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# ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS  
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NEW YORK ZOOLOGICAL SOCIETY



VOLUME XXIII

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# New York Zoological Society

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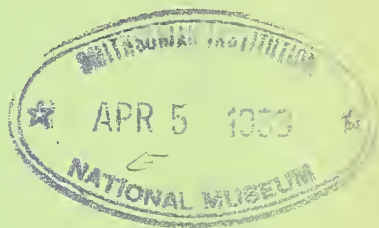


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# ZOOLOGICA

## SCIENTIFIC CONTRIBUTIONS OF THE NEW YORK ZOOLOGICAL SOCIETY

### 1.

#### The Significance of Differential Locomotor Activity as an Index to the Mass Physiology of Fishes.

C. M. BREDER, JR., & R. F. NIGRELLI

*New York Aquarium*

(Text-figures 1-8).

#### INTRODUCTION.

The existence of a measurable differential in the locomotor behavior of fishes under various conditions of companionship has been established by Schuett (1934) and confirmed by Breder and Nigrelli (1935b) and Escobar, Minahan and Shaw (1936). Each report mentions the use of similar physical equipment but somewhat different handling of the data. All three are almost purely descriptive with little attempt to interpret the possible significance of the data obtained or to explain the mechanism responsible for the observed differences in behavior.

It is the purpose of the present communication, therefore, to interpret the findings of the various investigators and to correlate these results, so far as possible, with other known data on the social attitudes of fishes. To this end a considerable amount of experimental work is reported, some of which was briefly referred to by Breder and Nigrelli (1935b). It was early found that before the observable results could be satisfactorily interpreted it was necessary to consider in some detail the various items of both the internal and external environment. Supplementary experiments, that may seemingly have little bearing on the problem of social attitude or mass physiology, were found necessary.

Briefly stated, the method of investigation, which was devised by Dr. Paul Escobar and associates, consists of observing the successive positions of a fish in each of the three dimensions through a system of coordinates ruled on the glass walls of an aquarium. From such observations the distance traveled, the configuration of paths and their relation to the three spatial axes may be calculated. That these differ for any one specimen with companions and when alone has already been established in the three reports mentioned. Before going into a full discussion of these data and presenting more details of related matters, a brief consideration of the factors involved may best be presented.

## FACTORS INVOLVED.

Of the numerous factors concerned, many are self evident, some are not, and a few have not been previously discussed in this connection. It does not follow, furthermore, that this list is exhaustive, but is intended to indicate only those factors that must be considered for any adequate understanding of social phenomena in fishes.

## EXTERNAL FACTORS.

All the factors in the external environment may be considered under this head and so include all influences extrinsic to the subject itself.

*Space.* The available space places strictures on the movements of the included organisms. For example, any calculations based on physical formulae that assume an infinite medium are accordingly modified by the limits of the container.

The shape of the space as well as the volume is distinctly important. This has been discussed in considerable detail by Escobar, Minahan and Shaw (1936). Thus, its relative extent in reference to the vertical and horizontal axes is an important differential. This latter element is apparently due extrinsically entirely to the unidirectional nature of the gravitational influence, illumination, etc.

*Radiant energy.* The impact of radiant energy is of extreme importance since, for example, the presence of visible radiation is essential to vision, the eyes being important receptors in the aggregating behavior of fishes. Other wave lengths have not been studied in detail but Beebe (1935) showed that a beam of ultra-violet would cause certain fishes to aggregate in a closely compacted mass within its radius.

*Temperature.* The effects of thermal differences and thresholds are obviously of considerable importance to the differential behavior of fishes. Schooling in some cases is clearly temperature controlled; Townsend (1916) and Breder and Nigrelli (1934, 1935a). In these cases the lowering of temperature induces the fishes to aggregate.

*Chemical conditions.* Many substances dissolved in the water have a clear effect on the "social" attitude of fishes, including the amount of CO<sub>2</sub> and O<sub>2</sub> present; Allee (1931), Allee and Bowen (1932), Breder (1934), Breder and Nigrelli (1934, 1935a). Eddy (1925) maintained that certain stimulants caused aggregation and certain depressants caused dispersal.

*Objects.* What, for want of better term, may be considered as objects may include both those that are inert and those that are active. Rocks, plants, etc., serve in part to act as physical boundaries to the subjects but more especially as boundaries to their vision which, as will develop, are of considerable importance in the behavior pattern. Food items present a vigorous stimulation to hungry subjects.

The companions may be here classified as homotypic and heterotypic, following the usage of Escobar, Minahan and Shaw (1936). These may be attractive or repellant according to the particular physiological state of the subject at the time.

## INTERNAL FACTORS.

Under this head may be considered all the effects of the internal environment. These then include the physical, chemical, and psychological make-up of the organism and cover all its inherent tendencies and characteristics.

*The Receptors.* Since all knowledge of the external world comes by way of the sensory receptors, considered in the broadest sense, they in their entirety may be taken as a starting point. It so happens that in all fishes



which have been used in experiments involving their attitude to their fellows, vision alone has been shown to be significant; Newman (1876) *Clupea harengus* Linnaeus; Parr (1927) *Pneumatophorus grex* (Mitchill); Spooner (1931) *Morone labrax* Linnaeus; Breder (1929) *Jenkinsia stolifera* (Jordan and Gilbert); Bowen (1931, 1932) *Ameiurus melas* (Rafinesque); Breder and Nigrelli (1934, 1935a) *Lepomis auritus* (Linnaeus). This has been in part demonstrated by the breaking up of schools on dark nights or by covering the eyes of individuals with vaseline and lamp black. While it has not been previously noted, the same holds for *Carassius auratus* (Linnaeus), the species on which Schuett (1934), Breder and Nigrelli (1935b) and Escobar, Minahan and Shaw (1936) chiefly worked. Consequently there is no need under the present limits of data to speculate on the possible significance of the other senses so far as response of fish to fish is concerned. However, the presence of chemically detectable food, mechanical jarring of the aquarium, etc., rapidly change the pattern of behavior and for the purpose of the present experimental studies have been rigorously guarded against.

*The Effectors.* After stimulæ are passed from the receptors and modified by the neuro-endocrine mechanism, the past conditioning of the fish, the particular drives that it labors under at the moment, etc., the effectors may produce appropriate movements or other responses. However, it cannot be assumed that such will be locomotor, although they clearly are in many cases. They may, for instance, be simply the rolling of an eye or the extension of the dorsal fin. Furthermore, undoubtedly many of the stimulæ may reach no evident effector at all, becoming "lost" in the internal environment with perhaps scarcely a quickened heartbeat. What such stimulæ may have to do with conditioning in fishes we can only speculate upon at present.

The locomotor effectors, the only ones which produce results which can be handled by the present technique, are distinctly axial. That is to say, because of the streamlined shape of a goldfish and its built-in locomotor mechanism, it is much more likely to move forward than in any other direction. While it is capable of backing up, its rising and falling movements are actually, under normal conditions, forward movements deflected up or down and its sidewise movements are forward ones which are laterally deflected. Escobar, Minahan and Shaw (1936) expressed the same thought as follows: "... the locomotor mechanism of fishes (with a few exceptions, e.g., seahorse) are adapted to propel the fish along the axis of the body, the latter being normally oriented in most species of fishes in a horizontal plane."

*The Drives.* The various internal urges that impel fishes to respond to stimulæ according to certain patterns obviously enter into the locomotor behavior and to a large extent control it. These stimulæ may arrive directly from either the external or internal environment. The seeking of comfort, suitable temperature, light, depth of water, current, contact with solids, which are ordinarily understood as the various tropisms, can be shown to be induced directly by external influences. For the purpose of the experiments many of these may be eliminated by having the factors uniform throughout the experimental tank. Others, such as gravity or light, which necessarily must have some axis, must be allowed for in the calculations. While thigmotropism in its full sense is not a characteristic of the goldfish, its desire to move close to solids is of considerable importance as will develop in some of the experiments.

Lest it might be thought that the agitation of water caused by the passage of another fish tends to keep schools intact, it need only be pointed out that, if fishes are at all aware of such movements, they are entirely inadequate to produce results obtained. As previously mentioned, the obscuration of vision results in the disintegration of schools.

The internal drives of hunger and sex are not easily controlled. By



adequate feeding apparently the first may be neutralized, and by using goldfish out of the breeding season the second may not be important, but as Escobar, Minahan and Shaw (1936) pointed out, "Even in immature individuals sex cannot be ignored, since there may exist dimorphisms and differential physiological abilities." Studies of both these items invite investigation. The above investigators further write: "In the case of animals with highly developed visual sense organs the contour and coloration of their fellows in homotypic or heterotypic groups may conceivably alter their movements resulting in various degrees of aggregation or dispersal." The known attitude of fishes to attempt mating with a variety of quite unfish-like objects does not support this view, however; Lissmann (1932) *Betta splendens* Regan; Breder and Coates (1934, 1935) *Lebistes reticulatus* Peters; Noble (1934) *Eupomotis gibbosus* (Linnaeus); Breder (1936) *Lepomis auritus* (Linnaeus). On the other hand, the abstract of studies by Noble and Curtis (1935) on *Hemichromis bimaculatus* is suggestive of some such differentiation.

Heterotypic schools of fishes are not uncommon and those of young fish are frequently of an ecological nature rather than a specific one, as discussed by Reighard (1915). Parr (1931) considered the temporary sexual dimorphism of *Gasterosteus* as a factor in the breaking up of the earlier non-sexual schools. Breder and Nigrelli (1935a) discussed other cases of heterotypic schools. Perhaps many of the vague controversial matters regarding fish schools and sex recognition could be cleared up by some modification of the technique here used for examining the factors in the simple aggregation of essentially non-schooling species.

The territorial attitude of fishes is well marked in many species, and is associated with tank dominance as has often been mentioned, Breder (1934, 1936). This seems to be strongest in nesting and thigmotropic species and weakest, if present at all, in schooling species. It is at least present to the extent of some aggregations being partial to some small area. Nothing can be said about homing instincts or migratory movements at this time but such would surely only be an influence evident outside of laboratory tanks. The behavior of animals on "home" territory and in unknown country is demonstrably different without the necessity of recourse to the plotting of paths or trajectories.

*Spiral Movements.* There is a well known tendency for animals when blindfolded or in an environment with inadequate points of reference to move in more or less circular or spiral paths. This seems to be an inherent element of all forms of life examined. Schaeffer (1931) expresses it as follows: "All motile organisms move spirally when guiding senses are not functioning, so far as known. By experiment and observation this has been found to hold true from bacteria to blindfolded aviators." That it is equally true of fishes is subsequently shown. The bearing that this feature has on mass physiology will be discussed in detail at that place. Schaeffer (1928) discusses the general problem of spiral movement and gives a good bibliography. Gordan (1936) detected such movement in the massed flight of insects.

*Random Movements.* It has been stated by Lotka (1925) that the movements of organisms in a uniform environment should be of a random character. They then follow the Einstein (1905) equation for Brownian movement which is usually given as follows:

$$\Delta_x^2 = \frac{RT}{3\pi N} \frac{t}{\eta\alpha}.$$

Expressed in non-mathematical terms, the law states that the mean squares of the displacement in any direction, in equal intervals of time, is proportional to the elapsed time. This may be expressed graphically by plotting time against the mean squares of the displacements. Then random movement is expressed by a straight line with its origin at the zero point in each axis.

This has been shown to be in agreement with the movements of protozoa by Przibram (1913). Applied in a larger sense to a non-uniform natural environment (in which the irregularities are essentially cancelling) Ross (1923), Pearson and Blakeson (1906), Brownlee (1911), Edgeworth (1920), Cole (1922), Hardy (1922) and others have shown similar phenomena in the migratory or other movements of non-captive organisms. Thompson (1933) has attempted to apply the equation of Einstein to the movements of tagged fishes. Certainly there would be expected to be a large degree of randomness under the conditions of the experiments to be discussed. Consequently by the application of the formula it should be expected to hold, except for the fact that the formula applies theoretically to a space of infinite volume. In the case of small containers and large objects, their early "reflection" back from the sides makes its application unsuitable.

The arbitrary limits of space available made it impossible in our circumstances to use a tank sufficiently large or a fish sufficiently small to apply the Einstein equation directly. However, by certain sub-experiments a fairly clear indication of the relationship of random to spiral movement was obtained which is adequate for the present purpose, at least.

Light, temperature, chemical conditions, objects, and gravitational differential were either controlled or, as in the case of the last, properly allowed for.

The food and sex drives were minimized by adequate feeding and performing the experiments out of the reproductive season. These were clearly sufficiently overcome to give comparable results. Small differential details are explained in connection with the items they modify.

#### EXPERIMENTAL STUDIES.

The data obtained by various experimental contrivances already referred to in the previous sections are given here in full descriptive detail. The interpretation based upon these results will be found in the section following.

*Experiments in Differential Locomotion.* For the purposes of this series of experiments a rectangular aquarium 20" x 16" x 14" high was used. This then represented a rectangular enclosure of 4,480 cubic inches. One side and an end were ruled faintly with a glass marking crayon in two inch intervals. The side was thus divided into 70 squares and the end into 56 squares. By viewing simultaneously from the end and side, any fish in the aquarium could be located in any one of the 560 two-inch cubes. Such positions were then noted at ten second intervals for uniform periods. The resulting data, a series of three reference numbers, one for each plane of projection, in a consecutive series (from "0" to "140") could then be calculated in various manners, both as to an estimation of the distance traveled and as to the actual position of the subjects in space. The data, then, which were obtained by all these experiments, are represented by a total of 5,499 points in space, each represented by three index figures or 16,497 projections. Exp. 35 and 36 are omitted because of the partial data taken.

By a suitable geometrical treatment of the data a trajectory of the fish, as measured, at ten-second intervals may be calculated. This, reduced to meters per hour, is given in Table I.<sup>1</sup> Obviously these figures are minimal values as the fishes do not necessarily travel in a straight line between the fairly long intervals. The methods used by Schuett (1934) and Escobar, Minahan and Shaw (1936), give closer approximations to the actual distance traveled. However, our readings were made basically for another purpose and are of course comparable among themselves, giving properly relative values. A study of the data will reveal that there is a very genuine separation between the rate of travel by a fish alone and one with com-

<sup>1</sup> All Tables will be found at the end of this paper.

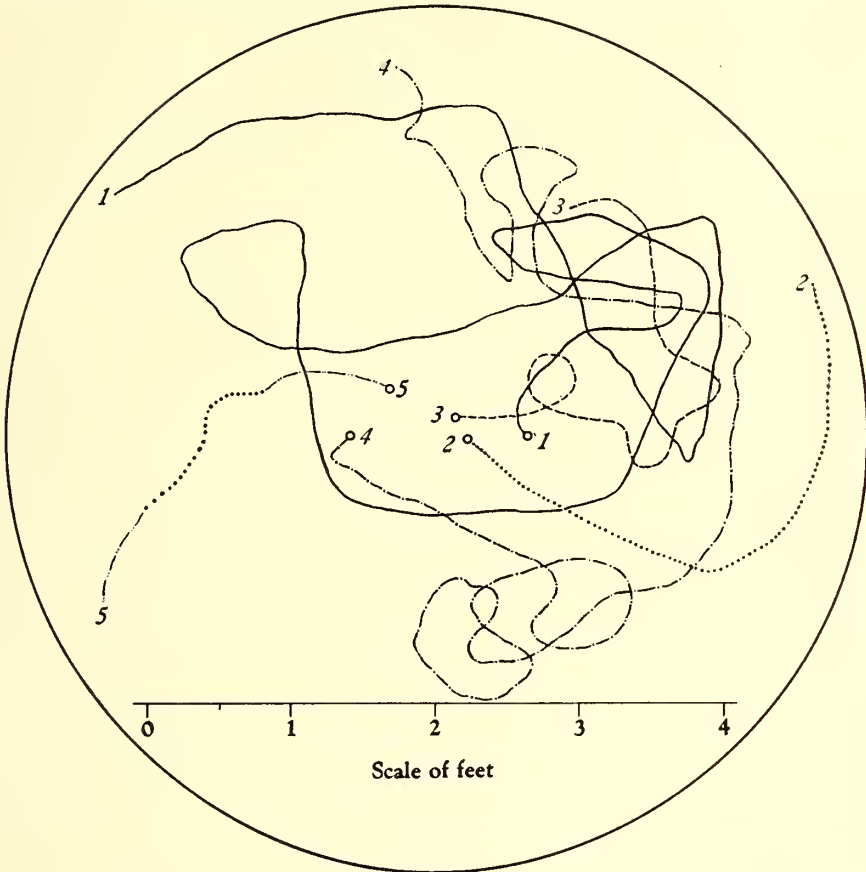


panions, the details of which are given in the discussion. The first 22 experiments were made by one observer by using a mirror set at an angle of  $45^\circ$  to the ruled end so that both side and end could be observed at one time. This was found to introduce slight complications, either by irregularities in illumination or perhaps by the fish seeing his image. This was subsequently overcome by enclosing the aquarium in a light-tight box, provided with a side and an end "peep hole" and with artificial illumination. This required the simultaneous observations of two people and even here certain irregularities in behavior could be traced to light entering laterally from around the viewing holes. The details of the separate experiments are given in Table I and discussed along with their interpretations.

Another method of handling the data is to consider the fish positions in each plane of projection separately and plot these as frequency curves. Obviously, any correlative changes in the shape of such curves to be found associated with the different conditions indicate a change in the swimming pattern of an active organism. These data are given in Table II. In certain cases it is more convenient simply to consider the aquarium as divided in half of each of its three axes and note the percentage of positions to either side of the mid-lines. These data are given in Table III. Still another way to treat the data is to count the number of crossings of these mid-lines in each plane. This is not the same as the previous treatment as various degrees of activity may give the same distribution or various speeds of travel may include more or less crossings of the mid-lines. Each of the three treatments, however, is nevertheless closely related to the others, and taken together they increase the emphasis on the differential behavior. Still another treatment is to note simply the number of changes in direction and finally to plot out the changes in position along a time axis. These items are considered at this point to indicate the flexibility of the technique rather than for the purpose in hand, the details of which are considered along with the inferences based upon them.

*Experiments in Random and Spiral Movements.* It is thoroughly evident that the aquarium used in the preceding experiments would be inadequate to make even a cursory study of random and spiral movements in any but nearly microscopic organisms. In order to obtain some estimation of these features a pan six feet in diameter and two inches deep was constructed. The bottom was covered with a uniform layer of sand and the vertical sides were enameled white to make them as little evident as possible under the circumstances. The pan was illuminated from six feet above by four electric fixtures spaced so as to provide a uniform vertical light, and was surrounded by a curtain of heavy white sail canvas to exclude extraneous light and disturbances. A motion picture camera was mounted directly over the center for the production of permanent records. This was found, however, not of any particular value as the experiments developed. The speed with which the fish found the edge of even this pan was so rapid as to give records of little value. It may be noted here that the restriction of the subjects to an essentially two-dimensional field in no way invalidates the calculations. Even a single dimension may be used for such purposes.

Sketch paths of five fish are shown in Text-figure 1. The longest represents not quite 15 seconds, as they were only continued until the subject responded to the side. This was always immediately evident because in every case the subject then began to circle close to it. Table VI gives the details of the data. There is very considerable evidence of typical spiral movements in both the figure and the tabular data. In these five cases the tendency was to turn to the left, resulting in a counter-clockwise traveling about the edge of the pan. These fish were gently placed at the points shown and had never been in the pan before. It was quickly found by a second trial that the conditioning had been such that the subjects learned that there was a sheltering edge not far away if they traveled in any



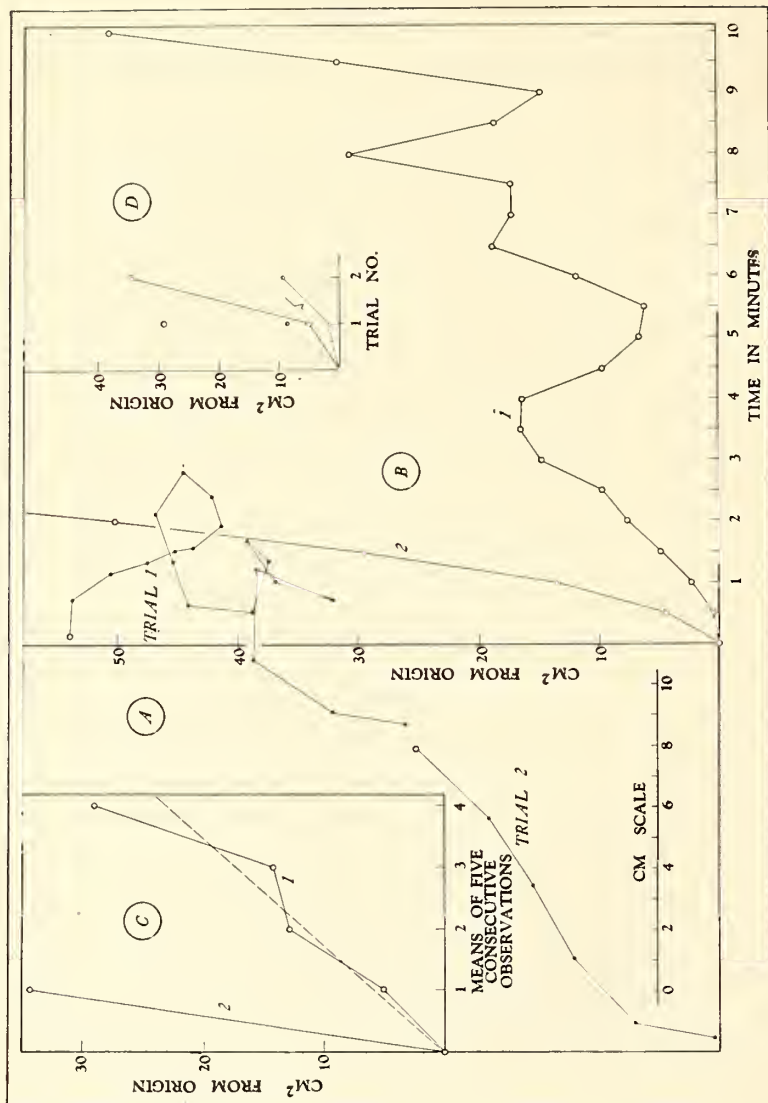
Text-figure 1.

Paths of five fishes of different species in a shallow pan, protected from outside influences. 1. *Carassius* No. 1. 2. *Carassius* No. 2. 3. *Lebistes reticulatus*, female (fish lost sight of at the point shown, but a moment later was found traveling counter-clockwise around edge). 4. *Brachydanio rerio*. 5. *Villariius catus*, 2 cm. long (heavy dotted portion of path picked from a motion picture record, each dot representing every eighth frame or at intervals of  $\frac{2}{3}$  of a second). All other paths are free-hand tracings.

straight line. This in itself is rather remarkable, since actual sight of the edge through two or more feet of water is not involved, as is evident from the fact that on second trials they seldom went to the nearest edge but seemingly struck out in a random direction when released but maintained practically a straight path. How this could be we do not yet understand. The short distances at which Breder and Coates (1935) found that *Lebistes* could distinguish even evident objects also bears on this.

After proceeding to this point it became evident that such an apparatus was inadequate for these studies and that suitable equipment was not available, on the basis of space alone, in the laboratories. Because of this, slow moving aquatic gastropods were substituted for fishes as subjects. Their behavior, readily followed, gave some interesting data on animal behavior, which would seem to be in accord with what the preceding fragmentary



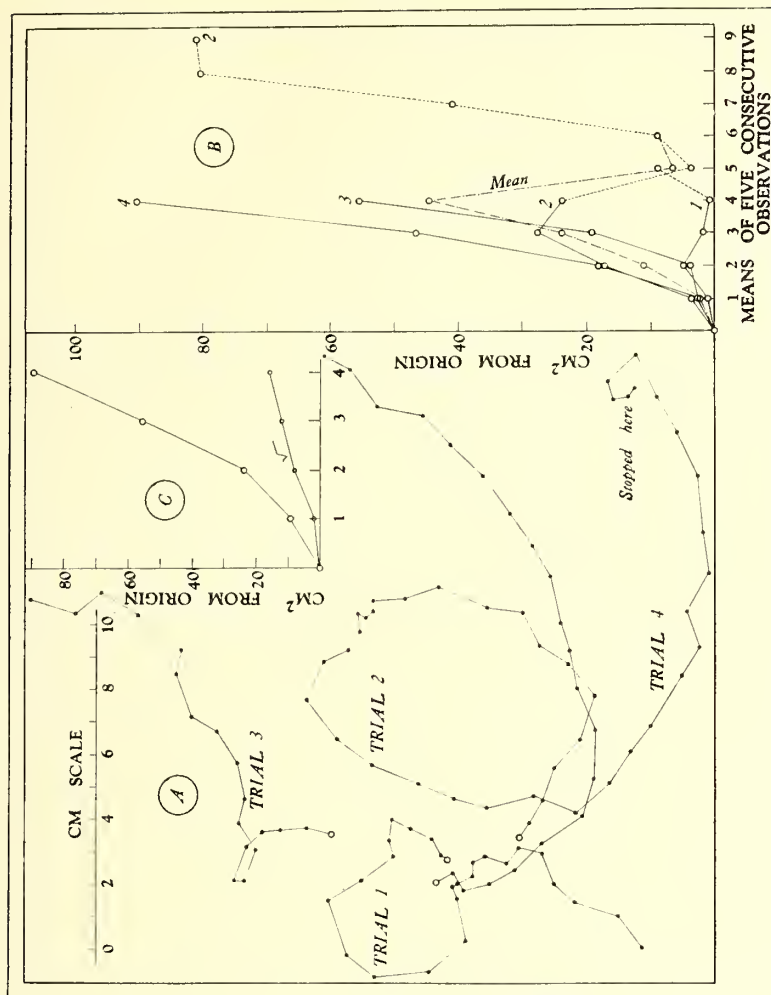


Text-figure 2.

Paths of *Physa*. First and second trials of snail No. 1 with resulting data plotted three different ways. **A.** Actual paths of trial 1 and 2. **B.** Square of displacements plotted against time. **C.** Means of five consecutive observations plotted as in "B". **D.** Mean positions and their square roots at the end of periods given in "C". The connected points correspond to the first period. The unconnected points correspond to the fourth, as there are no data for this from the second trial.

experiments would lead us to believe. Fortunately for the work, the snails all seemed dissatisfied with a position on a flat horizontal surface and showed a strong disposition to come to rest on the vertical sides of the pan. The only difference in physical equipment was the placing of a large piece of French plate glass over the sand so as to give the creeping snails an absolutely plane surface to move over. Under this was inserted a pale gray piece of cardboard, pencil ruled in small, scarcely discernible, squares.

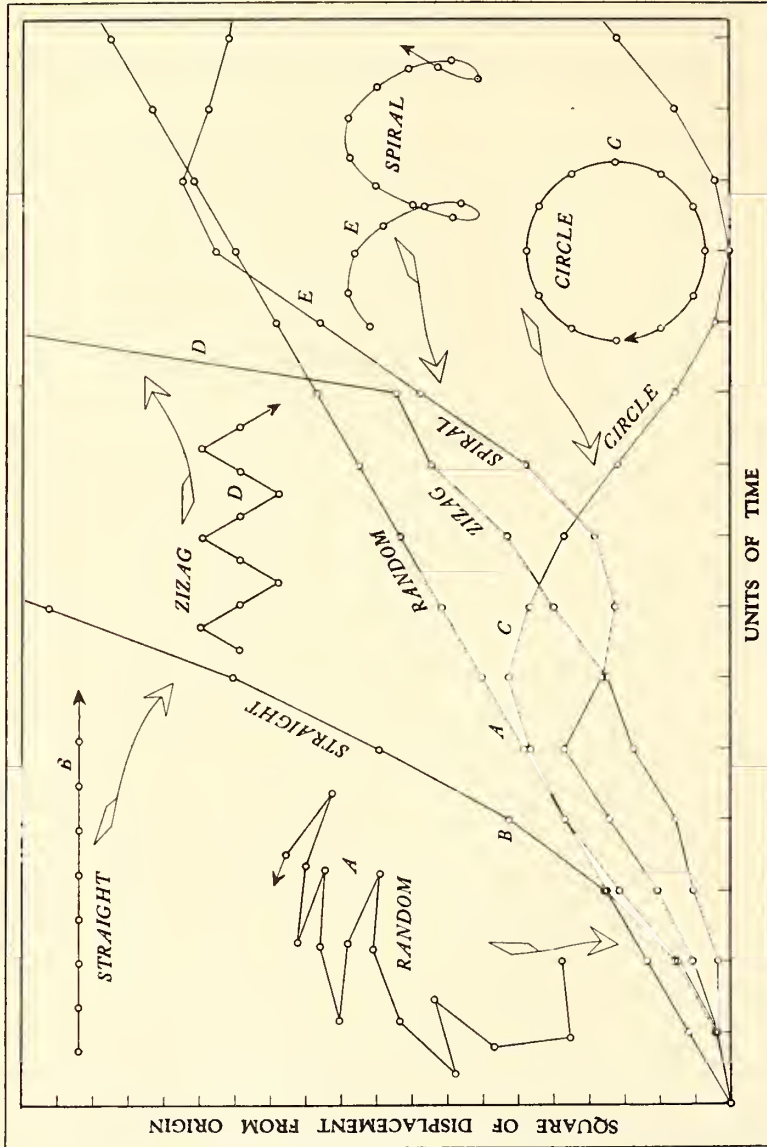
The trial paths of certain snails are given in Text-figures 2 and 3. Here, too, there are undoubted spiral movements, but the bias is slightly to the right. The behavior of these snails yielded further data bearing on the subject of random movement which is not entirely clear at this writing. It was found, for example, that the first trial of *Physa* No. 1 was much more nearly random than the second. The actual paths of these two trials are



Text-figure 3.

Paths of *Planorbis*. First to fourth trials of snail No. 1 with data plotted two different ways. **A.** Actual paths of trials 1, 2, 3 and 4. **B.** Means of five consecutive observations plotted as in Text-figure 2, C, as well as the mean of the four trials. **C.** Mean positions and their square roots at the end of periods given in "B".

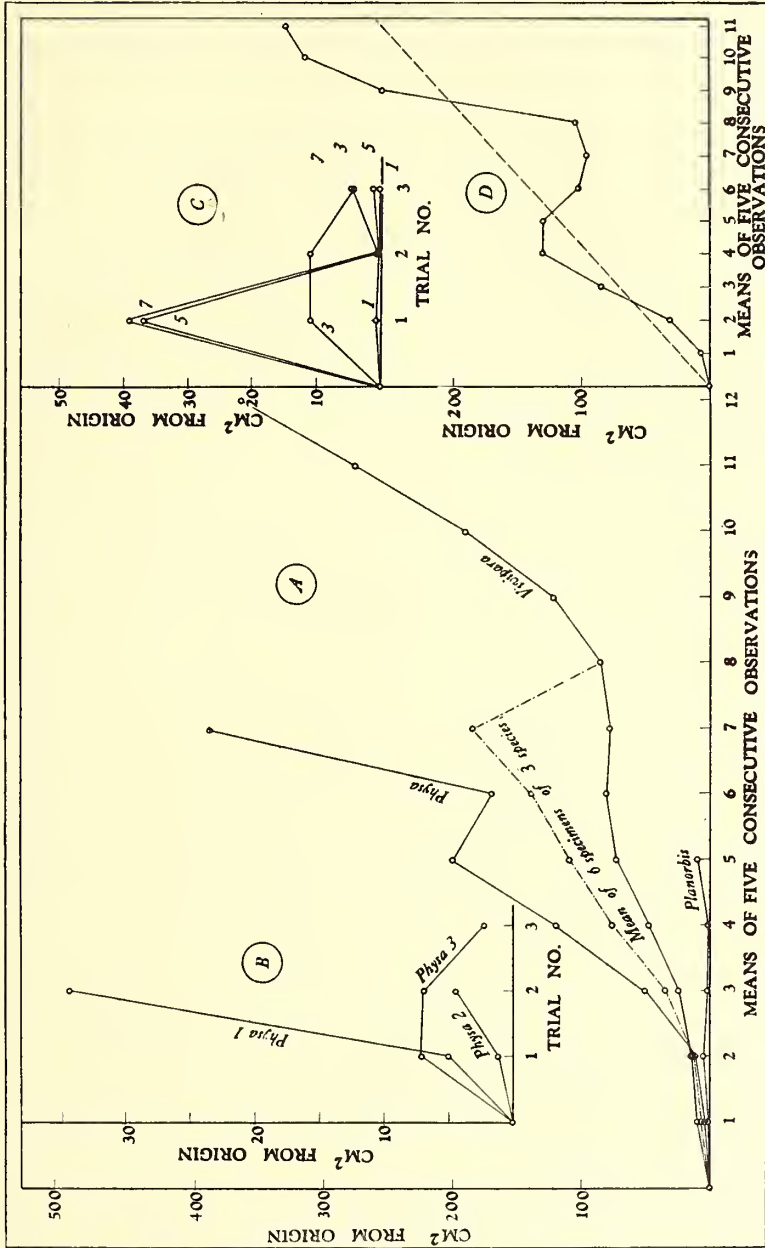
given to Text-figure 2A. The data of these, plotted according to the Einstein equation (i.e., square of the distance from the origin against time), are also shown here and indicate that the second more closely approximates that of a straight line while the first more closely resembles that of a spiral path (Text-figure 2B). See Text-figure 4 for illustrations of typical lines of translation and their representation by this type of plotting. If the means of 5 consecutive points be plotted, curves are obtained which are given in Text-figure 2C. Of the second little can be said because of the slight amount of data, although it is obvious that this line must become more and more nearly a straight one as the quantities taken to obtain mean values are increased. The first path in this graph also more nearly approaches a straight line, for similar reasons. The angle of these lines to the horizontal gives a measure of the speed of recession from the origin and insofar gives a measure of the behavior of the organism. At this point a difficulty inherent in the method becomes apparent, since by an appropriate selection of mean values a given path such as the first can be either represented as indicating a spiral movement or a random movement. This is not so serious as it might



Text-figure 4.

Geometrical paths and their representations in graphic form for comparison with Text-figures 2, B and C; 3, B; and 5, A and D. The indices indicate uniform units of time against squares of displacement from origin. The resulting curves are reduced to one-half the scale of the originating paths. A. Random movement. B. Straight path. C. Closed circular orbit. D. Zigzag path. E. Spiral path.

be first thought, since what it actually indicates is that elements of both are present and either one may be emphasized and studied according to the scale of operations under consideration. This seeming paradox becomes clear when it is considered that an animal or other object may be cutting close spirals, turning cart-wheels or showing other vagaries of locomotion and still be moving in a random fashion, if considered in a larger sense. On the other hand an animal may be moving in very large spirals on which are overlaid a measure of randomness considered in a finer sense. This only becomes confusing when the size of the spirals and the random paths are of similar magnitudes. However, it is just in such cases that the value of this approach is greatest.



Text-figure 5.

Resultant calculations from paths of *Physa*, *Planorbis* and *Vivipara*. A. Mean paths of all individuals studied by species plotted as in Text-figure 2. B. Mean positions at the end of periods of three specimens of *Physa*, plotted as in Text-figure 2. C. *Physa* No. 3 at the end of periods 1, 3, 5 and 7, indicating the inability of this individual to "learn"; compare with "B". D. Mean of three trials of *Physa* No. 3; compare with Text-figure 2, B and C.

The underlying biological causes of these differences between the snail paths No. 1 and No. 2 are not so evident but would seem to have their roots in some conditioning, orientation, or more broadly some learning process. By plotting the data still another way (i.e., trial number against distance from the origin at the end of fixed periods), what may tentatively be called a learning curve is obtained. This is given in Text-figure 2D. Further data of other individuals of *Physa* are given in Text-figure 5. The learning curves



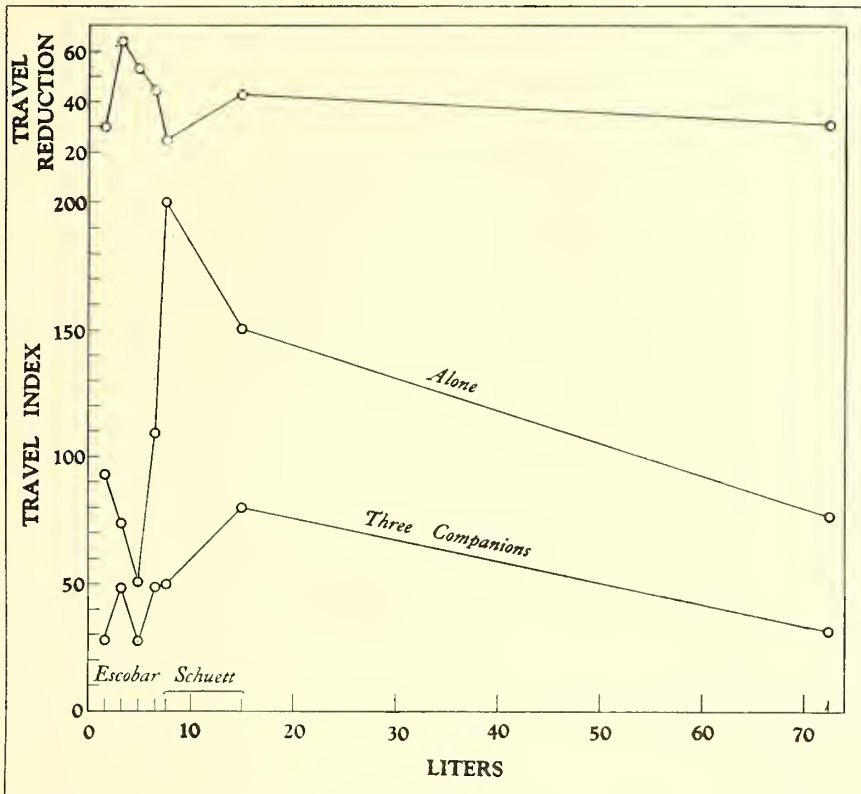
of three specimens show considerable differences, including one individual which apparently failed to learn, performing more poorly on each successive trials (Text-figure 5B). However, it is clearly evident that the mean of these three snails nevertheless shows some shift to an increasing speed of recession from the origin on successive trials. These observed differences may be due to individual background or other factors in the life of the animals. Text-figure 5C shows the positions of *Physa* No. 3 at the end of four different periods in each of its three trials, again indicating its lack of learning. The essential random and spiral nature of the paths are also indicated in Text-figure 5D in which the mean trial of the *Physa* No. 3 shows a marked resemblance to the first path of No. 1 given in Text-figure 2B. The means of all trials of these three *Physa* are likewise given, which emphasizes the characteristics common to all of them (Text-figure 5A).

Data on another species, *Planorbis*, are given in Text-figure 3 and show similar characteristics. The actual paths are given and the resulting plottings. The mean of four trials shows again the spiral and random tendencies inherent in these paths. The learning curve is well marked and, as in the other species, is shown both with the data as picked from the curve and the square roots of those values.

Similar studies of two specimens of *V. vivipara*, the data of which are not given in full, appear in the mean values for all in Text-figure 5A. This species was added to the previous two, since it is not a pulmonate. The essential similarity of its behavior is evident. The difference in shapes of the curves of the three species is referable directly to their activity and speed. It is to be noted how basically similar are all patterns.

#### SIGNIFICANCE OF OBSERVED BEHAVIOR.

The data obtained by means of the experiments previously described and presented in Tables I and V in most cases may be better understood if presented in graphic form. The index of the rate of travel under various conditions as expressed by the data of Experiments 1 to 22 of Table I is analyzed in Table IV. It may be seen at once from this table that the two fishes tested move much faster when alone than when with companions. This holds not only for the mean values obtained but also for both the maximum and minimum values. It is also to be noted that there is but one case of overlapping of extreme figures and that there is virtually complete separation between the two sets of values. Actually this is strictly true for all of the mean values, the only ones of full statistical significance. Maximum and minimum values show a separation of over 50% and the minimum considerably more. The close agreement between the two test fishes is to be especially noted. These data support the experiments of Schuett (1934) and Escobar, Minahan and Shaw (1936). The data of these investigators are given in Table III. This has been equated as well as is possible from their data to the present experiments. Since, however, their procedure differed somewhat from the present it cannot be thoroughly comparable, although it is fully adequate to establish the validity of the increase in speed of travel in *Carassius* with solitude. These data are presented in graphic form in Text-figure 6. Some of the irregularities are doubtless due to differences in technique and methods of calculation. This is largely obviated in the top-most line which represents the travel of a fish with companions as a percentage of the fish alone. The apparent differences smooth out to a considerable extent under such treatment, well indicating the basic agreement between the three sets of studies. Lest it may be thought that the different  $O_2$  and  $CO_2$  concentrations associated with various numbers of fish are responsible for these differences it is but necessary to point out that Schuett (1934) successfully ruled out this factor for a much smaller aquarium than the one here used.



Text-figure 6.

Comparison of the data of Schuett (1934), Escobar, Minahan and Shaw (1936), with the present. The topmost line was computed by reducing the amount of travel of the fish alone to unity. Then the indicated figures represent the extent of travel reduction with three companions.

The new experiments, each representing a special feature that in some cases shows more clearly just what transpired by other treatment of the data, may be now considered in reference to rate of travel. Another fish, "C", in the shadow box (Exp. 23) previously described and illuminated by a hundred watt light, showed a speed of 162.15 M/h when alone. The addition of other fish (Exp. 24) one-half hour later resulted in even a higher rate of travel (166.98 M/h). These fish changed abruptly from daylight were clearly worried and it would seem that their rapid movements were responsible for the failure of the accommodated test fish to reduce its speed. Further data on this appear in the consideration of the effect of light. Later, on the removal of the box (Exp. 25 and 26), the travel reduced to values comparable to those of "A" and "B" with companions; 61.70 and 33.39, mean 47.54.

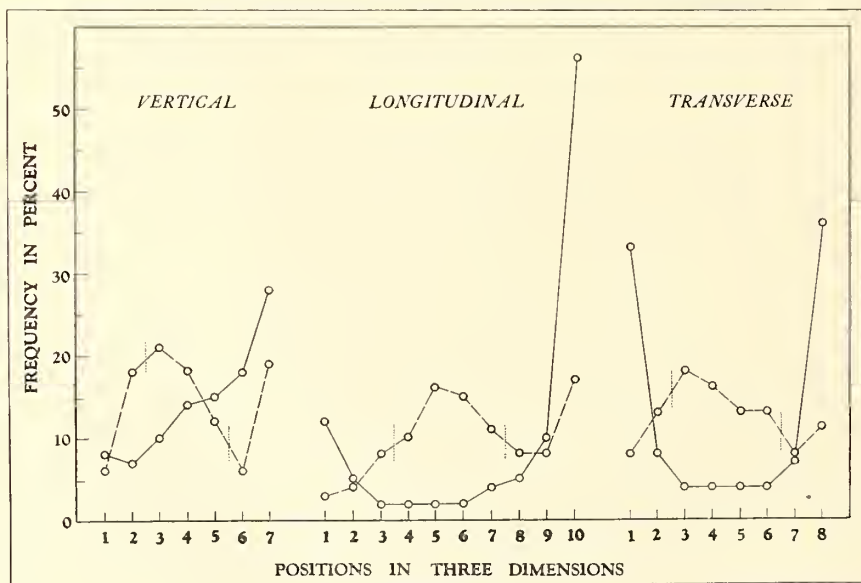
A rotating motor-driven disc placed under the electric bulb, causing the rapid passing of shadows, clearly caused fright and the speed increased (Exp. 27). Some hours later this was even higher (Exp. 28) and three days later (Exp. 29) the speed was still high although it is hard to imagine that this effect lasted that long. This feature needs further study.

Another fish, "D", was then studied in relation to the amount of light

used. The data are given in Experiments 30 to 35. If the values of fish alone are plotted, there seems to be an increase of speed with an increase of illumination but the data are inadequate for a thorough understanding of this phenomenon. The other items cannot be elucidated in terms of speed of travel at this time but are discussed in subsequent connections.

The distribution of the experimental fishes in space is given in Table V, expressed in terms of percentage. If again the first 22 experiments are combined their mean distribution alone and with companions may then be plotted and compared. These calculations are given in Table V and the resulting graphs are shown in Text-figure 7. It will be noted at once that the curves obtained from fishes alone are convex downwards and those from fishes with companions are convex upwards. An examination of the data of Table II will show that this is a consistent feature of each experiment. The separation is not so clear in some individual cases as in the integrated means of Text-figure 7, but in each of these there is a reasonably clear and evident reason because of the conditions of the experiments and to that extent forms a measure of the particular influences at work as noted in Table I. The minor distortions of the curves of Text-figure 7 are each indicative of tendencies in the subject and form an excellent quantitative measure of them. A consideration of the curves in detail yields the following data, each treated according to its separate coordinates.

The vertical curve of the fish alone shows that the fish tended in a regular manner to keep close to the bottom of the aquarium. Actually it occupied the bottom 2" of water 28% of the time and the surface 2" only 8%, with a quite regular grading of the intermediate strata. Considering the 14 individual experiments upon which this curve of the fish alone is based, there are the following extreme divergencies: Percentage of time



Text-figure 7.

Configurational behavior of goldfish alone and with companions in respect to three dimensions. Solid line: fish alone. Dotted line: fish with three companions. The short vertical pecked lines on the latter indicate the limits, counting from the central position that covers 50% of the readings. A projection of these on the solid line shows that over 50% is there excluded by them instead of included.



spent in the bottom layer varied from a minimum of 13% to a maximum of 60% while time spent in the surface layer varied from a minimum of 0% to a maximum of 31%. In only three of the experiments did the fish spend more time in the surface layer than in the bottom one, and in only one was a peak value reached in the middle layer. This may simply be taken as a mathematical expression of the normal attitude of a solitary *Carassius* as based on casual but extensive observations, to the effect that they are apt to be found near the bottom, and if not there, at the surface, and least commonly in mid-water.

If now the curve of the fish with companions be considered, it is clear that a considerable change in distribution has taken place, the peculiar S-shape of the curve apparently indicating two loci, or that the fish is hesitant between two sites of approximately equal preference. The bottom layer accounts for 19% of the time while an intermediate layer of from 6" to 8" from the surface accounts for 21% of the time. The surface layer is visited about as frequently as before (6%), but the distribution between surface and bottom is utterly different. Over 50% of the time is spent in layers 2, 3 and 4 (57%); the small values of the layers below these, except the bottom one, indicate rapid dashes through them to cruise along in the latter. With the same fish alone over 50% of the time was spent in layers 5, 6 and 7 (61%). If we divide the tank into a top and bottom half it appears that alone the fish spent 68% below and 32% above such a mid-line. With companions this was inverted to read 54% below and 46% above, indicating a more nearly uniform distribution.

The "longitudinal" curve running at right angles to gravity shows a strong tendency for the solitary fish to keep to either end of the tank, most markedly so at the right end. This was the end at which the mirror stood and the curve gives a measure of the attractiveness of this device. If it may be assumed that either end was equally attractive except for the mirror, then the difference of the readings at either end ( $56 - 12 = 44\%$ ) may be taken as a measure of this attraction. When companions are added and a more median position is selected, as evidenced by the shape of the curve, the strong attraction for the mirror end reduces but does not disappear. Thus, between the two sets of experiments the attractiveness dropped from a value of 56% as compared with all other influences in this plane to one of 17% on the addition of three companions. The non-mirrored end dropped from 12% to 3% and since the latter is the lowest value on the curve, presumably indicates that its attractive value fell to zero. The median positions 3, 4, 5, 6 and 7 account for 60% of the time, whereas when alone the terminal position 10 accounted for 56% of the time.

The "transverse" curve is essentially similar to the longitudinal one and with fish alone either side seemed to be equally attractive (33% and 36% respectively). Since there was no differential as in the longitudinal measure, this is what one should naturally expect. The addition of three companions caused the sides to lose their relative attractiveness to the extent that the four central coordinates, Nos. 3, 4, 5, and 6, accounted for 60% of the time.

