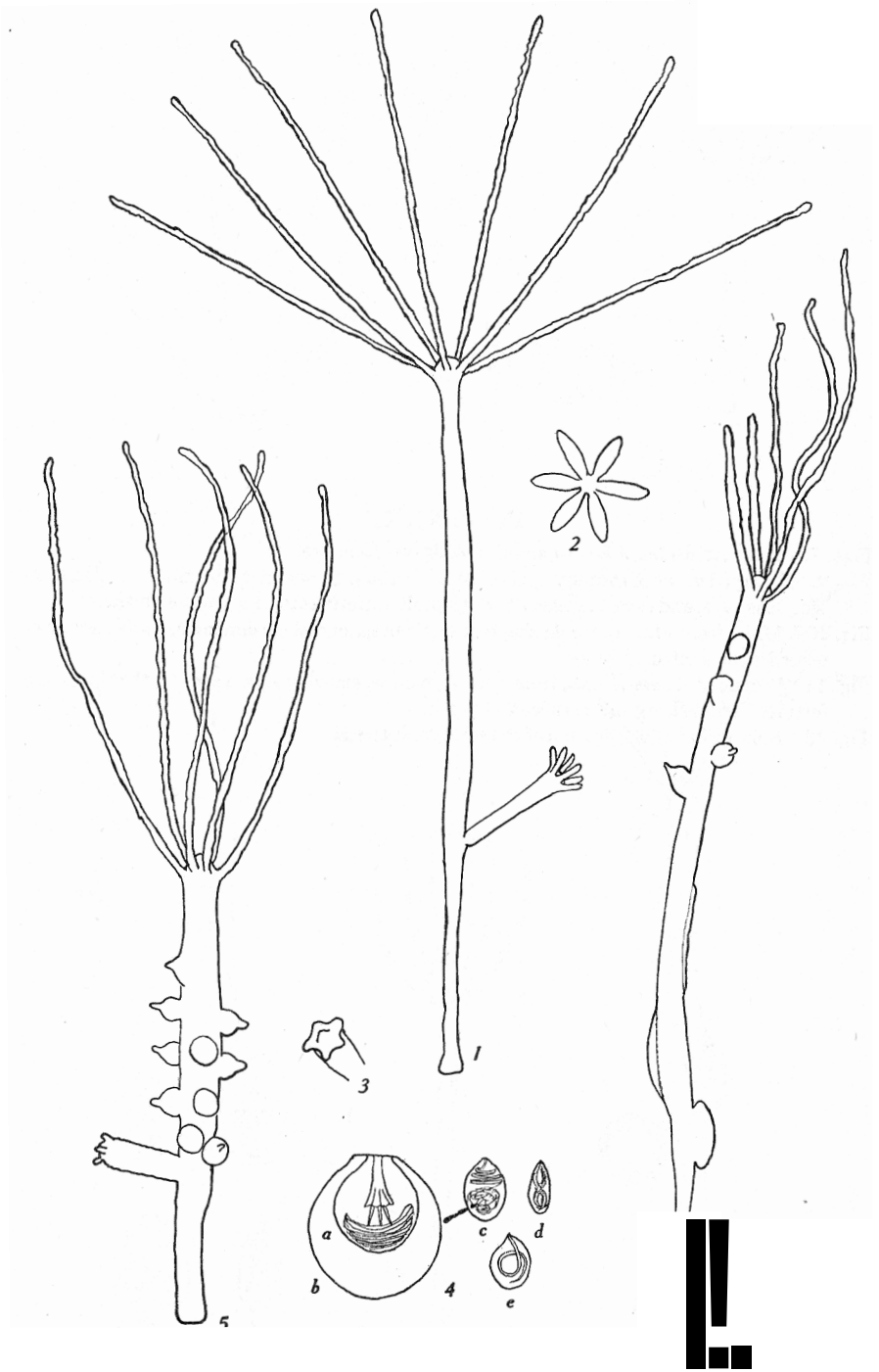

PLATE XXIX

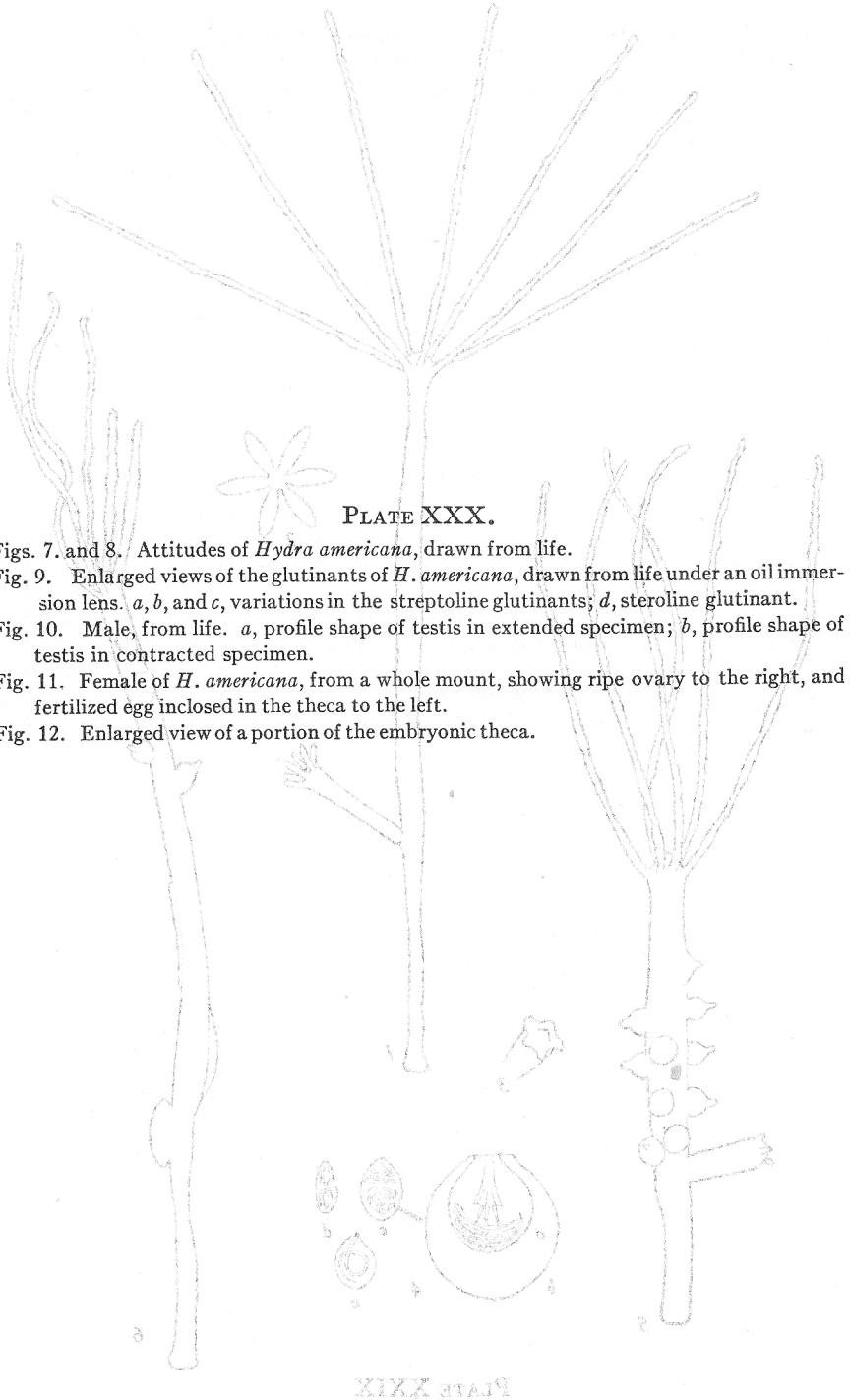

PLATE XXX.

Figs. 7. and 8. Attitudes of *Hydra americana*, drawn from life.

Fig. 9. Enlarged views of the glutinants of *H. americana*, drawn from life under an oil immersion lens. *a*, *b*, and *c*, variations in the streptoline glutinants; *d*, steroline glutinant.

Fig. 10. Male, from life. *a*, profile shape of testis in extended specimen; *b*, profile shape of testis in contracted specimen.