Dividing the transverse measures in half, we find that alone the distribution to left and right is 49% and 51% respectively and with companions 55% and 45%. These differences are likely too small to be significant and seem to indicate merely the degree of accuracy obtainable by this method on a half and half distribution. If, however, we take the longitudinal measure and handle it in the same way, the figures for the fish alone stand left 23% and right 77%. With companions this becomes 41% and 59%. The bias by the mirror in this is thus overcome by the introduction of three fish to the extent above indicated. The biological significance of the basic distortion of the spatial distribution curves of these fish with and without companions is quite apparent. The interpretation of them would seem to be somewhat as follows: Since goldfish are gregarious, the behavior re-



flected in these curves is evidently a measure of this social disposition. The species may be said to be an aggregating one but not a schooling one in the restricted sense, as may be checked by reference to goldfish in a fairly large pond. The exact behavior in a small aquarium, however, because of its limitations of space, can only be properly appreciated by some such treatment as the present. With these considerations in mind it would seem that both the increased speed of travel and the tendency to seek the walls of the aquarium would be due to an attempt to find company. This finding of company with the resulting slowing down of movement and the formation of an aggregation remote from the aquarium walls would then indicate a satisfaction of that drive. Since the aggregating tendency implies an urge to seek a position close to but not in contact with some object (another fish), it also may be that approach to some inanimate object or surface is used as a substitute to partially satisfy that urge when no companions are present. In fact, it may even be that the movements of the other fish is the determining factor in the expression of the preference of approach to a fish as against a surface. It must be borne in mind, however, that the glass walls of the tank are optically not very evident. If other sensory organs enter here they are not yet evident, for as previously mentioned the fish school in general appears to be a purely visual affair. The fact that aggregations form remote from the walls is not surprising on a purely mechanical basis. If each fish is considered as having a "field" of influence about it, the formation of the aggregation in mid-water would be expected. Fish in a central position would exert the effect of their presence at every point on the surface of a sphere at whose center they were located. Fish close to a side could exert only one-half that, i.e. on the surface of a hemisphere. Fish at the junction of two sides would exert a quarter as much and one in a corner one-eighth as much for similar reasons. It is not necessary to labor the point that such objects, moving either primarily at random or in spirals and mutually affecting each other, would aggregate at approximately the tank center equi-distant from the sides. Divergence from this would then indicate other influences.

If a space is enclosed that includes 50% of the positions, counting from the center both ways, Text-figure 7 indicates that it also includes the peaks of each of the curves of the fish with companions. Short vertical lines show these limits in that figure. These lines projected to include the curves of fish alone for the longitudinal and transverse readings include a very small percentage, i.e., 10% and 16% respectively. That for the vertical component is somewhat different because of the fact that it is at right angles to the main axis of the fish and parallel to the gravitational field. Here the curve of the fish alone is a gradual increase from one end to the other and the corresponding value is intermediate between the one on either side, i.e., 15%, 39%, and 46%.

Schuett (1934) in considering the speed of movement alone has shown that there is some optimum of crowding above and below which the fish move with greater rapidity. This would seem clearly to be for the reasons above outlined. Since these fish place themselves in regard to one another at some "standard" distance, the findings of Schuett would naturally follow and the whole phenomenon become one of seeking an equilibrium. Fast random swimming certainly would tend more quickly to restore a "lost" goldfish to its group as well as tend more quickly to disperse an aggregation too closely packed for comfort.

Having considered the primary significance of the configurational distribution of fishes, the details of the further experiments may be discussed. Experiment 23 made in the shadow box alone shows much greater equality of distribution at either end of the horizontal components; longitudinal 32% and 22%, transverse 32% and 28%. Here the confusing outside elements were eliminated, giving another evidence of the influence of the end

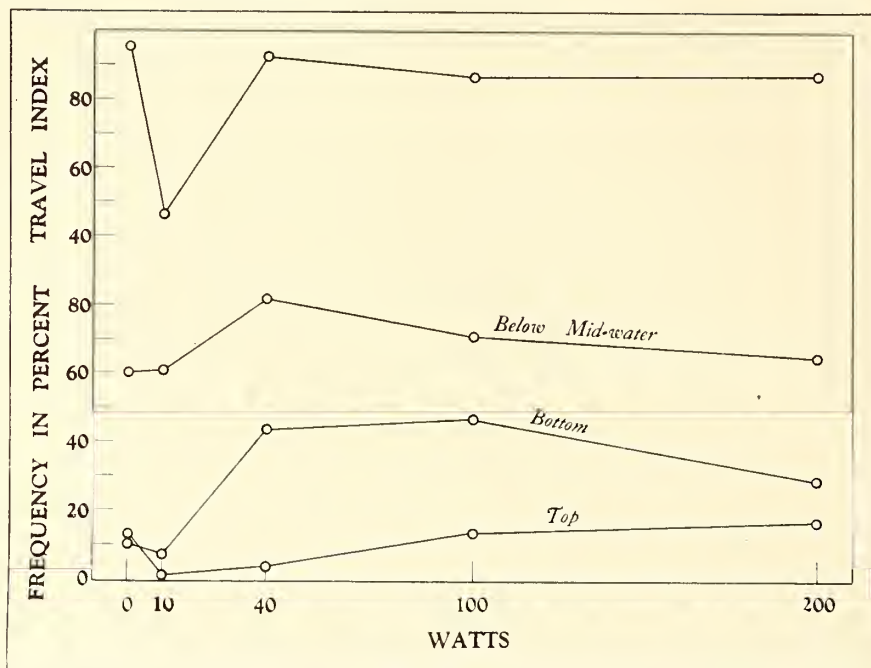
mirror of the 22 primary experiments. The vertical component was in essential agreement with the previous, the surface layer .01% and the bottom and highest figure 37%. This agreement is surprisingly close when it is considered that this single experiment was only 1/22 as long as the mean values previously discussed. Experiment 24 showed no change in speed, as previously noted, and agreeing with this it also showed no change in configuration. The presumed reason has already been mentioned, but it may be pointed out that the rate of speed and configuration of pattern are clearly not locked to each other on any mechanical basis. Consequently in the present case we have two separate approaches, both of which indicate that in this set of two experiments the expected response to companions that has already been established here and by others did not take place. Experiments 25 and 26, without the shadow box, showed irregularities not unlike those of the earlier experiments. As the speed of the fish slowed down, as previously noted, the configuration took on an approach to that of fish "A" and "B" with companions. All that can be said of this is that fish "C" either responded more slowly to companions or was simply not as reactive. Perhaps this could eventually be shown as a matter of individual difference in the "psychic" attitude of various goldfish.

The light was then interrupted (Exp. 27) and the fishes sought either end of the tank, spending 28% and 29% of the time in the two end divisions. The next day (Exp. 28) they returned to a more nearly normal distribution, the ends receiving only .08% and 19% of the positions.

Fish "D" with three companions (Exp. 30) behaved in a normal fashion. This fish was then tested alone with various degrees of illumination (Exp. 31 to 35). The results of this can be best understood by an inspection of Table V. Experiment 35, with a very faint light, just enough to enable the making of the necessary observations, showed the fish to have spent much time in mid-water. The three central coordinates accounted for 57% of the time. Experiment 31, with a 10-watt bulb, showed a considerable resemblance to this one with the same coordinates accounting for 66% of the time. These are the only two readings obtained with vertical characteristics of this nature and they are the two most weakly illuminated ones. This again suggests the visual nature of the movements and aggregating behavior in these fish. The other three experiments (32, 33 and 34) with 40, 100 and 200-watt bulbs all showed a strong predilection for the bottom, but the data cannot decide if there is a gradual change with increased illumination or whether it is simply a matter of passing some threshold. Text-figure 8 gives this data graphically. It is to be noted that in case of "no illumination" the fish spent more time in the top layer than in the bottom. The various elements of this figure, including that of speed, would seem to indicate that the lack of light was stimulating to locomotor activity but without any configurational influence, that a low illumination (10 watts) was quieting but again with no influence on the configuration, but that a higher illumination (40 watts) drove the fish sharply to the bottom and increased the locomotor activity. Increase of illumination above this point seemed to have very little effect, but seemed, if the figures can be trusted to such details, not to hold the fish so closely to the tank floor. It is doubted if such slight differences are significant, however. If anything, it would seem that there may be an activity and behavior threshold somewhere between the illumination of the 10 and 40 watt lamps.

Experiments 36 and 37 represent the simultaneous paths of "C" and "D". For practical reasons they could be taken in two ordinates only. The extent of agreement is close, but no closer than the agreement between successive observations on the same fish. Consequently it is inferred that these observed differences of such order are due to inherent variant characters in the fish rather than unrecognized extrinsic elements.

A fifth fish, "E", was tested in Experiments 38 to 41. The four fish,



Text-figure 8.

Behavior of goldfish in respect to vertical distribution under different amounts of illumination. See text for explanation.

A to D, which were examined at other times, were the companions of the test fish. The speed of travel under varying light conditions was less with companions than without, but the separation was not as great as in "A" and "B". The configuration, however, was in quite good agreement.

Another method of measurement of such activity is to plot the actual transit of the mid-line or to check the reversals of direction. The amount of labor involved in such calculations, however, is disproportionate to the results, which so far as can be seen from the present data give no further information than that already obtained from the more readily applied methods herein discussed.

An attempt was made to calculate the displacements according to the formula of Einstein (1905) for random movement, but it soon became apparent that the small size of the vessel in relation to the size and movement of the fish made it impossible of application. The thesis was taken that if such a fish moved at random, then any diversion from such randomness could be used as a measure of mental integration on the part of the fish. It is now clear, however, from a study of the movement patterns, that in any case such behavior is not of a fully random nature, but is at all times guided by a series of integrated perceptions, however slight.

Since the formula for Brownian movement, which may be used just as well in two dimensions, is so closely controlled by physical influences, recourse was made to the use of a large, shallow pan, virtually of two dimensions, employing much smaller fishes. Here, too, we encountered a difficulty, much different in nature, but one which finally led to the use of aquatic univalves. A description of this device is given in the experimental section together with the results obtained. The interpretation of these data involves the further confirmation of the tendency of organisms to travel in spiral



paths when there is an absence of "landmarks" to guide them. The simultaneous action of the innate tendency to spiral and move in a broader sense at random has been fully set forth in the experimental section. That this is readily modified by some sort of "learning" is also apparent from the experiments. Whether this is associated also with an obscure means of orientation similar to that of "homing" as found in many animals or simply that the snails were impelled by some drive is not fully clear. We suspect that it is the latter, however, for when left alone all three species came to rest on the vertical sides of the pan. The pulmonates had evident reason, but it is not clear in the case of the branchiate form. If the snails could detect these vertical surfaces at such a distance it is most surprising. That the re-crossing of their previous paths had no bearing on the subject is evident from the actual paths shown in Text-figures 2 and 3, as some did not cross at all and where they did there is no evidence of significant change of direction.

The points that these considerations bring out enable us to determine the minimum requirements for an adequate study of the phenomenon involved: 1. A vessel must be used in which it is possible for the organism to do considerable random and spiral wanderings without being able to "pick up" any landmarks. This may be a "two dimensional" space if necessary. For any animals of microscopic size the physical limitations of most laboratories present difficulties. 2. Photographic recording at suitable time intervals would be practically essential for any extensive survey of this field. Since neither space, time nor suitable equipment are available to us under present circumstances it was deemed best to indicate the progress of this work in the hope that someone better situated would be able to further it.

The fundamental nature and reasons for the existence of these spiral movements have been speculated on by various investigators, chiefly Schaeffer (1928). According to our views, certain features of them may be thought of in terms somewhat according to the following: It has been shown for invertebrate animals that those which move by means of muscular effort as opposed to ciliary efforts, behave differentially under various amounts of illumination (Welsh, 1933). The former move more rapidly, according to their phototropism, as the units of illumination are increased, while the latter show no such correlation. The present studies indicate a greater amount of movement under an increased illumination at right angles to the plane of activity. This suggests a similar increase in muscular effort under such stimulation in at least the lower vertebrates. It should follow from this that such spiral movements as may be present would tend to become exaggerated. Since the muscular efforts are being intensified, their unit acts come at shorter intervals and a given path is covered in a shorter period of time. This would seem to culminate in the spiral paths of insects about strong lights or even in the extreme conditions in some fishes discussed by Breder and Harris (1935). These remarks are undoubtedly an over-simplification of the condition, a more full examination revealing that a number of separate items enter into the complex of behavior, at least including the following:

1. Increasing speed of translation with increased illumination.
  - a. Direct positive or negative phototropism (Welsh, 1933).
  - b. Movements at right angles to axis of light (original).
2. Spiral movements inherent in organisms (Schaeffer, 1928, and others).
3. Tendency to expose dorsum (or other surface) to source of strong illumination (Breder and Harris, 1935).
4. Disturbance of neural integration by large changes in illumination (Breder and Harris, 1935).
5. Disturbance of neural integration by other environmental or pathological causes (Hollister, 1934).



It is not necessary for certain effects that all of these factors be present in evident form and there may be still others, as yet unanalyzed. As far as it is possible to understand these effects at present it would seem that the increasing speed of normal reactions to light due to increased illumination and the inherent tendency for organisms to show circling movements are basic to the rest and represent all that is necessary to account for them. The resulting movements from slight stimulæ may be of value to the individual, but beyond a certain point may lead to destruction.

It is evident from many quarters that the social relationship of a fish to its companions is not static but changes rather violently from time to time. Among adults this is most evident during the reproductive cycles as is emphasized in practically every paper on fish reproduction. Even in immature fish diverse influences are at work. Most recently this has been emphasized by Langlois (1935), who studied the relationships between young bass in fish-rearing ponds. Not only did he find that changes proceeded with their development, but that quite different associations appeared in ponds that were essentially similar in environment and original population. This he treated by measuring the output at the end of the season. From some he obtained a uniform group showing only the normal curve of variation in which all fed on the food supplied. In others he found a group of small fish and a group of large, the latter feeding on the smaller and refusing other food as well as showing different attitudes toward schooling. In all he enumerated eight different types of social organization, all derived from similar starting points. This is mentioned to emphasize the dynamic quality of fish aggregations and to indicate to some extent that the problem cannot be handled as one involving only the varying aspects of a continuing attitude on the part of the subjects involved.

Welty (1934) studied the learning of a maze by goldfish with and without companions that had been trained in the same maze. He found that those with trained companions learned the maze faster. The aggregating tendencies of this species certainly account for his results, as indeed might be expected. The results give a measure of the influence of an individual that "knows" where it is going over one that does not.

#### SUMMARY.

1. The relation of swimming speed to the number of fishes present as indicated by Schuett (1934) and Escobar, Minahan and Shaw (1936) has been further confirmed in larger bodies of water.

2. The mean positions of fish in relation to coordinates in three dimensions is shown to be modified by the numbers present in a significant manner, providing a quantitative technique for the study of environmental influences in active animals.

3. The inherent tendency for animals to travel in spiral paths has been shown for fishes and snails.

4. The essentially random nature of the broader movements of animals has been indicated, as have been the experimental requirements for its full study.

5. The equation of Einstein for the movement of Brownian particles should be applicable to the higher organisms if proper data could be obtained.

6. The basic nature of the tendency of organisms to travel in spiral paths may be influenced to various degrees by impingement of the environment on the neuro-mechanism and can be shown to reach from useful activity to self-destruction.

TABLE I.

Data on extent of locomotion and conditions of experiments. *Carassius auratus*, 2 to 3 inches. Each experiment covers 140 observations. Aquaria 20 x 16 x 14 inches high (50.8 x 40.6 x 35.6 cm.). Volume 4,480 cubic inches (72,427 cc.).

No.	Date.	Hour of Start.	No. of Companions.	Meters per Hour.	Condition.	Remarks.	Fish.
1	Aug. 21	1:45	0	72.96	Open tank with mirror.	{ One continuous reading.	A
2	Aug. 21	2:05	0	76.39	Open tank with mirror.		A
3	Aug. 21	2:25	0	87.20	Open tank with mirror.		A
4	Aug. 22	11:20	0	101.45	Open tank with mirror.		A
5	Aug. 22	1:55	0	93.60	Open tank with mirror.		A
6	Aug. 22	4:30	0	84.20	Open tank with mirror.		A
7	Aug. 27	9:30	3	27.98	Open tank with mirror.		A
8	Aug. 27	1:05	3	38.45	Open tank with mirror.		A
9	Aug. 27	4:00	3	26.45	Open tank with mirror.		A
10	Aug. 28	9:35	3	42.37	Open tank with mirror.		A
11	Sept. 5	3:10	3	17.17	Open tank with mirror.		A
12	Aug. 27	2:55	3	50.70	Open tank with mirror.		B
13	Aug. 28	10:00	3	34.38	Open tank with mirror.		B
14	Sept. 5	2:00	3	14.91	Open tank with mirror.		B
15	Sept. 5	4:30	0	49.38	Open tank with mirror.	{ 15 min. after companions were removed.	B
16	Sept. 6	9:25	0	70.12	Open tank with mirror.		B
17	Sept. 6	3:30	0	78.85	Open tank with mirror.		B
18	Sept. 7	9:05	0	58.45	Open tank with mirror.		B
19	Sept. 7	1:35	0	68.35	Open tank with mirror.		B
20	Sept. 8	11:15	0	62.50	Open tank with mirror.		B
21	Sept. 10	11:25	0	81.59	Open tank with mirror.		B
22	Sept. 11	11:00	0	89.48	Open tank with mirror.		B
23	Apr. 13	10:30	0	162.15	In box. 100 Watts.		C
24	Apr. 15	11:00	3	166.98	In box. 100 Watts.		C
25	Apr. 18	2:00	3	61.70	Out of box. Daylight only.		C
26	Apr. 19	11:30	3	33.39	Out of box. 40 Watts.		C
27	Apr. 19	12:00	3	63.35	Out of box. 40 Watts. (Rotor).		C
28	Apr. 19	4:30	3	91.95	Out of box. 40 Watts. (No rotor).		C
29	Apr. 22	2:30	3	79.48	Out of box. Daylight only.		C
30	Apr. 18	3:00	3	34.49	Out of box. Daylight only.		D
31	June 4		0	46.49	In box. 10 Watts.	Simultaneous with 37. Simultaneous with 36.	D
32	June 5		0	92.85	In box. 40 Watts.		D
33	June 6		0	86.95	In box. 100 Watts.		D
34	June 7		0	87.48	In box. 200 Watts.		D
35	June 10		0	95.10	In box. (No light).		D
36	Apr. 22	3:10	1	.....	Out of box. Daylight only.		C
37	Apr. 22	3:10	1	.....	Out of box. Daylight only.		D
38	Apr. 22	4:10	0	78.45	Out of box. 40 Watts.		E
39	Apr. 23		0	110.2	In box. 100 Watts.		E
40	Apr. 26		3	52.49	In box. 100 Watts.		E
41	Apr. 26	3:10	3	103.1	In box. 40 Watts.		E

TABLE II.

**V**, vertical index from top down. **L**, longitudinal index from left to right. **T**, transverse index from front to back. Numbers under **Position** indicate each 2-inch space of projection. Figures in body of Table equal percentage of period occupied.

Experiment.	1			2			3			4			5			6		
Position.	V	L	T	V	L	T	V	L	T	V	L	T	V	L	T	V	L	T
1	15	07	59	20	08	88	16	04	93	22	05	62	31	04	09	09	09	25
2	09	05	11	18	11	08	26	06	05	19	05	06	09	11	09	02	04	09
3	13	04	08	13	02	04	11	07	02	11	05	01	13	01	05	08	03	06
4	11	03	04	07	02	00	14	02	00	08	03	05	13	05	05	04	04	09
5	11	03	04	08	04	00	13	01	00	13	02	05	08	05	03	08	02	09
6	14	01	04	11	01	00	06	04	00	09	01	05	13	01	08	09	04	06
7	27	01	05	23	08	00	14	04	00	18	06	06	13	03	13	60	13	10
8		03	05		04	00		06	00		10	10		06	48		18	26
9		13			15			15			13			13			15	
10		60			45			51			50			51			28	
Experiment.	7			8			9			10			11			12		
1	07	04	20	06	05	09	12	10	08	10	05	23	01	00	03	00	00	03
2	19	01	10	13	02	21	10	17	28	27	07	24	14	02	02	05	00	07
3	25	00	20	14	21	37	14	07	16	19	21	14	36	01	13	12	00	05
4	23	09	20	19	18	05	23	12	14	10	13	19	18	13	19	17	00	09
5	10	25	12	18	22	16	07	17	10	05	09	12	20	20	25	24	00	05
6	03	19	10	07	13	05	06	21	09	05	07	02	02	16	38	18	01	07
7	13	06	07	23	05	06	28	10	13	24	12	05	09	36	00	24	03	03
8		16	01		02	01		03	02		15	01		09	00		01	61
9		10			06			02			09			02			10	
10		10			06			01			02			01			85	
Experiment.	13			14			15			16			17			18		
1	01	00	01	14	01	01	01	81	02	00	05	13	00	23	03	00	01	05
2	47	00	08	12	01	04	02	08	08	00	00	12	00	07	01	01	01	05
3	17	00	05	30	13	28	14	00	00	01	01	06	03	08	01	12	01	05
4	07	02	03	30	13	37	28	01	02	13	01	06	17	01	01	22	01	02
5	03	09	10	02	25	17	18	01	05	21	00	02	16	07	01	23	01	08
6	05	24	20	02	17	10	21	00	02	29	02	03	39	06	01	17	00	05
7	20	10	31	10	05	02	16	00	04	36	01	10	25	03	01	25	01	05
8		10	22		12	01		01	77		01	48		08	91		00	65
9		12			12			01			07			14			06	
10		33			01			07			82			23			88	
Experiment.	19			20			21			22			23			24		
1	00	13	05	01	00	24	01	00	32	01	05	36	10	32	32	00	35	31
2	00	02	07	05	01	14	02	01	15	03	05	15	03	12	08	01	06	11
3	05	01	06	13	01	03	17	00	09	07	02	01	06	05	05	03	08	06
4	12	04	02	21	01	05	13	00	05	15	02	05	13	04	05	07	04	06
5	16	04	02	23	00	05	15	01	07	13	02	05	11	05	04	24	04	08
6	16	01	02	13	01	05	26	01	10	24	02	02	15	03	06	21	03	06
7	51	06	07	24	01	21	26	01	06	37	02	05	42	06	12	44	03	08
8		04	69		01	23		01	16		02	31		06	28		06	24
9		06			06			02			10			05			06	
10		59			88			93			68			22			25	

TABLE II.—Continued

Experiment.	25			26			27			28			29			30		
Position.	V	L	T	V	L	T	V	L	T	V	L	T	V	L	T	V	L	T
1	01	63	23	00	32	10	00	28	17	01	08	04	01	38	28	00	04	08
2	06	08	28	00	05	14	01	07	20	05	06	10	03	11	19	01	04	20
3	11	04	08	00	05	04	01	04	12	23	09	09	05	07	08	01	12	08
4	06	01	13	00	20	03	04	04	06	18	11	09	19	02	07	03	05	09
5	12	01	06	03	08	04	05	03	06	07	06	10	12	04	09	05	06	08
6	18	04	05	05	00	22	16	03	09	16	05	31	18	01	10	13	10	06
7	46	01	08	92	00	42	73	04	13	30	06	16	42	03	13	77	09	13
8		03	09		05	01		06	17		12	11		03	06		14	28
9		06			05			12			18			11			17	
10		09			20			29			19			20			19	
Experiment.	31			32			33			34			35			36		
1	01	97	05	04	40	46	14	32	23	17	13	13	13	15	83	00	16	Not read.
2	09	01	21	04	04	13	05	02	12	07	04	08	06	08	10	01	03	
3	17	00	15	04	04	07	06	05	08	06	04	03	21	07	01	01	04	
4	23	00	13	09	08	03	07	04	08	10	07	04	20	09	01	09	14	
5	26	01	13	11	04	03	07	06	08	11	05	04	16	08	01	20	06	
6	17	00	12	24	04	04	14	07	07	20	07	05	14	05	01	24	07	
7	07	00	17	44	06	07	47	01	10	29	09	16	10	06	02	45	04	
8		00	04		07	17		09	24		07	47		12	01		07	
9		00			06			10			10			19			07	
10		01			17			24			34			11			32	
Experiment.	37			38			39			40			41					
1	04	04	Not read.	01	44	14	05	19	52	00	10	09	01	18	29			
2	00	01		06	11	12	11	08	04	01	10	13	00	06	05			
3	01	06		12	05	08	10	04	04	00	12	15	01	04	06			
4	09	08		17	06	06	16	08	04	00	09	18	09	06	11			
5	09	08		14	06	05	19	08	04	00	13	18	22	04	12			
6	32	07		16	04	06	12	10	04	00	10	12	23	06	09			
7	45	06		34	04	08	27	05	06	99	09	09	44	04	14			
8		03			09	41		06	22		09	06		03	14			
9		09			06			11			09			06				
10		48			05			21			09			41				



TABLE III.  
Data of others.

Compilation of published data for comparative purposes.						
Schuett (1934) <sup>1</sup>			Volume of Aquaria.		Two aquaria of similar shape were used but the dimensions were not given.	
			7,500 cc.	15,000 cc.		
	Companions.	Meters per Hour.				
		0	200—	150—		
		3	50—	80—		
	7	90+	40+			
	15	110+	90+			
Escobar, Minahan and Shaw (1936) <sup>2</sup>			Volume of Aquaria.			
			1,625 cc.	3,250 cc.	4,875 cc.	6,500 cc.
	Fish.	Companions.	Meters per Hour.			
			A	0	83.40	83.44
	A	3	17.26	55.47	32.54	58.43
	B	0	103.40	69.43	61.95	100.09
	B	3	39.10	39.65	13.08	50.04
	C	0	81.06	59.58	17.88	108.69
	C	3	24.15	51.84	51.14	17.58
Comparative travel of <i>Carassius</i> from all data.						
	Tank Size.	No. of Alone.	With 3 Companions.	Number of Observation Periods.	Difference.	Values Alone Reduced to Unity. Then Value with +3 =
Escobar	1 <sup>3</sup>	92.84	27.58	47	65.26	.30—
Escobar	2 <sup>3</sup>	73.95	48.20	47	25.75	.64—
Escobar	3 <sup>3</sup>	50.87	27.03	47	23.84	.53+
Escobar	4 <sup>3</sup>	109.07	48.77	47	60.30	.45—
Schuett	5	200.00±	50.00±	?	150.00±	.25
Schuett	6	150.00±	80.00±	?	70.00±	.53+
B. & N.	7	76.77	31.55	22	45.22	.41+

<sup>1</sup> Approximate values picked from the published graph.

<sup>2</sup> Heterotypic associations omitted from this Table. Fish A and B: each value represents the mean of 20 separate 20-minute periods. Fish C: each value represents the mean of 7 separate 20-minute periods. The aquarium used measured 24 x 12 x 24 cm. deep and only the volume of water was varied.

<sup>3</sup> These values are weighted A & B—20, C—7. (Range 75 to 34)

TABLE IV.  
Comparative travels of *Carassius* in certain experiments.

Rate of Travel M/H.					
Exp. No.	Fish.	Minimum.	Mean.	Maximum.	No. of Periods.
Alone.					
1-6	A	72.96	86.00	101.45	6
15-22	B	49.38	69.84	89.48	8
With 3 Companions.					
7-11	A	17.17	30.48+	42.37	5
12-14	B	14.91	36.66+	50.70	3
Averages.					
Alone		72.96	76.77—	101.45	14
3 Companions		14.91	31.55+	50.70	8

TABLE V.  
Mean distribution values for Fish A and B, expressed in percentage.

	A (1-6)			B (15-22)			Average 14		
	V	L	T	V	L	T	V	L	T
Alone.	19	6	56	01	16	15	8	12	33
	14	7	8	02	3	10	7	5	8
	12	4	4	9	2	4	10	2	4
	9	3	4	17	1	3	14	2	4
	10	3	3	18	2	4	15	2	4
	10	2	4	23	2	4	18	2	4
	26	6	6	30	2	7	28	4	7
		8	15		3	53		5	36
		14			7			10	
		47			62			56	
With 3 Companions.	(7-11)			(12-14)			8		
	7	5	12	5	01	2	6	3	8
	16	6	17	21	01	6	18	4	13
	21	10	20	20	4	13	21	8	18
	18	13	16	18	5	16	18	10	16
	14	18	15	10	11	11	12	16	13
	4	15	13	8	14	12	6	15	13
	20	14	06	18	6	12	19	11	8
		9	01		8	28		8	11
		6			11			8	
		4			39			17	

Effect of light on position and speed.

Exp. No.	Watts.	% at Surf.	% at Bott.	% Above Mid.	% Below Mid.	Speed.
35	0	13	10	40	60	95.10
31	10	01	07	39	61	46.49
32	40	04	44	17	82	92.85
33	100	14	47	29	71	86.95
34	200	17	29	35	65	87.48

TABLE VI.

Movements of animals in a shallow circular pan 6 feet in diameter, 2 inches deep.

Fishes.				
No. on Text-fig. 2.	Species.	Clockwise Loops.	Counter-clockwise Loops.	Direction at End of Path.
1	<i>Carassius auratus</i> No. 1	1	1	Counter-clockwise.
2	<i>Carassius auratus</i> No. 2	0	0	Counter-clockwise.
3	<i>Lebistes reticulatus</i> ♀	0	1	Counter-clockwise.
4	<i>Brachydanio rerio</i>	1	1	Counter-clockwise.
5	<i>Villarius catus</i>	0	0	Counter-clockwise.
Total		2	3	

Snails (First Trial).				
				Length of Observation.
Text-fig. 3	<i>Physa</i> No. 1	0	3	10.0 min.
6	<i>Physa</i> No. 2	3	0	13.5
6	<i>Physa</i> No. 3	0	1	16.5
4	<i>Planorbis</i> No. 1	0	0	12.5
6	<i>Vivipara</i> No. 1	1	0	30.0
6	<i>Vivipara</i> No. 2	1	0	30.0

Snails (Second Trial).				
Text-fig. 3	<i>Physa</i> No. 1	0	0	2.5
6	<i>Physa</i> No. 2	0	1	8.5
6	<i>Physa</i> No. 3	0	2	26.0
4	<i>Planorbis</i> No. 1	0	1	22.5

Snails (Third Trial).				
Text-fig. 6	<i>Physa</i> No. 3	1	4	24.0
4	<i>Planorbis</i> No. 1	0	1	

Snail (Fourth Trial).				
Text-fig. 4	<i>Planorbis</i> No. 1	0	0	
TOTAL		6	13	

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## 2.

A Study of the Anoplocephaline Cestodes of  
North American Rabbits.<sup>1</sup>

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(Text-figures 1-23).

## 1. INTRODUCTION.

Previous work on the anoplocephaline cestodes of North American rabbits has resulted in much confusion. Observations on internal anatomy, time of appearance of genital primordia, number of testes and other morphological details are so lacking in agreement that any interpretation is difficult. Baer (1927) and Sprehn (1932) have incorrectly cast all American leporine species of the genus *Cittotaenia* into synonymy with the European species *C. pectinata* (Goeze, 1782). The purpose of the present investigation was to secure precise information on the North American representatives of this genus, correct the errors, and eliminate the confusion that has existed in the knowledge of the rabbit cestodes of the family Anoplocephalidae.

## 2. ACKNOWLEDGEMENTS.

The present study was suggested by Professor Horace W. Stunkard and carried out under his direction. The author wishes to thank Professor Stunkard for helpful criticisms, for the loan of the European material used in comparison, and for the use of his private library. Grateful acknowledgement is also extended to Dr. Maurice C. Hall, U. S. Bureau of Animal Industry, U. S. Department of Agriculture, for the privilege of studying original material deposited in his care. The kindness of Dr. R. V. Boughton of the University of Manitoba, in lending specimens of *Cittotaenia pectinata americana*, is recognized. Lastly, the author gratefully acknowledges the assistance of Marion E. Arnold for criticisms and aid in the preparation of this paper.

## 3. MATERIALS AND METHODS.

The material used in this study consisted of both North American and European species. Specimens of all the American species and four of the five European ones provided material for a comprehensive treatment of the subject. *Andrya rhopalocephala* from European hares is rare and no material of that species was available. Since doubt has been expressed con-

<sup>1</sup> Contribution from the Biological Laboratory, New York University, University Heights, New York.



cerning the specific distinctness of the North American species, a detailed comparison has been made between North American and European forms.

Specimens of *Cittotaenia denticulata* (Rudolphi, 1804), *C. etenoides* (Railliet, 1890), *C. pectinata* (Goeze, 1782), and *Andrya cuniculi* (Blanchard, 1891) were loaned to the writer by Professor Stunkard, who collected them during 1931 and 1932 from the vicinity of Hamburg, Germany.

The American specimens of the family Anoplocephalidae were obtained from various sources. The writer examined the intestines of 9 cottontail rabbits, *Sylvilagus floridanus mallurus*, killed near New York City; 7 of the same species from Boylesville, Pennsylvania; 7 from cottontails killed in northern New York State; and 156 from cottontails, *Sylvilagus floridanus alacer*, killed near Wichita, Kansas. The material in the last two groups was obtained from slaughter houses in New York City. All the parasites were killed and fixed in a saturated solution of corrosive sublimate and were washed, stained, dehydrated, cleared, mounted and studied either as sections or *in toto*. Alcoholic and mounted specimens of the genera *Cittotaenia* and *Schizotaenia* were secured through the kindness of Dr. M. C. Hall. Similar specimens of *C. pectinata americana* were loaned by Dr. R. V. Boughton.

#### 4. HISTORICAL REVIEW.

The subfamily Anoplocephalinae was erected by Blanchard (1891), and the family Anoplocephalidae by Kholodkovsky (1902). Fuhrmann (1907) characterized the family Anoplocephalidae as follows: "Scolex meist kugelig, seltener gestreckt, unbewaffnet; Saugnäpfe verhältnismässig gross; Hals fehlt; Glieder kurz und breit; Genitalien einfach oder doppelt. Genitalpori randständig; Eier oft mit einem 'birnförmigen Apparat.' In Säugetieren und Vögeln." In his recent monograph, Fuhrmann (1931) gave a more extended diagnosis of the family. He stated: "Scolex immer ohne Rostellum. Glieder meist breiter als lang. 1 oder 2 Genitalapparate in einer Proglottis. Genitalöffnung beidseitig, einseitig, regelmässig oder unregelmässig alterierend. Weibliche Genitalöffnung oft verschwindend, selten fehlend. Hoden zahlreich. Weibliche Geschlechtsdrüsen häufig poral verschoben. Uterus sackförmig, retikulär oder sich in Ei-Kapseln auflösend oder mit 1 bis zahlreichen Paruterinorganen versehen. Eier mit 3 Hüllen, von welchen die innerste oft einen birnförmigen Apparat aufweist. Entwicklungsgeschichte vollständig unbekannt. In Reptilien (2 Genera), in Vögeln (7 Genera), in Säugern (21 Genera)."

Five species of anoplocephaline cestodes occur in European hares and rabbits. Three of them belong to the genus *Cittotaenia*, the others to the genus *Andrya*. The American leporine cestodes belong to the genera *Cittotaenia* and *Schizotaenia*. Although the genus *Andrya* is represented in North America, species have not yet been found in rabbits and hares. To facilitate description and avoid repetition, the diagnostic features of the three genera are listed.

*Andrya* Railliet, 1893, Anoplocephalinae: Segments much broader than long except in most distal parts of strobila. Single set of reproductive organs in each segment; genital pores irregularly alternate. Testes mostly on aporal side of segment; female genitalia on poral side. Uterus typically reticular to saccular. Pyriform apparatus present. Adults in mammals.

*Type species:* *A. rhopalocephala* (Riehm, 1881).

*Cittotaenia* Riehm, 1881. Anoplocephalinae: Segments broader than long. Double set of reproductive organs in each proglottid; genital pores in each lateral wall. Uterus saccular. Pyriform apparatus present. Adults in mammals and birds.

*Type species:* *C. denticulata* (Rudolphi, 1804) Stiles, 1896.

*Schizotaenia*, Janicki, 1906. Anoplocephalinae: Segments much broader

than long. Single set of reproductive organs to each segment; genital pores typically alternate. Testes in median field or segment; female genitalia slightly to aporal side. Uterus reticular. No pyriform apparatus present. Adults in mammals.

*Type species: S. decrescens* (Diesing, 1856).

A brief historical account of each species considered in the present paper is given later with the specific description. For more detailed historical data, the reader is referred to the original sources cited in the bibliography.

## 5. ANOPOLOCEPHALINE CESTODES FROM NORTH AMERICAN HARES AND RABBITS.

Anoplocephaline cestodes were first reported in North American rabbits by Curtice (1888), who described supposedly the early larval stages of *Taenia pectinata* in *Lepus sylvaticus*.

At present, four species of anoplocephaline tapeworms are recognized in North American hares and rabbits: (1) *Schizotaenia americana* (Stiles, 1895) (= *Andrya americana* = *Andrya americana leporis* = *Bertia americana* = *Bertia americana leporis* = *Schizotaenia americana leporis*); (2) *Cittotaenia perplexa* (Stiles, 1895) (= *Ctenotaenia perplexa* = *Cittotaenia mosaica*); (3) *Cittotaenia pectinata americana* Douthitt, 1915 (= *Cittotaenia pectinata* of Lyman, 1902); (4) *Cittotaenia variabilis* (Stiles, 1895) (= *Ctenotaenia variabilis* = *Cittotaenia variabilis variabilis* = *Cittotaenia variabilis angusta* = *Cittotaenia variabilis imbricata*).

### ***Schizotaenia americana* (Stiles, 1895) Janicki, 1906.**

(Text-figs. 1, 10).

This cestode was first described as *Andrya americana leporis* by Stiles (1895), and was transferred by him (1896) to the genus *Bertia* on the basis of its resemblance to *Bertia americana* (Stiles, 1895). Stiles, 1896, from the porcupine. Stiles postulated that *B. americana leporis* might eventually be elevated to specific rank, but that his five poorly preserved specimens did not warrant such a step. The material was collected by C. Curtice from *Lepus* sp. and the locality in the United States from which it was taken is unknown. Stiles and Hassall (1902) proposed the name *Bertiella* for *Bertia*, since the latter was preoccupied.

Cohn (1906) stated that *Bertia americana* was synonymous with *Taenia laticephala* Leidy. He retained the genus *Bertia* (he had apparently not seen Stiles' and Hassall's new allocation of the species), but placed the specific name, *americana*, in synonymy.

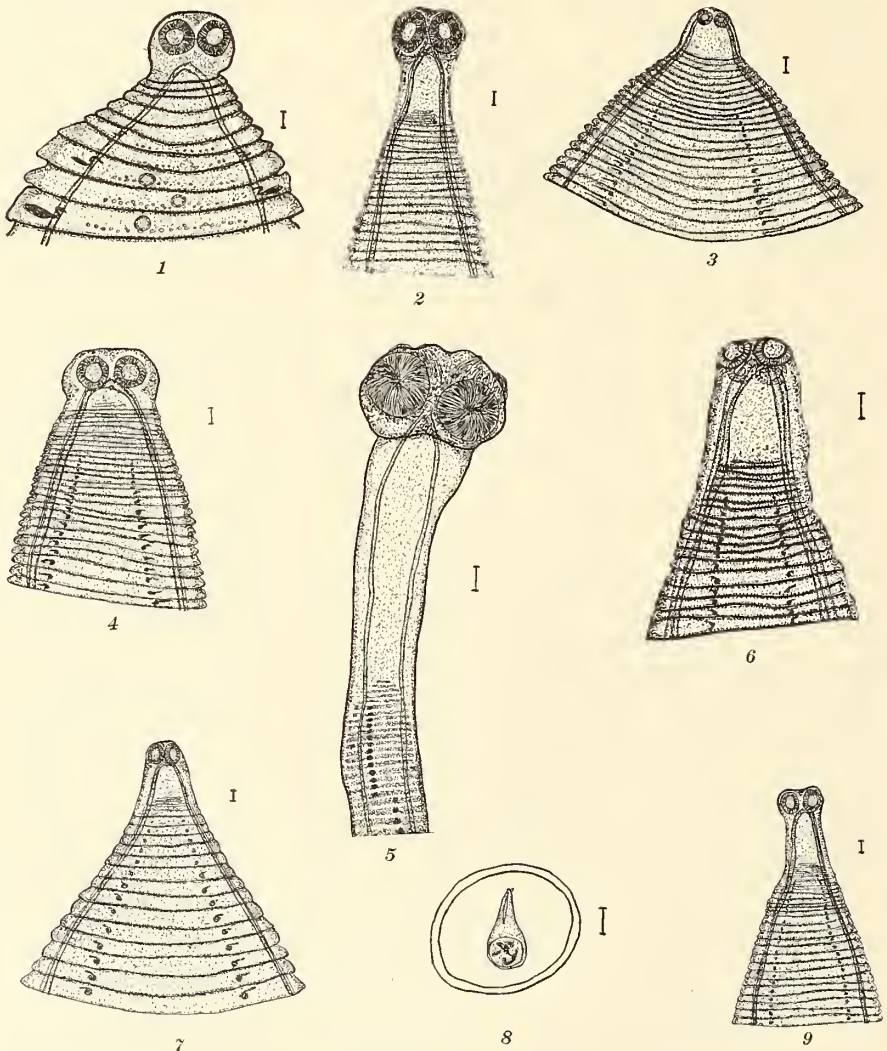
In his description of the cestodes of mammals, Janicki (1906) erected the new genus *Schizotaenia* with *S. macrorhyncha* (Rudolphi, 1810) as type and in it he included *Bertia americana* (Stiles, 1895) and *Bertia americana leporis* (Stiles, 1895).

Douthitt (1915) declared that the variety *Schizotaenia americana leporis* (Stiles, 1895) should be dropped in favor of *Schizotaenia americana*. He stated that the variety was too little known and too incompletely described to permit any distinction from *S. americana*. Douthitt gave sound and logical arguments to disprove Cohn's suggestion that *Bertia americana* and *Taenia laticephala* Leidy were identical.

Meggitt (1924) reestablished *Schizotaenia americana leporis* as a valid species. He reduced the species *S. americana*, which is from the porcupine, to synonymy with *S. laticephala*. In this he followed Cohn's contention and disregarded Douthitt's argument.

Baer (1927) removed *Schizotaenia americana* from synonymy with *S. laticephala*. Since he did not mention *S. americana leporis*, he apparently followed Douthitt and considered the leporine variety identical with the porcupine species.

Sprehn (1932), in his *Lehrbuch der Helminthologie*, did not even men-



Text-figures 1-9.

Abbreviations: c—cirrus sac. e—excretory duct. n—nerve fiber. o—ovary. p—pars prostatica. r—seminal receptacle. s—shell gland. t—testis. u—uterus. v—vitelline gland. va—vagina. vd—vas deferens. vs—seminal vesicle. All measurements are to a scale of 0.1 mm., with the exception of Text-figure 8 in which the scale is 0.01 mm. All drawings are camera lucida.

1. Scolex, *Schizotaenia americana*. 2. Scolex, *Cittotaenia variabilis*. 3. Scolex, *Cittotaenia perplexa*. 4. Scolex, *Cittotaenia denticulata*. 5. Scolex, *Andrya cuniculi*. 6. Scolex, *Cittotaenia pectinata americana*. 7. Scolex, *Cittotaenia pectinata*. 8. Ovum, *Cittotaenia denticulata*. 9. Scolex, *Cittotaenia ctenoides*.



tion the genus *Schizotaenia*, or give Janicki as a reference. He also failed to mention either *Bertiella americana* or *B. americana leporis*, although he recognized the generic name, *Bertiella*, proposed by Stiles and Hassall (1902).

The writer was fortunate to obtain a cotype of Stiles' original material of *Schizotaenia americana leporis* (U. S. Nat. Mus. 1170).

Since the specimen was incomplete and in poor condition, the total length and number of proglottids could not be determined. The fragment, consisting of 75 proglottids, measured 33 mm. in length and 6.5 mm. in maximal width. A neck, if present, was too contracted to be recognizable. The scolex (Text-fig. 1) was 0.63 mm. wide (Stiles found it to be 0.64 mm.) and the suckers measured 0.25-0.26 mm. in length and 0.21-0.25 mm. in width. This is a wider variation than found previously in either *Schizotaenia americana* or its variety, *S. americana leporis*.

The male genital primordia with evidences of the male ducts appeared first in the sixth proglottid. The cirrus and cirrus sac were well developed by the 20th segment, and the cirrus was seen extruded in the 23rd. Douthitt stated that the genital primordia were present in the first segment. According to Douthitt, sexual maturity was attained in the 80th proglottid (Text-fig. 10). The cirrus sac, containing the seminal vesicle and a long thin cirrus, was very muscular, especially at its proximal end. It measured as much as 0.69 mm. in length. It was Douthitt's opinion that part of the seminal vesicle was outside the cirrus sac. In one of the best preserved proglottids, 65-70 testes (Stiles reported 50) were observed in an irregular row in the distal half of the proglottid. The convoluted vas deferens extended from the region of the ovary to the cirrus sac and, just before it entered the latter, it was surrounded by glandular cells, probably the pars prostatica. The cirrus sac opened to the exterior at approximately the middle of the lateral margin. The vagina emptied just below the male opening. There were indications of a genital papilla.

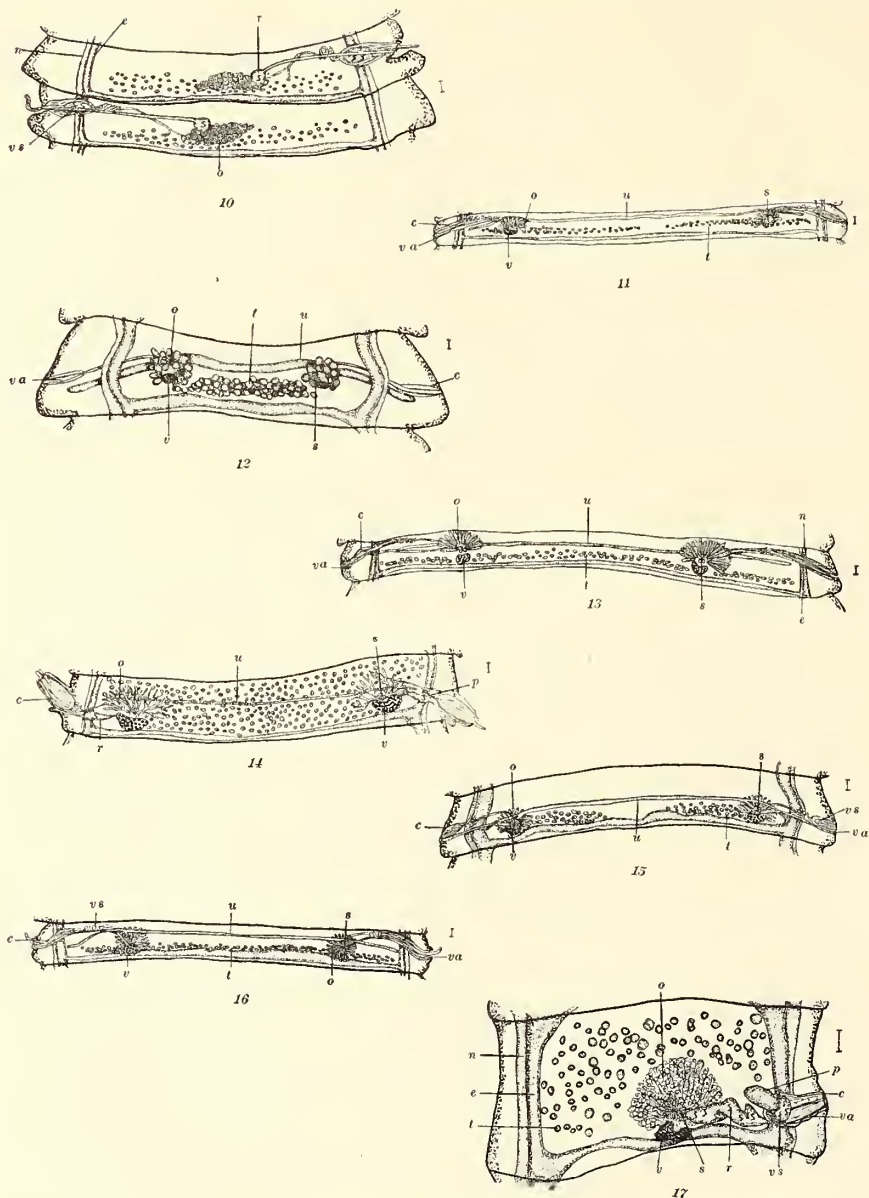
The primordium of the seminal receptacle first appeared definitely in the eighth segment, although indications were seen in the seventh proglottid. The structure present was rather spherical and was found alternately to the right and left of the median line. The details of the female reproductive system could not be made out. Only two ovaries were measured and their probable widths were 0.53 and 0.63 mm.; Douthitt's measurement of the ovary width was 1.3 mm. The uterus arose from the female genital complex as a fan-shaped structure, and was filled with eggs by the 58th segment. The ova measured 30-40  $\mu$  in diameter, with an average of 39  $\mu$ . According to Douthitt, the outer embryonic membrane ranges from 55-61  $\mu$  in diameter.

Comparison of the specific diagnoses (Stiles, 1896) of *Bertia americana* and *B. americana leporis* disclosed only minor differences which may be regarded as individual variations rather than specific characters. After examination of specimens of *S. americana leporis*, the writer agrees with Douthitt and Baer that the variety name should be suppressed.

From the above description and from a historical review, the following specific diagnosis may be derived.

*Diagnosis: Schizotaenia americana* (Stiles, 1895) Janicki, 1906. Strobilae from 23-47 mm. in length, and from 5-6.5 mm. in maximal breadth. Number of proglottids may exceed 95. Scolex varies from 0.6-0.7 mm. in breadth. Neck absent, strobilization beginning immediately. Genital organs single; pores lateral and regularly alternate. Male genital primordia appear first at the 6th segment; the female, between the 7th (?) -14th proglottids. Testes, 50-70 in number, found in an irregular row in distal half of proglottid. Muscular cirrus sac contains the seminal vesicle and a long thin cirrus. The vagina opens just below the cirrus sac, and the two tend to form a genital papilla. Ovary usually indistinct, median (?). Douthitt reported it was 1.3 mm. in width. Uterus arises from female genital complex in fan-like fash-





Text-figures 10-17.

Abbreviations: c—cirrus sac. e—excretory duct. n—nerve fiber. o—ovary. p—pars prostatica. r—seminal receptacle. s—shell gland. t—testis. u—uterus. v—vitelline gland. va—vagina. vd—vas deferens. vs—seminal vesicle. All measurements are to a scale of 0.1 mm. All drawings are camera lucida.

10. Mature proglottid, *Schizotoma americana*. 11. Mature proglottid, *Cittotaenia perplexa*. 12. Mature proglottid, *Cittotaenia variabilis*. 13. Mature proglottid, *Cittotaenia pectinata americana*. 14. Mature proglottid, *Cittotaenia denticulata*. 15. Mature proglottid, *Cittotaenia ctenoides*. 16. Mature proglottid, *Cittotaenia pectinata*. 17. Mature proglottid, *Andrya cuniculi*.

ion to fill median field. Ova range from 30-40  $\mu$  in material studied, but vary from 55-61  $\mu$ , according to Douthitt.

*Hosts*: Yellow-haired porcupine, *Erethizon epixanthes*; Canadian porcupine, *E. dorsatus*; and *Lepus* sp.

*Habitat*: Wyoming and New York.

### ***Cittotaenia perplexa* (Stiles, 1895).**

Stiles and Hassall, 1896.

(Text-figs. 3, 11).

This species was described by Stiles (1895) as *Ctenotaenia perplexa*, but was later transferred (Stiles and Hassall, 1896) to the genus *Cittotaenia* for reasons of priority. Later in 1896, Stiles published an inclusive diagnosis of the species.

In 1908, Hall described this same form as *Cittotaenia mosaica*, and later (1912) listed it from the intestine of *Sylvilagus nuttalli pinetis*, a cottontail rabbit of Colorado. The synonymy was pointed out by Douthitt (1915) who restudied Stiles' original specimens of *C. perplexa* (U. S. Nat. Mus., No. 1110). He found that Stiles' account was in error concerning the length of the cirrus sac and distribution of testes, and that the features which had been used to distinguish *C. mosaica* from *C. perplexa* were not significant differences.

Meggitt (1924) recognized *Cittotaenia perplexa* as a valid species with *C. mosaica* as a synonym. Baer (1927) reduced *C. perplexa* to synonymy with *Cittotaenia pectinata* (Goeze, 1782), which he considered to be exceedingly variable and widely distributed. Sprehn (1932) failed to mention either *C. perplexa* or *C. mosaica*.

In the present study, 26 incomplete specimens of *Cittotaenia perplexa* (Stiles, 1895) and *Cittotaenia mosaica* Hall, 1908, were loaned to the writer by Dr. M. C. Hall, U. S. Bureau of Animal Industry, U. S. Department of Agriculture. The specimens of *C. perplexa* bore the following numbers, U. S. Nat. Mus. Nos. 17226, 17246, and 17449. The specimens of *C. mosaica* were catalogued as U. S. Nat. Mus. Nos. 28429 and 24845. These included cotype material.

Of the fragments studied, the longest contained 150 proglottids and measured 70 mm. in length with a maximal width of 11 mm., the largest breadth yet reported. The greatest length reported previously (Hall, 1908) for *C. mosaica* was 100 mm. The scolex (Text-fig. 3) ranged from 0.32-0.45 mm. in width. The suckers were 0.11 mm. in diameter, which agrees with the measurement of Stiles. The scolex was not differentiated from a short and broad unsegmented neck, which measured from 0.30-0.35 mm. in length.

The genital organs were double and the pores opened anterolaterally. The female genital primordia appeared in the 10th proglottid and their ducts were first evident in the 16th. The male genital primordia first appeared about the 30th and their ducts in the 35th segment. The follicular ovary was well developed in the 70th segment, and disappeared in the 95th. This was correlated with the appearance of eggs in the uterus. This condition agreed with the observations of Hall and Douthitt. The ovary (Text-fig. 11) measured from 0.50-0.61 mm. in width. Douthitt reported a width of 0.85 mm. According to Hall, the yolk gland measured 0.20-0.23 in width, and the shell gland 0.074-0.092 mm. The seminal receptacle was rather large and situated within the longitudinal canals. The vagina was long and thin, opening below the cirrus sac. The ova ranged from 57-69  $\mu$  in diameter. Hall stated that they reached a maximum of 105  $\mu$ .

The testes, 120-125 in number, were in the distal half of the segment. In the younger proglottids, the testes were continuous from lateral canal to

lateral canal, while in more mature segments there was a definite median break in continuity of the chain. This was apparent both in Stiles' cotype material and in Hall's specimens of *C. mosaica*. The testes varied from 0.049-0.065 mm. in diameter. The maximal size recorded by Hall was 0.09 mm. The convoluted vas deferens proceeded from the region of the female glands to the long, narrow cirrus sac, which measured from 0.43-0.50 mm. in length. The maximal size recorded by Hall was 0.64 mm. In some of Stiles' material, Douthitt observed cirrus sacs as long as 0.55 mm.

The following diagnosis may be offered.

*Diagnosis: Cittotaenia perplexa* (Stiles, 1895) Stiles and Hassall, 1896. Mature specimens measure 3.8-10 cm. in length, and 11 mm. in maximal width. The scolex, 0.27-0.45 mm. in breadth, is not differentiated from a short, unsegmented neck region. Proglottids number over 150. Female genital primordia appear first in the 10th and their ducts in the 16th segment. Ovary well developed by the 70th segment; disappears at the 95th. Ovary, 0.50-0.85 mm. in width; ova 50 to 105  $\mu$  in diameter. Male genital primordia appear first in the 30th and their ducts in the 35th proglottid. Testes continuous from longitudinal canal to longitudinal canal in young proglottids, but divided into two groups in more mature ones. Testes 60-125 in number and 0.049-0.09 mm. in diameter. Cirrus sac 0.43-0.64 mm. long.

*Hosts: Sylvilagus nuttalli pinetis, Sylvilagus floridanus mallurus, and Sylvilagus floridanus alacer.*

*Habitat: Colorado, Maryland and Oklahoma.*

### ***Cittotaenia pectinata americana* Douthitt, 1915.**

(Text-figs. 6, 13, 19).

In 1896, Stiles declared that *Cittotaenia variabilis* (Stiles, 1895) is an American variant of *Cittotaenia pectinata* (Goeze, 1782) of Europe. Later discoveries have shown that *C. pectinata americana* of North America is much more closely related to *C. pectinata*. This American cestode was described by Lyman (1902) from *Lepus melanotis*, the common jackrabbit. Hall (1908) noted: "A hasty comparison of specimens of the European and American *C. pectinata* shows certain differences that should be determined as accidental or shown to be of specific or subspecific importance."

Later, Douthitt (1915) concluded that the American form "should be designated as a distinct variety to avoid confusion," and he proposed the name *C. pectinata americana*. This terminology was followed by Meggitt (1924), John (1926), Boughton (1932), and Rees (1933a).

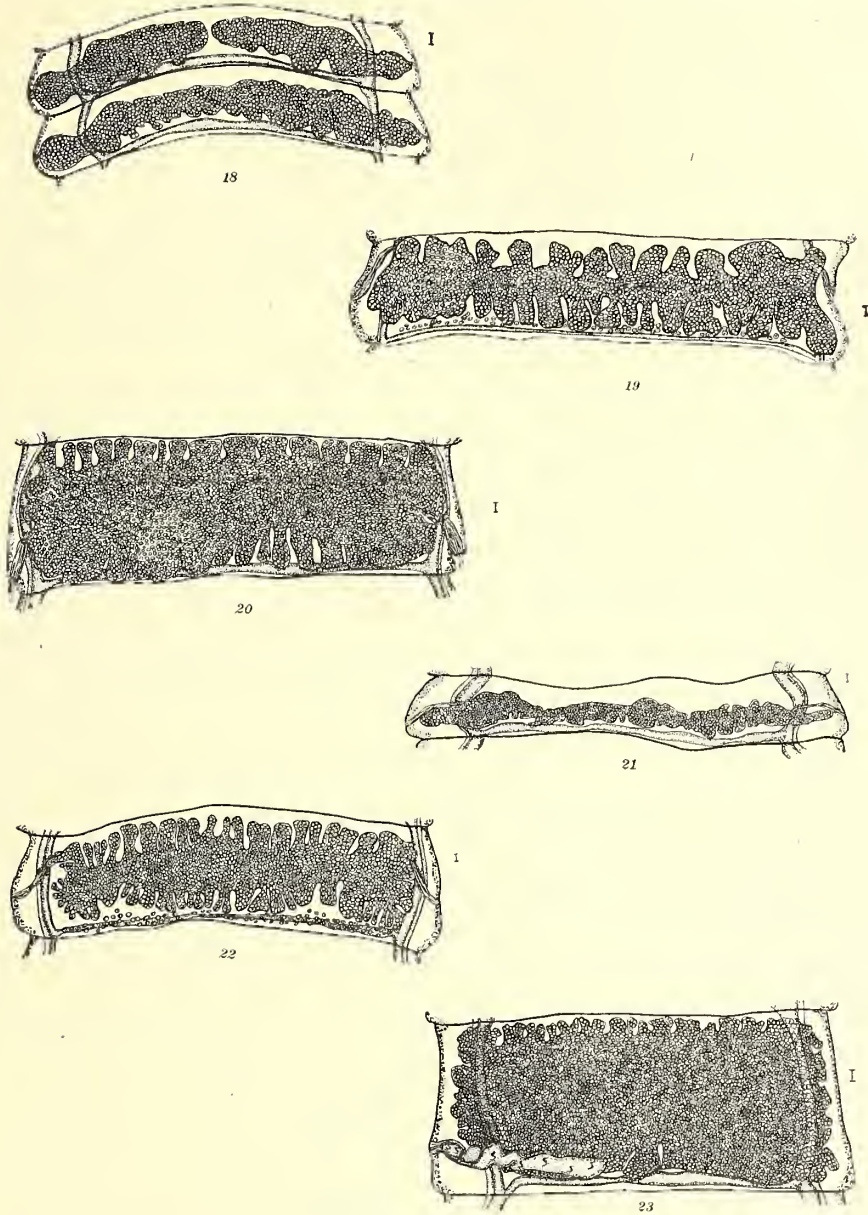
Baer (1927) and Sprehn (1932) failed to recognize any distinctly American variety.

The author was fortunate in obtaining several paratype specimens of *C. pectinata americana* from Dr. R. V. Boughton. The original specimens of *C. pectinata americana*, which were described by Douthitt, were not available.

Ten almost complete specimens were studied. The longest, consisting of at least 360 proglottids, was 110 mm., and the broadest 7.5 mm. The scolex (Text-fig. 6), varying from 0.23-0.30 mm. in width, was set off only slightly from the neck, which measured 0.14-0.30 mm. in length. The suckers, ranging from 0.11-0.17 mm. in diameter, were shallow, situated at an angle, and very close together.

The female genital primordia were indicated first in the 5th-6th, and their ducts in the 6th-7th proglottids. The ovary (Text-fig. 13), averaging about 0.60 mm. in breadth, reached maturity between the 60th-90th segments, and disappeared abruptly between the 90th-145th proglottids (Text-fig. 19). The cirrus sac and, just below it, the vagina, opened into a shallow





Text-figures 18-23.

Abbreviations: c—cirrus sac, e—excretory duct, n—nerve fiber, o—ovary, p—pars prostatica, r—seminal receptacle, s—shell gland, t—testis, u—uterus, v—vitelline gland, va—vagina, vd—vas deferens, vs—seminal vesicle. All measurements are to a scale of 0.1 mm. All drawings are camera lucida.

- 18.** Gravid proglottid, *Cittotaenia variabilis*. **19.** Gravid proglottid, *Cittotaenia pectinata americana*. **20.** Gravid proglottid, *Cittotaenia denticulata*. **21.** Gravid proglottid, *Cittotaenia ctenoides*. **22.** Gravid proglottid, *Cittotaenia pectinata*. **23.** Gravid proglottid, *Andrya cuniculi*.



depression or atrium in the posterior half of the proglottid. The vagina continued mediad and very soon enlarged to form the seminal receptacle. The latter, thin-walled and irregular in outline, led to the ovarian complex. Ova ranged from 70-130  $\mu$  in diameter, with an average of 80  $\mu$ . The uterus was typically single.

The male genital primordia appeared first in the 37th-45th segments, and their ducts were visible one or two proglottids behind the primary condensation. The testes, about 125 per segment, 0.062-0.11 mm. in diameter, were situated in the posterior half of the proglottid, between the longitudinal excretory canals, posterior to the ovaries. The short vasa efferentia emptied into the vas deferens, which joined the convoluted seminal vesicle located median to the longitudinal excretory canal. The cirrus sac, 1.0-1.76 mm. in length, was well developed and extended mediad from the longitudinal excretory canal.

The following brief diagnosis is proposed.

**Diagnosis:** *Cittotaenia pectinata americana* Douthitt, 1915. Mature specimens may contain 360 proglottids, with a length of 220 mm. and a width of 7.5 mm. Scolex 0.23-0.30 mm. broad; neck 0.14-0.30 mm. long. Female genital primordia appear in the 5th or 6th and their ducts in the 6th or 7th segments. Ovary, about 0.6 mm. in breadth, reaches maturity in the 60th-90th and disappears between the 90th-145th segments. Ova 70-130  $\mu$  in diameter. The male genital primordia appear first between the 37th-45th proglottids, and their ducts in each instance one or two segments later. Testes, 112-125 per proglottid, measure from 0.062-0.11 mm. in diameter. They extend from one longitudinal excretory canal to the other, in the posterior half of the segment. Cirrus sac, 1-1.76 mm. long, extends mediad from the longitudinal excretory canal.

**Hosts:** *Lepus californicus melanotis* and *Lepus americanus*.

**Habitat:** Nebraska, Kansas and western Canada.

After a careful comparison of *C. pectinata americana*, of North America, and *C. pectinata*, of Europe, it was felt that the only justifiable allocation of these species is to retain the former as a variety of the latter. The chief difference between the two is that *C. pectinata* attains a length of 400 mm. with 190 proglottids, whereas *C. pectinata americana*, with a length of 220 mm., has more than 360 segments. This difference is distinctive and worth variety rank, considering that the specimens were from different hosts and from different continents. On the other hand, careful comparison affords no justification in separating them by more than variety status. The writer, therefore, agrees with Douthitt (1915) that the American representative of *C. pectinata* should be designated as a variety, *C. pectinata americana*.

### ***Cittotaenia variabilis* (Stiles, 1895).**

Stiles and Hassall, 1896.

(Text-figs. 2, 12, 18).

This species was described by Stiles in 1895 as *Ctenotaenia variabilis*. The next year, Stiles and Hassall transferred it to the present genus because of priority. Stiles felt proper classification of *C. variabilis* necessitated breaking up the species into three varieties: *C. variabilis variabilis*, *C. variabilis angusta*, and *C. variabilis imbricata*. These varieties were recognized by Lyman (1902) but not by Hall (1908), Douthitt (1915) or John (1926). Meggitt (1924) considered the varieties as synonyms of *C. variabilis*.

In the present study some of Stiles' original material of *C. variabilis* and 97 other specimens of this species were studied. Maximal length of

strobilia was 450 mm., with as many as 750 proglottids, and maximal width was 10.5 mm. The scolex, measuring 0.44-0.61 mm. in breadth, was typically set off from the neck, although in a few contracted specimens there was no line of demarcation (Text-fig. 2). The suckers, spherical in outline, varied from 0.16-0.28 mm. in diameter and averaged 0.21 mm. The neck measured from 0.26-0.84 mm. in length, with an average of 0.50 mm.

The female genital primordia appeared first between the 40th-50th and their ducts between the 95th-105th segments (Text-fig. 12). The follicular ovary measured from 0.48-0.71 mm. in width. The seminal receptacle, first differentiated at about the 160th segment, lay median to the longitudinal excretory canal, with its proximal end near the ovarian complex. Near its origin, the oviduct was joined by the duct from the seminal receptacle and the combined duct received shortly those from the yolk and shell glands. The tubular uterus then proceeded to the saccular uterus which was either single or double. The opening of the vagina was immediately below that of the cirrus sac. The ova ranged from 52-68  $\mu$  in diameter, with an average of 64  $\mu$  (Text-fig. 18).

The first appearance of the male genital primordia was thought to be in the vicinity of the 125th proglottid, although their ducts were not located definitely until the 175th. The testes were confined between the two ovaries in the distal half of the segment. They numbered between 60-135 and ranged from 0.053-0.071 mm. in diameter, with an average of 0.062 mm. The short vasa efferentia emptied into the vas deferens which proceeded to the highly convoluted seminal vesicle, lying for the most part median to the longitudinal excretory canal. Distally the vesicle joined the small cirrus sac (0.32-0.45 mm. long, averaging 0.38 mm.) lying lateral to the longitudinal excretory canal. The cirrus sac, testes, ovary, and female ducts degenerate in ripe proglottids.

From the above data the following diagnosis may be given.

*Diagnosis: Cittotaenia variabilis* (Stiles, 1895), Stiles and Hassall, 1896. Mature specimens with as many as 750 proglottids attain a maximal length of 450 mm. and a maximal breadth of 10.5 mm. Scolex 0.44-0.61 mm. in width; may or may not be set off from the neck. Suckers 0.16-0.28 mm. in diameter, average 0.21 mm. Neck well defined; length 0.26-0.84 mm., average 0.50 mm. Female genital primordia appear between the 40th-50th and their ducts between the 95th-105th proglottids. Ovary measures 0.43-0.71 mm. in width, with an average of 0.58 mm. Ova 52-68  $\mu$  in diameter, with an average of 64  $\mu$ . Male genital primordia appear about the 125th proglottid and their ducts at the 175th. Testes (60-135) in the distal half of the proglottid between the two ovaries; diameter 0.053-0.071 mm. Cirrus sac small, 0.32-0.45 mm. long, lateral to longitudinal excretory canal.

*Hosts: Sylvilagus floridanus mallurus, S. floridanus alacer and S. palustris.*

*Habitat:* New York, Maryland, Kansas and Pennsylvania.

## 6. CORRELATION OF HOST-PARASITE RELATIONS.

In the present survey, 179 cottontail rabbits were examined. For identification the systematic arrangement of Nelson (1909) was employed. *Sylvilagus floridanus mallurus* was obtained from New York and Pennsylvania, and *S. floridanus alacer* from Kansas. *Cittotaenia variabilis* (Stiles, 1895) was the only cestode recovered. The parasites were usually found near the middle of the small intestine, although more anteriorly in a few cases.

Tables I and II give the data on infection in the rabbits studied.

TABLE I. *Sylvilagus floridanus mallurus*.

Locality.	No. Examined.	No. Infected.	% Infected.
Lake Mahopac, N. Y.	3	2	66 $\frac{2}{3}$
Pinebush, N. Y.	3	1	33 $\frac{1}{3}$
Carmel, N. Y.	1	1	100
New York, N. Y.	2	1	50
Northern New York.	7	6	85.9
Boylesville, Pa.	7	2	28.5
Total.	23	13	56.5

TABLE II. *Sylvilagus floridanus alacer*.

Locality.	No. Examined.	No. Infected.	% Infected.
Wichita, Kan. 1932	28	19	67.8
Wichita, Kan. 1933	50	19	38
Wichita, Kan. 1934	78	32	41
Total.	156	70	44.8

*Cittotaenia pectinata americana* (Douthitt, 1915) is found only in hares, namely, *Lepus californicus melanotis* Mearns and *Lepus americanus* Erxleben. *Cittotaenia perplexa* (Stiles, 1895) and *C. variabilis* (Stiles, 1895) are found only in cottontail rabbits. Both species are present in *Sylvilagus floridanus mallurus* (Thomas) and *Sylvilagus floridanus alacer* (Bangs), while only *Cittotaenia perplexa* has been found in *Sylvilagus nuttalli pinetis* (Allen) and only *C. variabilis* in *Sylvilagus palustris* (Bachman).

#### 7. ANOPLOCEPHALINE CESTODES FROM EUROPEAN HARES AND RABBITS.

##### ***Cittotaenia denticulata* (Rudolphi, 1804).**

Stiles and Hassall, 1896.

(Text-figs. 4, 8, 14, 20).

*C. denticulata*, type species of *Cittotaenia*, was first described by Rudolphi as *Taenia denticulata*. The original description was expanded in later papers (Rudolphi, 1805, 1810). The same species was subsequently described by Baird (1853) as *Taenia goezei*.

The next important work is that of Riehm (1881a), who described this worm first as *Cittotaenia latissima*, gen. nov., sp., nov., and then as a species of *Dipylidium*. *Dipylidium latissima* was transferred to the genus *Taenia* by Neumann in 1888.

*Taenia goezei* Baird was reduced to synonymy with *D. latissima* Riehm by Blanchard (1891) on reexamination of Baird's original material.

Riehm's *D. latissima* was placed in the genus *Ctenotaenia* by Railliet in 1893.

Stiles and Hassall (1896), upon study of the original specimens of Rudolphi's *Taenia denticulata*, Baird's *Taenia goezei*, and Riehm's *Dipu-*



*lidium latissima*, declared that they were all the same species which they recognized as *Cittotaenia denticulata*. Later descriptions of *C. denticulata* include those of Stiles (1896), John (1926), Baer (1927) and Sprehn (1932).

In the present study, 19 specimens of *Cittotaenia denticulata* were examined. They ranged from minute, immature forms to large, fully matured cestodes with as many as 260 proglottids. They measured 0.149-260 mm. in length and 8.5 mm. in maximal breadth (Text-fig. 4). The solices of the immature forms (worms 0.149-10.5 mm. in length) ranged from 0.10-0.50 mm. in width; those of mature worms (21-260 mm. in length) varied from 0.57-0.76 mm. in breadth. The scolex appeared to be rectangular in cross section. There was a short broad neck, not previously reported, which measured from 0.21-0.92 mm., depending on the degree of contraction. The suckers ranged from 0.23-0.30 mm. in diameter, averaging 0.27 mm. The sucker size was in close agreement with that found by other workers.

The female genital primordia were first seen between the 10th-15th, and their ducts between the 17th-40th proglottids. The ovarian follicles were not well developed until the 80th-100th proglottid (Text-fig. 14). The follicles continued to increase in size and then suddenly disappeared between the 135th-175th segments. The ovary measured from 0.32-1.42 mm. in width and averaged 0.97 mm. The disappearance of the ovary is correlated with the presence of eggs in the uterus (Text-fig. 20). The ovaries were found in the posterior two-thirds of the proglottid and just median of the longitudinal excretory canals. The oviduct originated about the middle of the ovarian mass, and after a short distance was joined by the short duct from the bulbous seminal receptacle. The combined duct then passed to the shell gland, where it was joined by the vitelline duct. The tubular uterus then proceeded anteriorly to the saccular uterus. The ova measured from 46-75  $\mu$  in diameter and averaged 61  $\mu$  (Text-fig. 8).

The male genital primordia were first seen between the 35th-60th, their ducts, between the 36th-70th proglottids. The testes increased in number very rapidly after the first appearance of their primordia. The follicles extended between the longitudinal excretory canals and were scattered between the anterior and posterior limits of the proglottid. The testes totaled between 225 and 250, a number very much greater than that previously recorded. Baer and Sprehn reported that there were 100 testes. Stiles and John merely stated that they were numerous. However, Stiles (1896) gave a drawing of one-half of a mature segment of *C. denticulata*. The writer counted the testes represented in that half segment and found that there were 124. Since Stiles worked on the original material of Rudolphi, Baird and Riehm, and his drawing was apparently taken from that material, it seems safe to assume that the number of testes is nearer 225-250 than 100. The vasa efferentia emptied on either side of the proglottid into a vas deferens which proceeded to the cirrus sac containing the seminal vesicle and a large cirrus. The cirrus sac measured from 0.50-0.97 mm. and averaged 0.77 mm. in length, which was within the range given by other workers. The testes ranged from 0.041-0.12 mm. and averaged 0.073 mm. in diameter. This range is much smaller than that given by other authors, but it is inclusive of some of the higher values found by others. The testes tend to disappear in ripe proglottids.

From the above description the following diagnosis may be drawn.

**Diagnosis:** *Cittotaenia denticulata* (Rudolphi, 1804) Stiles and Hassall, 1896. Type of the genus. Mature specimens range 20-800 mm. in length, with as many as 300 proglottids, and from 8-15 mm. in maximal breadth. Scolex 0.57-1.18 mm. wide; 0.43-1 mm. long. Suckers 0.2-0.3 mm. in diameter. The genital primordia appear early. Those of the female system are found between the 10th-15th proglottids, and their ducts between the 17th-40th proglottids. Ovary, 0.32-1.42 mm. in width, becomes well devel-



oped at about the 84th-100th and disappears about the 135th-170th segment. Male genital primordia appear first between the 35th-60th and their ducts between the 36th-70th segments. Testes range from 225-250 in number in mature proglottids, and vary between 0.041-0.12 mm. in diameter. Cirrus sac measures from 0.50-1.12 mm. in length and 0.26-0.3 mm. in width. Ova measure 46-75  $\mu$  in diameter.

*Host: Oryctolagus cuniculus.*

*Habitat: Europe.*

***Cittotaenia ctenoides* (Riehm, 1881).**

Stiles and Hassall, 1896.

(Text-figs. 9, 15, 21).

*Cittotaenia ctenoides* was first described as *Dipylidium leuckarti* by Riehm in 1881. Later it was transferred to the genus *Taenia* by Neumann (1888) and in 1892 it was replaced in the genus *Dipylidium* by the same author.

In 1890, Railliet changed the specific name from *Taenia leuckarti* to *Taenia ctenoides*. R. Blanchard (1891) placed *Dipylidium leuckarti* Riehm in the genus *Moniezia*. Railliet (1893) erected the genus *Ctenotaenia* and placed the species *Taenia ctenoides* in it. The synonymy of this genus with *Cittotaenia* was pointed out by Stiles and Hassall (1896). Later accounts of this species were given by Stiles (1896) (who studied Riehm's type specimens and others from Blanchard's collection), by Baer (1927), and by Sprehn (1932).

The writer examined 100 specimens of *C. ctenoides*, ranging from 6-460 mm. in length and from 1-10.5 mm. in width. The maximal length found was less than that previously reported, while the maximal width was somewhat greater. The scolex was small, although wider than the neck region and proximal proglottids. It measured 0.32-0.48 mm. in width (Text-fig. 9). This range is smaller than that reported by Stiles, Baer or Sprehn, although the higher value was in agreement. The suckers measured 0.12-0.25 mm. in diameter, with an average of 0.16 mm. There was a short broad neck which varied from 0.25-0.42 mm. and averaged 0.32 mm. in length. The neck was not measured by Stiles, and Baer and Sprehn did not mention it. The proglottids reached a number greater than 560. Stiles reported a maximum of 750 proglottids. The original, terminal 10-15 proglottids, when present, were sterile.

The female genital primordia appeared in the first few proglottids, but their ducts were not distinct until the 45th-50th segments. A well developed follicular ovary was first seen in the 130th-160th segments (Text-fig. 15). The ovary then continued to develop and later suddenly disappeared between the 183rd-232nd proglottids. This disappearance of the ovary was correlated with the presence of eggs in the uterus. The ovary measured from 0.40-0.88 mm. in width and averaged 0.61 mm. The oviduct arose posteriorly from the ovary and was joined almost immediately by the duct from the seminal receptacle. The convoluted oviduct proceeded posteriad to join the rather long vitelline duct, in the shell gland mass. The tubular uterus then proceeded antieriad and slightly laterad for a short distance, where it enlarged into the saccular uterus (Text-fig. 21). The ova ranged from 62-69  $\mu$ , and averaged 66  $\mu$  in diameter. This figure is slightly higher than those given by Stiles, Baer, and Sprehn. The seminal receptacle was not clearly delimited. The vagina opened to the exterior immediately below the opening of the cirrus sac. It proceeded as a small tube mediad and slightly posteriad for a short distance and then expanded to form the seminal receptacle. The seminal receptacle gradually narrowed to a duct which proceeded antieriad and mediad to join the oviduct.

The male genital primordia appeared first between the 85th-100th segments, and the ducts were found a few proglottids farther back. The testes were divided into two groups, one on either side of the proglottid, posterior to the ovaries and median to the longitudinal excretory canal. The testes numbered from 35-75 in each group, and the two groups contained approximately the same number of follicles. The number of testes found was less than that given previously by other workers. The testes varied from 0.046-0.081 mm. and averaged 0.056 mm. in diameter. The short vasa efferentia joined the vas deferens which proceeded antieriad and laterad to the cirrus sac. The small lateral cirrus sac, containing the seminal vesicle and a well developed cirrus, varied from 0.16-0.25 mm. in length, with an average of 0.23 mm. These measurements are slightly higher than those reported by Stiles, Baer and Sprehn.

The following brief diagnosis is suggested.

*Diagnosis: Cittotaenia ctenoides* (Railliet, 1890) Stiles and Hassall, 1896. Strobila, of 500-750 proglottids, may attain a length of 800 mm. and a maximal breadth of 10.5 mm. Scolex, 0.32-0.50 mm. wide, is broader than the neck and proximal proglottids. Suckers 0.12-0.25 mm. in diameter. Female reproductive primordia appear very soon after segmentation begins; their ducts at 45th-50th segments. Ovary, 0.40-0.88 mm. wide, develops between 130th-160th, and disappears about 183rd-232nd proglottids. Ova 62-69  $\mu$  in diameter. Male reproductive primordia appear first at 85th-100th segments and their ducts very soon thereafter. Testes, 0.046-0.081 mm. in diameter, arranged in two groups (35-80 in each). Cirrus sac 0.16-0.25 mm. long and 0.138-0.23 mm. wide.

*Hosts: Oryctolagus cuniculus* and *Oryctolagus cuniculus domesticus*.

*Habitat:* Europe.

### ***Cittotaenia pectinata* (Goeze, 1782).**

Stiles and Hassall, 1896.

(Text-figs. 7, 16, 22).

*Cittotaenia pectinata* was first described by Goeze (1782) as *Taenia pectinata* from hares and wild rabbits. His description was vague and inadequate, and pertained to material of more than one species.

Zeder (1800) transferred the species to the genus *Alyselminthes*. His description was supposed to cover *T. pectinata*, but subsequent workers feel he actually studied *Andrya rhopalocephala*. In 1803, Zeder placed *T. pectinata* in the genus *Halysis*.

Rudolphi (1810), Bremser (1824), and Diesing (1850) studied *T. pectinata* but their characterizations for this species were broad enough to include several species.

Riehm (1881) was the first to study the species in detail. After rectifying previous errors, he placed *T. pectinata* in the genus *Dipylidium*. In 1891, Blanchard reported this species at Briançon.

The species was included in the genus *Ctenotaenia* by Railliet in 1893, but Stiles and Hassall (1896) transferred it to the genus *Cittotaenia*.

Stiles (1896) obtained some of Riehm's original material and elaborated Riehm's diagnosis. Stiles summarized the works of previous authors and gave a more complete description.

Douthitt (1915) stated that *C. pectinata* was found only in Europe. This allocation was followed by Meggitt (1924), John (1926), and Rees (1933a).

Baer (1927) claimed that *C. pectinata* was very extensively distributed. He considered all American representatives of the genus *Cittotaenia* in

rabbits to be *Cittotaenia pectinata*. Sprehn (1932) followed Baer in his consideration of this species.

The author studied 29 specimens of *Cittotaenia pectinata* (Goeze, 1782), varying from 0.97-84 mm. in length and from 0.17-8 mm. in maximal breadth. Stiles reported a greater length than this, 400 mm. Blanchard found a width of 10 mm. The small scolex was rarely wider than the proglottids immediately following it. The scolex measured from 0.20-0.35 mm. in width, with an average of 0.28 mm. (Text-fig. 7). The suckers were set at an angle and were very close together. They ranged from 0.071-0.15 mm. in diameter, with an average of 0.12 mm.. The neck region measured from 0.10-0.35 mm. in length and averaged 0.20 mm. The proglottids were always much broader than long and numbered as high as 190. The terminal proglottids were found to be sterile, an anoplocephaline characteristic.

The female genital primordia appeared by the 8th proglottid, while their canals were found between the 10th-15th segments. The ovaries, measured only in mature proglottids, ranged from 0.21-0.67 mm. in width, with an average of 0.48 mm. (Text-fig. 16). The ovary developed steadily from the primordial stage to that found in fully mature proglottids, and then disappeared rather abruptly between the 75th-150th proglottids. The follicles of the ovary were not well developed until the 45th-60th proglottids. The oviduct arose medially from within the mass of the ovary and then proceeded anteriorly. Within a short distance it joined the duct from the seminal receptacle. The oviduct then proceeded posteriorly and soon met the ducts from the vitelline and shell glands. The convoluted tubular uterus passed anteriorly to meet the sacculus uterinus near its posterior limits. The uterus was either double or the two uteri became confluent in the middle of the segment to form a single continuous one. The former type was the one commonly encountered (Text-fig. 22). The ova ranged from 62-67  $\mu$  in diameter and averaged 65  $\mu$ .

The male and female reproductive systems opened to the exterior by a common genital pore, or by two pores which were situated exceedingly close together. The vagina opened to the exterior below the cirrus sac, or into the cirrus sac just at its opening to the outside. The latter condition seemed the more common. The vagina soon expanded into the seminal receptacle, a large, thin-walled structure, which was closely applied to the cirrus sac and seminal vesicle. Medially, the seminal receptacle became a duct that led to the oviduct.

The male genital primordia first appeared between the 25th-45th proglottids, or 1.4-5.6 mm. from the anterior end, and the male ducts between the 27th-47th segments. The testes, in mature proglottids, ranged from 80-160 in number, and averaged 130. They lay along the posterior border of the proglottid, between the longitudinal excretory canals, below the distal half of the ovary. They measured from 0.043-0.077 mm. in diameter, with an average of 0.06 mm. The vasa efferentia emptied shortly into the vas deferens, which proceeded to join the seminal vesicle near the anterior end of the proglottid. The seminal vesicle was much convoluted, and medial to the longitudinal excretory canal. The glandular cells of the pars prostatica surrounded the seminal vesicle. The cirrus sac was thick-walled, muscular and contained a well developed cirrus. The cirrus sac ranged from 0.36-1.03 mm. in length and averaged 0.69 mm. The cirrus sac and the seminal vesicle lay at a slight angle, and the genital pores (one on either side of the segment) were situated in the posterior half of the proglottid.

From the literature and the study of both whole mounts and sections, the specific diagnosis, given below, has been derived.

*Diagnosis: Cittotaenia pectinata* (Goeze, 1782) Stiles and Hassall, 1896. Mature specimens 400 mm. long and 10 mm. wide. Scolex 0.20-0.35 mm. wide. Broad, short neck measures 0.10-0.15 mm. in diameter. Female



genital primordia appear by 8th segment, their ducts, by 10th-15th segment. Ovary, 0.21-0.67 mm. wide, disappears between 75th-150th segments. Ova 54-90  $\mu$  in diameter. Male genital primordia appear first between the 25th-45th, their ducts between 27th-47th segments. Testes, 80-160 in number, 0.043-0.077 mm. in diameter, lying in distal half of proglottid, extend from one longitudinal excretory canal to other. Cirrus sac, 0.36-1.03 mm. in length, extends mediad beyond the longitudinal excretory canal.

*Hosts: Oryctolagus cuniculus, Lepus europaeus, Lepus timidus, Lepus variabilis and Marmota marmota.*

*Habitat: Asia and Europe (Germany, France and England).*

### ***Andrya cuniculi* (R. Blanchard, 1891).**

Railliet, 1893.

(Text-figs. 5, 17, 23).

*Andrya cuniculi*, first described by Riehm (1881) as *Taenia rhopalioccephala*, was placed in the genus *Anoplocephala* in 1891 by Blanchard when he changed the specific name to *cuniculi*. In regard to this transfer, he stated:

"*A. cuniculi* R. Blanchard, 1891 (*Taenia pectinata* Göze, 1782, pro parte; *T. rhopalioccephala* Riehm, 1881).—Chez le Lapin de garenne. Le nom proposé par Riehm ne peut pas être conservé, en raison de son identité avec le nom de *Taenia rhopalocephala*; ce dernier seul est valable: il a la priorité, puisque la ver auquel il s'applique est décrit par Riehm quelques pages avant le *Taenia rhopalioccephala* (3), et d'ailleurs est le seul dont le nom soit correctment formé."

Railliet (1893) erected the genus *Andrya* to contain *A. rhopalocephala* and *A. cuniculi*. Stiles (1896) restudied Riehm's original material and gave his own characterization of this species. He stated that he has never recovered this parasite from rabbits in North America. Douthitt (1915) and Meggitt (1924) both recognized this species as valid, but gave no further characterization of it. Baer (1927) and Sprehn (1932) studied this form, but gave nothing new in their monographs.

The present writer studied 38 specimens of *Andrya cuniculi*. They ranged from 13-325 mm. in length. The maximal breadth obtained was 3.5 mm. These measurements were only about one-third the maximum length and width previously reported. The scolex was large, varying from 0.40-0.67 mm. in diameter. It was definitely set off from a well differentiated neck (Text-fig. 5). The latter measured from 0.80-1.42 mm. in length. The large suckers ranged from 0.16-0.30 mm. in diameter, with an average of 0.25 mm. The immature segments were much broader than long, while the mature proglottids tended toward a quadrate condition. The segments numbered as many as 500. Stiles (1896) reported them to be as many as 800. He undoubtedly had more mature specimens than were studied in this survey. The original 2-7 terminal proglottids were sterile.

The reproductive organs were single. Their genital openings were irregularly alternate on right and left lateral margins (Text-fig. 17), but opened more often on one side than on the other, as previously observed by Stiles. The female genital primordia appeared first about the 5th-10th proglottids, and their ducts between the 95th-110th segments. The ovarian follicles were not well developed until the 225th-275th proglottids. The ovary measured from 0.43-0.50 mm. in width, and was median or on the poral side of the segment. The vagina was distal to the cirrus sac and its openings. It extended mediad to the longitudinal excretory canal and enlarged into the seminal receptacle. The latter extended to the ovarian mass, where it joined the oviduct. The latter duct, upon uniting with the yolk and shell glands, gave rise to the uterus (Text-fig. 23). Stiles (1896) stated that the



latter was characteristically a network structure. The ova measured from 49-57  $\mu$  in diameter, which was within the range given by Stiles (1896).

The male genital primordia were first evident about the 45th segment, and their ducts at the 110th segment. The testes extended between the two longitudinal excretory canals, and the anterior and posterior limits of the proglottid. They practically surrounded the ovary, although they were more predominantly distributed on the side opposite the genital pore. They numbered between 70-90 and varied from 0.049-0.065 mm. in diameter. The vasa efferentia very soon joined the vas deferens. Just before the latter emptied into the cirrus sac, it united with the pars prostatica. The cirrus sac was club-shaped, extended mediad of the longitudinal excretory canal and contained a definite seminal vesicle. The cirrus sac measured from 0.27-0.43 mm. in length. This range is lower than that given by Stiles, but may be explained by the fact that the specimens used in this study were not as mature (long) as those used by Stiles. There seemed to be a tendency for the formation of a genital papilla, which contained both male and female genital openings.

Summarizing the above surveys, the following diagnosis is derived.

*Diagnosis:* *Andrya cuniculi* (R. Blanchard, 1891) Railliet, 1893. Mature specimens, with as many as 800 segments, 1,000 mm. long and 8 mm. wide. Scolex 0.4-0.67 mm. wide. Well differentiated neck, 0.80-1.42 mm. long. Suckers 0.16-0.30 mm. in diameter, with an average of 0.25 mm. Female genital primordia appear first in 5th-10th and their ducts in 95th-110th proglottids. Ovary 0.43-0.50 mm. wide. Ova 49-57  $\mu$  in diameter. Male genital primordia appear first in about 45th proglottid and their ducts in 110th. Testes in median field, 70-90 per segment, varying from 0.049-0.065 mm. in diameter. Cirrus sac, 0.27-0.8 mm. long, extends mediad of the longitudinal excretory canal.

*Hosts:* *Lepus timidus* and *Oryctolagus cuniculus*.

*Habitat:* Europe.

## 8. COMPARISON OF EUROPEAN AND AMERICAN ANOPILOCEPHALIDAE OF RABBITS.

The members of the Anoplocephalidae from North American rabbits show constant differences from those of European rabbits.

*Schizotaenia americana* (Stiles, 1895) and *Andrya cuniculi* (R. Blanchard, 1891) are immediately distinguished from the several species of rabbit cestodes of the genus *Cittotaenia* by the fact that they possess only one set of genital organs to a proglottid. *S. americana* differs from *A. cuniculi* in regularity of alternation of the genital pores, length and width of body, lack of neck, number of proglottids, size of ovary, first appearance of male genital primordia and ducts, and number of testes.

*Cittotaenia denticulata* (Rudolphi, 1804) differs from *C. ctenoides* (Railliet, 1890) in size of scolex, number of proglottids, earliest appearance of female genital ducts, position of ovarian maturity and disappearance, first indication of male genital primordia and ducts, number of testes and their distribution, and size of cirrus sac. It is unlike *C. pectinata* (Goeze, 1782) in maximal length, number of proglottids, first appearance of female genital primordia and ducts, position of ovarian maturity, number and distribution of testes, and location of cirrus sac. *C. perplexa* (Stiles, 1895) is different from *C. denticulata* in maximal length, size of scolex, diameter of sucker, number of proglottids, appearance of ovarian follicles, number and distribution of testes, and location of cirrus sac. *C. denticulata* is dissimilar to *C. pectinata americana* Douthitt, 1915, in maximal length, maximal width, size of scolex, size of sucker, number and distribution of testes, and position of cirrus sac. *C. denticulata* is unlike *C. variabilis* (Stiles, 1895) in maximal length and width, size of neck, number of

proglottids, position of genital primordia and ducts of both male and female reproductive systems, number and distribution of testes, and size of cirrus sac.

*C. ctenoides* is unlike *C. denticulata* in scolex size, sucker diameter, proglottid number, first indication of female reproductive ducts, site of ovarian maturity and disappearance, earliest appearance of male genital primordia and ducts, number and distribution of testes, and size of cirrus sac. *C. ctenoides* differs from *C. pectinata* in maximal length, number of proglottids, first indication of female ducts, ovarian maturity and disappearance, location of male genital primordia and ducts, distribution of testes, and length and position of cirrus sac. *C. perplexa* is distinct from *C. ctenoides* in maximal length, size of suckers, number of proglottids, site of female genital duct appearance, maturity and disappearance of ovary, first appearance of male genital primordia and ducts, and size of cirrus sac. *C. ctenoides* is dissimilar to *C. pectinata americana* in maximal length and width, size of scolex, number of proglottids, first indications of female genital primordia, first appearance of male genital primordia and ducts, maturity and disappearance of ovary, distribution and size of testes, and position of cirrus sac. *C. variabilis* is different from *C. ctenoides* in maximal length, appearance of genital primordia and ducts of both male and female reproductive systems, distribution of testes, and length and position of cirrus sac.

*C. pectinata* differs from *C. denticulata* in maximal length, scolex width, sucker diameter, number of proglottids, location of ovarian maturity, testes number and distribution, and cirrus sac size. *C. pectinata* is unlike *C. ctenoides* in maximal size, number of proglottids, time of appearance of genital primordia and of ducts of both male and female reproductive systems, maturity and disintegration of ovary, distribution of testes and size and location of cirrus sac. The comparison of *C. pectinata* with the next three American species is of especial interest, since Baer (1927) and Sprehn (1932) considered them identical with *C. pectinata*. The latter is distinct from *C. perplexa* in maximal length, first appearance of female genital primordia and their ducts, site of first ovarian follicular development, and distribution of testes in mature proglottids. *C. pectinata* has a variant in *C. pectinata americana* but differs from it in maximal length and breadth and number of proglottids. *C. pectinata* is unlike *C. variabilis* in size of scolex, length of neck, size of suckers, number of proglottids, appearance of primordia and ducts of both male and female reproductive systems, distribution of testes, and length and location of cirrus sac.

*C. perplexa* differs from *C. denticulata* in maximal length, scolex width, sucker diameter, proglottid count, site of earliest complete follicular development and disintegration, testes number and distribution, and cirrus sac location. *C. perplexa* is different from *C. ctenoides* in maximal length, sucker size, number of proglottids, first appearance of female genital canals, location of ovarian follicular maturity and disappearance, earliest appearance of male genital primordia and ducts, and cirrus sac position. *C. perplexa* is unlike *C. pectinata* in maximal length, earliest appearance of female genital primordia and their ducts, location of first ovarian follicular development, and distribution of testes in mature segments. *C. perplexa* is dissimilar to *C. pectinata americana* in maximal length and breadth, maximal number of proglottids, earliest appearance of female ducts, first appearance of the male genital primordia and ducts, testes distribution, and cirrus sac characteristics. *C. perplexa* is distinct from *C. variabilis* in maximal length, scolex size, length of neck, sucker size, number of proglottids, place of appearance of genital primordia and ducts of both male and female reproductive systems, distribution of testes, and size and location of cirrus sac.

*C. pectinata americana* is unlike *C. denticulata* in maximal length, size of scolex and suckers, number of proglottids, number and distribution of



testes, and cirrus sac characteristics. *C. pectinata americana* differs from *C. ctenoides* in maximal length and breadth, number of proglottids, first appearance of female genital ducts, first appearance of male genital primordia and ducts, site of ovarian maturity and disappearance, testes distribution, and cirrus sac size and position. *C. pectinata* is different from *C. pectinata americana*, its variety, in maximal length and breadth, and number of proglottids. *C. pectinata americana* is unlike *C. perplexa* in maximal length and breadth, number of proglottids, first appearance of genital primordia and ducts of both male and female reproductive systems, testes distribution, and cirrus sac size. *C. pectinata americana* is distinct from *C. variabilis* in maximal length and breadth, size of scolex, number of proglottids, first appearance of genital primordia and of ducts of both male and female reproductive systems, testes distribution, and cirrus sac size and position.

*C. variabilis* is divergent from *C. denticulata* in maximal length, length of neck, number of proglottids, appearance of genital primordia and of ducts of both male and female reproductive systems, number and distribution of testes, and size of cirrus sac. *C. ctenoides* is distinct from *C. variabilis* in maximal length, length of neck, earliest appearance of male and female genital primordia and ducts, testes, distribution, and cirrus sac size. *C. variabilis* is dissimilar to *C. pectinata* in scolex width, length of neck, sucker size, segment count, appearance of male and female genital primordia and ducts, testes distribution, and cirrus sac length. *C. variabilis* is unlike *C. perplexa* in maximal length, size of scolex, length of neck, size of suckers, site of appearance of genital primordia and ducts of both male and female reproductive systems, distribution of testes, and length of position of cirrus sac. *C. variabilis* is unlike *C. pectinata americana* in maximal length and breadth, width of scolex, number of proglottids, earliest appearance of genital primordia and ducts of both male and female reproductive systems, distribution of testes, and size and position of cirrus sac.

#### 9. KEY TO SPECIES.

Contrary to the findings of Baer (1927) and Sprehn (1932), the anoplocephaline species of leporine cestodes in North America and Europe are separate and distinct. Representatives of three genera of the Anoplocephalidae have been found in hares and rabbits. The genus *Schizotaenia* Janicki, 1906, is represented by *S. americana* (Stiles, 1895) and this species is found only in North America. The genus *Andrya* Railliet, 1893, is represented by *A. cuniculi* (R. Blanchard, 1891) and is found only in Europe. Finally the genus *Cittotaenia* Riehm, 1881, has members in both North America and Europe and contains six species. They include *C. denticulata* (Rudolphi, 1804), *C. ctenoides* (Railliet, 1890), and *C. pectinata* (Goeze, 1782), all found in Europe, and *C. perplexa* (Stiles, 1895), *C. variabilis* (Stiles, 1895), and *C. pectinata americana* Douthitt, 1915, all found in North America. *C. pectinata* and *C. pectinata americana* are parasitic principally in hares (*Lepus*), whereas the other species of *Cittotaenia* occur chiefly in rabbits (*Oryctolagus* and *Sylvilagus*).

The Anoplocephalidae of rabbits may be distinguished by the following key:

1. (2) Two sets of reproductive organs to a segment. (5)
2. (1) One set of reproductive organs to a segment. (3)
3. (4) Genital pores alternating regularly to right and left lateral margins.  
*Schizotaenia americana*.
4. (3) Genital pores alternating irregularly to right and left lateral margins.  
*Andrya cuniculi*.
5. (6) Cirrus sac extending medial of longitudinal excretory canal. (10).
6. (5) Cirrus sac lying lateral of longitudinal excretory canal. (7).