Fig. 11. Female of *H. americana*, from a whole mount, showing ripe ovary to the right, and fertilized egg inclosed in the theca to the left.

Fig. 12. Enlarged view of a portion of the embryonic theca.

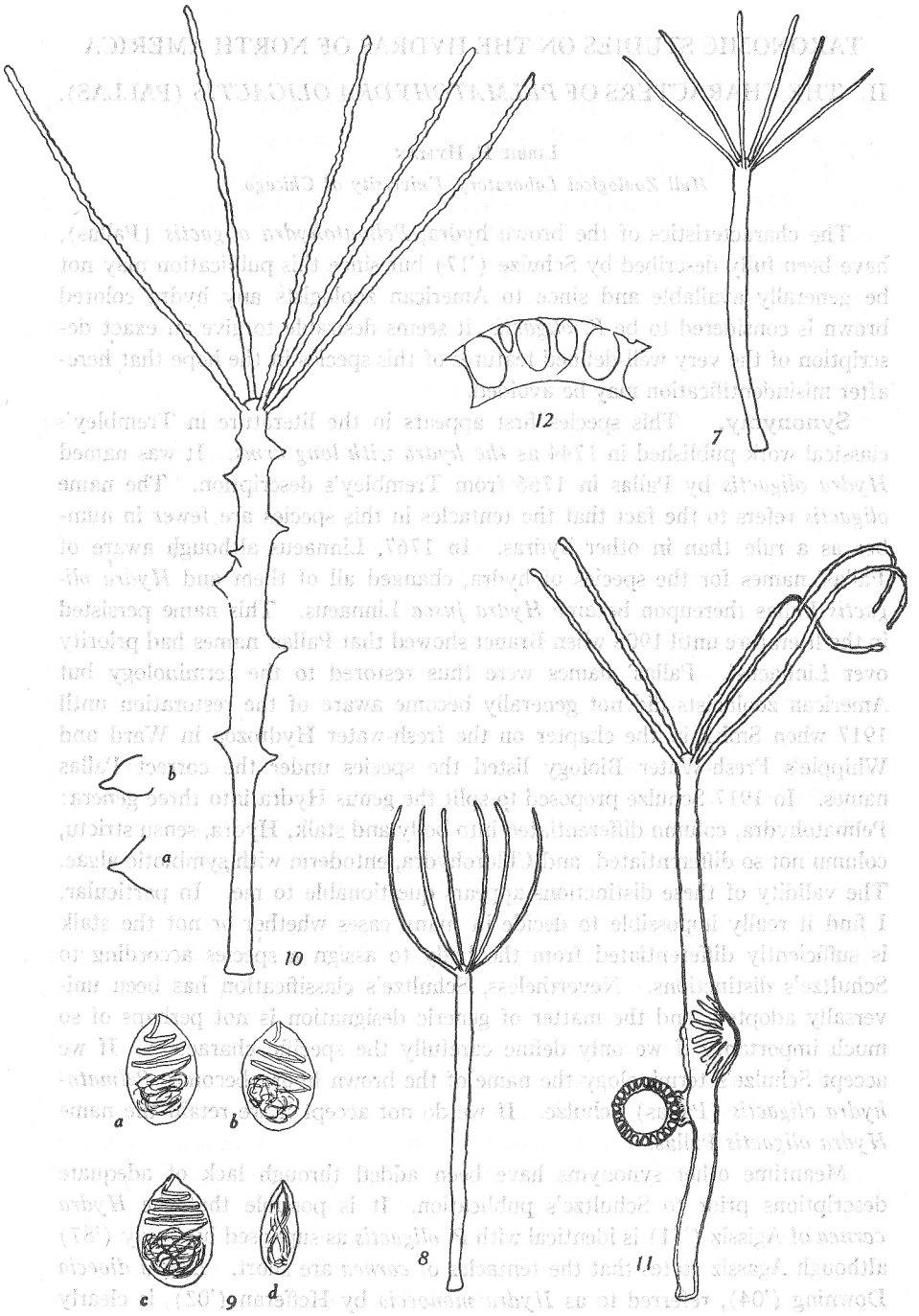

PLATE XXX