7. (8) Maximal number of proglottids—300; first appearance of female genital ducts between 17th-40th proglottids; earliest indication of male genital primordia and ducts from the 35th-60th and 36th-70th proglottids, respectively. *Cittotaenia denticulata*.
8. (9) Maximal number of proglottids—750; first appearance of female genital ducts between 45th-50th segments; first indication of male genital primordia and ducts between 75th-100th and 76th-105th proglottids, respectively. *Cittotaenia ctenoides*.
9. (7) Maximal number of proglottids—750; female ducts indicated first between the 95th-105th segments; male genital primordia and ducts originating at 125th-175th proglottids, respectively; well defined neck present. *Cittotaenia variabilis*.
10. (11) Cirrus sac just barely crossing longitudinal excretory canal, and with a maximal length of 0.64 mm.; maximal body length, 100 mm. *Cittotaenia perplexa*.
11. (12) Cirrus sac extending considerably mediad of excretory canal, and with a maximal length of 1.03 mm.; proglottids up to 190; maximal body length, 400 mm. *Cittotaenia pectinata*.
12. (10) Cirrus sac extending much mediad of longitudinal excretory canal; cirrus sac with a maximal length of 1.8 mm.; proglottid number, more than 360; maximal body length, 220 mm. *Cittotaenia pectinata americana*.

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## 3.

The Templeton Crocker Expedition. XIII. Penaeidae from the  
Region of Lower California and Clarion Island,  
with Descriptions of Four New Species.<sup>1</sup>

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(Text-figures 1-34).

[Note: This is the thirteenth of a series of papers dealing with the specimens collected on the Twenty-fourth or Templeton Crocker Expedition of the Department of Tropical Research of the New York Zoological Society; William Beebe, Director. For data on dredges, localities, dates, etc., concerning the capture of specimens treated in this paper, refer to the Volume XXII of *Zoologica*, No. 2 pp. 33 to 46. Unless otherwise noted the catalogue and station numbers referred to relate to the above-mentioned expedition.]

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<sup>1</sup> Contribution No. 550, Department of Tropical Research, New York Zoological Society.

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#### INTRODUCTION.

Of the seventeen or eighteen species of Penaeidae represented in the present collection, more than half were previously known more or less incompletely if at all. There are no less than five species in the collection which have not heretofore been recorded from Pacific America, of which three are new to science; in addition the material aids in the resurrection of a named species not generally recognized as valid and in the completion of descriptions of five species hitherto known only from juveniles or from a single sex, and also assists in the recognition as a new species of one form not included in the collection. That so large a part of the gathering is of the ultimate in systematic value is a tribute not only to the surprising richness of the region but to the capacity of those by whom the material was obtained. I am deeply indebted to Dr. William Beebe, the Director of the Expedition, and to his associates, for so valuable an opportunity to continue a study of the Pacific American peneids.

In a previous paper (Burkenroad, 1936, p. 6), it was stated that whereas the littoral peneids of the Atlantic and Pacific coasts of America are much more nearly related each to the fauna of the other coast than is either to the fauna of any other region, the deep-water peneids of the two regions seem to exhibit the inverse relationship. In explanation of this reversal of degree of relationship, it was suggested that the littoral peneids of the two coasts have had contacts less intimate (in terms of epoch and intensity) with the peneids of other regions than were their contacts with each other supplied by shallow Pleistocene and preceding transcontinental channels. It was suggested that by contrast, the oceanic faunas of the two coasts have presumably had no direct communication since the elevation of the Panama ridge before the late Cretaceous and have at the same time by their oceanic habit perhaps been placed in communication with

the faunas of other regions with relatively greater frequency than have the littoral forms. The new records supplied by the present collection are in agreement with the arrangement suggested above. Of the two newly added deep-water species, *Gennadas sordidus* is otherwise known only from the Indo-Pacific; while *G. scutatus*, although it occurs in the American Atlantic, is also known from the intervening Indo-Pacific regions.

It seems of interest to observe that the proportion of Eusicyoninae to Penaeinae in the region of Lower California is rather different from what seems usual elsewhere, the Eusicyoninae forming a relatively very conspicuous part of the littoral population. Thus, for instance, DeMan, 1911, records as the catch of the *Siboga* in East Indian waters 388 specimens of Penaeinae of about 30 species to 19 specimens of Eusicyoninae of 9 species (a ratio which I believe to be not unusual in unselected collections from most parts of the world). The *Zaca* took 156 specimens of Eusicyoninae of 7 or 8 species to 182 specimens of Penaeinae of 5 species, and the *Pawnee* in 1926 took 92 specimens of Eusicyoninae of 4 species to 43 of Penaeinae of 3 species, in the Lower California region.

#### GENNADAS Bate.

*Gennadas*, Burkenroad, 1936, p. 59.

#### *Gennadas sordidus* Kemp.

*Gennadas sordidus*, Kemp, 1910, p. 177.

*Amalopenaeus sordidus*, Balss, 1927, p. 262.

(Text-figure 1).

*Range*: Indian Ocean off India; Pacific off Lower California, Gulf of California; in midwater.

*Material*: A total of 37 specimens (about one-third of them males) was taken in the Gulf of California in the general neighborhood of Tortuga (Station 139) and San Ildefonso (Station 148) Islands; in the mouth of the Gulf of California (Stations 158 and 159); off the southern tip of Lower California (Station 134), and north of the Revillagigedo Islands (Station 165), at depths above 300 to 500 fathoms both inside and outside the 1,000 fathom contour, as follows:

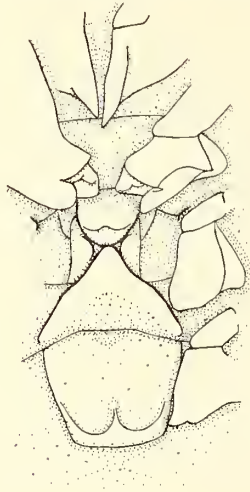
Station 130: T-1 (1 ♂); Station 134: T-2 (2 ♀), T-3 (1 ♀); Station 139: T-2 (1 ♂), T-3 (1 ♂), T-4 (1 ♀); Station 148: T-2 (1 ♀), T-4 (2 ♂, 5 ♀); Station 158: T-4 (2 ♂, 7 ♀); Station 159: T-2 (1 ♂, 2 ♀), T-3 (2 ♂, 4 ♀); Station 165: T-3 (3 ♂, 1 ♀). Cat. Nos. 36,950, 36,951, 36,952, 36,953, 36,954, 36,955, 36,956, 36,957, 36,958, 36,959, 36,960, 36,961.

*Dimensions and Sexual Condition*: Material ranges from adult individuals of carapace length 11 mm., total about 32 mm., to an uncertainly determinable early post-mysis probably of this species, of carapace 2 mm. The petasmas endopods are united in males above 8 mm. carapace length; females may and usually do bear ripened ovaries above 9 mm. Of the twelve fruitful hauls, the six made at 500 fathoms or more accounted for 28 of the 37 specimens; no clear indication of segregation according to size is apparent.

*Remarks*: The present Pacific American catches of *Gennadas sordidus* are unexpected, inasmuch as previous records have suggested a localization of the species in the Indian Ocean.

The female of the species has not previously been described. The thelycum bears a very great resemblance to that of *G. parvus* Bate, from which it differs in the slighter development of the median longitudinal carina of sternite XIV, the more narrowed anterior portion of the triangular

shield of sternite XIII, and the smaller size of the protuberance at the sides of sternite XIII behind the bases of the third legs. The median carina of XIV is variable in length and definition, ranging in form from a short, tooth-like crest at the posterior margin of the sternite to a very low ridge fading out anteriorly before it reaches a third of the way to the anterior margin (although a faint trace of median elevation sometimes reappears on the anterior part of the sternite and is very occasionally continuous with the more perceptible posterior ridge). In *G. parvus* the much stronger carina of XIV displays comparable variations, but seems always to reach beyond the anterior third of the sternite. The protuberance behind the bases of the third legs varies in strength in *G. sordidus* from complete absence to a low and inconspicuous weakly setose swelling (and is even, in one specimen, a conspicuous projection); but it seems never to acquire the strength of its homologue in *G. parvus*, which reaches as far median as to the lips of the openings of the sperm receptacles.



Text-figure 1.

*Gennadas sordidus* Kemp. Thelycum; adult ♀, D. T. R. 36,960, x 13.

The petasma of *G. sordidus* is adequately represented by Balss, 1927, fig. 18. It differs from that of *G. parvus* most conspicuously in that the distoventral lobe is not clearly subdivided, the cleft between the lobules in *G. parvus* being represented in *G. sordidus* only by a slight crenellation of the margin of the lobe and a short vertical crest on its posterior face (somewhat as in *G. tinayrei*); and also in that the accessory and the distomedian lobes are not subdivided, as they are in *G. parvus*.

In my discussion of *Gennadas* in 1936, p. 85, I have stated, on the basis of the undivided form of the distolateral lobe, that "The only other species of which the female is unknown, *G. sordidus* Kemp, undoubtedly belongs to a different section [I], and may be predicted with some confidence to have a thelycum with separated, independent spermathecal orifices;" a prediction which now stands confirmed. In a key to the species (1936, p. 64), however, *G. sordidus* has been placed in Group I A with the species (*G. capensis* and *G. kempi*) in which the distoventral lobe of the petasma is undivided and the orifices of the sperm receptacles very widely separated and not guarded posteriorly by conspicuous prominences; rather than in Group I B of forms (*G. elegans*, *G. brevirostris*, *G. tinayrei*, *G. parvus*) with divided distoventral lobe and guarded and less widely separated spermathecal orifices. The structure of the female of *G. sordidus* is clearly that of Group I B; and it is evident that I was mistaken in ignoring the trace of a



cleft in the distal border of the distoventral lobe of the petasma indicated in Balss' figure (but not, however, in that of Kemp, 1910, plate XIV, figs. 1, 2). It may be observed that both Kemp and Balss have placed the male of *G. sordidus* in its correct relationship, as most closely allied to *G. parvus*.

The diagnostic key published by me in 1936 thus requires to be modified by elimination of I A 1 and transfer of *G. sordidus* to I B 2 b (2) as follows:

I B 2 b (2). MALE. Distolateral lobe much narrower than the distoventral, and not reaching so far distally as does the latter; accessory lobe much larger than the distolateral.

FEMALE. Elevation of XIV with a median longitudinal ridge.

I B 2 b (2) (a) MALE. Division of the distoventral lobe indicated only by a slight crenellation and thickening of the margin; accessory and distomedian lobes entire.

FEMALE. Median longitudinal ridge of XIV very short, not well defined, if present, on the anterior two-thirds of the sternite.

6. *G. sordidus* Kemp; Balss, 1927, ♂ [♀, figure 1].

I B 2 b (2) (b). MALE. Distoventral lobe conspicuously bipartite; accessory lobe tripartite; distomedian lobe bipartite.

FEMALE. Median longitudinal ridge of XIV well defined and extending two-thirds or more the length of the sternite.

7. *G. parvus* Bate; Balss, 1927, ♂ and ♀.

### ***Gennadas scutatus* Bouvier.**

*Gennadas scutatus*, Bouvier, 1906, p. 9; Burkenroad, 1936, p. 83.

*Gennadas clavicarpus*, part, DeMan, 1911, p. 19.

? *Gennadas clavicarpus*, Boone, 1930, p. 129.

*Range*: Cosmopolitan, in midwater.

*Material*: Two female specimens were taken 145 miles north of Clarion Island (Station 165 T-3), 20° 36' N. Lat., 115° 07' W. Long., at a depth above 500 fathoms (Cat. No. 36,962).

*Dimensions and Sexual Condition*: Carapace length 9 mm., total about 31 mm. The specimens equal in length the largest heretofore recorded (Milne Edwards and Bouvier, 1909, p. 194). Both have well-developed ovaries; in one a small mass of material in one sperm-receptacle seems to mark an interrupted mating.

*Remarks*: The record from Pacific America is new.<sup>2</sup>

The present material differs in genital sculpture from that known from the Atlantic and the Indo-Pacific in that the free flap from the anterior margin of the fourteenth sternite is very slender (about three times as long as broad), tapering, and pointed, being widest at the base; the anterior margin of the anterior lip of the sperm receptacles is heavily setose; there are a pair of conspicuous setose prominences between the bases of the fourth pair of legs; and the coxal projection of the fourth legs has an elongate deeply concave distal margin. Comparison of the present specimens and others (including both sexes) taken by the *Arcturus* in the American Pacific, with Atlantic material of *G. scutatus* in the Bingham Oceanographic Collection and with the literature, leads however to the belief that the *Zaca* females are to be considered as an extreme variation falling within the specific limits.

<sup>2</sup> It is possible that the record by Boone, 1930, of "*Gennadas clavicarpus* DeMan" from off Cape Mala, may refer to the present species. However, although Miss Boone's description of the petasma applies to *Gennadas scutatus*, her description of the thelycum applies to *Gennadas propinquus* Rathbun, just as in the account of "*G. clavicarpus*" by DeMan, and what her specimens may actually correspond to therefore seems doubtful.

In females of *G. scutatus* from the Gulf of Mexico and the Caribbean, the free flap of XIV is very broad, not more than one and one-third times as long as wide. In Plate II, figure 3k, DeMan, 1911, of the thelycum of an Indo-Pacific female of *G. scutatus* ("*G. clavicarpus*"), the flap is shown as about one and three-quarters times as long as wide; in Bouvier's figure of a North Atlantic female (1906, fig. 8), as two and one-third times as long as wide. In an *Arcturus* female from the American Pacific the flap is two and one-third times as long as wide. In available Atlantic females the tip of the flap is sometimes truncate or even emarginate, sometimes pointed.

The Atlantic females bear a pair of very inconspicuous and weakly setose prominences, placed just median to the bases of the fourth legs; these prominences, which were overlooked in my previous account, seem the equivalents of the much more conspicuous ones in the *Zaca* females; and indeed, are not very much less distinct in Atlantic specimens than in small *Arcturus* females from the American Pacific.

The inner margin of the coxa of the fourth legs in Atlantic females generally resembles that indicated in DeMan's Plate II, figure 3k, of an Indo-Pacific specimen; in some Atlantic females, however, the distal projection is farther below the coxobasilar articulation and is more pronounced, thus approaching the form characteristic of the Pacific American specimens.

Finally, the petasma of an *Arcturus* male from the American Pacific, as compared with the same organ in Atlantic specimens, seems to show no differences lying outside the range of those fairly considerable variations in relative length of the different lobules which are indicated in the literature.

#### HYMENOPENAEUS Smith.

*Hymenopenaeus*, Burkenroad, 1936, pp. 101, 102.

#### ***Hymenopenaeus doris* (Faxon).**

*Haliporus doris*, Faxon, 1893, p. 214; 1895, p. 191.

*Range*: Off the Pacific coasts of southern Mexico and Guatemala; mouth of the Gulf of California. Midwater (300-500 fathoms) and bottom, in 1,500-2,000 fathoms.

*Material*: One female was taken in the mouth of the Gulf of California (Station 159 T-3, Cat. No. 36,963) at a depth above 500 fathoms.

*Dimensions and Sexual Condition*: The specimen is a juvenile of carapace 9 mm., total length about 29 mm.

*Remarks*: The thelycum of the present small female differs considerably from that of the much larger types of *H. doris* in that the median vertical projection of the posterior margin of the thirteenth sternite has a very bluntly acuminate rather than a truncated distal margin; and the pair of projections laterally flanking the median projection are very much lower than the median one instead of reaching as high as it does. The posterior margin the twelfth sternite lacks the pair of posteriorly directed projections present in the types.

In my opinion, the thelycum described above cannot be that of a juvenile of *H. nereus*, particularly since a strong cusp like that of the adult *H. doris* is present on the fourteenth sternite, instead of the low untoothed ridge of *H. nereus* adult. In Penaeinae, a tooth or spine is usually present on the fourteenth sternite in larval or juvenile stages, which may later disappear in the adult. According, however, to the results of examination of mysis and post-mysis larvae and of juveniles of Solenocerinae, a tooth develops on the fourteenth sternite of this subfamily only in juveniles of species which continue to bear it as adult.

As to whether the present specimen actually refers to *H. doris* rather

than to some undescribed form it is impossible to be certain. However, the thelycum in juveniles of the closely related species *H. laevis* differs from that of adults in somewhat the same manner as, although to a lesser degree than, the thelycum of the present juvenile differs from that of *H. doris*.

A comparison of the present specimen of *H. doris* and of another similar but still smaller juvenile with two adult females of *H. nereus* (the three last-mentioned specimens being undescribed Pacific American material taken by the *Arcturus*), reveals no striking differences between the two forms other than those in genitalia. A less detailed comparison of the female types of *H. nereus* with those of *H. doris* (the males being known in the former species only), made during a visit to the Museum of Comparative Zoology, also indicated that, about as stated by Faxon, the two species agree so closely except in thelycum "that one description would serve for both." Both forms are extremely like *H. laevis* (Bate), and differ from the remainder of the genus [save possibly *H. villosus* (Alcock and Anderson)] in bearing both pterygostomial and branchiostegal spines (cf. Burkenroad, 1936, pp. 103 seq.). The only non-genital differences from *H. laevis* seem to be that the eyes are somewhat larger in the two Pacific American species and the tip of the telson, beyond the lateral spines, is more slender and elongate than in *H. laevis*.

It may be noted that in a preceding reference to *H. nereus* and *H. doris* (1936, p. 111), I have done an injustice to Faxon by the incorrect statement that "only three" of the five teeth arming the median lobule of the distolateral lobe of the petasma of *H. nereus* "are indicated in Faxon's figure."

Faxon (1895, p. 192) calls attention to the possibility that those of his specimens of *H. doris* which were obtained at Albatross Station 3414 might possibly have been taken pelagically, inasmuch as Agassiz records the capture of some "transparent Penaeidae" in the tow-net at this station; it is possible, however, that Agassiz refers to the "*Sergestes edwardsii* Kr." which Faxon records from Station 3414. On the other hand, there is no possible doubt that the present juvenile of *H. doris*, and another taken by the *Arcturus* off Cocos Island at 300 fms., were captured pelagically, since both were caught in nets lowered to not more than 500 fathoms, in areas well outside the 1,000-fathom contour. In the present Californian juvenile, the statocyst contains a flattened agglomeration of transparent, sharp, irregularly shaped granules, the largest of which is about 0.15 mm. in greatest dimension. These granules, which are not affected by dilute HCl, appear siliceous; although they are rather readily fractured by pressure with the dissecting needle. In the Cocos juvenile, the statocyst contains a flattened plate of the delicate shells of minute pelagic foraminifera cemented together with cuticular secretion. In two large specimens of *Hymenopenaeus nereus*, taken by the *Arcturus* on bottom at Station 74 and examined for comparison, the statolith is composed of pelagic foraminifera, heavy calcareous fragments apparently of molluscan shells, and granules of siliceous appearance similar in nature to those composing the statolith of the Californian juvenile of *H. doris*. I am inclined to think that as in the case of the pelagically captured specimens of *H. laevis* and *H. aphoticus* discussed by Burkenroad, 1936, p. 106, the present juveniles of *H. doris* had obtained their statoliths from bottom, and had later swum up to the levels where they were captured.

SOLENOCERA Lucas.

***Solenocera mutator*, sp. nov.**

(Text-figures 2-5).

*Type*: Type male and cotypes: Cat. No. 36,969, Department of Tropical Research, New York Zoological Society; taken at Station 150, Dredge 5



(5 ♂, 2 ♀); from Gorda Banks, tip of Lower California, 23° 01' 30" N. Lat., 109° 30' W. Long., 4-foot dredge at 40 to 100 fathoms; April 21, 1936.

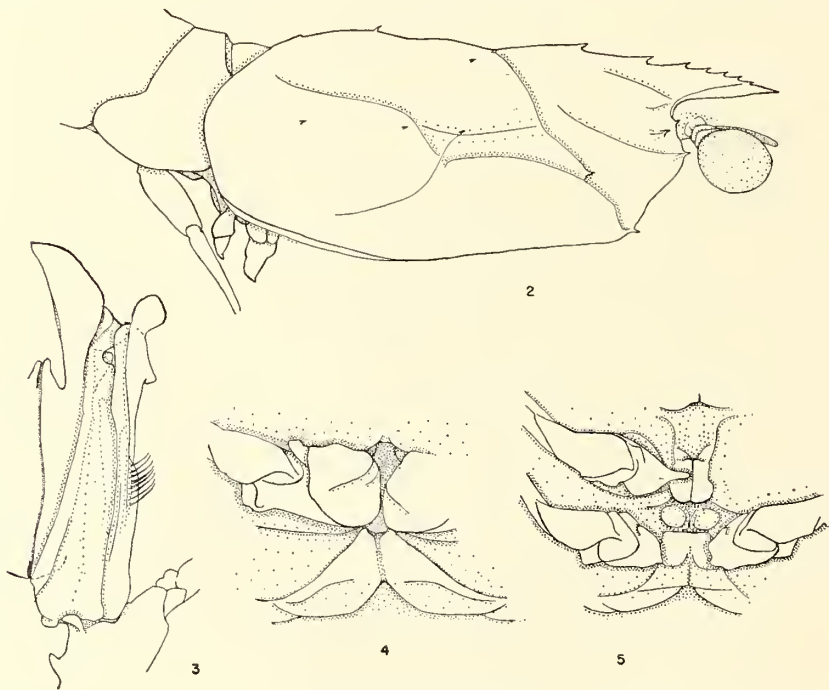
*Range:* Bay of Panama; Pacific coast of Mexico off Manzanillo and Mazatlan; Lower California, both coasts; 20-117 fathoms.

*Material:* A total of 33 specimens (somewhat more than half of them males) was taken, at depths of 20 to 100 fathoms, east of Cedros Island (Stations 125 and 126), in Santa Inez Bay (Stations 141 and 143), on Gorda Bank (Station 150) and off Mazatlan (Stations 154 and 155), as follows:

Station 125: D-1 (2 ♂); Station 126: D-3 (2 ♂, 1 ♀), D-4 (1 ♂, 1 ♀); Station 141: D-4 (1 ♂, 1 ♀); Station 143: D-3 (5 ♂, 2 ♀); Station 150: D-5 (5 ♂, 2 ♀); Station 154: D-1 (3 ♀ plus 1 fragment); Station 155: (3 ♂, 3 ♀). Cat. Nos. 36,964, 36,965, 36,966, 36,967, 36,968, 36,969, 36,970, 36,971.

In addition to this material, I have been enabled through the kindness of Dr. W. L. Schmitt of the U. S. National Museum to examine four males ranging in carapace length from 12 to 13.5 mm. and five females ranging in carapace length from 12.5 to 16 mm., taken off Manzanillo, Mexico, in 117 fathoms (U. S. N. M. 28489); as well as a large female 19 mm. in carapace length from Panama Bay (*Albatross* Station 2804) at a depth of 47 fathoms (U. S. N. M. 28488).

*Dimensions and Sexual Condition:* Males ranging in size from carapace length 16 mm., total about 62 mm., to carapace 9 mm.; females from carapace 14 mm., total 56 mm., to carapace 7 mm. In the four males of



Text-figures 2-5.

*Solenocera mutator*, n. sp. 2. Carapace (lateral view); juvenile Mazatlan ♀, D. T. R. 36,970, x 6. 3. Petasma (left half, posterior view); type ♂, T. R. 36,969, x 6. 4. Fourteenth sternite; adult ♂, D. T. R. 36,965, x 6. Thelycum; subadult ♀, D. T. R. 36,968, x 6.



carapace 10 mm. or less, and in one of carapace 11 mm., the petasmal endopods are unjoined; in the rest, of carapace 11 mm. or more, the petasma is of adult form.

**Diagnosis:** Pterygostomian spine meeting the frontal margin at nearly a right angle; cervical carina not notched above the level of the hepatic tooth; postorbital spine well developed; orbital angle dentiform. Cervical sulcus not continuous across the dorsum; postrostral carina of the carapace obliterated behind the level of the cervical sulcus. The rostrum is short and deep, with convex ventral margin; it bears from 5 to 7, usually 6, teeth in addition to the epigastric, of which the posteriormost (and sometimes the preceding also) is behind the orbit. The posteriormost tooth of the rostral series is separated from the preceding by an interspace equal to one-third to one-fifth, usually more than one-fourth, of the interval between the posteriormost rostral tooth and the dorsal end of the cervical sulcus. The epigastric tooth is placed at a point from three-fifths to more than two-thirds, usually about two-thirds, of the way from the orbital margin to the cervical sulcus. In specimens from other localities than Lower California there is a small slender spine on the dorsum of the carapace near its posterior end, and still other spines not present in Lower Californian material may occur on carapace and pleon. It is to the inconstant presence of this armature that the specific name refers.

The fourth, fifth and sixth pleonic somites are dorsally carinated; the third rather weakly ridged. The telson is short, with a conspicuous pair of fixed marginal teeth.

The antennular flagella vary from somewhat shorter than the carapace minus the rostrum, to more than one and two-thirds this length. They are usually quite slender, except in a few of the larger males where the distal portion of the inferior flagellum is expanded to twice its basal breadth.

The emargination of the posterior end of the fourteenth sternite of the male is deep but broad. The paired teeth of the anterior part of the fourteenth sternite of the female are usually represented by broad, low, obtuse swellings; which may in large specimens, however, be somewhat produced, acuminate and turned medioanteriorly. The posterior margin of the thirteenth sternite of the female is, although narrowly incised by a median groove, on the whole conspicuously convex; the V-shaped anterior edge of the posterior part of the sternite is sharply defined; the anterior part of the sternite bears a low ridge not rising into a setose protuberance at its hinder end. The coxae of the fourth legs of the female are often considerably produced, so that they may overlap considerably in the midline.

The petasma is particularly characterized by the considerable size of the triangular lamellate projection of the dorsal face of the distolateral lobe (which is even visible in ventral view, projecting beyond the lateral margin of its lobe); and by the elongated subtriangular shape of the acuminate median lobule of the distolateral lobe. The distoventral lobe is crowned by a free distoventral projection.

**Remarks:** In a preceding paper (1936, p. 123), I have described in detail, under the heading "*Solenocera* species," a small male with joined petasmal endopods taken in the Gulf of Panama, which differs in several respects from the much larger types of *S. agassizii* Faxon from the same region. It was thought possible at that time that this specimen might represent a young form of *S. agassizii*; chiefly for the reason that a small female of *Solenocera* from the Gulf of Mexico, described in the same paper (1936, p. 122) under the heading "*Solenocera vioscai* Burkenroad" and regarded as a young adult of that species, was found to differ in bodily characters from the much larger types of *S. vioscai* in somewhat the same manner as the small Panamanian male differed from the types of *S. agassizii*.

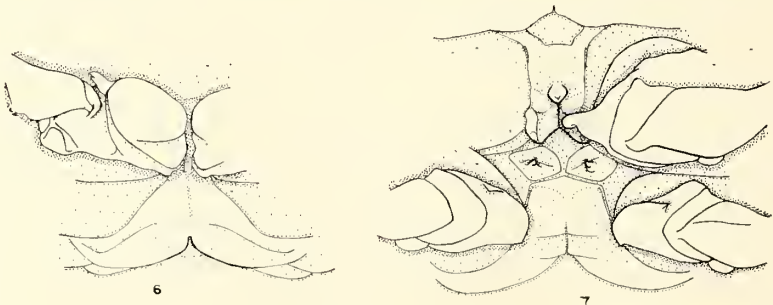
A study of the very much more adequate material of *Solenocera* from

American waters which has now become available from various sources, demonstrates, however, that not only do both "*Solenocera* species" and the supposed young specimen of *S. vioscai* represent species distinct from those to which it was previously thought that they might refer, but there are still other distinct forms, one from the Gulf of Mexico, and the present one included in the *Zaca* collection. The American species of the genus therefore number six, of which only two, *S. agassizii* Faxon and *S. vioscai* Burkenroad, have been named until the present. The third form, *S. mutator* sp. nov., has been named and diagnosed in preceding paragraphs. A fourth form is a peculiar one from the Gulf of Mexico represented by the supposed "juvenile" erroneously referred to *S. vioscai* in 1936; a fifth form, also from the Gulf of Mexico, is closely related to *S. mutator*; these will be described in a forthcoming paper. The sixth form, the "*Solenocera* species" from Panama, which is also closely related to *S. mutator*, may be given a name in this place, as follows:

***Solenocera florea*, sp. nov.**

*Solenocera florea*, sp. nov. Holotype, B. O. C. No. 132 (a male described by Burkenroad, 1936, p. 123, figs. 68-69). Paratypes (Text-figs. 6-7 below) U. S. N. M. No. 28486, five males and five females, all adult, taken in Panama Bay at a depth of 33 fathoms. The paratype material has been made available to me by the very great kindness of Dr. W. L. Schmitt of the U. S. National Museum. The males range in size from carapace 17.2 mm., total length 68 mm., to carapace 15 mm.; the females from carapace 22.8 mm., total length 77 mm. to carapace 21.5 mm. The paratype material agrees very well with the previous description of the holotype; it may however be noted that the antennal scale usually overtops the antennular peduncle by a fifteenth or more of the length of the scale. The figure of the petasma of the holotype (Burkenroad, 1936, fig. 69) is in error, in that the distal margin of the median lobule of the distolateral lobe should be shown as folded over anteriorly, not posteriorly; the description is also in error in that the "pair of rigid lamellar projections" on the posterior face of the distolateral lobe actually represent the two ends of a single lamella, the midsection of which is broken in the holotype. Diagnostic distinctions between *S. florea* and related species of the genus are given in succeeding paragraphs.

The three Pacific American species of *Solenocera* are distinguished from their three Atlantic American congeners by the fact that the blade of the epipodite of the tenth through thirteenth somites is in all of the former deeply bifurcate, the shorter ramus being half or more the length of the undivided portion of the blade (not including peduncle); whereas in the



Text-figures 6 & 7.

*Solenocera florea*, n. sp. 6. Fourteenth sternite; adult, U. S. N. M. 28,486, x 5. 7. Thelycum; adult ♀, U. S. N. M. 28,486, x 5.

Atlantic forms the epipodites are only shallowly furcated or even mitten-like, the shorter ramus being at most less than a third as long as the undivided portion of the blade. *S. mutator*, *S. florea* and one of the undescribed species from the Gulf of Mexico are all three distinguished from *S. agassizii* and *S. vioscai* by their less numerous rostral teeth (minimum 6, maximum 8 in the former as compared with minimum 8, maximum 10 in the latter); the right angle made by the juncture of their pterygostomial spine with the frontal margin of the carapace dorsal to it, this juncture being a smooth concavity in the two latter forms; and the presence of a scale-like projection on the anterior face of the distolateral lobe of their petasma, which is not represented in *S. vioscai* and *S. agassizii*. The former three species are also, so far as their maxima are known, smaller (55-80 mm.) than the latter two (total lengths respectively exceeding 100 and 200 mm.). The second unnamed species from the Gulf of Mexico, which was erroneously described as the juvenile of *S. vioscai* in 1936, agrees with the *S. mutator* group as regards number of rostral teeth, but with the *S. agassizii* group in pterygostomial spine; its petasma is unknown.

In non-sexual characters, typical (Californian) material of *S. mutator* is not very easily distinguished from *S. florea* although the epigastric tooth of the latter is usually placed somewhat nearer to the orbit (only about one and one-quarter times as far from the orbit as from the cervical sulcus) and the posteriormost tooth of its rostral series is less widely separated from the tooth preceding it (interval between the two teeth from a fourth to a fifth of that between the posterior tooth and the cervical sulcus) than in *S. mutator*. The scale of the inner margin of the basal segment of the antennular peduncle (prosartermia) of *S. florea*, which reaches well beyond the eye, seems to be longer than that of *S. mutator*.

Females of *S. florea* are readily distinguished from those of *S. mutator* by the fact that in the former the posterior margin of the thirteenth sternite is acutely concave rather than roundedly convex; and that there is no sharp boundary between the anterior and posterior parts of the same sternite except medially, where the median groove of the posterior part of the sternite ends at a conspicuous, unpaired, setose conical projection set just in advance of the fourth legs. The pair of teeth of the anterior part of the fourteenth sternite also seems to be somewhat more sharp and slender in females of *S. florea*, and the coxal nubs of the fourth legs are less extended than is sometimes the case in *S. mutator*.

The emargination of the posterior edge of the fourteenth sternite is a narrow notch with parallel sides in males of *S. florea*, rather than a sloping concavity as in *S. mutator*. In petasma the two species are strikingly different; particularly as regards the subtriangular rather than subrectangular shape of the median lobule of the distolateral lobe of *S. mutator*, and the form of the distoventral lobe which is in *S. mutator* very nearly identical with that in *S. agassizii*.

Certain peculiar variations in structure within the material which I have here assigned to *Solenocera mutator* seem to require attention. In the specimens from Mexico and Panama, the integument is thin and membranous, the tissues are rather flabby, and the pleon seems relatively quite slender. In Californian material, on the contrary, the integument is thick and rigid, the flesh solid, and the habitus is of the Penaeine type usual in the American species of the genus. These differences are difficult to define precisely, and there is considerable intergradation between the groups; but nevertheless specimens from Lower California do give a general impression different from that of the Mexican material. That this impression may not be the result of differences in method of preservation is suggested by the fact that the Lower Californian and one of the available lots of Mexican material are derived from one collection, the other lot of Mexican and Panamanian material from another.



Of more precisely definable differences between the peninsular and the mainland material of *S. mutator*, in all but one of the nineteen Mexican and Panamanian specimens the dorsum of the carapace about midway between the cervical sulcus and the posterior margin bears a small, slender spine which is absent in all of the twenty-four Californian specimens. In the mainland material there is also a well-developed vestige of the posterior dorsal organ found in many peneid larvae, which is not perceptible in Californian specimens. In small mainland specimens from Mazatlan (the smallest a female of carapace length 9 mm.), the carapace bears four additional pairs of spines of which no traces appear in peninsular specimens, two pairs on the branchial region below the cardiaco-branchial carina, and two pairs on the sides behind the cervical sulcus. The cardiaco-branchial carina, which is in Californian specimens obsolescent, is in these small individuals strongly developed; and there is also a short carina, not represented in peninsular material, which runs between the posterior section of the cardiaco-branchialis and the cervical carina. One of the pairs of lateral spines is set on the middle of this carina, from the midpoint of which another ridge not perceptible in Californian specimens slants in a sinuous oblique toward the posteroventral margin of the carapace. There is also in these small specimens a spine at the posterior end of the dorsal carina of the fourth and fifth pleonic somites as well as of the sixth to which such spines are limited in the peninsular material. Altogether, the small specimens recall to mind in many ways various of the species of *Hymenopenaeus*; thus the carapacic carination and pleonic armature, as well as the habitus, are to some extent comparable with those of *H. laevis* (Bate); the dorso-lateral postcervical spines with the pair present in *H. diomedee* (Faxon) (or in *Solenocera hextii* Wood Mason); and the posterior dorsal spine of the carapace with that of *H. steindachneri* (Balss). In somewhat larger specimens from Mazatlan, the extra carapacic carinae are weaker, and the extra lateral spines of the carapace and the posterior spine of the fourth pleonic somite are absent, although the dorsal carapacic spine and that of the fifth pleonic somite are present. In the largest specimen from Mazatlan, a male of carapace length 13.5 mm., all of the extra spines of carapace and pleon are absent and the animal nearly approaches the Californian types in habitus. In all available specimens from Manzanillo, of whatever size, the dorsal spine and the two dorsal of the extra lateral pairs are present. A spine is present on the fifth pleonic somite in all but one small male from Manzanillo; that of the fourth pleonic somite occurs in only two of the ten specimens. In the large female from Panama, of carapace length 19 mm., the dorsal and two pairs of extra lateral carapacic spines are present, but only the sixth pleonic somite is dorsally armed.

There are a number of other inconstant differences between mainland and peninsular material; thus there are eight rostral teeth in 5 of 7 Mazatlan specimens and in 2 of 9 Manzanillo specimens as compared with a maximum of seven in all of the 22 Californian individuals with unbroken rostrum; and the antennular flagella are shorter, or at most no more than slightly longer, than the carapace in Mazatlan and Manzanillo specimens.

However, despite the many differences pointed out above, the mainland and the peninsular specimens are identical in petasma and thelycum, and for this reason I am unable to consider them as systematically distinct. It seems possible, especially because of the change with size among the Mazatlan specimens, that the peculiar features of the mainland material are of larval derivation. However, the mainland specimens are quite as well developed sexually as are Californian specimens of similar size, and the Panamanian female is by far the largest of the known individuals of *S. mutator*; while at the same time juveniles from Lower California, smaller and less developed sexually than are any from the mainland, display no traces of the extra spines and carinae characteristic of the latter. The



question of the significance of the differences between the Californian and the mainland specimens is a most interesting one, and it is to be regretted that no more satisfactory an account than the above can be offered.

### PENAEUS Fabricius.

*Penaeus*, Burkenroad, 1934a p. 74.

DIVISION 2, Burkenroad, 1934a, p. 75.

### *Penaeus californiensis* Holmes.

*Penaeus californiensis*, Holmes, 1900, p. 218; Pesta, 1915, p. 113.

*Penaeus canaliculatus*, Holmes, 1895, p. 581.

*Penaeus brevirostris*, part, Rathbun, 1902, p. 287; 1904, p. 146; Schmitt, 1921, p. 21; Burkenroad, 1934a, p. 91.

*Penaeus brasiliensis*, part, Schmitt, 1935, p. 16.

(Text-figures 10, 11, 14, 15).

*Range*: San Francisco, California; Santa Monica, California; Gulf coast of Lower California; west coast of Mexico near Esquinapa. Beach to 45 fathoms; Juveniles in lagoons and estuaries.

*Material*: A total of 3 specimens (1 ♂, 2 ♀) was taken on Arena Bank, 45 fathoms (Station 136 D-2, Cat. No. 36,972).

*Dimensions and Sexual Condition*: Larger female impregnated, of carapace 34 mm., total length about 140 mm.; smaller female of carapace 30 mm., unimpregnate. Male fully adult, carapace length 30 mm.

*Remarks*: No more than two American species of Section 2 of *Penaeus* have in the past been recognized. The names generally applied to these have been, for Atlantic specimens, *P. brasiliensis* Latreille; for Pacific ones, *P. brevirostris* Kingsley. In the two most recent considerations of the group, Burkenroad (1934a, pp. 91 seq.) has advanced some reasons for believing that Atlantic is specifically distinct from Pacific material, while Schmitt (1935, pp. 16-17) refers all American material to a single name, *P. brasiliensis*.

It now appears, however, that there are no less than five species of Division 2 in the American waters, three Atlantic and two Pacific ones. As the account of the Atlantic forms will appear in a forthcoming paper, it is proposed to describe and to differentiate only the two Pacific species in this place.

Although there seems in the past to have been no suspicion of the existence of more than one species of the *P. brasiliensis* group in Pacific America, names are already available for both of the newly separated forms. Some juvenile specimens from Nicaragua were described by Kingsley, 1878, p. 98, as the new species *Penaeus brevirostris*.<sup>3</sup> In 1895, Holmes incorrectly referred specimens of the *brasiliensis* group from Southern California and San Francisco Bay (which he thought likely to be identical with Kingsley's material) to the Indo-Pacific *P. canaliculatus* (Olivier). In 1900 Holmes retrieved this error by describing the Californian specimens as the new species *P. californiensis*; but as he failed at this time to refer to Kingsley's species, his name has subsequently been regarded by most workers as synonymous with *P. brevirostris*. *P. californiensis* Holmes is entered in his list of peneid species by DeMan, 1911, p. 10, but it is intentionally omitted from the account of *Penaeus* by the same author, who according to p. 131 accepts its identity with *P. brevirostris*. Pesta, 1915, p. 113, identifies mate-

<sup>3</sup> This name was later incorrectly referred to the synonymy of *P. brasiliensis* by Kingsley himself (1879, p. 427), thus antedating the similar action by Verrill in 1922 and by Schmitt, 1935, p. 17.

rial from San Francisco Bay as *P. californiensis* Holmes, but considers it likely that Kingsley's specimens are juveniles of the same form; he remarks "Es scheint mir jedoch zweckmässiger den *P. californiensis* Holmes, von dem eine gut Diagnose mit abbildungen gegeben ist, bestehen zu lassen, und vielleicht die Spezies Kingsley's als fragliches Synonym hierher zu stellen."

Since I am informed by Dr. F. M. MacFarland of the California Academy of Sciences that the types of *P. californiensis* Holmes were destroyed in the earthquake and fire of 1906, a specimen from Santa Monica, California, is designated below as neotype. The specimen from San Francisco which is figured by Pesta seems to belong to the same species as the neotype. Cotypes of *Penaeus brevirostris* Kingsley, although juvenile, are easily differentiated from the form which occurs in the type locality of *P. californiensis*. Material of the two Pacific American species of the group available to me in addition to that obtained by Dr. Beebe, is listed below. For material credited to the respective institutions, I am deeply indebted to the authorities of the American Museum of Natural History, the Museum of Comparative Zoology, and the U. S. National Museum.

*Penaeus californiensis* Holmes.

NEOTYPE. U. S. N. M. 23942. Santa Monica, California. 1 ♂ adult, carapace 33 mm.; total length 140 mm.

B. O. C. 18. Concepcion Bay, Lower California; May 3, 1926. *Pawnee II*. 1 ♀ adult, impregnated, carapace length 43 mm.; 8 ♂ adult, carapace 29 to 34 mm.; 3 ♀ juvenile, carapace 14.5 to 20 mm.; 2 ♂ juvenile, carapace 17.5 to 20 mm.

B. O. C. 14. Angeles Bay, Lower California; May 13, 1926; 17-23 fms. *Pawnee II*. 3 ♀ adult (2 impregnated), carapace lengths 31.5 to 38.5 mm.; 2 ♂ adult, carapace lengths 29.5 and 30 mm.

A. M. N. H. 4620 [A]. Lagunaje de las Lomitas, Esquinapa, Sinaloa, Mexico (just south of the Gulf of California); November 15, 1919. Sr. M. Gallegos. 2 ♀ juvenile, carapace lengths 18 mm. and 20 mm.

*Penaeus brevirostris* Kingsley.

(Text-figures 8, 9, 12, 13).

COTYPES. M. C. Z. Estero at Realejo, Nicaragua; March, 1867. 1 ♀, juvenile, carapace length 13.2 mm.; 1 ♂, juvenile, carapace length 11 mm.

B. O. C. 15. Pearl Islands, Bay of Panama (8° 29' 40" N, 78° 52' 30" W); March 31, 1926. *Pawnee II*. 5 ♀, subadult to juvenile, carapace length 9 mm. to 22 mm.; 2 ♂, juvenile, carapace lengths 10.5 mm. and 11 mm.

B. O. C. 102. Panama City Market (reported locality, Chame River); February 10, 1934. M. D. B. 1 ♀ adult, impregnated, carapace length 38 mm.

B. O. C. 103. Tide-pool, Panama City; February 12, 1934. M. D. B. 1 ♂ juvenile, carapace length 8 mm.

B. O. C. 16. West coast of southern Mexico (14° 48' 40" N, 92° 54' 40" W); April 9, 1926; 30 fms. *Pawnee II*. 3 ♀ adult, impregnated, carapace lengths 46 mm. to 50 mm.

U. S. N. M. 28417. Panama Bay (*Albatross* Station 2795); 33 fms. 1 ♂ adult, carapace 30.5 mm.; 1 ♀ adult, impregnated, carapace 43.5 mm.

U. S. N. M. 28419. Panama Bay (*Albatross* Station 2804); 47 fms. 2 ♂ adult, carapace 31 mm.

A. M. N. H. 4620 [B]. Lagunaje de las Lomitas, Esquinapa, Sinaloa, Mexico; November 15, 1919. Sr. M. Gallegos. 2 ♀, juvenile, carapace lengths 18 mm. and 20 mm.

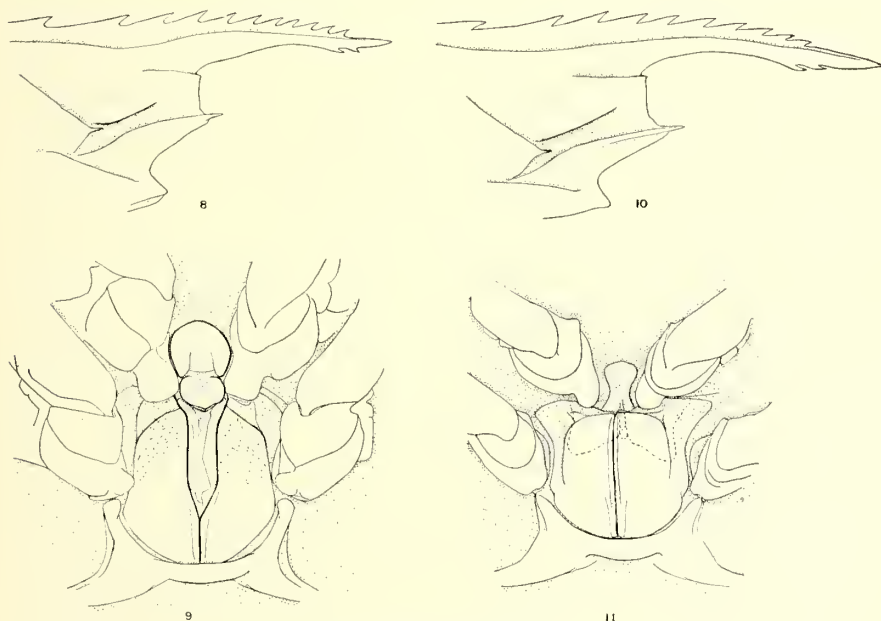
A. M. N. H. 4621. Estero del Puyequ, Esquinapa, Sinaloa, Mexico; November 29, 1919. Sr. M. Gallegos. 1 ♀ juvenile, carapace length 19 mm.; 1 ♂ juvenile, carapace length 17.5 mm.

A. M. N. H. 4622. Pesqueria Caligüey, Esquinapa, Sinaloa, Mexico; November 22, 1919. Sr. M. Gallegos. 1 ♂ juvenile, carapace length 19 mm.

A. M. N. H. 4623. Estero del Puyequ, Esquinapa, Sinaloa, Mexico; November 29, 1919. Sr. M. Gallegos. 1 ♀ juvenile, carapace length 15.5 mm.; 2 ♂ juvenile, carapace lengths 18 and 19 mm.

The sharpest non-sexual diagnostic between *P. brevirostris* and *P. californiensis* is supplied by the carina forming the postero-dorsal margin of the antennal sulcus. In *P. californiensis* this carina reaches to within nearly half its length at least of the orbital angle (usually, and in adults almost always, to within one-third); whereas in *P. brevirostris* the carina does not reach to within more than three-fifths its length of the orbital angle, often not within its length.

The orbital angle is more produced and the postorbital carina more pronounced in *P. californiensis* than in *P. brevirostris*; thus in the former the sharply defined posterior part of the crest (best seen in dorsal view) is longer, usually considerably longer, than the more obtuse anterior portion, while in the latter species the anterior obtuse part is usually the longer. The posterior part of the ridge is in *P. brevirostris* often no sharper than is the anterior part in *P. californiensis*, and the anterior part is sometimes hardly discernible.



Text-figures 8-11.

*Penaeus brevirostris* Kingsley. 8. Carapace (anterior part, lateral view); juvenile ♀ cotype, M. C. Z., x 4. 9. Thelycum; impregnated adult ♀, B. O. C. 102, x 4.

*Penaeus californiensis* Holmes. 10. Carapace (anterior part, lateral view); juvenile ♀, B. O. C. 18, x 4. 11. Thelycum; unimpregnated adult ♀, D. T. R. 36,972, x 4.



The adrostral carinae of *P. californiensis* are somewhat longer and more widely separated than are those of *P. brevirostris*, generally extending toward the posterior margin of the carapace to within the breadth of the interval separating their posterolateral ends; and are posteriorly better defined than in *P. brevirostris*, being continued medially at the posterior ends of the adrostral sulci. In *P. brevirostris* these carinae usually extend to no more than about three-quarters of the interval between them toward the posterior margin, and are usually not continued medially, so that the adrostral sulci lack a defined posterior margin. These differences in form of adrostral carina are very much less distinct in juveniles than in adults.

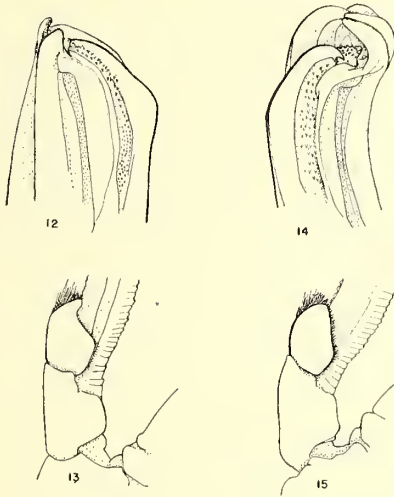
The modal number of dorsal carapacic teeth is different in the two species, as far as the present material serves to indicate, being nine in *P. californiensis*, ten or eleven in *P. brevirostris*. The exact counts are shown in the table:

Number of Rostral Teeth.	Number of Individuals.	
	<i>P. californiensis</i> .	<i>P. brevirostris</i> .
7 + 1 epigastric	1	0
8 + 1	14	2
9 + 1	7	11
10 + 1	1	11
11 + 1	0	1

Finally, the two species seem distinct in thelycum, petasma and appendix masculina. In adult Panamanian females of *P. brevirostris*, the posterior part of the median elevation of the thirteenth sternite forms, in ventral view, a roughly oval or diamond-shaped cup with elevated rim and depressed center, against which the anteromedian lips of the lateral plates of the fourteenth sternite abut, and by which these lips are held apart so that they do not meet in the midline anteriorly. The anterior part of the ventral surface of the lateral plates is quite heavily pubescent. The characteristic form of the median elevation of XIII and the pubescence of the ventral surface of the lateral plates are recognizable in Panamanian juveniles down to a carapace length of 14 mm., though the pubescence cannot be discovered in smaller specimens. Since the lateral plates of XIV gape widely in juveniles of *Penaeus*, the separation of the anteromedian lips of the lateral plates loses its value as a diagnostic in juveniles. In the juvenile female cotype from Nicaragua, of carapace 13.2 mm., the form of the median elevation of XIII is characteristic, but the specimen seems below the size at which the pubescence of the lateral plates appears. In adult females of *P. brevirostris* from southern Mexico, the structure of the thelycum is similar to that in Panamanian specimens, but the anterior parts of the ventral plates are in some individuals only very lightly pubescent. In juvenile females from Esquinapa, of carapace lengths 15-20 mm., the ventral surfaces of the lateral plates are not pubescent at all; and while the posterior part of the median elevation of XIII has the characteristic cup-like form, its posterior end is more extensively produced in a posterior direction, to form an obliquely vertical ridge, than in the Panamanian juveniles.

In adult females of *P. californiensis* from the Gulf of California, the posterior part of the median elevation of XII shows at most no more than a trace of the cup-like form found in *P. brevirostris*; instead, it bears a median longitudinal carina representing an elongation of the posteromedian rim of the cup in *P. brevirostris*. The lateral plates of XIV meet in the

midline for their entire length, their anterior ends thus overlying and concealing the posterior part of the elevation of XIII, as is clearly indicated in Pesta's figure of a female from San Francisco. The lateral plates are not pubescent on their ventral surface. Juveniles of *P. californiensis* maintain the characteristic form of the thelycum (except as regards the meeting of the lips of the lateral plates) down to a carapace length of 18 mm. at least. Although the juveniles of *P. californiensis* are not too readily distinguishable in these features from the Sinaloa juveniles of *P. brevirostris* described above, it is my belief that the Sinaloa juveniles would as adults resemble material from southern Mexico, and would thus, although differing slightly from the Panamanian stock of *P. brevirostris*, fall easily within the same specific limits and be clearly distinct in female genital characters from *P. californiensis*.



Text-figures 12-15.

*Peneus brevirostris* Kingsley. 12.

Petasma, (distal part, lateral view from right side); adult ♂, U. S. N. M. 28,419, x 5. 13. Appendix masculina (of right second pleopod, anterior view); as in 12, x 5.

*Peneus californiensis* Holmes. 14.

Petasma (distal part, lateral view from left side); adult ♂, D. T. R. 36,972, x 5. 15. Appendix masculina (of right second pleopod, anterior view); as in 14, x 5.

The petasma of adult males of *P. californiensis* displays the following critical characters: The medially curved distal ends (distoventral lobes) of the heavily chitinized lateral ribs of the petasma terminate in a sharply pointed recurved tip which is free from the membranes forming the median parts of the petasma. The distolateral or free margin of the distal ends of the ribs is unarmed; the proximomedian margin which is attached to the membranes forming the median parts of the petasma is most frequently armed on its anterior or dorsal side with a single proximally directed tooth-like spine (the range in armature being from no such teeth to five). Just median to the tip of the lateral rib is a large, fleshy posteriorly projecting flap the area of which is nearly comparable with that of the distomedian lobe. This flap, which probably represents a part of the distolateral lobe, is armed on its free edge with several series of spines like those arming the anterior surface of the membranes median to the lateral rib and those on the median edge of the lateral rib itself. The posteriorly curved distomedian lobes are quite long, and overlap the distal ends of the lateral ribs by a considerable amount. The characteristic features of the adult petasma are well-developed in the two available juvenile males with separated petasmal endopods.

In adult males of *P. brevirostris* from Panama the petasma differs from that of *P. californiensis* as follows: The medially directed distal ends of the lateral ribs terminate in a blunt tip not projecting free of the median membranes; this tip is armed on its distolateral or free edge with one or two

conspicuous axially-directed teeth which seem not to be homologous with the projecting, recurved, acutely-pointed tip in *P. californiensis*. The proximomedian margin of the anterior, or dorsal side of the distal parts of the lateral ribs bears a row of 8 to 11 spines along its juncture with the membranous median parts of the petasma. The folded distal edge of the median parts, at the point of juncture with the tip of the lateral rib, does not project inward as a conspicuous fleshy flap, and is here unarmed. The distomedian lobes of the petasma are relatively short, and do not much overlap the distal ends of the lateral ribs. In the four juvenile males of *P. brevirostris* from Sinaloa, the disunited petasml endopods are very much like the above, although there is in all but one tooth visible on the free margin of the tip of the lateral ribs, and although there may be as few as four teeth on the proximomedian margin. Juvenile males from Nicaragua and Panama are too small to display recognizable petasml characters.

In adult and juvenile males of *P. californiensis*, the external margin of the appendix masculina of the second pair of pleopods is approximately straight. In adult males of *P. brevirostris* from Panama and in juveniles from Sinaloa the external margin of the appendix is deeply concave. In Panamanian and Nicaraguan juveniles, the carapace length of which is less than 10.5 mm., the external margin of the appendix masculina is straight, but this organ, like the petasma, is extremely small and undeveloped in these very small specimens and presumably does not yet display the adult characters.

PENAEOPSIS A. Milne Edwards (Bate).

*Penaeopsis*, Burkenroad, 1934b, p. 7.

Subgenus METAPENAEOPSIS Bouvier.

*Metapenaeopsis*, Burkenroad, 1934b, p. 8.

SECTION I, Burkenroad, 1934b, p. 8.

***Penaeopsis (Metapenaeopsis) kishinouyei* (Rathbun).**

*Parapenaeus kishinouyei*, Rathbun, 1902, p. 288.

*Penaeopsis kishinouyei*, Schmitt, 1924, p. 161.

Not *Penaeopsis kishinouyei*, Boone, 1930, p. 108; 1931, p. 176.

(Text-figures 16, 17).

*Range*: Galápagos Islands; Revillagigedo Islands; 2-55 fathoms.

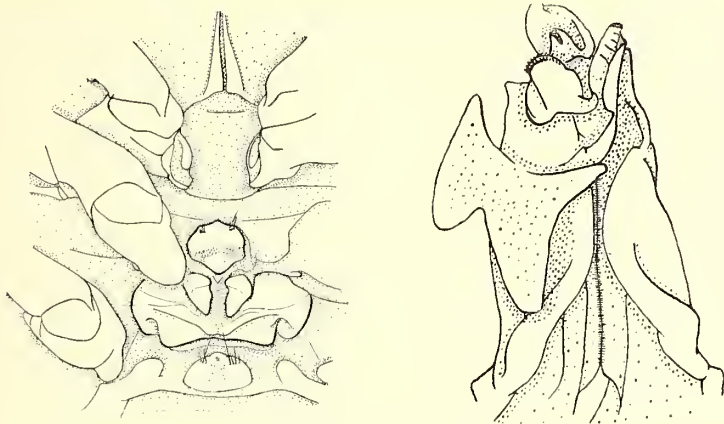
*Material*: Two specimens (1 ♂, 1 ♀) were taken 3 miles off Pyramid Rock, Clarion Island, Revillagigedo Islands (Station 163 D-2, Cat. No. 36,973) in 55 fathoms.

*Dimensions and Sexual Condition*: Female an impregnated adult of carapace 12 mm., total length about 56 mm. Male a subadult with joined petasml endopods of carapace 5 mm., total length about 27 mm.

*Remarks*: The present record of *Penaeopsis kishinouyei*, although from a locality nearly 20° to northward of the Galápagos from which the species is otherwise definitely known, and from deeper water, refers like the original record to the neighborhood of an isolated group of oceanic islands. Whether the species occurs on the mainland, from which it has twice been recorded by Boone, is extremely doubtful; thus the Panamanian specimen in the collection of the American Museum of Natural History, referred to *P. kishinouyei* by Boone, 1931, p. 176, is entirely distinct from Rathbun's species and will be discussed in a further paragraph as *P. beebei* sp. nov. (not *P. mineri* Burkenroad, to which closely related form I have erroneously



referred the Panamanian specimen in 1934b, p. 28). As to the Costa Rican specimen referred to *P. kishinouyei* by Boone, 1930, p. 108, according to her Plate 33 the fifth legs of this specimen are nearly as long as the third, the telson lacks conspicuous lateral armature, the antennular flagella are longer than their peduncle, and the exopodites of the walking-legs are swollen and bladder-like; I would therefore infer that it may perhaps belong to another genus than *Metapenaeopsis*. As a possible analogy, mention may be made of figure 4B in the same paper, which although referred to "*Penaeopsis goodei*," obviously represents the petasma of *Trachypeneus*. If the Costa Rican specimen is not a *Metapenaeopsis*, it is necessary to assume that such portions of Boone's description as that (p. 110) referring to the sternal spines characteristic of *Metapenaeopsis* may, like the descrip-



Text-figures 16 & 17.

*Penaeopsis kishinouyei* (Rathbun). 16. Thelycum; adult ♀, D. T. R. 36,973, x 10.

*Penaeopsis kishinouyei* (Rathbun). 17. Petasma (posterior view, "dust-cap" bent down to expose distal parts); subadult ♂, D. T. R. 36,973, x 25.

tions of thelycum and petasma in the same account, be drawn from Rathbun's remarks on *P. kishinouyei* rather than from the animal figured on Plate 33. Boone's unrecognizable figure 3A, given as an original drawing of the thelycum of *P. kishinouyei* (although the material which she has examined is stated to have consisted of "one adult male") bears a great resemblance to the similarly unrecognizable figure 4A given by the same author as that of "*Penaeopsis goodei*." It must be admitted that this figure is rather suggestive of *Metapenaeopsis*, by reason of the occurrence of a spine at the anterior end of what seems intended to represent the median plate of XIII; however, it seems unlikely the drawing can refer to *P. kishinouyei*, since at a carapace length of 11 mm. the median plate seems to have lost its armature in that species.

Accepting that *P. kishinouyei* has not yet been taken on the mainland, its limitation to oceanic islands off the Pacific American coast would seem a matter of considerable interest, inasmuch as the mainland would seem as readily accessible to a littoral animal of the Galápagos as would the Revillagigedo Islands.

For comparison with the present Revillagigedo specimens, one of the two juvenile females taken off Indefatigable Island by the Williams Galápagos Expedition, and reported by Schmitt, 1924, p. 161; as well as three

juvenile females (the largest of carapace 5.2, total length about 25 mm.) and a juvenile male (of carapace 4 mm.; petasmas endopods not joined) taken at *Arcturus* Station 54 (Gardiner Bay, Hood Island, Galápagos; April 25, 1925; 15 feet), from the collection of the Department of Tropical Research, have been available.

*P. kishinouyei* differs from the related American species in that the basis of the second leg is constantly unarmed. Its rostrum also seems to bear a smaller number of teeth than in the other species, the average for the six available specimens being  $8 + 1$ .

The petasma of the juvenile male from the Galápagos displays in recognizable form the peculiarities of the Revillagigedo subadult. The distinctive features of the petasma of *P. kishinouyei* are, that the lateral shoulder of the distolateral lobe of the right endopod bears a short obtuse conical projection; the main or ventral lobule of the distolateral lobe is a blunt cone armed on the dorsal rim of its distal end with a single lunate row of spinules; the dorsal lobule of the distolateral lobe is an undivided projection much smaller than the ventral lobule; the projection or "dust-cover" of the distoventral lobe is distally deeply cleft into a small right and large left lobule, the right partially folded under the left.

The present Revillagigedo female, by far the largest specimen of *P. kishinouyei* so far recorded, agrees with Rathbun's figure 15, Pl. XII, 1902, of the Galápagan type of 33 mm., total length, in that the anterior margin of the median plate of the thelycum is unarmed. As regards certain other features of Rathbun's drawing, particularly the enormous bilobed form indicated to characterize the coxa of the fourth legs, I find no correspondence with available material. Rathbun's figure is incomplete, the posterior part of the fourteenth sternite not being represented. In the available juvenile females from the Galápagos, the thelycum differs from that of the northern adult in that the posterior parts of the median plate are shorter and broader, and the anterior margin armed with a median spine; these differences seem however to be referable to youth. The thelycum of *P. kishinouyei* differs from that of the related Pacific forms (aside from the disappearance of the anteromedian spine in adults, a unique feature) in that the semicircular median elevation of the thirteenth sternite is not posteromedially depressed; and the posterior parts of the median plate of XIII are moderately elongate, little elevated, and taper to their posterior ends. There appears to be a pair of sac-like membranous sperm-receptacles invaginated beneath the lateral hoods of sternite XIV. The transverse plate of XIV is about three or four times as broad as long; its posterior half slopes sharply down to well below the level of the median part of the transverse ridge of the posterior margin of the sternite. The anteromedian edge of the transverse plate does not overhang the posterior parts of XIII or the anteromedian prolongation of XIV.

***Penaeopsis (Metapenaeopsis) beebei*<sup>4</sup> sp. nov.**

(Text-figures 18, 19).

*Type*: Type and cotypes, Cat. No. 36,983 (4 ♂, 4 ♀), Department of Tropical Research, New York Zoological Society. Taken at Station 136, Dredge 30, Arena Bank, Gulf of California, 23° 27' N. Lat., 109° 24' W. Long., 4-foot dredge, 35 fathoms, May 1, 1936.

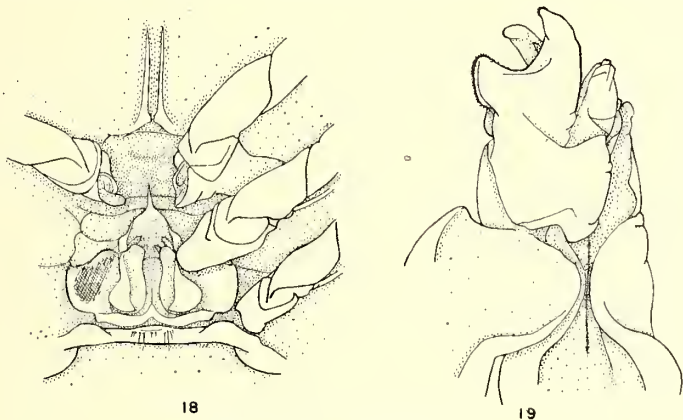
*Range*: Gulf of Panama; Lower California, 3 to 50 fathoms.

*Material*: A total of 106 specimens (almost equally divided as to sex) was taken at San Lucas Bay (Station 135) and at Arena Bank (Station

<sup>4</sup> Named for Dr. William Beebe of the Department of Tropical Research, New York Zoological Society.

136), at the southern end of Lower California, as follows: Station 135: D-1 (4 ♂, 1 ♀), D-9 (20 ♂, 21 ♀), D-11 (9 ♂, 16 ♀), D-20 (1 ♂), D-18, D-19, D-21 to D-25 (4 ♂, 5 ♀), D-26 (1 ♂, 1 ♀); Station 136: D-6 (1 ♂, 1 ♀), D-21 (1 ♂), D-24 (2 ♂, 5 ♀), D-26 (1 ♂), D-27 (2 ♂, 1 ♀), D-30 (4 ♂, 4 ♀). Cat. Nos. 36,974, 36,975, 36,1027, 36,977, 36,978, 36,979, 36,980, 36,981, 36,982, 36,983, 36,1028.

*Dimensions and Sexual Condition:* Females ranging in carapace length from 13.5 mm. (impregnated adult) to 4.5 mm. (juvenile); total length at carapace 10 mm. about 44 mm.; at 5 mm. about 21 mm. Males ranging in carapace length from 11 mm. (adult) to 4 mm. (juvenile); total length at carapace 9 mm. about 42 mm., at 5 mm. about 23 mm. Petasmas endopods joined and of adult appearance down to a carapace length of 6 mm. Both juveniles and adults are included in all of the more extensive samples, without any indication of segregation as to either locality or depth.



Text-figures 18 & 19.

*Penaeopsis beebei*, n. sp. **18.** Thelycum (position of right sperm-receptacle indicated by cross-hatching); adult ♀ type, D. T. R. 36,983, x 7. **19.** Petasma (posterior view, "dust-cap" bent down to expose distal parts); adult ♂ type, D. T. R. 36,983, x 15.

*Diagnosis:* Vestigial anterior arthrobranch present on the thirteenth somite. Distoventral projection of the left side of the asymmetrical petasma reduced to a vestige.

Rostrum modally with 9 teeth in addition to the epigastric. The second pleonic tergite lacks any trace of median longitudinal carina; the third is compressed but not sharply carinated. Posterior pair of mobile lateral spines of the telson exceeding by little or nothing the fixed pair succeeding them. Stylocerite less than half as long as the external margin of the basal segment of the antennular peduncle. Basis of second leg usually spinose but sometimes unarmed.

Median elevation of thirteenth sternite of the female with a subtriangular outline, its posteromedian portion much depressed below the anterior and lateral rim; the anteromedian margin armed with an anteriorly directed spine of moderate size. Posterolateral parts of the median plate of XIII tear-shaped in outline, anteromedially depressed, posterolaterally elevated. A pair of membranous sperm-receptacles invaginated to lie internal to the lateral hoods of the fourteenth sternite. Transverse plate near the posterior margin of XIV more than six times as broad as long; the anteromedian margin slightly convex but not produced to overhang the postero-



lateral parts of XIII; the posterior margin depressed below the level of the posterior rim of the sternite.

Lateral shoulder of the distolateral lobe of the right endopod of the petasma a gently curved swelling; main or ventral lobule in ventral view a saddle-shaped transverse elevation crowned with a row of spinules on each of its two peaks, the lateral of the two rows of spinules much more extensive than the median one. Dorsal lobule of the distolateral lobe a subdivided projection nearly as bulky as the ventral lobule but almost entirely concealed behind it in ventral view.

*Remarks:* *Penaeopsis beebei* very nearly resembles *P. mineri* Burkenroad; and indeed, was confused with the latter by Burkenroad, 1934b, pp. 25-26, since the Panamanian male in the collection of the American Museum of Natural History which was there considered to be a variant individual of *P. mineri* can now be recognized as a representative of *P. beebei*.

*P. beebei* is distinguishable in non-sexual characters from *P. goodei* (Smith) [and from the African *P. pubescens* (Bouvier)] by its relatively shorter stylocerite and the weaker carination of its pleon; and from *P. pubescens* by the relatively much shorter mobile lateral spines of its telson. It differs from all of the American members of its section in the inconsistency of the armature of the basis of its second leg, which appendage appears to be constantly unarmed in *P. kishinouyei*, constantly armed in *P. mineri* and the two Atlantic American species. In the available material of *P. beebei*, a well-developed spine is present on the basis of the second leg in 78 individuals, a rudimentary one in 8 individuals, and no spine at all in 19 individuals. Although the spine modally diminishes in relative size with decrease in size of the individual, its absolute presence or absence seems to be independent of the size or sex of the individual. Even at its maximum, the spine is smaller in *P. beebei* than in *P. mineri*.

In rostral, as in pereopodal armature, *P. beebei* falls between *P. kishinouyei* and *P. mineri*, as tabularly indicated below.

Number of Rostral Teeth.	Number of Individuals.		
	<i>P. kishinouyei.</i>	<i>P. beebei.</i>	<i>P. mineri.</i>
13 + 1 epigastric	0	0	1
12 + 1	0	0	5
11 + 1	0	0	23
10 + 1	0	4	23
9 + 1	2	63	5
8 + 1	2	22	0
7 + 1	2	0	0

In the 4 individuals of *P. beebei* with ten rostral teeth, and in somewhat more than half of the 63 with nine, the anteriormost tooth is rudimentary. Variations in rostral armature show no conspicuous correlation with size of individual, but the number of teeth tends to be greater in the females. The rostrum of *P. beebei*, as that of other species of the section, varies in length with size of the individual, ranging in extent from the end of the first to the middle of the second segment of the antennular peduncle. As in *P. kishinouyei* and *P. mineri*, the rostrum of *P. beebei* is somewhat deeper proximally than it is in the Atlantic American species.

*P. beebei* agrees with all of the American species except *P. goodei*

(Smith) in that the females possess a pair of sac-like, membranous sperm-receptacles invaginated from the lateral portions of the groove between the twelfth and thirteenth sternites. The thelycum is very similar to that of *P. mineri* from which it differs as regards the subtriangular rather than semicircular outline of the median elevation of XIII which is armed with a somewhat smaller anteromedian spine (this spine being relatively larger in *P. mineri* than in any of the other American species). The posterior parts of XIII are in *P. beebei* much less narrow, elongate and elevated than in *P. mineri*; the transverse plate of XIV is shorter and its anterior margin much less produced; the thelycum thus appears much less cuplike than in *P. mineri*. The anteromedian margin of the transverse plate of XIV is convex rather than notched as in *P. mineri*.

To an even greater extent than as regards thelycum, the petasma of *P. beebei* resembles that of *P. mineri* much more nearly than that of any other species. The principal differences are that in *P. mineri* the lateral of the two rows of spinules crowning the eminences of the ventral lobule of the distolateral lobe is hardly more extensive than the median row, instead of much more extensive as in *P. beebei*; and the lateral part of the dorsal lobule of the distolateral lobe projects considerably beyond the ventral lobule in ventral view instead of being hidden behind it as in the present species.

### ***Penaeopsis (Metapenaeopsis) mineri* Burkenroad.**

*P. (M.) mineri*, Burkenroad, 1934b, p. 25, part.

*Range*: Lower California, both coasts, 7 to 30 fms.

*Material*: A total of 61 specimens (the males slightly outnumbering the females) was taken at Magdalena Bay, Pacific coast of Lower California (Station 131), San Lucas Bay on the southern coast (Station 135) and Santa Inez Bay on the Gulf coast (Stations 141 and 142) at depths of 6 to 30 fathoms, as follows: Station 131: D-1 (6 ♂, 10 ♀); Station 135: D-11, D-12 (2 ♂); Station 141: D-1 (3 ♂), D-4 (2 ♂, 5 ♀); Station 142: D-1 (23 ♂, 10 ♀). Cat. Nos. 36,984, 36,985, 36,986, 36,987, 36,988.

*Dimensions and Sexual Condition*: Females ranging in carapace length from 11.5 mm. (impregnated adult) to 5 mm. (juvenile); males from 11 to 5 mm. The petasmal endopods are already joined distally in the smallest specimen available, but are of fully adult condition only above 6 mm. No particular indication of local segregation as to size or sex is discernible.

*Remarks*: Although *P. mineri* has so far been recorded only from Lower California, the fact that there is but one specifically determinable record of the genus from the Pacific American mainland south of 22° N. permits no speculation as to the actual range of the species. It is perhaps interesting that although their ranges overlap, *P. mineri* was taken in company with *P. beebei* only once, at Station 135, and then in very small number.

The present extensive material requires modification of the original description in certain particulars. The rostral armature varies from 9 + 1 to 13 + 1, the modal number being 10 or 11 teeth in addition to the epigastric; the extremes are infrequently found. Recognition of the "variant" Panamanian male erroneously referred to the present species in 1934b (p. 26) as representing the closely related but distinct species *P. beebei* disposes of the opinion previously held that the basal spine of the second leg in *P. mineri* is variable in occurrence. The distoventral projection of pars externa of the right petasmal endopod is not, as described in 1934b (p. 28), shallowly cleft into "a small right and a large left lobe," but into two subequal lobes the left of which partially conceals the right in ventral view; the essential distinction between the projection in *P. mineri* and in *P. kishinouyei* is therefore that in the latter the left lobule is actually as

well as apparently considerably larger than the right. Rathbun's statement that the "left half" of the "petasma" of *P. kishinouyei* is longer than the right evidently refers to the distoventral projection of pars externa of the right endopod only; and not, as interpreted in 1934b (p. 28) to the actual halves of the petasma, the two endopods.

In the comparison of the thelycum of *P. mineri* with that of the Atlantic American species of *Metapenaeopsis*, given in 1934b, the statement is made (p. 28) that the transverse groove between sternites XIII and XIV is in *P. mineri* "anteromedially so shallow . . . that it is probably no more than a vestige bereft of the sperm-storing function which this portion of the groove possesses in *P. goodei* and *P. smithi*;" and I have also stated (p. 10) that "in the American species of *Metapenaeopsis*, no portion of this depression [the transverse groove] is especially expanded; the spermatophores enter each lateral half of the groove by median openings, the sperm being extruded at the lateral, anterior ends of the groove." These statements are not entirely correct, and a more precise description of sperm-storage in these forms is therefore offered here, as follows:

In *P. goodei* (as described in 1934b, p. 18), the transverse groove is on either side quite deep in its entire length, and the spermatophore is introduced into the elongate, U-shaped receptacle of either side at its antero-median end, on the *inner* side of the posterior part of the median plate. The median limb of the U is occupied by an elongate cylinder of sperm-free material; while the sperm lie near the exit of the receptacle, at the anterolateral end of the U, which is not particularly expanded for this function. In *P. smithi*, on the contrary, the part of the transverse groove homologous with the median limb of the U in *P. goodei* is shallow, and is not employed in spermatophore storage; and the entrances of the receptacles seem to lie near the posterior ends of the lateral limbs of the transverse groove, on the *outer* sides of the posterior parts of the median plate; instead of on the inner sides of the posterior parts at the anterior ends of the median limbs of the transverse groove, as in *P. goodei*. Further, the anterior ends of the lateral limbs of the transverse groove in *P. smithi*, near the exits, are quite definitely expanded as membranous sacs into which the sperm-bearing portion of the spermatophores is introduced; the sperm-free secretion of the spermatophore seems much reduced in quantity as compared with *P. goodei*, commensurate with the reduction of that part of the groove in which the secretion might be stored. The receptacular arrangements in the three Pacific American species of the subgenus are very similar to those of *P. (M.) smithi*, although there is little resemblance in superficial sculpture. It therefore appears that as regards the method of sperm storage, *P. goodei* is unique among its American congeners; and it seems possible that *P. mineri*, *P. beebei*, and *P. kishinouyei* are more closely related to *P. smithi* than to *P. goodei* and *P. pubescens* (to which *P. kishinouyei* displays some superficial resemblance in sculpture of the thelycum). It is probable, however, that the three Pacific species are more closely related to one another than they are to any of the Atlantic forms.

#### TRACHYPENEUS Alcock.

Subgenus TRACHYSALAMBRIA Burkenroad, 1934b, p. 49.

SECTION 1, Burkenroad, 1934a, p. 94.

#### *Trachypeneus similis pacificus* Burkenroad.

*T. (T.) s. pacificus*, Burkenroad, 1934b, p. 50.

*Range*: Gulf of Panama; Lower California, both coasts; 12-24 fms.

*Material*: Five specimens (1 ♂, 4 ♀) were taken at Magdalena Bay,



Pacific coast of Lower California, in 12 fathoms, March 29, 1936. (Station 131 D-1, Cat. No. 361,026).

*Dimensions and Sexual Condition:* Females ranging in carapace length from 8 to 12 mm.; male 7.5 mm. Juvenile.

*Remarks:* In the adults of *T. s. pacificus* the anterior margins of the produced posterior lips of the transverse groove are conspicuously truncated, as stated in the original description. In the juveniles, however, this truncation is hardly discoverable, the anterior margins of the lips being roundedly convex somewhat as in the Atlantic American species *T. constrictus* (Stimpson). In the Atlantic American *T. s. similis* (Smith) the truncation develops with age as in *T. s. pacificus*, but the lips are never so decidedly convex as they are in the juveniles of the Pacific subspecies. Other diagnostic differences between *T. similis* and *T. constrictus*, listed in 1934b, are little affected by growth in subadult stages.

SECTION 2, Burkenroad, 1934a, p. 94.

***Trachypeneus (Trachysalambria) brevisuturæ* Burkenroad.**

*T. (T.) brevisuturæ*, Burkenroad, 1934b, p. 55.

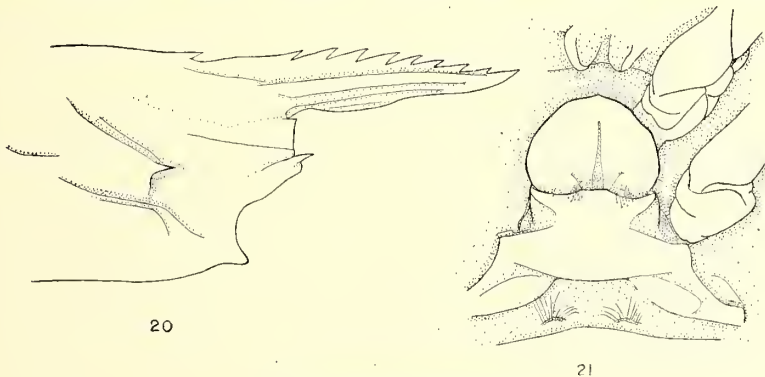
(Text-figures 20, 21).

*Range:* El Salvador; Lower California; 3-35 fms.

*Material:* A total of seven specimens (of which two are males) was taken at San Lucas Bay (Station 135) and at Arena Bank at the southern end of Lower California (Station 136) in 3 to 35 fathoms, as follows: Station 135: D-1 (1 ♂, 3 ♀), D-6 (1 ♂), D-18 (1 ♀); Station 136: D-30 (1 ♀). Cat. Nos. 36,989, 36,990, 36,991, 36,992.

*Dimensions and Sexual Condition:* Females ranging from carapace length 15 mm., total about 58 mm. (impregnated adult) to carapace length 5 mm. (juvenile). Both males of carapace length 7 mm. (subadults with joined petasml endopods).

*Remarks:* The present Californian material seems in close agreement with the Salvadorean holotype of the species, a subadult male of carapace length 6.5 mm. There is very little difference in non-genital features between adults and juveniles or males and females; except that in the larger



Text-figures 20 & 21.

*Trachypeneus brevisuturæ* MDB. 20. Carapace (anterior part, lateral view); adult ♀, D. T. R. 36,991, x 5.5. 21. Thelycum; as in 20, x 12.

specimens the rostrum is somewhat longer than in the holotype, reaching as far as to the middle of the second segment of the antennular peduncle. In 4 of the present specimens there are seven rostral teeth in addition to the epigastric; in 3, eight. The branchiostegal carina is very shallow, but quite perceptible; it is obsolescent, rather than "obsolete" as stated in the original description.

Confirming the allocation of *Trachysalambria brevisuturæ* to Section 2 of the subgenus, the thelycum resembles that of the other, Indo-Pacific, species included in the Section, in that the posteromedian lip of the transverse groove is not produced forward as a pair of flaps divided by a deep incision in the manner diagnostic of Section 1. The posterior lip of the transverse groove of the present species, although it is continuous across the midline in the fashion diagnostic of the subgenus, overhangs a median cavity much shallower even than that in the other species of the Section. The thelycum is superficially distinguishable from that of *T. curvirostris* and its allies in that the posterior lip of the transverse groove is in adults (but not in juveniles) medially convex, rather than concave; and in that the portion of sternite XIV lying behind the level of the bases of the fifth legs is longer than the anterior part, rather than shorter. The heart-shaped median plate, which is considerably depressed in the midline, especially posteriorly, bears an anteromedian spine reminiscent of that in *Metapenaeopsis* in the three juvenile females of *D. T. R.* 36989.

#### EUSICYONIA Stebbing.

DIVISION I, Burkenroad, 1934b, p. 71.

#### *Eusicyonia disparri* Burkenroad.

*E. disparri*, Burkenroad, 1934b, p. 83.

(Text-figures 22, 23).

*Range:* Southern and Gulf coasts of Lower California, beach<sup>5</sup> to 35 fathoms.

*Material:* A total of 3 specimens (2 ♂, 1 ♀) was taken at Arena Bank (Station 136) and at Santa Inez Bay (Station 142) in 30 to 35 fathoms, as follows: Station 136: D-30 (1 ♂); Station 142: D-1 (1 ♂, 1 ♀). Cat. Nos. 36,993, 36,994.

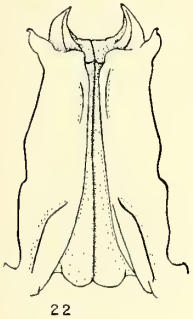
*Dimensions and Sexual Condition:* Female of carapace length 7 mm., total about 29 mm. Larger male of carapace length 6.9 mm.; smaller of carapace 4 mm., total length 15.5 mm. The petasma of both males is of adult form.

*Remarks:* The female of the present collection is in detailed agreement with the types. The larger male, taken in the same catch as the female, agrees well as to sculpture and armature of carapace and pleon, except that the posteriormost rostral tooth is somewhat farther in advance of the orbital margin than in material previously recorded. The small male (*D. T. R.* 36993) differs quite considerably from other known specimens of *E. disparri*, which are all of considerably larger size, in that the rostral tip bears only four teeth, the third rostral tooth is not a great deal farther behind the tip than it may be in *E. laevigata* (Stimpson), the first or posteriormost rostral tooth is not a great deal closer to the orbit than it sometimes is in *E. laevigata* (Stimpson), the anterior postrostral tooth is conspicuously smaller than the two following ones (although it is relatively much larger than even the extreme in *E. laevigata*), and finally, the anterior three pleonic somites bear a trace of posterior pleural sulcus, much shorter and

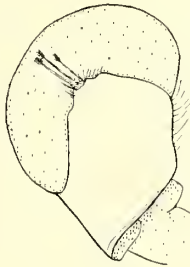
<sup>5</sup> "Beach" record based on specimens taken in the seine by the *Pawnee*, at depths presumably not greater than 5 fathoms.

shallower than in *E. parri* Burkenroad, but quite definite; and the anterior tergal of the fourth somite is continuous, as in *E. carinata* (Olivi), not interrupted as in *E. laevigata*, *E. parri*, and the other available specimens of *E. disparri*. In spite of these differences from the specific norm it seems to me safest for the present to identify *D. T. R.* 36993 with *E. disparri*.

The petasma of *E. disparri*, which has not previously been described, very nearly resembles that of *E. laevigata*; the distolateral projections are however turned conspicuously inward, somewhat as in *E. carinata*, instead of extending straight distally in ventral view as in *E. laevigata*. A male of *E. parri* taken by Dr. Beebe in Bermuda (which agrees very well in non-sexual characters with the female holotype from the Bahamas) resembles the present males of *E. disparri* in form of sexual appendage, except that the proximal border of the notch in the lateral margins of the petasma protrudes beyond the margin proximal to it as a prominent shoulder.



22



23

#### Text-figures 22 & 23.

*Eusicyonia disparri* MDB. 22.

Petasma (posterior view); adult ♂, *D. T. R.* 36,994, x 14. 23. Eye (of left side, dorsal view); adult ♀, *D. T. R.* 36,994, x 14.

Since the variant small male referred with some doubt to *E. disparri* above softens several of the differences previously given as distinguishing this species from related forms, especially *E. parri*, certain additional distinctions between the Atlantic and the Pacific forms may be considered.

In all five of the available specimens of *E. disparri* the middle part of the posterior margin of the pleura of the fourth pleonic segment is decidedly concave and is ventrally set off by a well-developed angle which in the largest specimens is acute. In both specimens of *E. parri* (as in *E. laevigata* and *E. carinata*), the midsection of the posterior margin of the fourth pleura is straight and the posterior rounds into the ventral margin without a defined angle. In the five specimens of *E. disparri* the ventral margins of the rostrum, near its distal end, bear one or two small but conspicuous mobile spinules on either side, which are absent in both specimens of *E. parri*. In four of the five specimens of *E. disparri* the rostrum bears a fourth tooth on its dorsal margin just behind the tip, which is not present in either example of *E. parri*.

The first of the above characters may perhaps be subject to variation; the second probably is (inasmuch as in a male and a female of *E. laevigata* from the west coast of Florida the mobile rostral tooth [similar to those of *E. disparri*] present in all fourteen members of the species previously examined by me, is absent); and the third is certainly variable; these differences therefore appear not to be diagnostic. A diagnostic between *E. parri* and *E. disparri* seems however to be provided by size and shape of eye. In the Atlantic form the distal, cornea-bearing section of the ocular peduncle is relatively longer and is much less expanded at its distal end; and the cornea is smaller and is set more transversely than in the Pacific material. The difference in peduncular proportions may be expressed by the ratio of the length of the outer margin of the peduncle to that of the carapace and



to the breadth of the peduncle across its dorsal surface at base of cornea, as follows:

Species.	<i>Eusicyonia parri.</i>		<i>Eusicyonia disparri.</i>				
Sex.	♀	♂	♂	♂	♀	♀	♀
Carapace length in mm.	6.3	8.0	4.0	6.9	7.0	9.2	9.3
Ratio of length of outer margin of distal part of ocular peduncle to carapace length.	.14	.13	.10	.11	.11	.09	.09
Ratio of length to breadth of ocular peduncle.	.83	.76	.58	.52	.53	.52	.53

DIVISION II, Burkenroad, 1934b, p. 73.

***Eusicyonia disedwardsi* Burkenroad.**

*E. disedwardsi*, Burkenroad, 1934b, p. 86.

*Range*: Lower California, Gulf coast and southern tip; 6 to 50 fathoms.

*Material*: A total of 33 specimens (about half of them males) was taken at San Lucas Bay (Station 135), Arena Bank (Station 136) and Santa Inez Bay (Stations 141, 142, 143) in 6 to 50 fathoms, as follows: Station 135: D-1 (3 ♂, 1 ♀), D-9, D-10 (1 ♀), D-26 (1 ♀); Station 136: D-1 (1 ♀), D-6 (2 ♂), D-24 (2 ♂, 2 ♀), D-30 (4 ♂, 2 ♀); Station 141: D-1 (1 ♀), D-3 (1 ♂, 1 ♀), D-4 (3 ♂, 1 ♀); Station 142: D-1 (2 ♂, 3 ♀), Station 143: D-1 (1 ♀). Cat. Nos. 36,995, 36,996, 36,997, 36,998, 36,999, 361,000, 361,001, 361,002, 361,003, 361,004, 361,005, 361,006.

*Dimensions and Sexual Condition*: Females ranging in carapace length from 16.2 mm. to 7 mm.; males from 15.3 mm. to 4.6 mm. Total length of the largest male, about 59 mm. The haul from Station 136, D-24, composed of the four largest specimens, is the deepest one yielding material of the species; but although the smaller specimens are often those from the least depths, the correspondence is by no means complete. The size of the males at maturity seems quite irregular; there are specimens with unjoined petasmal endopods ranging in carapace length from 6.8 mm. to 8 mm., and specimens with the endopods hooked together at the distal end only ranging in carapace length from 5.5 mm. to 10 mm.

*Remarks*: *Eusicyonia disedwardsi* was described with some misgivings from a single subadult male; and it is therefore with considerable satisfaction that a confirmation of its right to specific distinction is now offered on the basis of an ample material.

Petasma, male genital sternites, and thelycum are practically identical with those of *E. edwardsi*, except that the tips of the distolateral projections of the petasma are often directed rather conspicuously away from the midline instead of parallel to it. Differences from *E. penicillata* in petasma, previously described, are completely constant in adults and are recognizable even in very juvenile stages. Differences in male genital sternite and in thelycum between *E. disedwardsi* and *E. penicillata*, identical with those between the latter and *E. edwardsi*, are constant in adults but are somewhat obscure in very juvenile individuals. The divergence of the tips of the stylets of the ocular somite, constant at all sizes, provides a clear though minute distinction from *E. penicillata*.

Differences in pleonic sculpture from *E. edwardsi* are constant and diagnostic; although the traces of posterior pleural sulcus are often stronger than in the holotype, there is generally a faint trace of posterior tergal on the first somite, and the dorsal end of the posteromedian pleural often reaches the anterior margin as a groove which although shallower than in *E. edwardsi* and *E. penicillata* is not completely obliterated. In large adults the pleura of the fourth somite often bear a posterior ventral tooth or angle.

The rostrum is almost constantly longer than the maximum in *E. penicillata*, and is usually more elevated than in the related Pacific form. As a very obvious distinction from both *E. edwardsi* and *E. penicillata*, it may be observed that the rostrum of every available individual of *E. disedwardsi* bears two teeth behind the bifurcated tip (in addition to the "anterior tooth of the carapace" which is occasionally placed in advance of the orbital margin); whereas in the two related species not more than one individual in ten bears more than one rostral tooth behind the tip.

It may be noted that in one specimen of *E. disedwardsi* the middle tooth of the carapace, in contrast to its usual position, lies anterior to the level of the hepatic spine.

Like *E. penicillata* and several other Pacific species less closely related, *E. disedwardsi* is marked with a large and conspicuous ring or ocella of pigment on the branchial region which seems, peculiarly enough, to be absent in *E. edwardsi* and in the other Atlantic members of the genus.

### ***Eusicyonia penicillata* (Lockington).**

*Sicyonia penicillata*, Lockington, 1879, p. 164; Pesta, 1915, p. 118.

*Eusicyonia penicillata*, Burkenroad, 1934b, p. 88.

*Range*: Lower California, both coasts; beach to 40 fathoms.

*Material*: A total of 37 specimens (somewhat more than half of these being males) was taken at Santa Inez Bay (Station 144), at San Lucas Bay (Station 135), east of Cedros Island (Station 126), and at Magdalena Bay, in 2 feet to 40 fathoms, as follows: Magdalena Bay, "In 2 to 3 feet of water under stone" (17 ♂, 14 ♀); Station 126: D-3 (3 ♂, 1 ♀); Station 135: D-11, D-12, (1 ♂); Station 144: D-7 (1 ♀). Cat. Nos. 361,007, 361,008, 361,009, 361,010.

*Dimensions and Sexual Condition*: Material from Station 126 (a female of carapace length 18 mm. and males of 12.4 to 16.5 mm.), falls within the range of sizes previously recorded (1934b, p. 88) and is fully adult; while the male from Station 135, of carapace length 9.6 mm., although of smaller size, appears to be adult. The series from very shallow water in Magdalena Bay is however composed exclusively of juveniles, the first which I have been able to examine. Females of this series range from carapace length 12 mm. down to carapace 4 mm., total length 17.5 mm.; and males from carapace 8 mm. to carapace 4.9 mm., total length 18.5 mm. The single female from Station 144 is also a juvenile, of carapace length 6.9 mm.

*Remarks*: The present seem to be the first records of the species from outside the Gulf of California.

In my previous account of *E. penicillata*, I have unfortunately overlooked the description by Pesta, 1915. It may be noted that the otherwise excellent figure 7 of the petasma, there given, is inaccurate in one detail, in that the accessory filaments originate near the middle of the distolateral projections, rather than, as shown, at their bases.

The present juveniles of *E. penicillata* display little change from adult form in non-sexual characters, except that as in many related species the sharp angle terminating the hinder end of the dorsal carina of the fifth pleonic somite becomes more rounded with diminishing size until in the

smallest individuals there is no trace of it. The notch in the posterior margin of the thirteenth sternite loses its narrow subrectangular outline in the juveniles and becomes a shallow concavity; and the ridge across the posterior margin of the thirteenth sternite of the male loses its well-bowed appearance, chiefly by the reduction in relative size and the increased separation of the lateral protuberances.

In males of carapace length 7.5 to 8 mm. the petasmata are hooked together only at their anterior ends, and the filaments of the various projections are relatively shorter than in the adult. Below 7.5 mm. the endopods are unattached, but the adult characteristics of the petasma are recognizably indicated even in the smallest individuals, where the accessory filament is represented by a well-defined shoulder about one-third from the tip of the curtailed but very slender distolateral projection.

### ***Eusicyonia aliaffinis* Burkenroad.**

*Eusicyonia aliaffinis*, Burkenroad, 1934b, p. 92.

(Text-figures 25, 27).

*Range*: Pacific coast of Mexico; southern tip of Lower California; 13 to 30 fathoms.

*Material*: One male was taken at San Lucas Bay in 13 fathoms (Station 135 D-26, Cat. No. 361,011).

*Dimensions and Sexual Condition*: The specimen, of carapace length 8.4 mm., is smaller than the holotype, but its petasma is fully developed and of adult form, rather than disunited and juvenile as in the type.

*Remarks*: The present male agrees precisely in critical non-sexual characters with the Mexican holotype. The petasma shows no very striking differences from that of *E. affinis*, except in the non-projection of a small cusp near the median base of the distolateral projections which is conspicuous in an available large type male of Faxon's species.

In addition to the large specimens of *E. affinis* contained in the collection of the Museum of Comparative Zoology, a comparison of which with *E. aliaffinis* has been presented in my previous discussion of that species (1934b), I have recently been enabled by the kindness of Dr. W. L. Schmitt of the U. S. National Museum to examine the juvenile male of *E. affinis* (U. S. N. M. 21169) which Faxon, 1895, p. 179, records from *Albatross* St. 3369, off Cocos Island, in 52 fathoms. This specimen (figure 24), of carapace 8.8 mm., total length 35 mm., is of the same size as the holotype of *E. aliaffinis*. The agreement of this specimen in all critical characters with the much larger individuals of *E. affinis* previously examined, and its sharp contrast with *E. aliaffinis*, seems to provide justification for my dismissal in 1934b, p. 94, of the possibility that *E. aliaffinis* might "represent a developmental stage of *E. affinis*." The possibility that *E. aliaffinis* and *E. affinis* may represent extremes of variation connected by intergrading forms is discussed in the next paragraph.

### ***Eusicyonia* species.**

(Text-figures 26, 28, 29, 30).

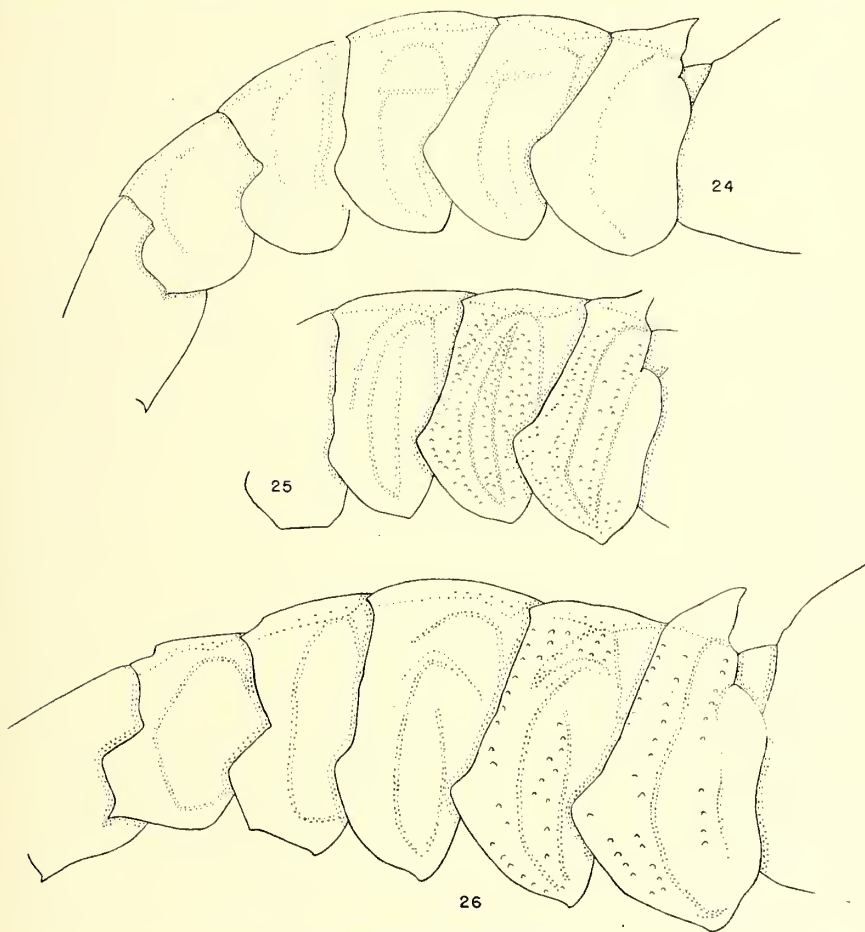
*Range*: Known only from Arena Bank at the southern tip of Lower California; 45-50 fathoms.

*Material*: Two specimens (1 ♂, 1 ♀) were taken at Arena Bank at depths of 45 to 50 fathoms, as follows: Station 136: D-13 (1 ♂), D-24 (1 ♀). Cat. Nos. 361,012, 361,013.



*Dimensions and Sexual Condition:* The male from Station 136 has a carapace length of 12 mm., total length about 60 mm. The carapace length of the female is 12 mm. Both specimens appear to be fully adult.

*Remarks:* The present material, representing a species closely related to if distinct from *E. aliaffinis* Burkenroad, agrees with the two known specimens of the latter and differs markedly from *E. affinis* Faxon (figure 24 above) as regards the sharp definition of the angle terminating the dorsal carina of the fifth pleonic somite; the angular outline of the ventral margins of the pleonic pleura (especially those of the fourth somite, the posterior ventral angle of which is in the male even spiniform; and of the first somite, the anteroventral margin of which is in all decidedly concave rather than conspicuously convex as in *E. affinis*); and the coarse tubercula-



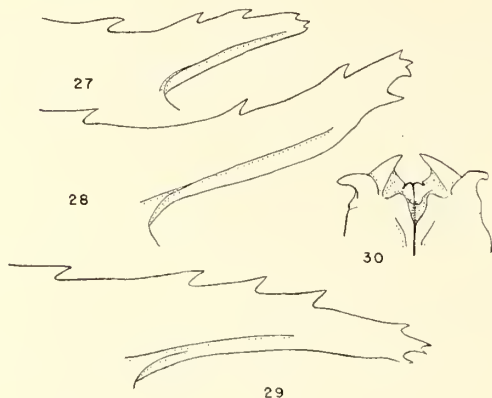
Text-figures 24-26.

*Eusicyonia affinis* (Faxon). 24. Pleon (lateral view); juvenile ♂, U. S. N. M. 21,169, x 5.5.

*Eusicyonia aliaffinis* MDB. 25. Pleon (lateral view of anterior part, tubercles indicated for first two somites only); subadult ♂, D. T. R. 361,011, x 5.5.

*Eusicyonia* species. 26. Pleon (lateral view, tubercles indicated for first two somites only); adult ♀, D. T. R. 361,013, x 5.5

tion of the pleonic surface. On the other hand, however, the two specimens from Station 136 differ considerably from *E. aliaffinis* and approach *E. affinis* in that the posteromedian pleural sulci of the second and third pleonic somites extend dorsally only to within a third of the height of the somite from the dorsal midline (instead of to within a fourth or nearer), turn anteriorly at their dorsal ends, and are margined above by a conspicuous longitudinal ridge.



Text-figures 27-30.

*Eusicyonia aliaffinis* MDB.  
27. Rostrum (lateral view); as in 25, x 6.

*Eusicyonia* species. 28. Rostrum (lateral view); as in 26, x 6. 29. Rostrum (lateral view); adult ♂, D. T. R. 361,012, x 6. 30. Petasma (distal part, posterior view); as in 29, x 13.5.

The anteromedian pleural sulci of the first, second and third pleonic somites of the two specimens from Station 136 seem to fall about midway in length and definition between those of *E. affinis* and *E. aliaffinis*. The rostrum seems longer than that of either *E. affinis* or *E. aliaffinis*, being approximately half instead of two-fifths or less as long as the carapace and extending far beyond the eyes; and it bears six teeth instead of five in both specimens. While, however, the rostrum of the male from Station 136 is recurved nearly to the horizontal and the third tooth of the dorsal margin lies far behind the trifurcate tip, that of the female is recurved to an angle of elevation much greater even than in the two available specimens of *E. aliaffinis*, the third dorsal tooth forms part of a trifurcate tip, and the sixth tooth is placed on the ventral margin more than half as far from the tip as the penultimate dorsal tooth; the rostrum of the female thus superficially somewhat resembles that of *E. carinata* (Oliv). The transverse ridge at the posterior margin of the fourteenth sternite of the male from Station 136 resembles that of *E. aliaffinis* as regards its dimensions, but is strongly arched. The petasma differs slightly both from that of *E. aliaffinis* and that of the available large male *E. affinis*, in that the distolateral projections are quite convergent; and in that the small cusp near the median base of the distolateral projections is more conspicuous than in *E. aliaffinis*, less so than in *E. affinis*.

Whether the present material should be regarded as a distinct species, as a variant form of *E. aliaffinis*, or as an intergrade between *E. aliaffinis* and *E. affinis* seems difficult of decision. The fact that the pleonic sculpture is the same in *E. affinis* of both large and small size, which is in harmony with what is known of other members of the genus, suggests that differences between the various available groups of individuals of the *E. affinis* superspecies are at least not the correlates of differences in size. The provenance of the present material seems to rule out local variation as an explanation of its attributes. However, the total number of available individuals of the superspecies is not yet sufficient to exclude the possibility that differences between groups of these individuals are referable simply to individual variation (and it may be noted that if the small specimen discussed on

p. 80 actually refers to *E. disparri*, its pleonic characters imply that considerable departure from the specific norm may sometimes occur in species of the genus). Although it seems to me possible that the present specimens represent a third species distinct from both *E. affinis* and *E. aliaffinis*, their systematic status may be left undefined until further material has become available.

### ***Eusicyonia picta* (Faxon).**

*Sicyonia picta*, Faxon, 1893, p. 210.

*Eusicyonia picta*, Burkenroad, 1934b, p. 95.

**Range:** Off Mariato Point and in the Gulf of Panama, 127 to 182 fathoms; southern and Gulf coasts, Lower California, beach<sup>6</sup> to 60 fathoms.

**Material:** A total of six specimens (including 1 male) was taken at Arena Bank (Station 136) and at Santa Inez Bay (Station 147) in depths of 30 to 45 fathoms; as follows: Station 136: D-11 (1 ♀), D-12 (1 ♀), D-15 (1 ♀); Station 147: (1♂, 2 ♀). Cat. Nos. 361,014, 361,029, 361,016.

**Dimensions and Sexual Condition:** Females ranging in length from carapace 14 mm., total 56 mm., to carapace 8 mm. Male of carapace length 7.5 mm. The largest female is considerably smaller than Faxon's type-specimen of 70 mm. The petasma of the male is of adult form.

**Remarks:** The rostral armature varies in the present material from three dorsal and two terminal to four dorsal and three terminal teeth. The spacing and position of the dorsal rostral teeth, and the length, elevation and curvature of the rostral blade are quite variable. Although Californian material of *E. picta* has not been directly compared with the Panamanian types, there seems little reason to doubt its identity with the latter.

A direct comparison of *E. picta* with two females and a male, paratypes of *E. stimpsoni* (Bouvier), from Blake Station 293, Barbados, 82 fms., which were very kindly loaned by Dr. F. A. Chace, Jr., of the Museum of Comparative Zoology, confirms the suggestions previously made (Burkenroad, 1934b, p. 96) as to characters distinguishing the two species. In addition to the conspicuously greater breadth and depth of its carapace and pleon, its longer rostrum with ventral tooth very distinctly separated from the two dorsal elements of the tip, and the deeper sculpture of its pleon, *E. stimpsoni* seems to differ from *E. picta* as follows: Its pleon is tuberculate, not punctate only as in *E. picta*. The lateral ridge of its rostrum is usually concave dorsally, so that the ridge is closer and more nearly parallel to the ventral margin of the rostrum than in *E. picta* where the ridge is usually concave ventrally. Its eye and the peduncle of its antenna seem somewhat smaller and shorter and its stylocerite longer. The distolateral projections of its petasma are curved much more to median than is usual in *E. picta*. Finally, whereas in a male of *E. picta* of carapace 11 mm. (*B. O. C. No.* 81) the petasma is 2.9 mm. long by 1.3 mm. broad, and in the present male of *E. picta* of carapace 7.5 mm. the petasma measures 1.3 x 0.7 mm., in the available male of *E. stimpsoni*, of carapace 7.0 mm., the petasma measures 2.5 x 1.2 mm., a size relatively much greater than in *E. picta*.

### ***Eusicyonia disdorsalis* Burkenroad.**

*E. disdorsalis*, Burkenroad, 1934b, p. 96.

**Range:** Gulf of Panama, southern tip of Lower California, 3 to 24 fathoms.

<sup>6</sup> "Beach" record based on specimen taken in the seine by the *Pawnee*, at a depth presumably not greater than 5 fathoms.



*Material:* A total of 10 specimens (of which about half are males) was taken at San Lucas Bay (Station 135) in 3 to 20 fathoms, as follows: Station 135: D-11, D-12 (2 ♂, 4 ♀), D-18, D-19 (2 ♂), D-20 (2 ♀). Cat. Nos. 361,017, 361,018, 361,019.

*Dimensions and Sexual Condition:* All of the specimens are of very small size, the females ranging in carapace length from 6 mm. to 8 mm., the males from 5 mm. to 7 mm. The petasma is, however, of adult form and condition in all of the males, which are presumably adult.

*Remarks:* No distinction between the present material and that previously known, from the Gulf of Panama, is apparent.

### ***Eusicyonia ingentis*, sp. nov.**

(Text-figures 31-34).

*Type:* Type and Cotypes, Cat. No. 361,025, Department of Tropical Research, New York Zoological Society (6 ♂, 4 ♀). Station 127, Dredge 1, off east coast of Cedros Island, west coast of Lower California, 28° 05' N. Lat., 115° 09' W. Long. 4-foot dredge, 38 fathoms, March 27, 1936.

*Range:* Known only from the present records, from east of Cedros Island on the Pacific coast of Lower California, in 38 to 60 fathoms.

*Material:* A total of 63 specimens (of which number about three-fifths are males) was taken east of Cedros Island (Stations 125, 126 and 127) in depths of 38 to 60 fathoms, as follows: Station 125: D-1 (7 ♂, 1 ♀); Station 126: D-2 (4 ♂, 6 ♀), D-3 (21 ♂, 12 ♀), D-4 (1 ♀), D-10 (1 ♀); Station 127: D-1 (6 ♂, 4 ♀). Cat. Nos. 361,020, 361,021, 361,022, 361,023, 361,024, 361,025.

*Dimensions and Sexual Condition:* Females ranging in length from carapace 27 mm., total length 105 mm., to carapace 7 mm., total 30 mm. Males ranging in length from carapace 22 mm., total 86 mm. to carapace 5 mm., total 20 mm. There is no clear evidence of local segregation as to size or sex. The petasmal endopods are of adult form and are joined together in males down to 10.5 mm. in carapace length.

*Diagnosis:* Antennal angle with a buttressed tooth; dorsal carina of the second pleonic somite not incised; basis and ischium of the first chelipeds unarmed. The carapace is armed with two middorsal teeth, one before and one behind the level of the hepatic spine; the rostrum is armed above with three teeth and has a bifurcate tip.

The rostrum is more than one-third as long as the carapace and is distally quite slender; it is proximally decurved, but the tip is often turned up somewhat at an angle to the proximal part. The lateral ridge of the rostrum parallels the ventral margin of the blade throughout its length. The ridge (cardiacobranchial) extending posteriorly on the sides of the carapace from behind the hepatic spine, is conspicuous, especially in large individuals.

The telson is long and slender, the width of its base being no more than a quarter of its length; and is armed with a conspicuous pair of fixed lateral spines. The middorsal carina of the fifth pleonic somite descends very gently at its posterior end. The anteromedian pleural sulcus of the first pleonic somite is faintly continued below its well-defined dorsal section as a very shallow depression. The pleural margin of the first pleonic somite, anterodorsal to the ventral angle, is straight.

The dorsal surface of the distal part of the ocular peduncle bears, near its distolateral margin, a pencil of hairs which when unbroken reaches far beyond the eye in large adults, although it is sometimes much shorter in small specimens. The terminal segment of the antennal peduncle is very

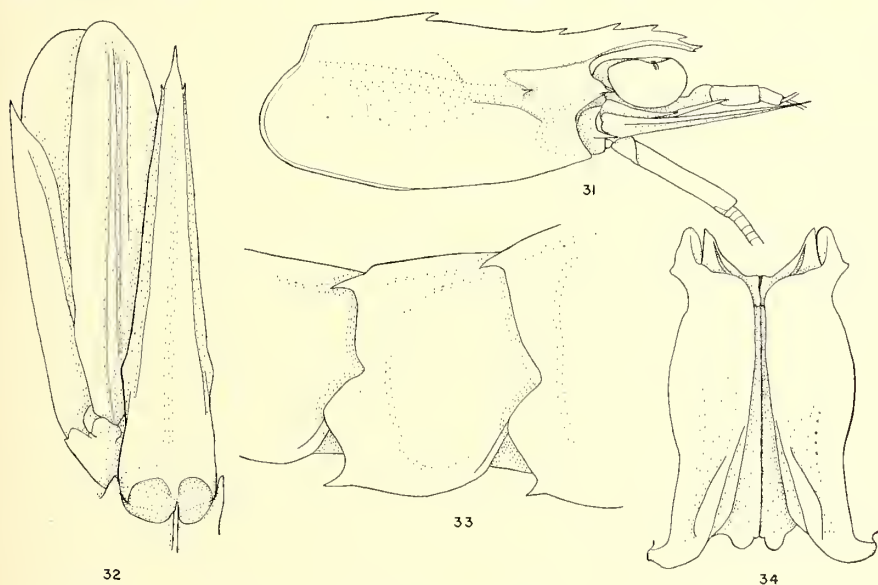
long and slender, its diameter being no more than one-fifth its length. The telson does not extend as far as do the uropods in adults, although it may exceed them in juveniles.

The blunt-tipped distoventral projections of the petasma bear a shallow proximolateral prominence, distal to which the projections extend parallel to and nearly or quite as far as do the distolateral lobes. The distolateral lobes are divergent from the median plane.

The depressed median interspace between the raised posterolateral parts of the buttress of the median spine of the thirteenth sternite in the female is little if at all wider than are the raised parts. The spine between the first pleopods of the female is broadly subtriangular in ventral outline, with convex lateral margins.

*Remarks:* The length attained by *E. ingentis* is somewhat greater than seems heretofore to have been recorded for the subfamily, although the animal, being a relatively slender one, is outbulked by the corpulent species next it in length, *E. brevirostris* (Stimpson).

*Eusicyonia ingentis* is closely related to *E. dorsalis* (Kingsley) and its Pacific congener *E. disdorsalis* Burkenroad, from which it is most strikingly distinguished by the form of its petasma. Aside from being a much larger species, its habitus is relatively more elongate and slender than in the related forms, a tendency particularly pronounced as regards rostrum, telson, and antennal peduncle. The details in which *E. ingentis* differs most markedly from *E. disdorsalis* are those listed in the paragraphs of the diagnosis subsequent to the first; thus in *E. disdorsalis* the lateral ridge of the rostrum usually arches up from the ventral margin near the distal end; the broad ridge posteriorly continuing the hepatic buttress is ill-defined; the lateral teeth of the telson are very minute and inconspicuous, especially in large



Text-figures 31-34.

*Eusicyonia ingentis*, n. sp. **31.** Carapace (lateral view); juvenile ♀, D. T. R. 361,021, x 4.5. **32.** Telson and right uropod (dorsal view); adult ♂ of total length 64 mm., D. T. R. 361,021, x 4.5. **33.** Fifth pleonic somite (lateral view); as in 32, x 4.5. **34.** Petasma (posterior view); as in 32, x 10.

specimens; the posterior end of the dorsal carina of the fifth pleonic somite is in adults sharply angular, although in juveniles it may descend gently; the anteromedian pleural sulcus of the first pleonic somite is not continued below its well-cut dorsal section; the anteroventral pleural margin of the first pleonic somite is concave in adults, although it is straight in juveniles; the pencil of setae on the dorsal surface of the ocular peduncle extends no more than half way across the cornea; the telson exceeds the uropods; the distolateral lobes of the petasma curve toward the midline; the proximo-lateral ramus of the distoventral projection of the petasma exceeds the acute, laterally directed distal part in size; the depressed area of the base of the spine of sternite XIII of the female is much wider than the raised parts flanking it; and the tooth between the first pleopods in females is narrow and usually with concave lateral edges.

At dimensions at which *E. ingentis* is juvenile, with minute undeveloped petasmas and endopods, *E. disdorsalis* presents all the characters of maturity.

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## 4.

Fibro-epithelial Growths of the Skin in Large Marine Turtles,  
*Chelonia mydas* (Linnaeus).

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&amp;

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(Plates I-XVIII).

Diseases of turtles have received but relatively little study up to the present time and not much is known about the benign or malignant tumors of these reptiles. In a report on the causes of deaths in the London Zoological Gardens, Plimmer (1912, 1913) reported two cases of such growths. Scott and Beattie (1927), referring to Plimmer's observation, state that one tumor was a glandular cancer of the stomach in an elephantine tortoise and that the second was a multi-nucleated tumor involving heart muscle of *Sternotherus niger*, a fresh water turtle from the Cameroon area of West Africa. These authors point out that of six thousand reptiles of various kinds autopsied at the London Zoological Gardens, only two showed tumors as the cause of death. Pick and Poll (1903) described an adenomatous growth of the thyroid of the Brazilian fresh water turtle, *Platemys geoffroyana* (*Hydraspis geoffroyana*). This was a large mass measuring 6 x 4 x 2.5 cm., consisting of narrow cylindrical cells in small acinar arrangement with lumina containing granular material.

In December, 1936, it came to our attention that one of the large marine turtles, *Chelonia mydas* (Linnaeus), of the New York Aquarium presented multiple warty growths of the skin. This turtle, shipped from Key West, Florida, two years previously, occupied a large harbor water tank with two others of the same species and with two large loggerhead turtles, *Thalassochelys caretta* (Linnaeus). None of the other four turtles exhibited papillomatous lesions, although an exposure to possible infection had existed for more than a year. The water supply of the tank is a continuous flow of harbor water, which is brackish and changes density with the change of tide.

The turtle showing multiple warts weighed approximately one hundred and fifty pounds. Papillomata were distributed in the region over the dorsal part of the neck in both non-pigmented and pigmented areas and in the light gray or whitish areas of both axillae and both groins (Figs. 1 and 2). There were in addition several small warty excrescences in the outer regions of the upper eyelids involving the conjunctivae. Tissues were



removed from the neck for microscopic study and a month later more tissues were excised from several sites for transplantation experiments.

Recently (December, 1937) it was determined that cutaneous fibro-epithelial growths occur in *Chelonia mydas* (Linnaeus) under normal conditions of wild life. Three instances of this disease were found in these large marine turtles (weighing from sixty to two hundred pounds) in the course of an examination of some two hundred turtles of this species caught in the waters south of Key West. The distribution of the growths in the wild turtles likewise occupied the dorsal aspect of the neck, the axillae, groins and eyelids. The histological details of the lesions in the wild turtle resembled in general those of the original turtle studied in the New York Aquarium and it was thought probable that the disease in wild life and that seen in the Aquarium represented the same condition.

For purposes of pathological description, the cutaneous growths of the large marine turtle now under consideration may be referred to as fibro-epithelial in character. There appeared to be considerable variety in the size, form and arrangement of the masses of tissue (Figs. 3 to 8). Outstanding were the papillary, coral or cauliflower-like growths (Figs. 5 to 8). Figure 7 represents a growth arising from non-pigmented skin, while the tumor in Fig. 8 is derived from a pigmented area. Less frequently smooth oval or round fibromata projected above the level of the skin (Figs. 12 and 13). Both papillomata and fibromata, caused perhaps by the same agent, appeared as single or confluent masses in the same turtle. Papillomata and fibromata at times grew in immediate apposition. All growths had a firm gritty consistency and areas of calcification at the surface of tumors were not uncommon. In the preparation of histological sections, it was found advisable to subject all tissues to decalcification. Papillomata varied in size from 3 mm. to 3 cm. while solitary fibromata measured as much as 2.5 cm. in diameter.

The internal structure of papillary growths became clear on sectioning the gross specimens and inspecting their cut surfaces (Figs. 9 to 11). Attached to the skin by a sessile or pedunculated base, the stroma of the various growths was composed of dense intermingling fibrous tissue which spread out toward the surface in many lesser ramifications to form rounded, bulbous or pointed terminal tips covered with thickened surface epithelium.

The microscopic structure of normal skin of *Chelonia mydas* is shown in Fig. 17. Compared with this the epithelium covering papillomata appeared to be somewhat thickened and covered with an irregular mass of keratin (Fig. 21). The size and shapes of epithelial cells varied greatly and intercellular bridges of prickly cells were strongly developed (Fig. 23). Epithelial columns and cords often dipped down deeply into the supporting stroma (Fig. 22). So-called epithelial "pearls" were frequently encountered, not unlike those found in mammalian epithelial tumors (Fig. 24). The vascular supply of papillomata is a network of small blood vessels. It was not unusual to have collections of lymphocytes grouped around small blood vessels, indicating possibly a low grade of inflammation (Fig. 27). Cell inclusions were not demonstrated in the sections examined. Dendritic pigment cells frequently accompanied blood vessels (Fig. 25), or they existed in diffuse distribution in the stroma below the surface epithelium (Fig. 26). In highly pigmented areas, numerous melanophores were found at the surface between epithelial cells.

The fibromata of the turtle's skin (Figs. 12 and 13) were relatively simple in microscopic architecture, being composed of intermingling bands of fibrous tissue varying in density (Figs. 28 and 29), covered on the surface with but slightly thickened epithelium (Fig. 28). Although the skin covering fibromata could appear non-pigmented so that tumors looked white on external examination, the interiors were usually gray or a streaky black due to the presence of pigment cells which followed the course of blood

vessels (Fig. 28). Small nerve trunks were found in one of the sections of a fibroma (Fig. 30).

It was noted that papilloma and fibroma existed at times in a combined form of tumor. This was illustrated very well in a large growth measuring 8 x 6 x 5 cm., taken from the right side of the neck of one of the Key West turtles (Fig. 15). The large bosses (F) of this growth were fibromata, while at point P a distinct papilloma existed, fused with the rest of the mass. Figure 16 shows the interior of this tumor to be composed of five smaller fibromata, white or partly pigmented. Nearly all fibromata showed microscopic evidences of peri-vascular melanophores (Fig. 28).

These fibro-epithelial tumors of the turtle show no malignant changes. Mitotic figures are few in number.

#### COMMENT.

The stimulus to the formation of cutaneous fibro-epithelial growths in *Chelonia mydas* remains for the present undetermined. It is interesting to note that fishermen of the white population at Key West, exposed for many years to the sun, frequently develop keratoses and malignant changes of the skin, whereas it is said that with fishermen of the colored population such changes are rare occurrences. It is conceivable that these great sea turtles, even though in an aquatic environment, may respond to exposure to the sun prolonged over many years by papillomatous changes affecting the skin. A different explanation for the etiology of the disease other than the above mentioned is more likely, such as infection by parasites or by an unknown virus. No parasites were noted so far in the tumor tissues of the four turtles examined. It is known that certain infectious warts of man, dog and cattle are of virus origin. Infectious papillomatosis of rabbits has been shown by Shope (1933) and Rous and Beard (1934) to have its origin in a virus. Such an etiology for the cutaneous turtle fibro-papillomata is not unlikely. The study of the transmissibility of the turtle papilloma has been begun and it is hoped to report on this at a later date.

#### SUMMARY.

Cutaneous fibro-epithelial growths in four large marine sea turtles, *Chelonia mydas* (Linnaeus), are described, with a discussion of their microscopic structure.

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## EXPLANATION OF THE PLATES.

## PLATE I.

Figs. 1 & 2. Marine turtle, *Chelonia mydas*, weighing about 150 pounds, showing distribution of papillomata on neck, axillae and eyelid.

## PLATE II.

Fig. 3. Small papillomata. A pigmented growth at x.

Fig. 4. Papillomata of various shapes. E is tissue removed from upper eyelid with papilloma growing on the margin of eyelid.

## PLATE III.

Figs. 5 & 6. Larger forms of papillomata.

## PLATE IV.

Fig. 7. One of the larger forms of papillomata. Shows papilloma arising from non-pigmented skin.

## PLATE V.

Fig. 8. One of the larger forms of papillomata. Shows papilloma derived from pigmented skin.

## PLATE VI.

Fig. 9. Cut surfaces of gross specimens of papillomata.

## PLATE VII.

Fig. 10. Cut surface of gross specimen of papilloma.

Fig. 11. Cut surface of gross specimen of papilloma, showing a deeply pigmented stroma.

## PLATE VIII.

Fig. 12. Solitary fibroma of the skin. F marks the fibroma; C marks the site of a calcified plaque of the skin.

Fig. 13. Solitary fibromata of the skin.

## PLATE IX.

Fig. 14. Inner surfaces of fibromata with pigmentation.

## PLATE X.

Fig. 15. Large fibromatous masses, FF, with associated papilloma, P.

## PLATE XI.

Fig. 16. Interior of tumor shown in Fig. 15, exhibiting smaller fibromata; 1, 2, 3, 4 and 5.

## PLATE XII.

Fig. 17. Normal skin of *Chelonia mydas*. x 80.

Fig. 18. Papilloma with broad base of fibrous tissue supporting irregularly-shaped papillary processes tipped with thickened epithelium. x 40.

## PLATE XIII.

Figs. 19 & 20. Low power magnification of papillomatous tissue. x 20.

## PLATE XIV.

Fig. 21. Bulbous tips of a papilloma. Stroma slightly hyalin in character. x 100.

Fig. 22. Surface epithelium of papilloma illustrating down-growth of epithelium. x 60.

## PLATE XV.

Fig. 23. Surface epithelium of papilloma showing prickle cells united by thick intra-cellular bridges. Masson stain. x 650.

Fig. 24. Deep-lying epithelial cord with epithelial "pearl." x 250.

## PLATE XVI.

Fig. 25. Section from a papilloma with melanophores arranged around small blood vessels. x 125.

Fig. 26. Melanophores in diffuse arrangement lying in stroma close to epithelium. x 200.

## PLATE XVII.

Fig. 27. A collection of lymphoid cells around blood vessels in a papilloma. x 350.

Fig. 28. Section taken from solitary pigmented fibroma showing compact fibrous tissue below skin. Numerous pigment cells accompany blood vessels. x 50.

## PLATE XVIII.

Fig. 29. Dense, wavy, hyalin, fibrous tissue taken from the center of a non-pigmented fibroma.

Fig. 30. In center of photograph a small nerve trunk traversing loosely arranged fibers of a fibroma. x 275.



FIG. 1.

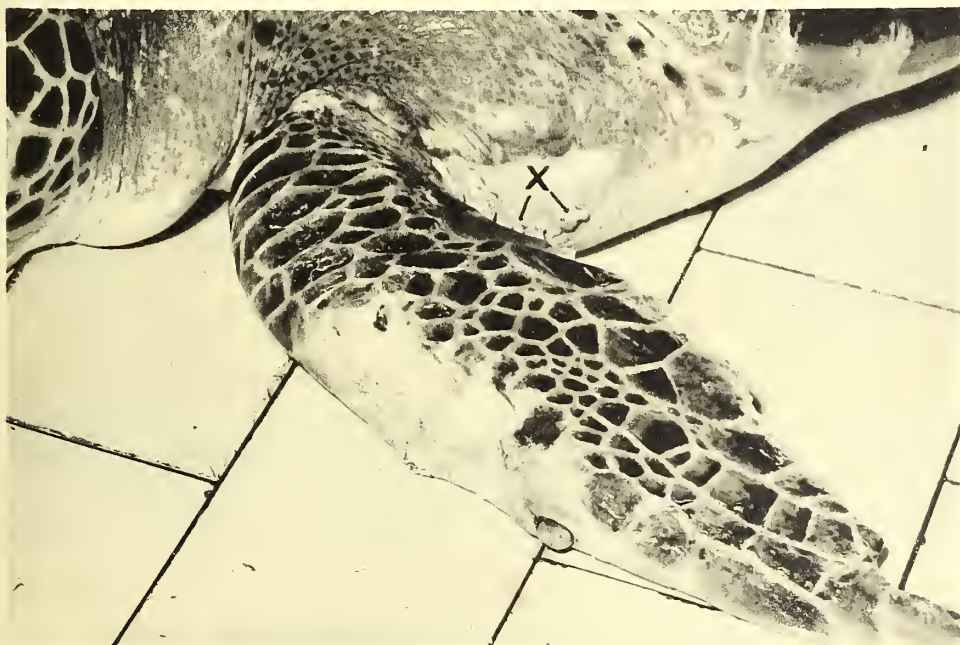


FIG. 2.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).





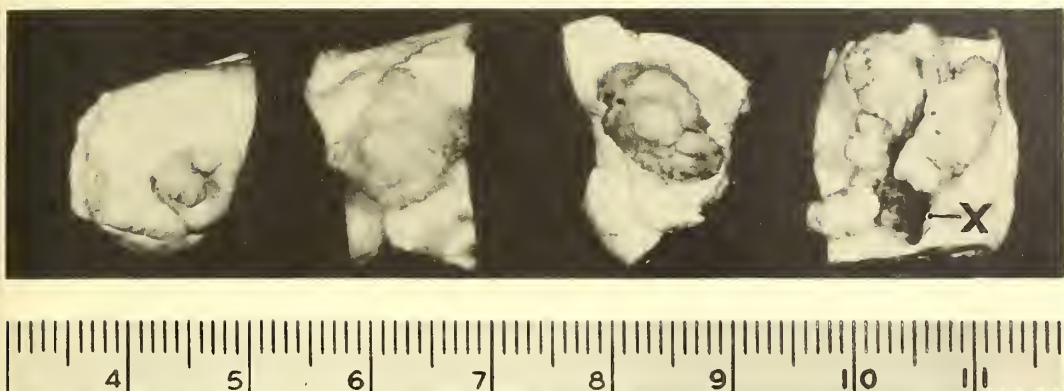


FIG. 3.

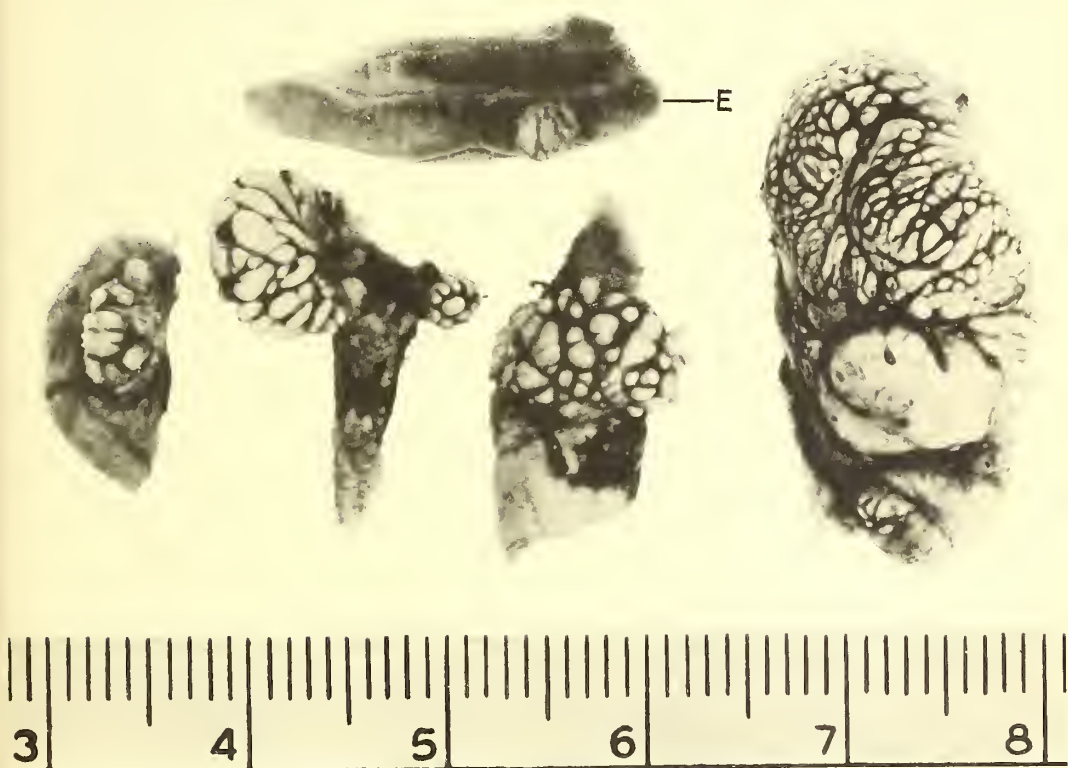


FIG. 4.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).





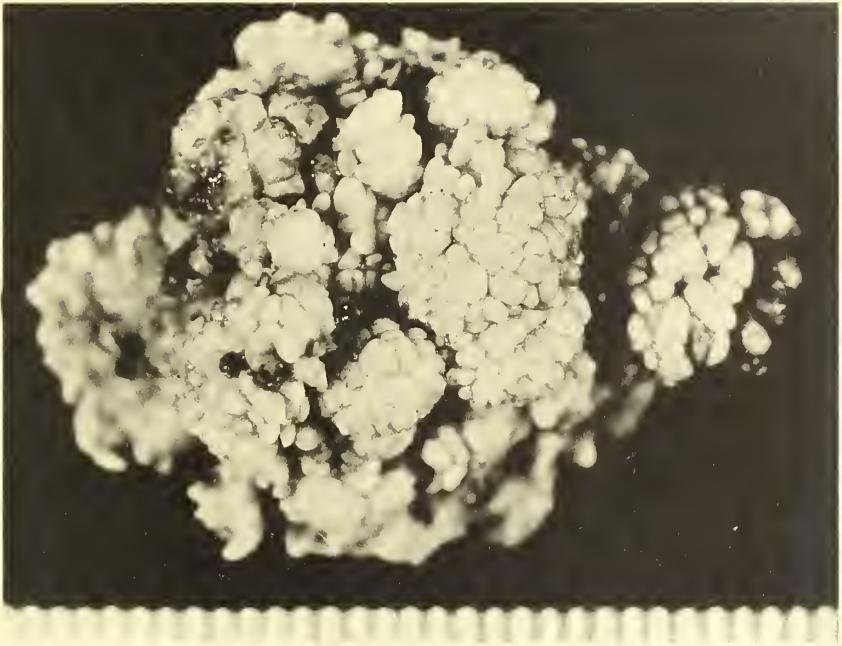


FIG. 5.



FIG. 6.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).



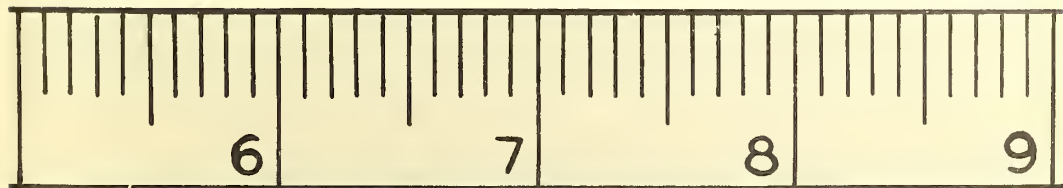
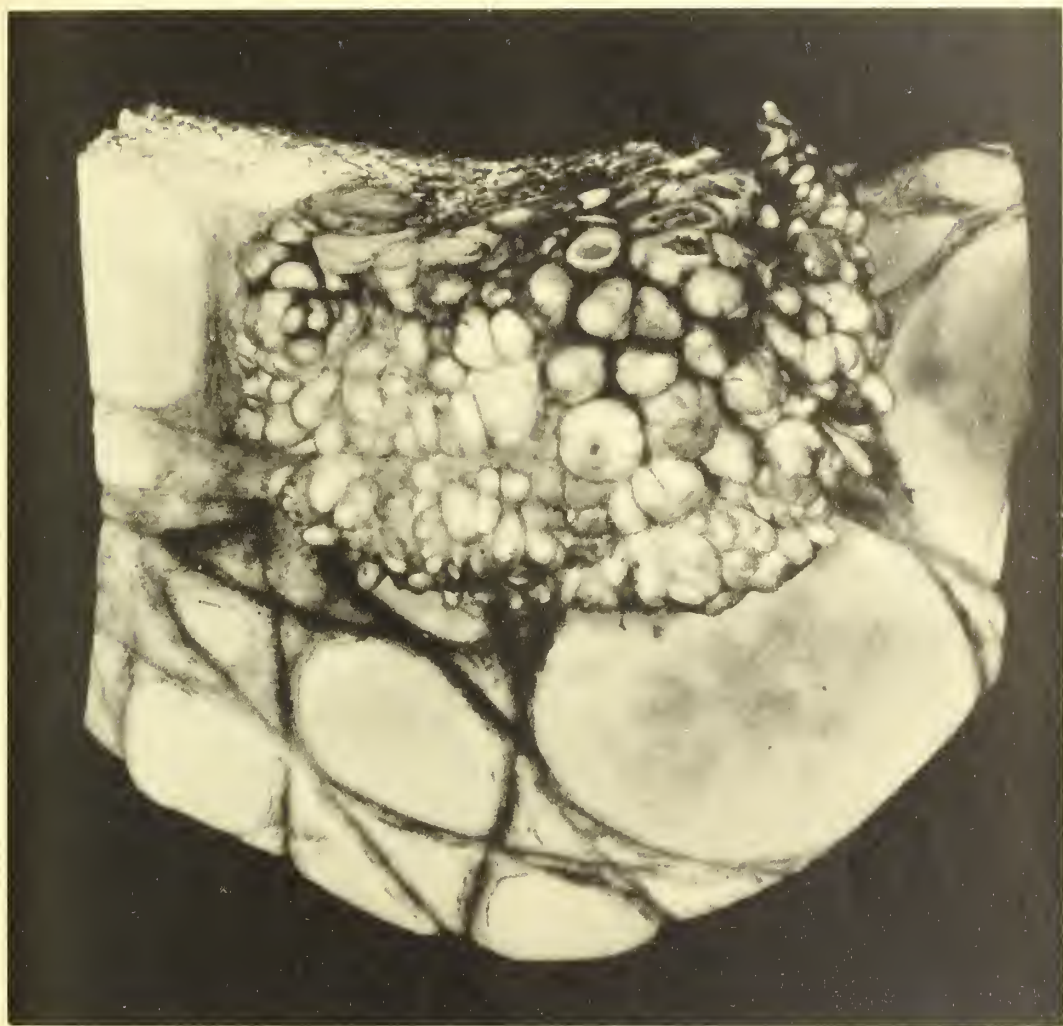


FIG. 7.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).







FIG. 8.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).





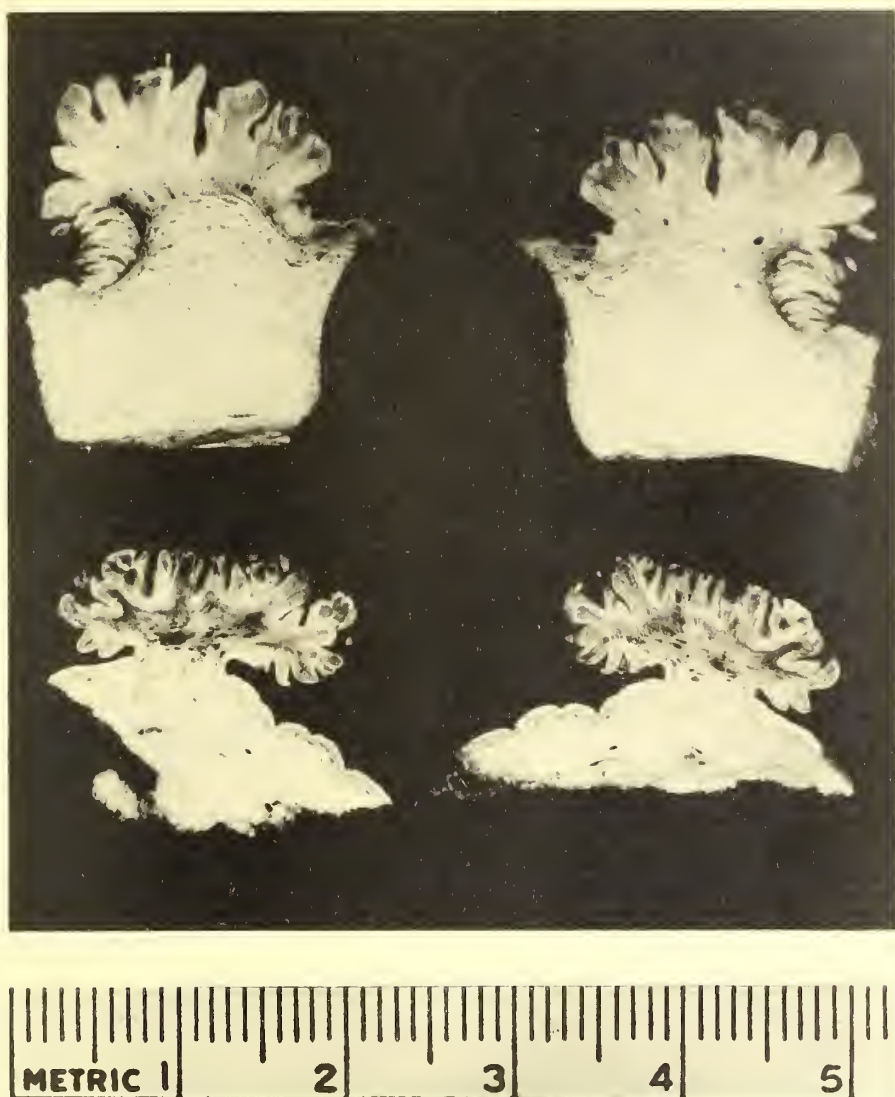


FIG. 9.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).



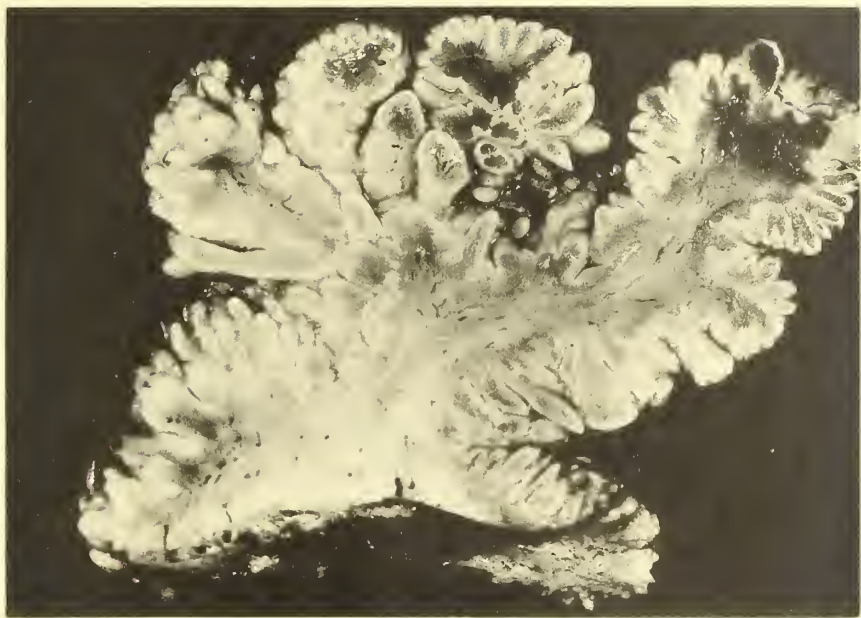


FIG. 10.



FIG. 11.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).





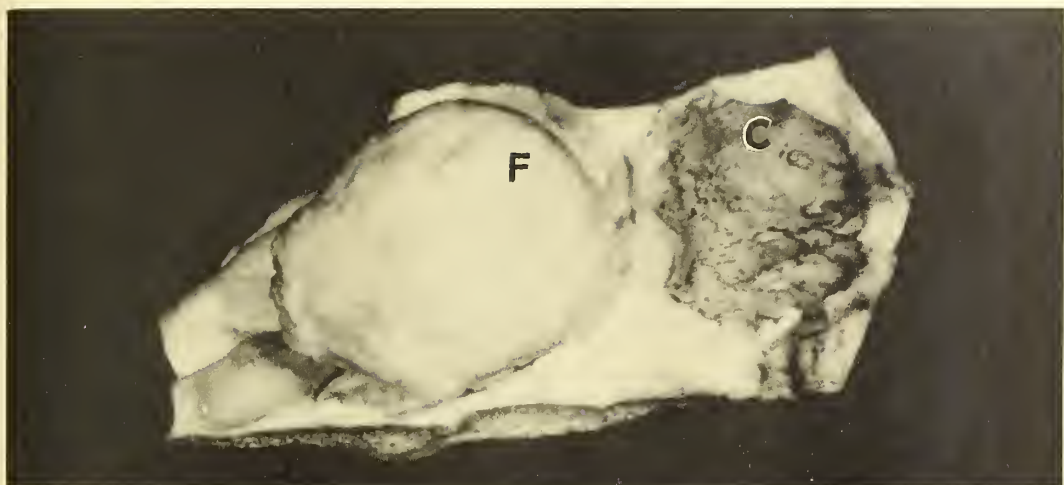


FIG. 12.

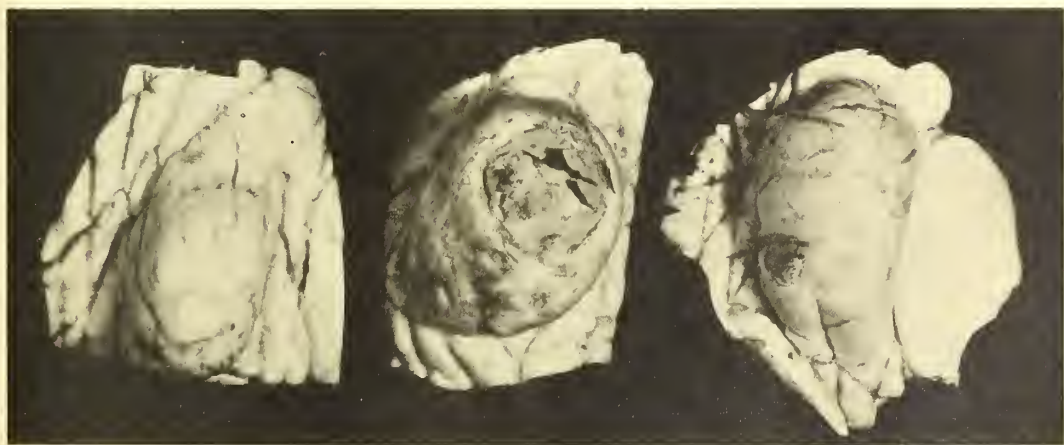


FIG. 13.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).



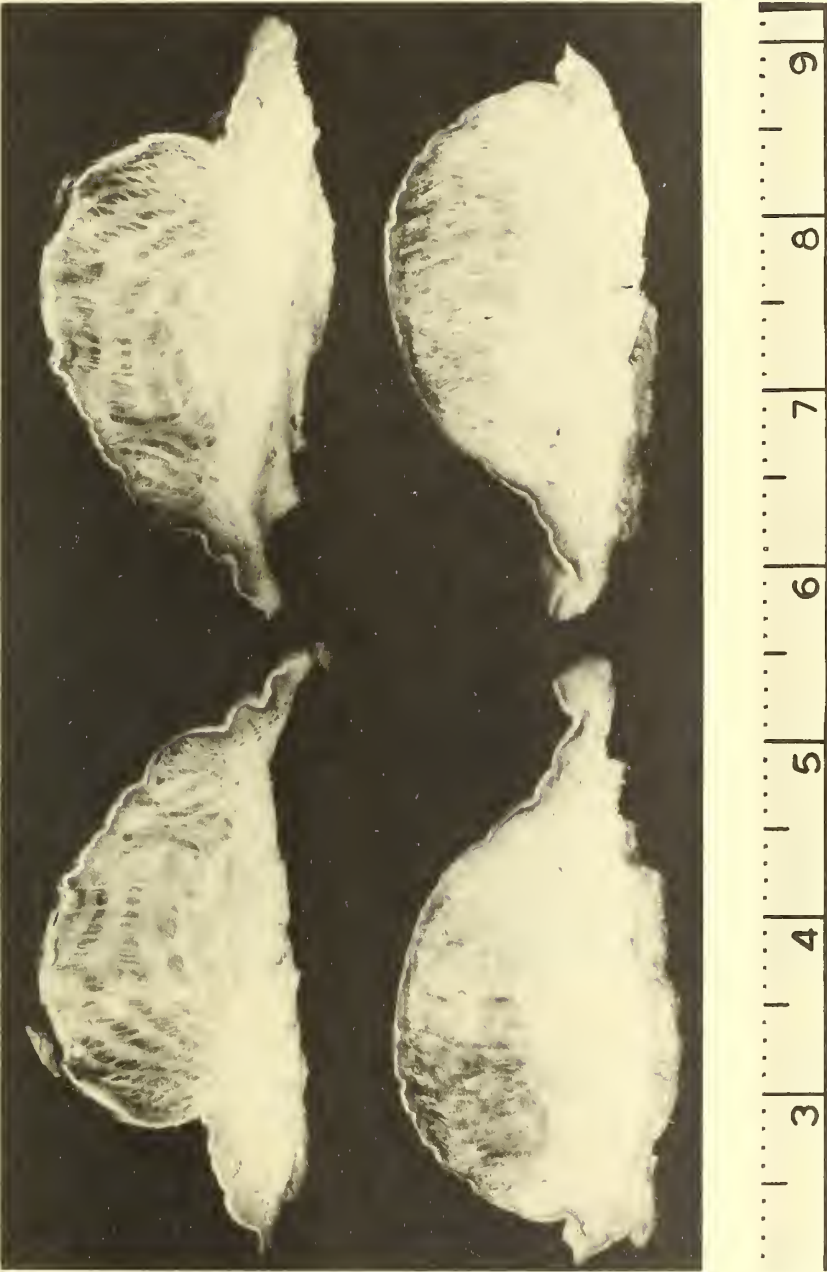


FIG. 14.  
FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).







FIG. 15.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).





FIG. 16.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).





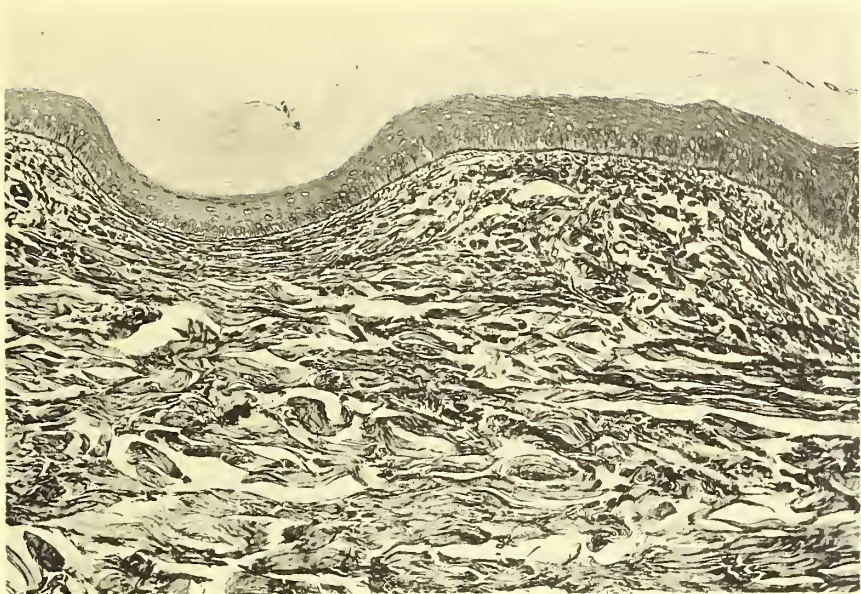


FIG. 17.

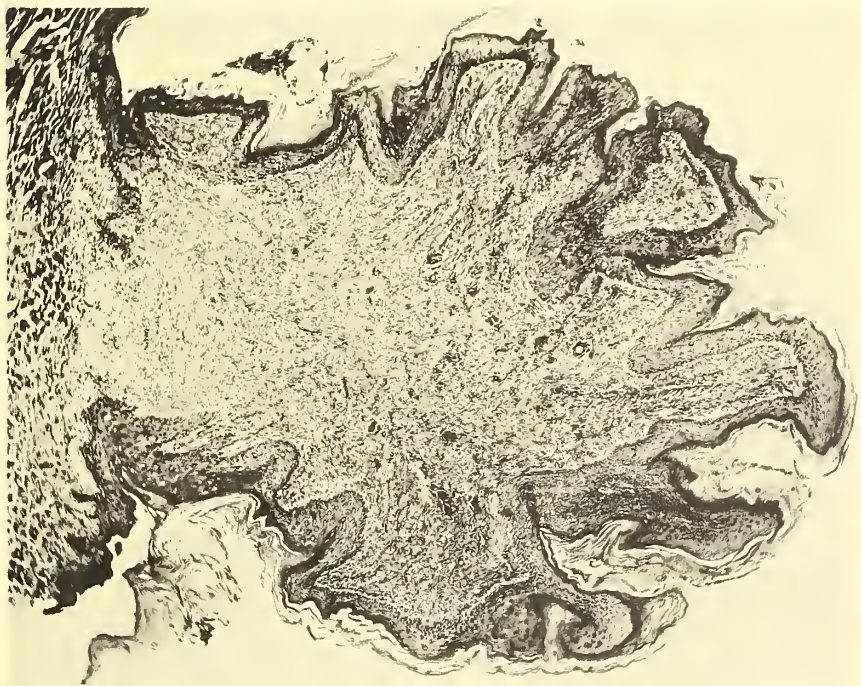


FIG. 18.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).



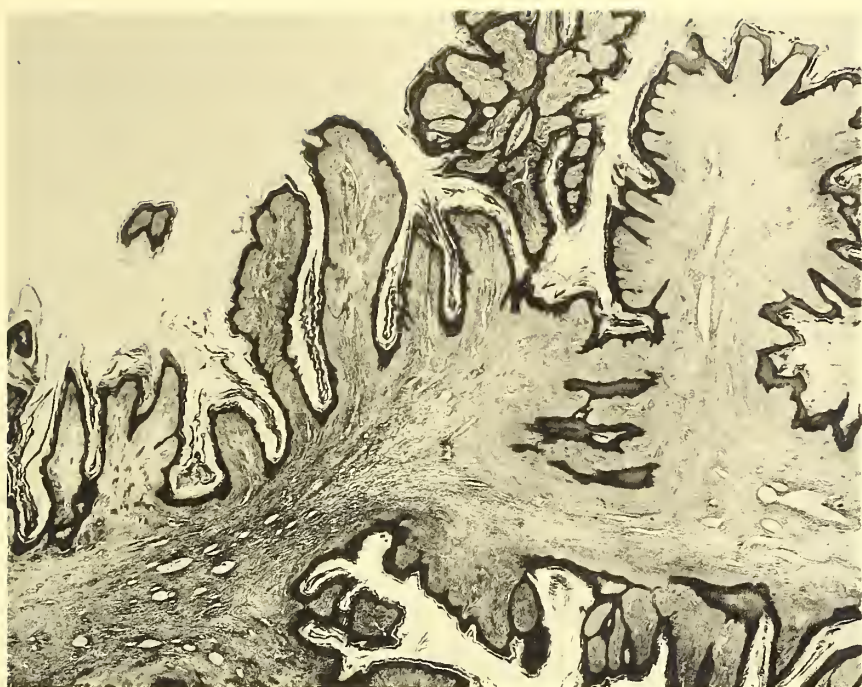


FIG. 19.



FIG. 20.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).







FIG. 21.

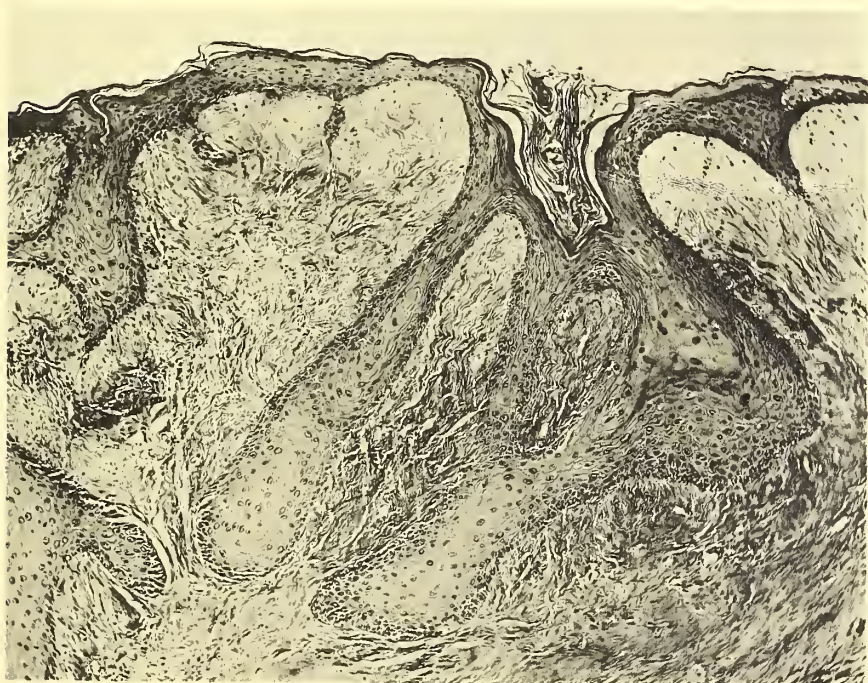


FIG. 22.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).



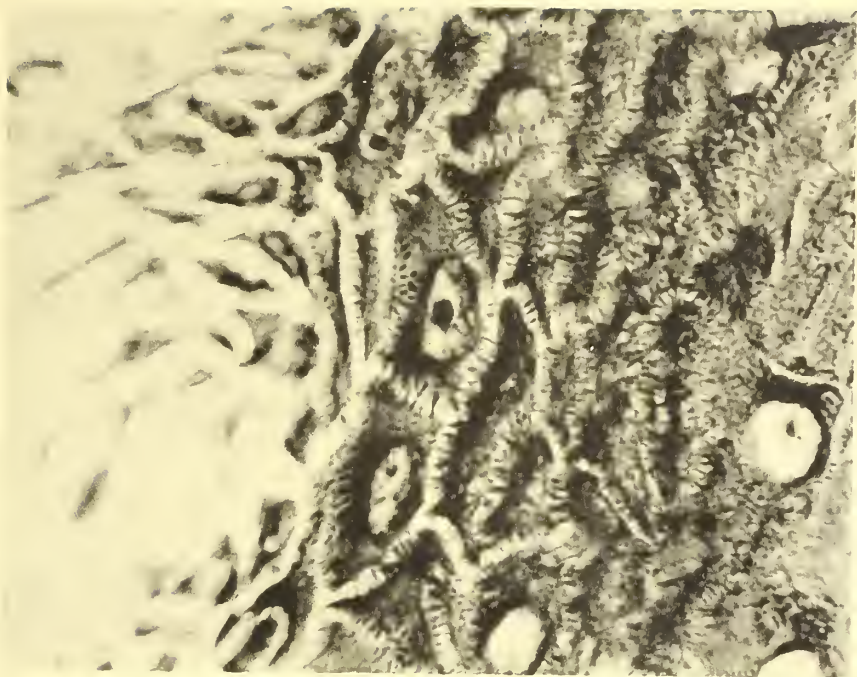


FIG. 23.

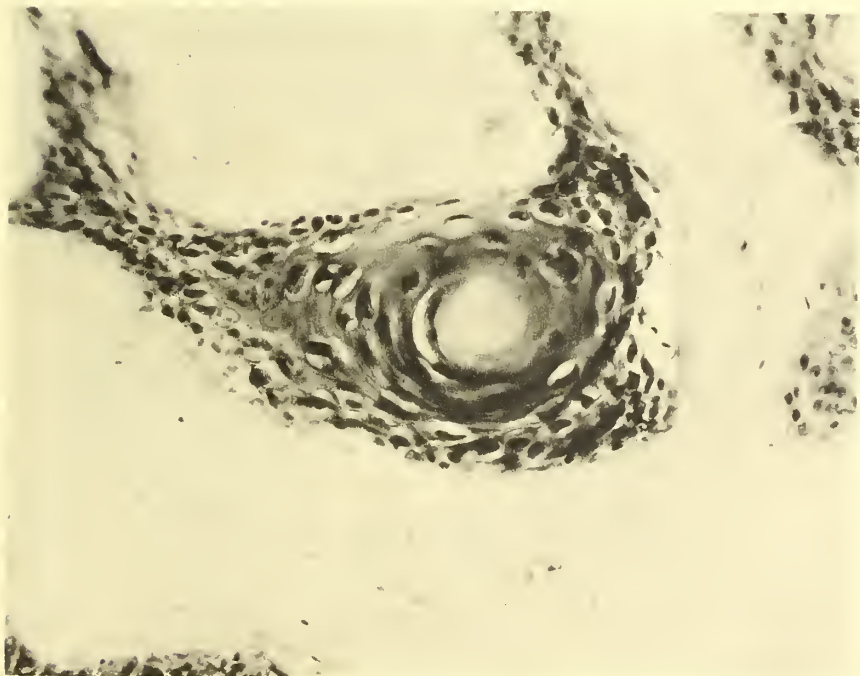


FIG. 24.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).





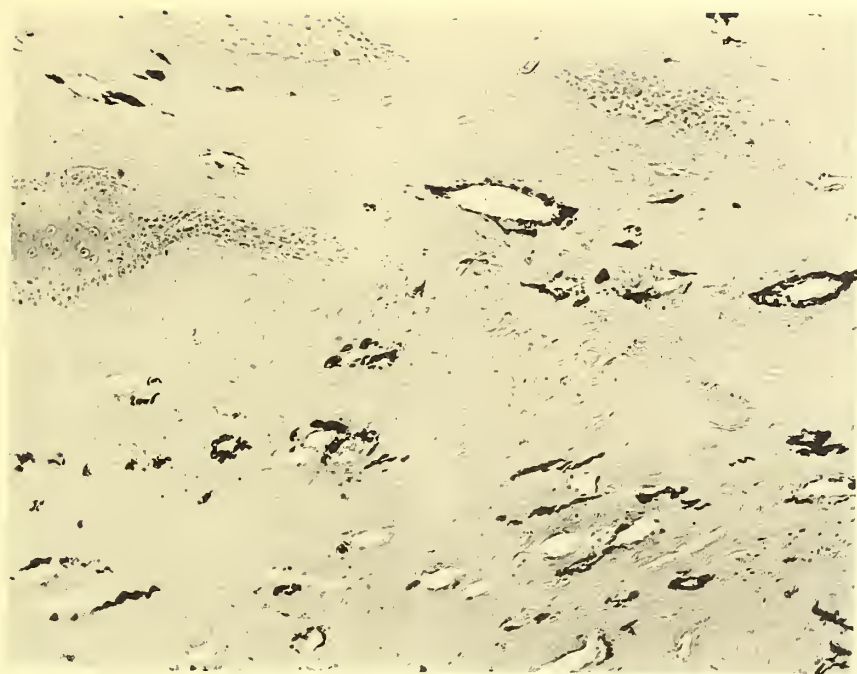


FIG. 25.

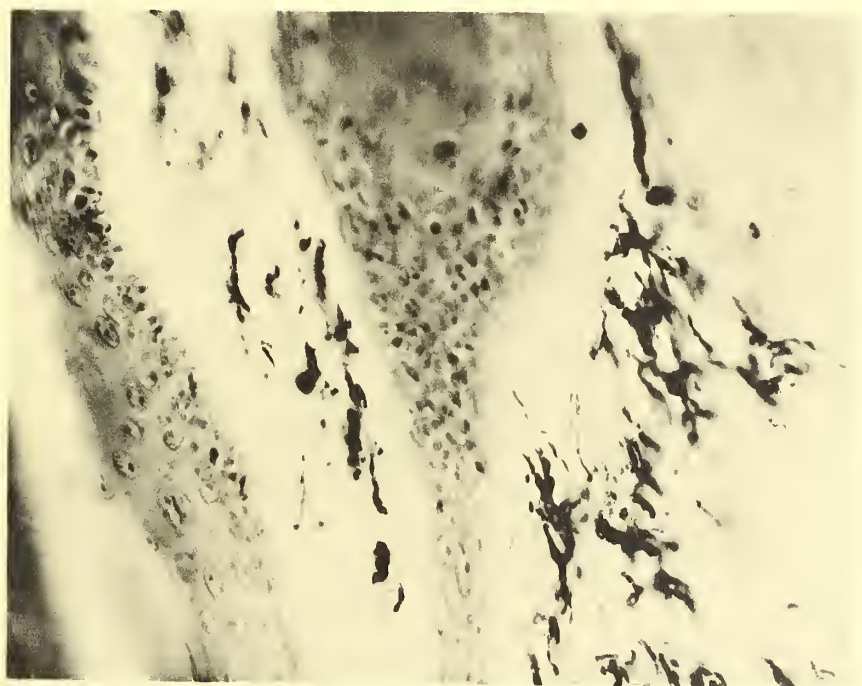


FIG. 26.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).



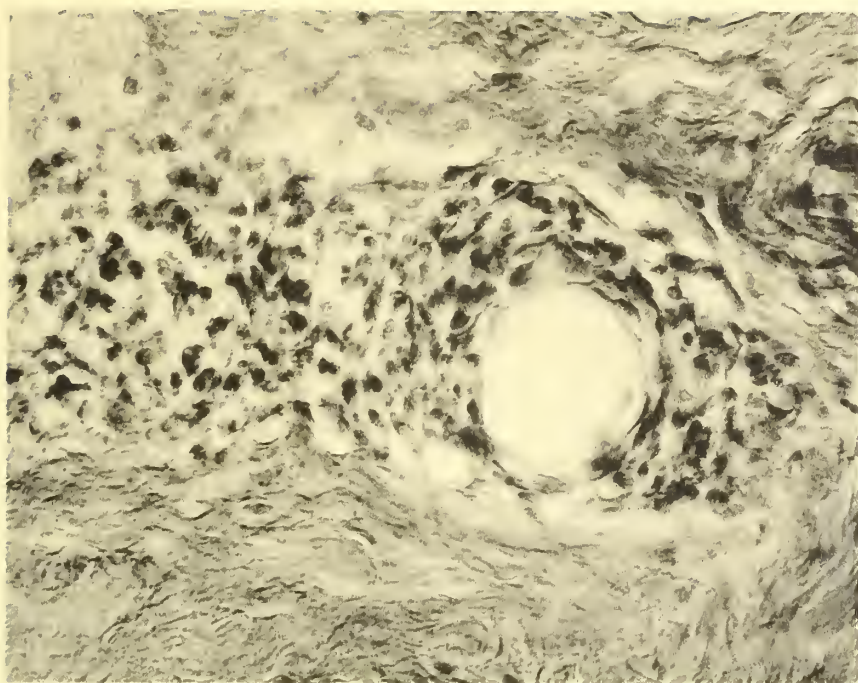


FIG. 27.

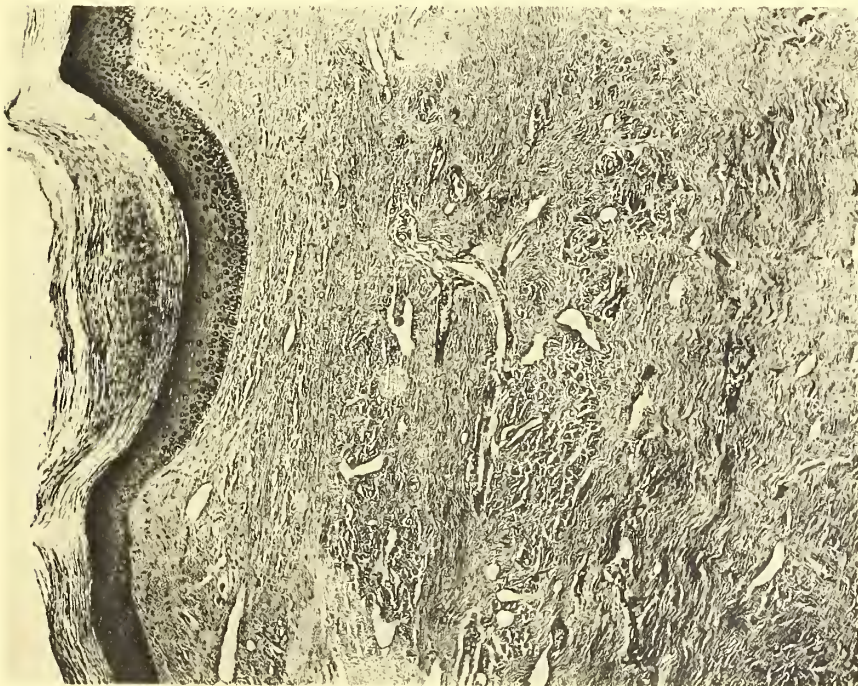


FIG. 28.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).





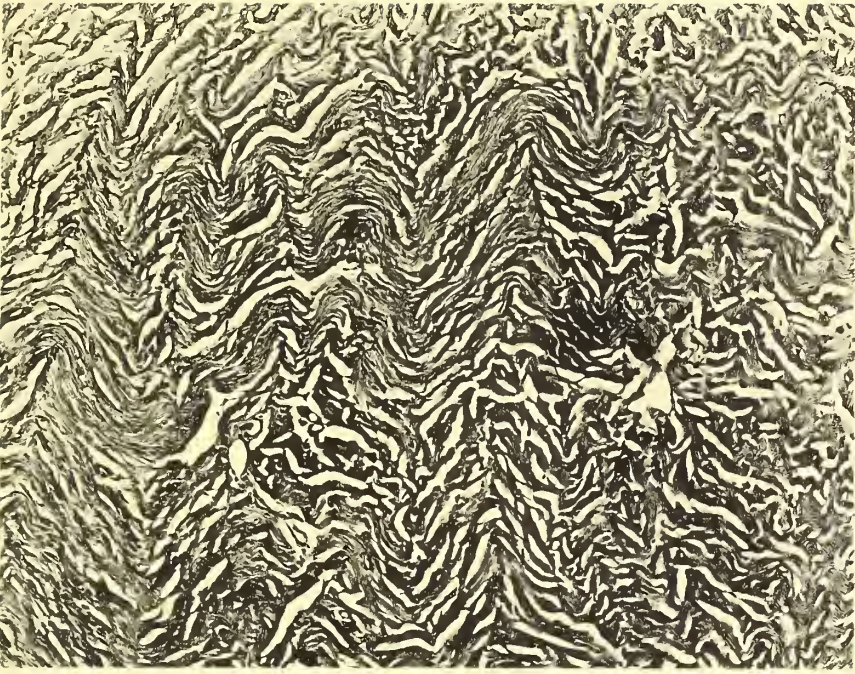


FIG. 29.



FIG. 30.

FIBRO-EPITHELIAL GROWTHS OF THE SKIN IN LARGE  
MARINE TURTLES, *CHELONIA MYDAS* (LINNAEUS).



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## 5.

Plankton of the Bermuda Oceanographic Expeditions. VIII.  
Medusae Taken During the Years 1929 and 1930<sup>1</sup>.

HENRY B. BIGELOW

*Museum of Comparative Zoology, Harvard College.*

(Text-figs. 1-23).

[This is one of a number of papers dealing with the planktonic contents of nets drawn at various levels off the coast of Bermuda on the Bermuda Oceanographic Expeditions of the New York Zoological Society under the direction of Dr. William Beebe. Full details of the nets, locality, etc., will be found in *Zoologica*, Volume XIII, Numbers 1, 2 and 3, and Volume XXI, Numbers 3 and 4.]

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<sup>1</sup> Contribution No. 554, Department of Tropical Research, New York Zoological Society.  
Contribution No. 147 of the Woods Hole Oceanographic Institution.  
Contribution from the Bermuda Biological Station for Research, Inc.

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### INTRODUCTION.

The medusae recorded in the following pages were taken by Dr. William Beebe within a roughly circular area, some eight miles in diameter, centering about 9 miles about south-southeast from the eastern end of the Bermuda archipelago. Within the area of study, the depth ranges from 1,357 to somewhat less than 1,500 fathoms.

Horizontal towing with open nets was carried out in each year at frequent intervals from April through September, at various levels from the surface down to 2,195-0 meters, the total number of tows being 528 for 1929, 488 for 1930. An account of methods of collection, with list of tows, has been given by Beebe (1931). In this list, the depths stated are those at which the horizontal parts of the tows were made, determined—at least in some cases—by a recording pressure-gauge or "Bathygraph" (Beebe, 1931, p. 13, Fig. 6). But one must remember that as the nets used were of the ordinary open type, which fish nearly as effectively while being lowered as while being towed horizontally, and as effectively while being hauled up again, there is no way of determining from what depth any particular specimen may have come. The depths of the hauls, given under the several species in the following pages, are therefore stated accordingly. However, so many hauls were made on each towing day, and at so many different levels, that differential results show fairly well the upper limits of occurrence; also the chief levels of abundance for the more common species. But none of the species was taken in numbers large enough to allow calculation of the probable degree to which the catches were contaminated by specimens picked up during the vertical parts of the tows (for further discussion of this subject see Bigelow and Sears, 1937, p. 69).

The collection contains no new species. But it adds to morphological knowledge of several. And it is especially interesting from the distributional standpoint, being the only intensive and long-continued campaign of deep towing that has yet been made at one place in the open ocean. With so many hauls, made at such close intervals, it is unlikely that any medusa was missed that was at all common, or that occurred other than sporadically. It is therefore safe to assume that the catches listed below give a representative picture of all the species of medusae that occurred with any regularity between the surface and the bottom of the sea, at the chosen station, during the summers of 1929 and 1930, except *Cyanea*, which as Dr. Beebe informs me, was occasionally seen at the surface.

## ANTHOMEDUSAE.

## CLADONEMIDAE.

**Zancleopsis.**

This genus was proposed by Hartlaub (1907, p. 116) for a bitentaculate medusa from the Tortugas, described by Mayer (1900) as *Gemmaria dichotoma*, but which differs from typical *Gemmaria* (the latter is probably a synonym of *Zanclea*) in the fact that its tentacles are branched, with the branches as well as the main trunk terminating in swollen bulbs; structures very different from the stalked nematocyst knobs with which the tentacles of *Gemmaria* (or *Zanclea*) are armed. *Zancleopsis* also possesses ocelli, which are lacking in *Gemmaria*. And the new genus was accepted by Mayer (1910) in his subsequent monograph.

*Zancleopsis* was not reported again until 1928 when Kramp (1928, p. 40) described a second species—*tentaculata*—from a single specimen from the Pacific. The Bermuda series now yields a third record of the genus.

Mayer's specimens from the Tortugas had only two developed tentacles. But it appears that they were juveniles, for while he stated that the gonads are developed on the inter-radial sides of the manubrium, his illustrations give no indication that the sex tissue had actually appeared, which accords with the small size of the specimens (3 mm. high), contrasted with the Bermudian example (20 mm. high). Therefore, it is entirely possible that the bulbs alternating with the formed tentacles of Mayer's specimens would later have developed filaments, thus raising the tentacle number to four. And this is made the more likely by the fact that Kramp's Pacific specimen (4.5 mm. high) showed just this state, i. e., one pair of large branched tentacles and one pair of much smaller simple tentacles. It also showed a more advanced stage in the sexual development, with the gonads forming "a number of vertical folds, four on each of the inter radial sides of the stomach" (Kramp, 1928, p. 41). The Bermuda example illustrates a stage still more advanced, the sex folds being more numerous (p. 104), the secondary tentacles about as long as the primary, though still continuing simple, and the size much greater. In short, it seems altogether probable that we have to do here with the final stage in growth of Mayer's juvenile *Z. dichotoma*, a conclusion favored by the fact that there is no faunistic discontinuity, so far as medusae are concerned, between Bermuda and southern Florida.

But it appears that the Pacific *Z. tentaculata* is distinct, for not only does it have large gonads at a much smaller size, but the tentacular spurs, bearing the ocelli, are not so highly developed, and the edges of its radial canals are pictured by Kramp as smooth, whereas they are jagged in the Bermuda specimen.

***Zancleopsis dichotoma* Mayer.**

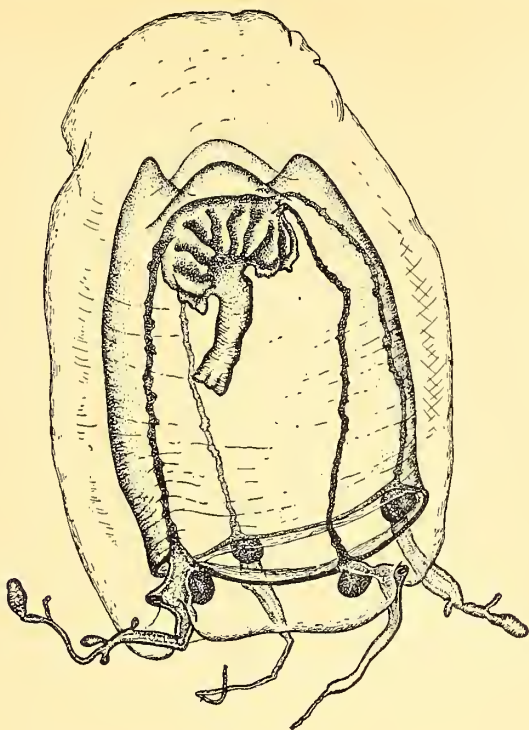
*Gemmaria dichotoma*, Mayer, 1900, p. 35, Pl. 17, Fig. 40.

*Zancleopsis dichotoma*, Hartlaub, 1907, p. 115; Kramp, 1928, p. 42.

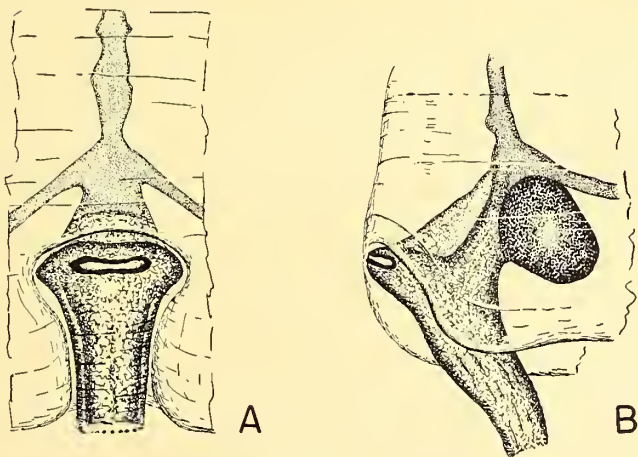
**Material:** Net No. 922, 1,097-0 meters, September 20, 1930, 1 specimen, 20 mm. high by 14 mm. broad, in good condition.

As the adult has not been seen previously, an account of the significant features follows:

The bell is high domed, moderately thick walled, especially apically (Text-fig. 1), resembling Kramp's (1928, Fig. 14) picture of the Pacific *tentaculata* in general form, except that the apex is rounded instead of pointed. And this minor difference may be merely the result of the preservative. The exumbrella is smooth as Hartlaub has also noted, without any



Text-fig. 1.  
*Zancleopsis dichotoma*. Bermudian specimen,  
20 mm. high.



Text-fig. 2.  
*Zancleopsis dichotoma*. Tentacular bulb. A., Abaxial  
view; B., Lateral view. x about 12.



trace of the nematocyst-ribs so conspicuous in *Zanlea*. The subumbrella occupies about  $\frac{2}{3}$  the height of the bell, with the bell-cavity projecting, pouch-like, apically, in the interradial, in form easier pictured (Text-fig. 1) than described; again much as Kramp figured it for the Pacific species. The four radial canals are of moderate breadth, their margins distinctly jagged (smooth in *tentaculata*). The margins of the circular canal are smooth.

The four subspherical tentacular bulbs, about equal in size, are prominent axially. Just distal to its bulb, the tentacle base is also expanded, abaxially, as a spur (Text-fig. 2) lying in a furrow of the exumbrella, and with a curious cap-like mass of large, clear cells (apparently ectoderm) on its outer (abaxial) side. On its outer angle the spur bears a prominent, long oval ocellus (Text-fig. 2A). The four tentacular filaments are all of about the same length—in the preserved state about  $\frac{1}{3}$  as long as the bell is high. One pair are simple, the other pair branched. Of the latter, one bears a branch out near the tip, two sessile knobs about mid-way the length of the filament (distal to which the latter narrows abruptly), besides a swelling apparently the forerunner of an additional branch. The other tentacle of this pair bears two small branches, but is so strongly contracted that it is impossible to tell how extensible the latter may have been. The two branched primary tentacles terminate in large knobs. The two secondary tentacles do not, but their tips are in poor condition.

The area of connection between the base of the manubrium and the subumbrella is cruciform, much as described by Kramp for *tentaculata*; its upper  $\frac{1}{3}$  is thrown into a very characteristic series of vertical folds. These are no doubt the sites of the sexual tissue, as interpreted by Kramp, but eggs not being visible (i.e., the specimen apparently being a male), this point could not be determined positively without microscopic sectioning. In the Pacific specimen of *tentaculata*, there were 3-4 such folds in each interradial sector of the manubrium (Kramp, 1928, p. 41, Fig. 15). In the present specimen the number is greater, 4-6 per interradius, precise enumeration depending on what does, or does not, deserve the name "fold." Below the level of attachment of the radial canals the folds apparently form a continuous series surrounding the manubrium, but as Kramp points out, sectioning would be required to show to what extent the masses of sex tissue are confluent. In the preserved state, the distal tube-like portion of the manubrium hangs to about the mid-level of the bell cavity. But as it is much wrinkled, it is probably contracted, hence may have been considerably longer in life.

After preservation with formalin, manubrium and tentacular bulbs are of an opaque, dull brownish hue; the pigment ring of each ocellus, dull red.

A comparison of Text-fig. 1 with Kramp's (1928, Figs. 14-18) illustrations of *Z. tentaculata* will sufficiently emphasize the close resemblance between the two, especially as regards the structure of the tentacles. The chief differences—probably sufficient to separate two species—are summarized above (p. 102). Minor differences in the outline of the bell and the shape of the manubrium are probably to be credited to the preservative.

#### BOUGAINVILLIIDAE.

##### ***Bougainvillia*.**

##### ***Bougainvillia niobe* Mayer.**

*Bougainvillia niobe*, Mayer, 1894, p. 236, Pl. 1, Fig. 2; 1900, p. 42; 1904, p. 11, Pl. 2, Figs. 14-15c; 1910, p. 166, Pl. 18, Figs. 1-3; Bigelow, 1918, p. 368.

*Material*: Surface, July 11, 1929, 1 specimen, 9 mm. diameter, with medusa buds.



Net No. 562, 914-0 meters, May 10, 1930, 1 specimen, 9 mm. diameter, with medusa buds.

Net No. 738, 1,463-0 meters, June 28, 1930, 1 specimen, 9 mm. diameter, with gonads.

Net No. 812, 1,463-0 meters, August 28, 1930, 1 specimen, 10 mm. diameter, with gonads.

Net No. 862, 1,463-0 meters, September 8, 1930, 1 specimen, 10 mm. diameter, with gonads.

Net No. 915, 549-0 meters, September 19, 1930, 1 specimen, 6 mm. diameter, with medusa buds.

Net No. 935, 1,463-0 meters, September 23, 1930, 1 specimen, 10 mm. diameter, with gonads.

These specimens confirm conclusions earlier reached from the study of the more extensive *Bache* series (Bigelow, 1918, p. 368) as to the relationship of *B. niobe* to other species of the genus, for they fall well within the recorded range of *niobe* in number of marginal tentacles and in branching of the oral tentacles. As in previous collections, the smaller specimens, up to 9 mm. in diameter, bear the medusa buds well described by Mayer (1910), whereas the gonads have so far been found only in specimens of 8 mm. in diameter or larger. In the specimens listed above, as in those of the *Bache* collection, the sex-masses are adradial, in which *niobe* resembles *fulva* and *britannica*. It was not possible to determine on the *Bache* specimens whether or not the masses of sexual tissue were discontinuous in the interradii, at the base of the manubrium. This, however, seems definitely to be the case in the specimen from Net No. 862; apparently so in the specimen from Net No. 812 (see list above). Hence, while the other two specimens with gonads are too much contracted to show this feature, it can now be added to the specific diagnosis.

The medusa buds in the smaller specimens add nothing to Mayer's (1910) account, except for confirmation.

I may note also that one specimen (Net No. 562) is infested with the parasitic larval stages of a Narcomedusa, probably *Cunoctantha*.

The large specimens are so much contracted that exact counting of the marginal tentacles is difficult. They appear to range from 13-14 up to 16; in one bundle possibly 18, the latter a somewhat greater number than reported previously. For this same reason, the number of branchings of the oral tentacles can be stated only tentatively; the maximum number of branchings appears to be not less than 8 or 9.

On the basis of cumulative evidence the following diagnosis may now be given for this species: Marginal tentacles, usual maximum 12-16 per bundle at sexual maturity, perhaps up to 18-19; gonads adradial, discontinuous in the interradii and entirely confined to the manubrium proper; manubrium sessile, i.e., there is no gelatinous peduncle; ocelli are present; oral tentacles branch a maximum of 7-9 times. Medium sized individuals may produce medusa-buds. It is not known whether the same individuals produce first buds, then gonads in succession, or whether some individuals exhibit the asexual reproduction only, others the sexual.

The closest ally of *niobe* is the wide-ranging Pacific species, *fulva*; so close in fact, that no constant difference has been found, to separate them, other than the common occurrence of budding in the former, its absence, so far as known, in the latter.

*General Distribution:* Records for *B. niobe* are so far confined to the waters between southern Florida, Cuba, the Bahamas, and Bermuda. The common occurrence of this species, close to the surface, proves it a shoal water form, hence it is probable that the specimens taken in deep hauls (all with open nets) were picked up not far below the surface.

## PANDEIDAE.

**Pandea.*****Pandea conica*** Quoy and Gaimard.

*Dianaea conica*, Quoy and Gaimard, 1827, p. 182, Pl. 6A, Figs. 3-4.

For synonymy, see, Mayer, 1910, p. 118; Hartlaub, 1914, p. 338; Kramp, 1924, p. 8; Uchida, 1927, p. 214; Ranson, 1936, p. 84.

*Material*: Net No. 649, 1,646-0 meters, May 29, 1930, 1 specimen, about 17 mm. high.

The single example is much contracted, the margin being strongly recurved; gonads, radial canals, and tentacular bulbs are, however, in good condition, and it is chiefly on the basis of the former that the specimen is identified as *P. conica*.

The several recent accounts of this species agree that, at maturity, its gonads form an irregular net-work completely occupying the interradian areas of the gastric wall (see especially, Mayer, 1910, p. 117, Fig. 63B; Hartlaub, 1914, Figs. 283, 286; Uchida, 1927, Fig. 38; Ranson, 1936, Pl. 1, Fig. 2). Conditions in the present specimen suggest a somewhat more advanced stage in development, for while the upper portion of the manubrium shows much the type of network—the most distinctive generic feature—usually figured, this gives place in the distal zone next the lip to an irregular series of folds and knobs, a formation not shown in any of the earlier figures, though perhaps indicated by Uchida (1927).

There are 34 or 35 tentacles—a number falling well within the recorded range, the maximum so far recorded being 44 in a specimen 30 mm. high (Uchida, 1927). The tentacles also show the characteristic laterally compressed basal bulbs, each with a well marked, dark red, abaxial ocellus, repeatedly described for *P. conica*.

Earlier accounts have varied as to whether the walls of the radial canals are smooth (Hartlaub, 1914, p. 339), or more or less jagged (Mayer, 1910, p. 117, Fig. 63; Uchida, 1927, p. 214). In the present example, they are of the latter type, much as pictured by Uchida (1927) and reported by Kramp (1928) for a large specimen from Japan. The only feature specifically characteristic of *P. conica* that is not clearly shown is the ribbing of the exumbrella with nematocyst ridges. The bell does show a definite ridge in the radius of each tentacle. But the exumbrellal surface has been so badly rubbed, that one cannot be certain whether these ridges actually represent the locations of nematocyst ribs, or are merely contraction phenomena. But the specimen agrees so well in all other respects with the accounts of *conica*, and with good specimens of the latter from Naples, with which I have been able to compare it, that its identity, as such, seems assured.

*General Distribution*: *P. conica* has already been found at a station not far from Bermuda (Bigelow, 1918).<sup>2</sup> Other captures show a wide distribution, including many localities in the Mediterranean (Kramp, 1924), off Scotland, the South Atlantic, Japan, and the Philippines.

*Vertical Range*: Recorded depths of capture indicated that *P. conica* occupies a considerable depth zone, for while all stages have been found commonly at the surface (Kramp, 1924; Ranson, 1936), a fair proportion of the records have been from nets working down to considerable depths.<sup>3</sup> But the deep hauls yielding it have all been with open nets, nor are data extensive enough to allow any conclusion as to the lower limit to its normal occurrence.

<sup>2</sup> Identification of this specimen was provisional, but subsequent studies of *P. conica* show that it fell well within the varietal range of this species.

<sup>3</sup> See especially the table of *Thor* captures, given by Kramp (1924, p. 9).

***Pandea rubra* Bigelow.**

*Pandea rubra*, Bigelow, 1913, p. 14, Pl. 2, Figs. 1-7; Hartlaub, 1914, p. 340; Kramp, 1920, p. 4; 1926, p. 96, Pl. 2, Fig. 15; Ranson, 1936, p. 81.

*Material*: Net No. 562, 914-0 meters, May 10, 1930, 1 specimen, about 25 mm. high.

Net No. 607, 914-0 meters, May 20, 1930, 1 specimen, about 40 mm. high.

Net No. 613, 1,097-0 meters, May 21, 1930, 1 specimen, about 40 mm. high.

Net No. 800 1,463-0 meters, July 15, 1930, 1 specimen, about 40 mm. high.

The specimens from Net Nos. 562, 613, and 800 are in good enough condition to show that they agree closely, even as to details, with the original series from the North Pacific, and with those subsequently collected in the North Atlantic by the *Armauer Hansen* (Kramp, 1920; 1926.) The most diagnostic morphological features of this species, as contrasted with its relative *P. conica*, are its lack of exumbrellal nettle ribs, the thin bell wall, the very complex and fine meshed network formed on the walls of the manubrium by the development of the gonads, the complexly crenulated lips, the small number of tentacles, and the large size attained at maturity. Another difference is that most accounts of *conica* credit it with ocelli, whereas such organs have not been detected in any of the specimens of *rubra* so far seen.

The largest example yet recorded (from the Pacific) about 75 mm. high, had about 20 tentacles (Bigelow, 1913); Pacific examples of 35-47 mm. had 14-18. Present indications are that the number of tentacles may average somewhat smaller in medium-sized examples from the Atlantic than from the Pacific, for in 2 Bermudian specimens about 38-40 mm. high, and in one of Kramp's (1920; 1926), of about the same size, the number ranged from 12-14. But larger series might well show that there is actually no regional difference in this respect. Specimens 25-31 mm. high (1 Pacific, 2 Atlantic) may have 8 (Kramp, 1926, p. 96), 9 (Bermudian specimen, Net No. 562), or 12 or 13 tentacles (Bigelow, 1913, Pl. 2, Fig. 6).

The gonads of *P. rubra* are extremely characteristic, the sexual convolutions of the manubrium taking the form of an extremely fine and numerous-meshed network; comparison of a photograph of a Pacific specimen (Bigelow, 1913, Pl. 2, Fig. 2)—which would equally well represent the Bermudian specimen from Net No. 613—with illustrations of *P. conica* by Mayer (1910, Fig. 63) and by Ranson (1936, Pl. 1, Fig. 2) will illustrate how widely the two species differ in this respect; how widely, in fact, *rubra* differs from any other pandeid yet known. Seen from the inner side, the sexual thickenings appear as a great number of knobs.

The most arresting feature of *P. rubra*, among its relatives, is that it shows extreme development of what might now be termed "bathypelagic" pigmentation. The Bermuda specimens about 40 mm. high show the same reddish or chocolate brown coloration as the Pacific specimens of the same size or larger, the entire manubrium, tentacles, and subumbrella surface being densely pigmented, with the more palely colored radial canals showing as pale bands. In the Bermudian example of 25 mm., however, in which the manubrium and tentacles are equally densely colored, the subumbrella is pigmented only in the immediate vicinity of the base of the manubrium, so that the pigmented canals—radial and circular—show as dark bands in the transparent bell, as was also the case in the smaller of the Pacific specimens. As Pacific examples of intermediate size (35-40 mm.) showed an intermediate stage (Bigelow, 1913, p. 16), it appears that it is not until the medusa is well-grown that pigment spreads out over the subumbrella—perhaps accompanying a descent into deeper water.



Ranson (1936, p. 82) does not consider the coloration diagnostic in this genus. The pigmentation of *P. rubra* is, however so peculiar in its density and opacity, and in its eventual extension over the subumbrella (quite apart from the precise shade of color), and *P. rubra* differs so widely in these respects from *P. conica*, that it must be regarded as a specific characteristic even though it may not be a safe criterion for identification except for large specimens.

*General Distribution:* Previous records include high latitudes in the northwest Pacific and Bering Sea (Bigelow, 1913); and, more recently, two oceanic stations to the west of Ireland (Kramp, 1920). The captures at Bermuda now make it likely that its range will finally prove to be as extensive as that of other bathypelagic medusae.

*Vertical Range:* The shoalest of the 6 hauls that have so far yielded it was from 411-0 meters (Albatross Sta. 4800); others have been from 549-0 meters or deeper.

#### BYTHOTIARIDAE.

##### *Heterotiara.*

##### *Heterotiara anonyma* Maas.

*Heterotiara anonyma*, Maas, 1905, p. 19, Pl. 3, Figs. 19-21; Bigelow, 1909, p. 216, Pl. 41, Figs. 12-13; 1913, p. 25; 1918, p. 382; Mayer, 1910, p. 107, 489; Vanhöffen, 1911, p. 211, Pl. 22, Figs. 3, 4; Hartlaub, 1914, p. 350.

*Material:* Net No. 79, 1,280-0 meters, May 8, 1929, 1 very fragmentary specimen, about 20 mm. high by 17 mm. in diameter.

Net No. 977, Surface, May 12, 1931, 1 specimen, 13 mm. high by 9 mm. in diameter, with 10 tentacles.

The specimen from Net No. 977 is in excellent condition. As regards size, in relation to the number of tentacles, it falls well within the range already recorded (Bigelow, 1913, p. 26; 1918, p. 382; 1919, p. 287).

The larger specimen is in such poor condition that identification is only tentative. Its general appearance seems, however, to warrant reference to *Heterotiara*, and its large size to *H. anonyma* rather than to *H. minor*.

*General Distribution:* Previous Atlantic records are between Florida, the Bahamas, and Cuba (Bigelow, 1918). Elsewhere, it is known from Malayan waters, the Indian Ocean and several localities in the Pacific, South and North, including Bering Sea (for list of Pacific localities, see Hartlaub, 1914, p. 351).

*Vertical Range:* The recorded vertical range includes various depths from the surface downward. The comparative frequency with which the *Bache* took it shoaler than 100 meters (Bigelow, 1918, p. 382), makes it likely that specimens from deep hauls with open nets were actually taken in the upper water layers.

##### *Calycopsis.*

##### *Calycopsis* sp.?

*Material:* Net No. 959, 914-0 meters, September 29, 1930, 1 specimen about 22 mm. high; 1 specimen, much crumpled, about 9 mm. high.

The larger specimen is fragmentary, having lost all but the cruciform base of the manubrium. And it apparently represents an abnormality of the same type as pictured by Kramp (1924, p. 15, Fig. 11B, 11D) for *Bythotiara murrayi*, for the canals are connected in an irregular network,



the arrangement differing on the halves of the bell. To attempt to give it a specific name would only add to the difficulties with which the student of the genus is faced.

## LEPTOMEDUSAE.

### LAODICEIDAE.

#### ***Chromatonema*.**

The systematic location of this genus, originally described by Fewkes (1882), is still a moot question: it is placed by Kramp (1919; 1933) among the Laodiceidae, which by common consent, are the leptomedusan group most closely related to the higher Anthomedusae, whereas Ranson (1936) refers it to the latter, as a member of the Williidae. Discussion of this point necessarily revolves chiefly around the relationship of the gonads to the gastrovascular system, i.e., whether the perradial diverticula from the corners of the stomach, along which the sexual tissue is developed, are actually part of the manubrium, whether they are merely the dilated proximal sectors of the radial canals, or whether (as I believe) no sharp distinction can be drawn between gastric and canalar portions. This last view has already been proposed by Kramp (1933, p. 552) who says, for the Laodiceidae as a whole, that the separation of the gonads from the manubrium is not "durchgeführt." The Bermudian series are not in good enough condition to throw light on this point. But successive growth stages in the closely allied *C. erythrogonon*, from the Pacific (Bigelow, 1909), show, on the one hand, that the development of the gonads does take place along the radial canals (cf. Bigelow, 1909, Pl. 39, Fig. 6 with Figs. 2-3), but, on the other hand, that as the sex masses increase in size and complexity, the canal-sectors that they occupy expand in breadth and so become morphologically incorporated into the cruciform angles of the manubrium proper. Thus, it is only distal to the extremities of the gonads that the canals continue to retain their narrow tubular nature. It also seems probable from the corresponding expansion of entodermal pigment that Kramp (1919) was correct in crediting a digestive function to the expanded proximal portions.

If this view be correct, the primary question is no longer whether we are to regard *Chromatonema* as a Leptomedusa or as an Anthomedusa, for it bridges the gap, but to which of the borderline groups it belongs, or is most closely related. Basing the decision chiefly on the marginal sensory clubs, it seems wisest to follow Kramp (1919; 1933) in referring it to the Laodiceidae—at least, provisionally. But future study may well show that *Chromatonema* deserves a separate family, for as Kramp (1919) has emphasized, its gonads are fundamentally similar to those of *Calycopsis*, rather than to those of *Laodicea* or *Ptychogena*. I cannot follow Ranson (1936) in referring it to the Williidae (if his own definition of the latter is to be accepted), because he confines this family to forms lacking a circular canal, which is present in *Chromatonema* as Kramp (1919, p. 9) has shown and as Ranson (1936, p. 103) himself remarks, and because the typical members of the Williidae (*Willia* and *Proboscidactyla*) lack marginal organs other than tentacles.

#### ***Chromatonema rubrum* Fewkes.**

*Chromatonema rubrum*, Fewkes, 1882, p. 305, Pl. 1, Fig. 41.

For subsequent references, see Kramp, 1919, p. 7; 1933, p. 552; Ranson, 1936, p. 102.

*Material*: Net No. 368, 1,280-0 meters, August 14, 1929 and Net No.

959, 914-0 meters, September 29, 1930, 2 very fragmentary specimens, respectively about 17 and 15 mm. in diameter.

One of these specimens still bears fragments of a few tentacles, though no cordyli; the other has lost the marginal zone altogether. Identity seems, however, reasonably assured by what remains of the gonads, which are of very characteristic appearance in this genus.

The Bermuda capture extends the known range of *C. rubrum* southward, previous records being west of the Azores (Ranson, 1936); off the American continental slope in Latitude about 40° N. (Fewkes, 1882); and at numerous localities farther north, including Davis Strait (Kramp, 1919, Chart I, p. 13).

The depths of capture of the Bermudian specimens are in line with previous experience that *C. rubrum* inhabits chiefly the mid-depths, the great majority of captures (all with open nets) having been in hauls reaching down to at least 700 meters, and as Kramp (1933, p. 553) remarks "nur ein paar mal in höheren Wasserlagen."

#### AEQUORIDAE.

#### *Aequorea*.

The few Aequoreas in the collection represent the subdivision of the genus in which the stomach is only  $1/4$ - $1/5$  as broad as the diameter of the disc. In contrast to the multiplicity of names under which large-stomached Aequoreas have appeared in literature, the small-stomached group includes only two named forms, *tenuis* and *floridana*. The first of these is now generally accepted as a good species (Bigelow, 1913; Kramp, 1933; Ranson, 1936), size of stomach having proved one of the most dependable characters in this widely variable genus. But the status of the second has remained doubtful, awaiting critical examination of the supposed differences—all minor—between it and *tenuis*. The Bermuda specimens agree so closely with A. Agassiz's (1865) account of *floridana* as to leave no doubt of their identity with the latter. And the need of giving them a name makes pertinent a decision as to the relationship of *floridana* to *tenuis*; names which appeared on the same page in the original publication. According to the original accounts, and to Mayer's (1910) more recent comparison, the chief differences between the two are that *floridana* has more tentacles at a smaller size, about four times as many otocysts as tentacles instead of an equal number, a somewhat smaller stomach (about  $1/7$  instead of  $1/5$  as wide as the diameter of the bell), and that its radial canals are very narrow, its tentacles minute.<sup>4</sup> Hargitt (1905), however, had already shown that in *tenuis* from Woods Hole (i.e., from the type region) numerical characters are all highly variable. Thus, a specimen of only 36 mm. may have even more tentacles than one of 47 mm. Canals not only vary in number, but show much irregular branching and anastomosis. The number of otocysts (described by A. Agassiz as alternating regularly with the tentacles) may be one, is often two, and sometimes even more between every two tentacles and series of typical *tenuis* from Woods Hole in the collection of the Museum of Comparative Zoology, similarly show from 1-4; most frequently 2 or 3; the number depending, it seems, on the distance apart of the large tentacles, and on how many rudimentary tentacles there are in the interspaces. I may note in passing, that while A. Agassiz (1865, p. 96, Fig. 138) stated that there is always a single otocyst between 2 tentacles in *tenuis*, the segment of margin he illustrated was one in which two large tentacles stood close together with no small ones intervening.

The contracted condition of the specimens in the present collection

<sup>4</sup> Mayer's (1910, Pl. 43, Fig. 6) illustration of *Ae. floridana* is obviously labelled incorrectly, for it shows a very wide stomach.

makes it difficult to make sure of the total number of otocysts. But in other specimens from Bermuda, in the collection of the Museum of Comparative Zoology, there are from one to three between every two large tentacles, most frequently one or two in the sectors on the margin on which the otocysts are still intact, which agrees with the Woods Hole specimens of *tenuis*. And the number of small tentacles, between 2 adjacent large ones, varies from none to an observed maximum of six, usually 1-3.

Evidently, then, one can no longer invoke numerical precision in the number of otocysts relative to tentacles as an alternative character between *tenuis* and *floridana*. Neither can the number of large tentacles finally developed, for while, by published accounts, this is somewhat larger for *floridana* (up to 100) than for *tenuis* (up to 90), there is no discontinuity in this respect. Comparison of the Woods Hole series, just mentioned, with the Bermudian specimens shows, however, that at diameters of 24-35 mm. (*tenuis* is only half grown at this size), *tenuis* consistently has significantly fewer large tentacles than *floridana*, the number in the one case ranging from 43-58, in the other from 63-103. And a still sharper distinction appears in the number of canals, for while in the *tenuis* within this size range that I have examined, the number of complete canals arising from the stomach, varies from 22-31 (plus 1-4 blind centrifugals in 5 of the seven specimens), which corroborates previous reports of 24-32, the number in the Bermuda specimens is 16 in every specimen (large or small) where countable, except for two (respectively of 25 and 28 mm.) in which it is 15. And no blind centrifugals are to be seen in any. A. Agassiz's (1865, Fig. 139) illustration of *floridana* also shows 16 complete canals, though with one short centrifugal also, besides indications of an early stage in formation of several more, while Mayer (1910, p. 330) reports 16-24 complete canals.

Thus it appears that while occasional specimens of *floridana* may have as many canals as an occasional—perhaps stunted—*tenuis*, the number is usually only  $\frac{1}{2}$  to  $\frac{3}{4}$  as great in the former as in the latter, with strong indications of a normal determinate number of 16 in the one case, of 32 in the other. And this difference seems sufficient to warrant recognition of both species. A minor difference is that *floridana* (so far as known) is full grown and has its maximum number of large tentacles at a maximum reported diameter of only about 50 mm.; whereas *tenuis*, at Woods Hole, is known to reach a diameter of 100 mm. (Mayer, 1910, p. 332).

### ***Aequorea floridana* L. Agassiz.**

*Rhegmatodes floridanus*, L. Agassiz, 1862, p. 361; A. Agassiz, 1865, p. 97, Fig. 139.

*Rhegmatodes floridana*, Haeckel, 1879, p. 223.

*Aequorea floridana*, Mayer, 1910, p. 330; Bigelow, 1913, p. 37; 1919, p. 309.

*Material*: Net No. 840, Surface, September 3, 1930, 1 specimen about 19-20 mm. in diameter, stomach diameter, 4 mm., 16 canals, 72 tentacles; 1 specimen, 23-24 mm. in diameter, stomach diameter about 5 mm., 16 canals and about 50 large tentacles. As the margin in each case is damaged, exact measurement of diameter is not possible.

Also, 16 other Bermudian specimens, 12-37 mm. in diameter (besides fragments) collected in the summers of 1903, 1904, 1911 and 1916, now in the Museum of Comparative Zoology.

The following tabulation for the Bermuda specimens is pertinent to the foregoing discussion of the relationship of *Ae. floridana* to *Ae. tenuis*.



Date of Collection.	Approximate Diameter.	Approximate Diameter of Stomach.	Approximate Number of Large Tentacles.	Canals.
1904	12	3	37	16
1904	15	3	45	16
1930	20	4	72	16
1930	23	5	50	16
1904	23	6	63	16
1904	25	5	67	16
1911	25	6	63	15
1911	28	7	46	15
1911	28	5	81	16
1911	33	7	74	16
1916	33	7	87	16
1916	33	7	85	?
1904	35	7-8	83	16
1916	37	8	103	16

Relative counts of large tentacles and of small cannot be precise, there being no sharp demarcation between the latter and rudimentary knobs of various sizes, the variety in size of which is evidence that while some would have developed into large, others would have remained permanently rudimentary.

The specimens of 12-15 mm. have no gonads; in those of 20-23 mm., gonads have appeared on the outer  $\frac{1}{3}$ - $\frac{1}{2}$  of the radial canals; in those of 25-28 mm., they occupy the outer  $\frac{1}{2}$ - $\frac{2}{3}$  and the outer  $\frac{2}{3}$ - $\frac{3}{4}$  in the larger specimens of 33-37 mm.

In *Ae. tenuis* of corresponding sizes, the gonads occupy about the same sectors of the canals, but with continued growth they finally come to occupy nearly the whole length of canals, though (as Mayer, 1910, p. 332, remarks) "not quite reaching the circular canal."

According to Mayer (1910, p. 330), the stomach is relatively smaller in *floridana* (only  $\frac{1}{7}$  as wide as the disc) than in *tenuis* (about  $\frac{1}{5}$  the width of the disc). However, A. Agassiz (1865, Fig. 139) pictures its greatest diameter as about  $\frac{1}{5}$ . And as the preceding tabulation shows, it ranges about  $\frac{1}{4}$ - $\frac{1}{5}$  the diameter of the disc in the Bermuda specimens. But since the stomach is rarely—if ever—circular, its breadth depends on what particular radius be chosen for measurement. Total diameter similarly depends on the degree of contraction (cupping) or relaxation of the disc.

*General Distribution*: So far as I am aware, previous records of small-stomached Aequoreas referable to *floridana* have been confined to the waters around the southern extremity of Florida. Bermuda is thus a considerable extension of the known range.

## TRACHOMEDUSAE.

### OLINDIIDAE.

#### *Olindias*.

Recent studies of considerable series from different parts of the world (Bigelow, 1909; 1919; Mayer, 1910; Neppi and Stiasny, 1913) have made it reasonably certain that the two named forms from the western Atlantic (*sambaquiensis* F. Müller and *tenuis* Fewkes) represent but a single species, for the supposed differences between them in number of tentacles, of marginal knobs, and of blind centripetal canals, and in the diameter of the disc indicate, at most, that *tenuis* is a dwarf race of *sambaquiensis*, or that the de-



scriptions of the former have been based on specimens that had not attained their maximum growth and development. It has in fact been repeatedly suggested that both of these are simply varieties—if as much—of the well-known *O. phosphorica* of the Mediterranean. And the necessity of naming the Bermudian example listed below makes discussion of this question pertinent.

The only ostensible differences between *phosphorica* and *sambaquiensis* are that the original account of the latter (Müller, 1861) credits it with a larger number of secondary tentacles (200-300) and of centripetal canals (21-27 per quadrant), than have ever been recorded for *phosphorica*, for which the maxima are 100-120 tentacles and 19 centripetal canals in one quadrant (for tabulation of numerical characters, see Bigelow, 1909, p. 109; Mayer, 1910, p. 353). That is to say, *phosphorica* bears the same sort of relationship to *sambaquiensis* as does *tenuis* to *phosphorica*. By present indications it is not possible to make any definite specific separation, within this series, because the three forms intergrade in numerical characters. On the other hand, to unite the three definitely under one name, would obscure the very interesting fact that all the records from the West Indian-Bermudian region are for the *tenuis* (or to some extent paedogenetic) form, which is not known to occur at all in the Mediterranean. Neither, on the other hand, has *Olindias* from the latter sea, ever been found to attain the extreme development described for the Brazilian form. The case, analogous to that of the representatives of *Charybdea* from these same regions (p. 137), seems best handled taxonomically, by the recognition of subspecies. For further discussion of the reasons for this procedure, in the case of geographic races of medusae, see page 137.

### ***Olindias phosphorica tenuis* Fewkes.**

*Halicalyx tenuis*, Fewkes, 1882, p. 277, Pl. 7, Fig. 15.

To the references given by Mayer, 1910, p. 354 ("*Olindias tenuis*"), add:

*Olindias phosphorica* [Partim], Bigelow, 1919, p. 317.

*Olindias tenuis*, Boone, 1933, p. 32.

*Material*: Net No. 840, Surface, September 20, 1929, 3 specimens, approximately 10, 10, and 25 mm. in diameter.

The larger specimen has large gonads, between 45 and 50 primary tentacles, and about 40 centripetal canals, the contracted and recurved state of the margin preventing exact enumeration. The chief interest of the series is as cumulative evidence that the Bermudian-West Indian representatives of *O. phosphorica* are characterized by fewer primary tentacles and canals at maturity than are their Mediterranean relatives; consequently that the recognition in nomenclature of *tenuis*, as a local subspecies, is justifiable. Owing to the condition of the large specimen, I was not able to count the secondary tentacles.

*General Distribution*: *O. tenuis* has already been reported from Bermuda (Bigelow, 1909, p. 109); other records are from the Bahamas and the coast of southern Florida (Fewkes, 1882; Mayer, 1910; Boone, 1933).

## TRACHYNEMIDAE.

### ***Rhopalonema*.**

#### ***Rhopalonema velatum* Gegenbaur.**

*Rhopalonema velatum*, Gegenbaur, 1856, p. 251, Pl. 9, Figs. 1-5.

For synonymy, see Bigelow, 1909, p. 129; Mayer, 1910, p. 378; Thiel, 1936, p. 10.

*Material:* Net Nos. 32, 35, 39, 43, 44, 67, 69, 97, 98, 100, 102, 362, 581, 620, 632, 634, 682, 720, 730, 793, 915, 916, 945, 959, 967; hauls at 549-0 to 1,829-0 meters; 39 specimens, 6-12 mm. in diameter; 1-5 specimens per haul.

These specimens, all of which are more or less fragmentary, call for no special comment, this being one of the best known of Trachomedusae. I need merely note that as all of them are large enough to show the situation of the gonads, there is no possibility that the list includes any examples of *Sminthea eurygaster*, a species somewhat similar in appearance, and which Thiel (1936, Fig. 2) has recently shown to be much more generally distributed on the high seas than formerly supposed.

*General Distribution:* *R. velatum* was to be expected near Bermuda, there being many previous records for the eastern side of the Sargasso Sea region, as well as elsewhere over the warmer belts of all three oceans, including also the Mediterranean and Red Sea. For a recent chart of distribution, see Thiel, 1936, Fig. 1.

It is interesting that 108 hauls shoaler than 549-0 meters did not yield it, for it often occurs close to the surface, with its center of abundance shoaler, in general, than 100 meters (Thiel, 1935, Fig. 21).

### ***Pantachogon.***

The definitions for this genus adopted by Mayer (1910), also recently by Broch (1929) and by Thiel (1932), would likewise include the medusa reported here (p. 117) as *Colobonema*. But for reasons stated on page 116, it seems to me preferable to retain the latter genus as distinct, because of the peculiar order in which its tentacles are developed, and because of the structure of its radial canals. The structure of its tentacles may perhaps be of generic significance, likewise. Opinions have also differed as to whether the generic limits of *Pantachogon* should be interpreted broadly enough to include the various species usually reported as *Homoeonema*, in which the gonads are localized along restricted sectors of the radial canals (Bigelow, 1913, p. 44), or should be restricted to forms in which these organs are developed more diffusely along the whole length of the canals (Broch, 1929; Thiel, 1932, 1936; Ranson, 1936). As the present collection contains representatives of the latter sort, only, it does not aid in the solution of this question.

The group with diffuse gonads includes three named forms, *haeckeli* (Maas, 1893), *rubrum* (Vanhöffen, 1902), and *scotti* (Browne, 1910). I have already expressed doubt as to whether the first two could be separated, the color being the only difference. As Ranson (1936) again emphasizes, successive studies of considerable series have revealed no anatomical differences whatever between them, hence he has now united them provisionally, Thiel (1936) definitely, and I believe with good reason. I may add that the capture near Bermuda of several specimens, lacking any trace of pigment (i.e., of the *haeckeli* type), now answers the last argument in favor of considering the two color-forms as distinct, i. e., that the colorless *haeckeli* was restricted to high latitudes. Nomenclatural rules require the choice of *haeckeli* Maas as the name for the joint species, because Maas' account, with clearly recognizable illustration showing the gonads and tentacles correctly, was published many years prior to the description of *rubrum* (Vanhöffen, 1902).

*P. scotti*, an Antarctic species, is separated from *haeckeli* by much more numerous tentacles (104-128, contrasted with a maximum of 64 in *haeckeli*). And so many specimens of the latter have now been examined that this difference seems established.

***Pantachogon haeckeli* Maas.**

*Pantachogon haeckeli*, Maas, 1893, p. 17, Pl. 1, Fig. 2; 1904, p. 29; Mayer, 1910, p. 389; Bigelow, 1913, p. 44, Pl. 3, Figs. 4-8; Broch, 1929, p. 503; Thiel, 1932a, p. 152; 1936, p. 26.

*Pantachogon rubrum*, Vanhöffen, 1902a, p. 63, Pl. 9, Fig. 9, Pl. 10, Figs. 19-20, Pl. 11, Fig. 25; Maas, 1905, p. 55, Pl. 10, Fig. 66; Mayer, 1910, p. 389; Kramp, 1913, p. 274; 1914, p. 433; 1920, p. 5; 1924, p. 22; Bigelow, 1913, p. 44; Browne, 1916, p. 195; Broch, 1929, p. 504; Thiel, 1931, p. 330; 1932a, p. 153; Ranson, 1936, p. 147.

*Pantachogon rubrum* [Partim], Thiel, 1936, p. 24.

*Material*: Net Nos. 36, 42, 52, 64, 234, 296, 539, 552, 554, 575, 582, 598, 628, 648, 657, 658, 659, 666, 684, 685, 691, 695, 698, 709, 717, 718, 736, 739, 742, 757, 780, 789, 805, 809, 854, 862, 864, 866, 881, 897, 916, 964; 549-0 to 1,829-0 meters; 65 specimens; 1-5 per haul.

Also, 12 very fragmentary specimens, from Net Nos. 556, 640, 698, 709, 721, 748, 862, 929; 1,280-0 to 1,646-0 meters, are provisionally referred to this species.

The specimens are all more or less fragmentary—most of them very much damaged—but those included in the first of the two preceding lists have enough of the margin and of the subumbrella intact to show that the tentacles are so spaced as to accord with the number characteristic of this species (maximum, 64), and that the radial canals are of even bore throughout their lengths. I have also been able to compare them with the series collected by the *Albatross* in the northwestern Pacific (Bigelow, 1913).

*Tentacles*: Vanhöffen (1902a) counted 7 tentacles per octant, between every two perradials, in all his specimens. Maas (1905), however, found smaller numbers in some octants, i.e., intermediate stages in development. And the Bermuda series again illustrates this, for while the sub-radials are seven in number in most of the octants in which complete counts can be made, only 6 are to be seen in some octants. And one specimen seems to have not more than 6 in any octant, i.e., a total of only 56. On the other hand, a greater number than 7 sub-radials has never been found in any octant, nor have additional tentacular bulbs been observed. That the number is determinant in *Pantachogon* (as it is in *Colobonema*) thus seems sufficiently established. The order of development of the different series of tentacles has not been traced; nor is this point clarified by the present series, preservation not being good enough for dependence to be placed on differences in size between different tentacles. It is, however, suggestive that a tentacle does not always stand exactly opposite a canal, i.e., it appears that in some cases none can be described as strictly "perradial;" neither are those most nearly opposite the canals appreciably larger than the others.

An interesting question, still awaiting answer, is whether the tentacles of *Pantachogon*, like those of *Colobonema*, are stump-like, as suggested by the fact that they have been very short, and of sub-equal length, in all the specimens so far examined, or whether Maas (1905) was correct in his suggestion that they are of ordinary filamentous type, but so easily broken off that all except the bases have been lost. None of the Bermudian and northwest Pacific specimens are in good enough condition to settle this point, though the general appearance of the tentacles—especially the fact that in many cases, they are square tipped—favors the second alternative.

*Gonads*: In one small specimen, about 8 mm. high, in which the gonads are intact, they represent about the same early stage in development illustrated for a North Pacific specimen of corresponding size (Bigelow, 1913, Pl. 3, Fig. 5). In the larger specimens, the gonads have either been lost



entirely, or are represented by fragments only, here and there along the canals.

**Musculature:** The circular musculature of the subumbrella is strongly developed (Bigelow, 1913; Ranson, 1936); a development as striking, in fact, as it is in *Colobonema*. In *Pantachogon*, as in *Colobonema*, however, the musculature is not only entirely discontinuous along the lines of the radial canals, but terminates, apically, at the level where the general contour of the subumbrella changes from sub-cylindrical to domed, leaving a considerable clear space surrounding the base of the manubrium. And Ranson (1936) has recently pointed out that the outlines of the apical ends of the interradial muscular fields provide at least a specific character, being transversely truncate in *P. haeckeli*, as appears clearly in the few Bermuda specimens in which the musculature is still intact, whereas in *Colobonema* they are ovoid, corresponding to the contours of the interspaces between the apically expanded radial canals (p. 118). The latter, as Ranson (1936) has emphasized, are narrow and of uniform caliber, throughout their lengths, from bell margin to union with the manubrium, contrasting strongly with their state in *Colobonema*.

**Color:** Occasional specimens show a pinkish tinge. But the few in which the subumbral musculature is more or less intact are colorless: interesting evidence, as noted above (p. 114), that the unpigmented form of this species, as well as the rosy-colored, occurs in the warm belt of the North Atlantic. Thiel (1936, p. 24), in fact, has already shown that the two may exist side by side, the *Meteor* having taken one of each at a station in the South Atlantic. No recent student of *Pantachogon* has considered this color difference a sufficient ground *per se* for specific separation. But it is an interesting question, how the existence of the two color phases is to be interpreted. As the present series throws no light on this point, I need only note that the pigmentation of the rosy form (*P. rubrum*, auct.) is not of the peculiarly dense and opaque sort characteristic of many bathypelagic medusae.

**General Distribution:** Locality records for *P. haeckeli*, as here defined, are widespread in the Atlantic, including Spitzbergen, Irminger Sea and Davis Strait in the north, sundry localities off Ireland, in the Bay of Biscay, and in the region between the Canaries, Azores, and Gibraltar; the Mediterranean; the eastern side of the tropical and South Atlantic south to Lat. 64° S.; the Antarctic (Weddell Sea); South and North Indian Oceans and Red Sea; Malaysia; and the extreme northern Pacific including Bering Sea and the Sea of Okhotsk. With the Bermuda records extending the known range to the western Sargasso Sea,—the nearest previous record was in mid-Atlantic—*P. haeckeli* is evidently world wide in the ocean basins, right up to the subpolar zones.

**Vertical Range:** The great majority of captures have been in open nets working as deep as 500-0 meters, the only exception being a single young specimen taken by the *Valdivia* in a haul from 60 meters (Vanhöffen, 1902).

### **Colobonema.**

There has been much discussion recently as to whether *Colobonema* is generically separable from *Pantachogon*. Thiel (1936) at the one extreme, has even included its unique representative in the synonymy of *P. rubrum* (= *P. haeckeli*). But this seems definitely precluded not only by the constant difference in the number of tentacles, but also by the structure of the proximal sectors of the radial canals. Other students who have recently written of *Colobonema* (Bigelow, 1913; 1919; Kramp, 1924; Broch, 1929; Ranson, 1936) have therefore retained it as a separate genus, either definitely or provisionally. And that course is followed here.

The question what specific name should be applied to the one known representative of *Colobonema* is one that will not down, because a final an-



swer depends on decision as to the accuracy, or the reverse, of the published description of a specimen no longer extant. Accepting Maas' (1905) subsequent statement that his earlier (1897) account of his *Homoeonema typicum*, which credited the latter with more than 32 tentacles, was an error resulting from the poor condition of the specimen, Mayer (1910), Uchida (1928), and I (Bigelow, 1913; 1919) have used this specific name, for in all other respects, Maas' *typicum* appears to resemble the form later described by Vanhöffen (1902a) as *Colobonema sericeum*. Kramp (1920; 1924), Broch (1929), and Ranson (1936), however, take the opposite view, that Maas' (1897) original *typicum* cannot be identified with *sericeum*, hence use the latter name.<sup>5</sup>

The present series adds nothing toward solution of this nomenclatural puzzle, beyond the opportunity for pointing out that choice of *typicum* as the specific designation has the advantage of providing a resting place for a name which is likely otherwise to remain permanently without connection with any actually existant medusa.

### ***Colobonema typicum* Maas.**

*Homoeonema typicum*, Maas, 1897, p. 22, Pl. 3, Figs. 1-3.

For early synonymy, see Mayer, 1910, p. 385.

It has been referred to, subsequently, under the following names:

*Colobonema sericeum*, Kramp, 1920, p. 5; 1924, p. 28; Ranson, 1936, p. 152, Pl. 2, Figs. 14-15.

*Homoeonema (Colobonema) sericeum*, Broch, 1929, p. 500.

*Colobonema typicum*, Bigelow, 1913, p. 46; 1919, p. 322.

*Homoeonema typicum*, Uchida, 1928, p. 81.

**Material:** Net Nos. 26, 39, 94, 95, 99, 105, 240, 292, 293, 295, 296, 400, 434, 565, 597, 605, 606, 607, 610, 625, 626, 637, 641, 653, 680, 732, 760, 777, 802, 805, 813, 853, 867, 874, 937, 939, 964; 732-0 to 1,829-0 meters; 47 specimens; 1-3 per haul, mostly in poor condition.

The specimens range from about 8 to about 33 mm. in height. Features especially to be examined on any considerable series of this species that may now come to hand, are: (a), number and order of appearance of the tentacles, whether as constant as earlier records have indicated; (b), number of otocysts; and (c), contours of the proximal parts of the radial canals, which Ranson (1936, Pl. 2, Fig. 14) has found to differ significantly from those of *Pantachogon*.

**Tentacles:** Successive examinations have yielded cumulative evidence, not only that the final number of tentacles in this species is 32, but that variations from this number are so unusual that none has been found among 123 specimens collected by the *Valdivia* (Vanhöffen, 1902a) *Siboga* (Maas, 1905), *Research* (Browne, 1906), *Albatross* (Bigelow, 1909; 1913; 1919), *Thor* (Kramp, 1924), and by the Prince of Monaco (Ranson, 1936). The peculiar order of development—perradials, adradials, and finally interradials—first reported by Maas (1905), has proved equally unvarying, judging from the relative sizes of the different orders of tentacles on small and medium-sized specimens. Both these findings are further corroborated by the present series, for in every octant on which they can be counted, there is the usual interradial, and pair of adradials in the larger specimens. In one of the smaller specimens about 20 mm. high (Net No. 26), the interradial has not yet appeared in one of the octants, while in 6 of the other octants<sup>6</sup> it is represented by a rudimentary knob only, illustrating a stage between that in which the per- and adradials alone have appeared (Maas,

<sup>5</sup> The species subsequently described by Maas (1905) from the *Siboga* collection, as *typicum*, undoubtedly was identical with Vanhöffen's *sericeum*.

<sup>6</sup> The margin of the eighth octant has been torn off.

1905, Fig. 64), and the final stage in which the interradials are also well developed.

In all specimens so far examined (including the Bermuda series) the tentacles have been short, stump-like. And it seems now established that this is normal, and not the result of mutilation, for in the better preserved specimens the tips are rounded and apparently uninjured, i.e., with their ectodermal covering complete. And the fact that in large specimens the members of the per- and adradial series (sometimes the interradials also) are all about equal in length, suggests that they are but little extensible.

*Otocysts*: The otocysts of this species must be very easily detached, for only in one case has a single otocyst been detected, among the earlier collections (Bigelow, 1919, p. 323). One of the Bermuda specimens (Net No. 26) also bears one otocyst—agreeing in structure with the earlier account—between a per- and an adradial tentacle. But I have not been able to detect even a trace of any others, in this, or on any of the other specimens. To determine positively whether otocysts normally alternate with tentacles, as earlier observations suggest (Bigelow, 1913, p. 321), requires examination of specimens with undamaged margin.

*Radial Canals*: Ranson (1936, p. 154, Pl. 2, Fig. 14) has recently pointed out (what seems to have been overlooked previously) that the radial canals of *Colobonema* are expanded proximally so that their walls are in close contact (though discontinuous) in the interradia across the domed apex of the subumbrella, narrowing again toward their union with the narrow base of the manubrium, which gives characteristic ovoid contours to the apical ends of the 8 muscular zones. The better preserved of the Bermuda series corroborate this interpretation, so far as can be determined from surface views, though in all cases the base of the stomach is damaged.

*General Distribution*: *Colobonema*, as distinguished from *Pantachon haeckeli*<sup>7</sup> had been taken already at many stations in regions as widely scattered, as the central Sargasso Sea; the eastern North Atlantic; west of Ireland; between the Azores, Canaries, and the coast of Spain; Straits of Gibraltar; Mediterranean; equatorial and South Atlantic down to Latitude 42°S.; the Indian Ocean from Lat. 9°N. to Lat 34°S.; Malaysian region; Philippines; Japanese waters; and the eastern tropical Pacific. It is, in short, cosmopolitan in the warm and temperate belts, at appropriate depths, but has not yet been reported from Arctic or from Antarctic latitudes.

*Vertical Range*: So far as I have been able to learn, the shoalest haul that has so far yielded *Colobonema* was with an open net, from about 241-0 meters, most of the captures (all but one with open nets) being from hauls deeper than 500-0 meters; and there is one record from a closing net from 900-1,500 meters. Its bathypelagic habit is thus well established.

### Crossota.

*Crossota*, originally classed with the Ptychogastridae (Vanhöffen, 1902a; Bigelow, 1909), was soon shown to be a trachynemid (Bigelow, 1913). But it is not yet possible to give any precise generic definition for it that can be depended upon to stand the test of time. During the first years of its history it was, indeed, regarded as a very sharply defined genus, for while the type species (*C. brunnea* Vanhöffen) agrees with *Aglaura* and *Aglantha* in the structure of the gonads, it differs markedly from them not only in lacking any trace of a gelatinous peduncle, but also—and from all other Trachynemidae as well—in having more than one row of tentacles. Shortly, however, other species were described, one of which (*rufobrunnea*, Kramp, 1913) apparently had the tentacles in a single row,<sup>8</sup> while in another (*C.*

<sup>7</sup> Thiel's (1936) chart of distribution for *Pantachogon* also includes the *Colobonema* records, for he classes the latter as a synonym of the former.

<sup>8</sup> Broch (1929, p. 506) says "Ersichtlich in einer Reihe."

*pedunculata* Bigelow, 1913), there is a short gelatinous peduncle. The former partially bridges the gap between *Crossota* and *Pantachogon*, the latter between *Crossota* and *Aglantha*, i.e., between the subfamilies Rhopaloneminae and Aglaurinae, as defined by Broch (1929) and by Thiel (1936, p. 9). Indeed, *pedunculata* is tentatively referred to *Aglantha* by Thiel (1936, p. 22). But this course would involve expanding that genus to include species with tentacles in more than one series, for in *C. pedunculata* these are in three or four irregular rows, much as in *Crossota brunnea*. Until Kramp and Damas' (1925, p. 317) characterization of the tentacles of *norvegica* as being in a single row is confirmed, it seems simplest to confine *Crossota* to Trachynemidae with sausage-shaped gonads hanging free from the sub-umbrella and with many closely crowded tentacles, in more than one row, irrespective of whether or not there is a short peduncle. Data as to the number of otocysts is much to be desired. In the only species in which any estimate of this has been possible, they have proved much more numerous than they are in *Aglantha*.

### ? *Crossota brunnea* Vanhöffen.

*Crossota brunnea*, Vanhöffen, 1902a, p. 73, Pl. 9, Figs. 11-13, Pl. 12, Figs. 34-38, 43-47; Bigelow, 1909, p. 135, Pl. 2, Fig. 7, Pl. 45, Fig. 9; Mayer, 1910, p. 396.

*Crossota brunnea* [Partim], Thiel, 1936, p. 20<sup>9</sup>.

*Crossota brunnea*, var. *norvegica*, Bigelow, 1913, p. 48.

*Crossota norvegica*, Broch, 1929, p. 507.

? *Crossota norvegica*, Kramp, 1920, p. 5.

Non *Crossota norvegica*, Vanhöffen, 1902a, p. 75; Kramp and Damas, 1925, p. 317.

See Thiel (1936, p. 21) for a recent summary of the checkered history of *C. norvegica* Vanhöffen and for the reasons why *norvegica* cannot be used as the name for a variety of *C. brunnea* as I formerly did (Bigelow, 1913).

**Material:** Net Nos. 241, 642, 665, 733, 787, 794, 854, 869; 1,097-0 to 1,829-0 meters; 11 very fragmentary specimens, all approximately 14 mm. in diameter.

These specimens are all in such poor condition that identification is only tentative; in every case all trace of the manubrium and gonads has been lost and only faint indications of the radial canals are to be seen. At first sight, it seemed that they might belong to *C. rufobrunnea* Kramp, for in most cases the tentacular bases—in their present state—have the appearance of being in a single row. But in one specimen in which the margin is in somewhat better condition than in the others, the larger (older) tentacle-bases arise at a slightly higher level than do the smaller (younger) ones, for which reason it seems more probable that the whole series belongs to *C. brunnea*. In some parts of the margin, 3 successive sizes—or rows—of tentacles can be recognized, in others only two, as was the case in the *Meteor* specimen recently described by Thiel (1936, p. 20). In the specimens of *brunnea* that I have seen, in good enough condition to show the tentacles (Bigelow, 1909; 1913), the arrangement in different rows has been less regular than Vanhöffen (1902a, Pl. 12, Fig. 47) pictured it, the tentacles being more crowded and the older only a very short distance above the younger, instead of well above the latter: this distribution is more correctly represented in Vanhöffen's 1902a, Pl. 12, Fig. 46) section of the margin.

<sup>9</sup> Thiel (1936) includes *C. alba* Bigelow in the synonymy of *C. brunnea*.



It was not possible to make a reliable count of the tentacles, even in any one octant, owing to the uncertainty as to the precise location of the radial canals. In the specimen just mentioned, the spacings of the tentacular-bases suggests a total of at least 200. No otocysts were to be found.

In most of the specimens enough of the subumbral pigmentation is still intact to show that it was of the characteristic opacity and chocolate or reddish brown color.

*General Distribution:* Previous records probably referable to *C. brunnea*, as mapped by Thiel (1936, p. 23), are widely scattered in the eastern side of the Atlantic from Latitude about 50° N. down to the Antarctic—extended, now in all probability to the western half of the Sargasso Sea—; in both sides of the Indian Ocean; and in the parts of the eastern tropical and far northern Pacific traversed by the *Albatross* on the cruises of 1904-1905 and 1906. It has not been taken, however, in the Mediterranean. And while reaching high latitudes in the south, it apparently does not inhabit the North Polar regions.

*Vertical Range:* All captures have been in deep hauls.

### ? *Crossota*.

The following fragments (now mere shells) are tentatively referred to *Crossota* because such indications of the locations of the tentacles as are still to be seen suggest that these were numerous and close crowded, and because most of the specimens still show some trace of subumbral pigment. But specific identification is out of the question.

Net Nos. 41, 66, 74, 75, 101, 114, 137, 138, 220, 295, 640, 644, 647, 666, 724, 748, 770, 779, 807, 812, 815, 844, 849, 867, 885, 891, 917, 935, 959, 967, 970; 914-0 to 1,830-0 meters; fragments of 37 specimens.

### TRACHYNEMIDAE gen. ?

Medusae, apparently belonging to the Trachynemidae, but in such poor condition as to preclude even provisional identification, were taken in Net Nos. 110, 145, 269, 295, 317, 322, 327, 341, 449, 574, 577, 598, 613, 644, 680, 715, 718, 726, 738, 767, 785, 795, 799, 807, 824, 827, 867, 882, 885, 896, 926, 968; a total of 51 specimens, 1-4 per haul.

### HALICREIDAE.

#### *Halicreas*.

Opinions have differed whether such of the Halicreidae as have only 8 canals, and tentacles in a continuous row (i.e., not grouped as they are in *Botrynema*) should all be referred to the one genus, *Halicreas*, or to two genera; and if the latter, whether generic separation should be based on number of tentacles alone, as by Vanhöffen (1902a), on this character combined with the form of the umbrella, as by Ranson (1936); or on the presence or absence of exumbral papillae, as formerly by me (1909).

Even granting eventual agreement as to the relative taxonomic value of different characters, we still face a nomenclatural difficulty (if two genera are to be recognized), in the fact that the decision as to the correct name of the second genus would depend on the true identity of the specimen originally described by Maas (1893) as *Homoeonema platygonon*, and later declared by him (Maas, 1906, p. 3) to be a halicreasid, not a trachynemid as he originally supposed.

Examination of the type specimen of *H. platygonon*, if this be still in existence, would settle the point. Meanwhile it seems simplest to follow Broch (1929) and Thiel (1936), in uniting, in *Halicreas*, all halicreasids



with 8 canals and continuous series of tentacles, whether the exumbrella be papillate or smooth, and whether the tentacles be few or numerous, all of one size, or of two sizes. For further discussion, see Ranson (1936) and Thiel (1936).

Among the named forms referable to *Halicreas* as thus expanded, two (*H. minimum* Fewkes and *H. papillosum* Vanhöffen) are set apart by the presence of exumbral papillae. Thiel (1936), it is true, bases the specific distinction within *Halicreas* solely on whether the tentacles are of one size or of two sizes. I see no reason, however, for abandoning the presence or absence of exumbral papillae as of specific value here, even if it be not of generic worth as I formerly suggested; not only are these structures highly distinctive features, but no variation has ever been found in their number. And Ranson (1936) also considers them as specific.

*H. papillosum* is the best-known member of the genus, and large series of it have been taken on most of the recent expeditions that have done deep towing. It has, however, long been generally recognized that it might eventually prove to be identical with the *H. minimum* of Fewkes (type species of the genus) which was described 20 years the earlier, consequently *minimum* has repeatedly been classed as a doubtful synonym of *papillosum* in the lists of references to the latter. Fortunately, the collection of the Museum of Comparative Zoology contains one of Fewkes' original two specimens (previously overlooked); evidently the one described by him (1882, p. 306) as "expanded" and "preserved in spirit." Although this specimen has subsequently been dessicated, then restored to alcohol, the typical exumbral papillae (each with several conical projections) are still to be seen, while the locations of the 8 radial canals are marked as broad, flat ridges on the subumbrella. And fragments of the circular lip are still recognizable. What Fewkes took for the velum was in reality the marginal zone of the bell, distal to the exumbral papillae. Thus, while the tentacles have all been lost—as indeed Fewkes pointed out—there is no reason to doubt that it is the same species that Vanhöffen (1902a) later described as *papillosum*, while Fewkes' specimens were from a locality where many *papillosum* have since been taken, on the cruises of the Woods Hole Oceanographic Institution. Consequently, there need no longer be any hesitancy in superseding *papillosum* by *minimum*, thus making one more step toward stability in the nomenclature of the medusae.

It has long been obvious that the five named representatives of the smooth-belled subdivision of the genus (*conicum*, *album*, *glabrum* and *rotundatum* Vanhöffen, 1902a; *racovitzae* Maas, 1906) stand in need of drastic reduction, successive studies (Bigelow, 1909; Ranson, 1936) having proved that the features on which Vanhöffen (1902a) laid chief stress (degree of doming of the exumbrella, and precise location of the gonads on the radial canals), are too variable to be of taxonomic significance. Thiel's (1936) recent grouping, based on whether there are two sizes of tentacles or only one, is a decided advance. It is certain that the tentacles are all alike in *racovitzae*, for Maas (1906) definitely states as much; likewise in *conicum* (Vanhöffen, 1902a, Pl. 11, Fig. 33). On the other hand, it seems equally certain that the original specimens of *glabrum* had tentacles of two sizes, because Vanhöffen (1902a, p. 70) describes them as "ebenso wie bei *H. papillosum* angeordnet." Hence—as *glabrum* has page priority in Vanhöffen's original paper—this name may be accepted for smooth-belled *Halicreas* with 2 sizes of tentacles.

Unfortunately, Vanhöffen gave no definite information on this point, either for his *Halicreas album* or his *Halicreas rotundatum*. The first of these is placed by Thiel (1936) in the group in which the tentacles are all of one size (i.e., grouped with *racovitzae* and *conicum*). And the original accounts certainly would allow this interpretation. But Vanhöffen's (1902a, p. 68) statement that "so wohl *Halicreas* wie *Haliscera*" has tentacles of

two sizes, makes it seem more likely that this was true of his specimens of *album* and *rotundatum*. Hence it seems justifiable to class these names provisionally as synonyms of *glabrum*, recognizing, however, that the wide variation in numbers of tentacles between the several forms may finally warrant a further subdivision on this basis.

### *Halicreas minimum* Fewkes.

*Halicreas minimum*, Fewkes, 1882, p. 306.

*Halicreas papillosum*, Vanhöffen, 1902a, p. 68, Pl. 9, Figs. 7-8; Pl. 11, Fig. 30.

For the more important subsequent references, see *Halicreas papillosum*, Mayer, 1910, p. 391; Ranson, 1936, p. 164; *Halicreas papillosum* [Partim], Thiel, 1936, p. 34.

*Material*: Net Nos. 25, 26, 41, 43, 44, 56, 60, 62, 65, 66, 67, 68, 69, 75, 76, 81, 83, 108, 110, 115, 124, 138, 144, 157, 203, 241, 247, 269, 270, 271, 293, 295, 297, 357, 360, 383, 401, 405, 406, 442, 466, 468, 481, 488, 501, 566, 569, 570, 576, 590, 599, 640, 648, 654, 682, 683, 684, 701, 703, 717, 718, 722, 723, 724, 727, 728, 730, 736, 741, 746, 750, 751, 756, 765, 767, 774, 781, 787, 788, 795, 799, 815, 852, 857, 858, 863, 864, 869, 875, 887, 893, 898, 919, 931, 932, 933, 935, 940, 942, 947, 963, 969, 970; at depths ranging from 0 to 2,012-0 meters; a total of 186 specimens; 1-6 specimens per haul, except for one catch of 17 specimens in Net No. 271.

The specimens, ranging from about 13 mm. to about 36 mm. in diameter, are all fragmentary, having lost every trace of marginal organs and of the gastrovascular system. Hence, they add nothing to previous accounts of the morphology of this interesting bathypelagic medusa. This species is, however, made so easily recognizable by the marginal papillae—structures so resistant that they persist even after the roughest handling—that identity seems assured. Most of them also show more or less trace of the gelatinous apical projection, though the discs of others are apically rounded, in their present condition.

*General Distribution*: Earlier records of capture are widespread over the eastern side of the tropical Pacific, also the tropical and subantarctic belts of the Indian Ocean, the East Indies and Philippines, Japan, Sea of Okhotsk, Bering Sea, the South Atlantic down to the Antarctic, north boreal and east temperate belts of the North Atlantic (Thiel, 1935, Fig 38; 1936, p. 36, Fig. 7; Ranson, 1936). It had been taken on the continental slope of America in the offing of Woods Hole. Curiously, however, there was no previous record of it in the Sargasso Sea region. The Bermuda records, proving it abundant there, are therefore interesting as cumulative evidence that it is cosmopolitan in the ocean basins at suitable depths, at low and mid-latitudes.

However, it has not been taken in the Mediterranean, in spite of the great number and wide distribution of deep hauls that have been made there by the *Thor* and by the Prince of Monaco (Kramp, 1924; Ranson, 1936). And its absence, or at least rarity, there is puzzling, for the comparative frequency of records from small depths at low latitudes in the Atlantic (see below), makes it unlikely that the shoalness of the sill depth of the Straits of Gibraltar can offer a permanent barrier to its entrance into the Mediterranean, as it apparently does in the case of certain more strictly bathypelagic animals (Bigelow and Sears, 1937, p. 128). For further discussion of its distribution and dispersal in the South Atlantic, see Thiel, 1935, p. 72.

*Seasonal Distribution*: The seasonal distribution of the hauls yielding *H. minima*, for the two years combined, appear from the following tabulation:

Month.	Hauls Yielding <i>H. minimum</i> .	Total Hauls, 1,280-0 Meters or Deeper.	% Yielding <i>H. minimum</i> .
April.	6	20	30
May.	24	77	31
June.	22	135	16
July.	17	109	15
August.	5	40	12
September.	29	158	19

This shows a somewhat greater abundance in spring, for the two collecting seasons combined, than during the summer months.

*Vertical Range:* The early records were all from hauls with open nets, leaving in doubt the precise depths from which the specimens came, but the great majority of the catches were from hauls that sampled down to 500 meters or deeper. Thus, the shoalest of the 40 *Valdivia* hauls that yielded specimens positively identified as *H. minimum* was from 600-0 meters, 37 of them at least 1,000-0 meters<sup>10</sup> or deeper (Vanhöffen, 1902). All of the 30 *Albatross* catches were, similarly, in hauls from 550-0 meters (Bigelow, 1909; 1913; 1919), while the records of the Prince of Monaco were all from 1,000-0 meters or deeper (Ranson, 1936).

The *Meteor* records have shown, however, that *H. minimum* is not exclusively restricted to great depths, but may populate the whole column from, say, 75 meters down to 800-900 meters, as appears from the distribution of catches in closing nets, tabulated below, from data presented by Thiel (1935, Tables 10, 21, Fig. 27; 1936, p. 34):

Depth in Meters.	Number of Cases.	Number of Specimens.
50- 70	1	1
50-100	7	8
100-200	2	2
200-400	5	7
400-600	4	5
600-800	2	1

And still more recent captures by *Atlantis* of the Woods Hole Oceanographic Institution make it unlikely that there is any definite lower boundary to its occurrence, any more than for various siphonophores (Bigelow and Sears, 1937, p. 137), for horizontal closing net hauls of uniform duration at 3 stations as described by Leavitt (1935) in the summer of 1935, yielded the following catches:

Depth in Meters.	Number of Cases.	Number of Specimens.
600	1	6
1,200	1	4
1,800	1	3
2,000	1	2
2,200	2	2

<sup>10</sup> One juvenile, perhaps of this identity, was taken at 200-0 meters.



The Bermuda collection amplifies the foregoing, proving that *H. minimum* may occasionally come right up to the surface (Net No. 654, 1 specimen). But in this part of the Sargasso Sea, where the thickness of the superficial stratum of warm water is great, the chief center of abundance lies deeper than in most parts of the oceans, or at least as deep as 1,400-1,800 meters, as appears from the following tabulation for the two seasons combined:

Depth in Meters.	No. of Hauls with <i>minimum</i> .	Total Number Hauls.	% with <i>minimum</i> .
732-0	2	40	5
913-0	3	132	2
1,097-0	2	134	2
1,280-0	8	132	6
1,463-0	21	132	15
1,646-0	34	135	25
1,829-0	31	135	22
2,012-0	3	4	45

*H. minimum* (seemingly also *H. glabrum* and *Halitrephes*) thus is a marked exception to the general rule that medusae having their center of abundance so deep, are densely pigmented.

Thiel (1935, p. 47) has shown, from the catches made in closing nets by the *Meteor*, that the individuals of the genus *Halicreas*, as a whole, average larger, the greater the depth. This suggests that the young stages are passed chiefly in the shoaler strata and that the medusae tend to sink as they grow larger. But we still await positive evidence whether the eggs, as a whole, rise to the surface, as he suggests (Thiel, 1935, p. 72).

### ? *Halicreas glabrum* Vanhöffen.

*Halicreas glabrum*, Vanhöffen, 1902a, p. 70, Pl. 9, Fig. 3; Mayer, 1910, p. 392; Ranson, 1936, p. 167.

*Homoeonema glabrum*, Bigelow and Leslie, 1930, p. 564.

*Haliscera alba*, Vanhöffen, 1902a, p. 71, Pl. 9, Fig. 5.

*Homoeonema alba*, Bigelow, 1909, p. 142, Pl. 3, Fig. 1-2, Pl. 33, Figs. 6, 11, Pl. 34, Fig. 9.

*Halicreas album* [Partim], Thiel, 1935, p. 48; 1936, p. 37.

*Halicreas rotundatum*, Vanhöffen, 1902a, p. 71, Pl. 9, Fig. 4; Maas, 1905, p. 57; Mayer, 1910, p. 392.

*Halicreas papillosum* [Partim], Thiel, 1936, p. 34. [Non *H. papillosum*, Vanhöffen, 1902.]

*Material*: Net Nos. 25, 43, 56, 62, 68, 75, 83, 89, 106, 114, 144, 145, 157, 218, 242, 247, 269, 270, 271, 295, 297, 315, 339, 345, 346, 347, 354, 359, 449, 466, 488, 501, 506, 539, 710, 742, 890, 942, 962; hauls from 914-0 meters to 2,012-0 meters; 66 specimens, 1-5 per haul.

These specimens—like Ranson's—agree very closely with Vanhöffen's (1902, p. 9, Fig. 3) illustration of *H. album* in the form of the bell, with high conical apex, and thin marginal zone, without any sign of the exumbral protuberances. But as already suggested (Bigelow and Leslie, 1930, p. 564), and as indicated above (p. 122), it is probable that *album* is specifically identical with Vanhöffen's *H. glabrum* and the latter name has page priority.



In every case, all trace of all the tentacles has been lost, preventing positive identification; in fact the great majority are mere shells. But in a few, parts of the subumbrella still remain. And one from Net No. 890, another from Net No. 942, are especially interesting, being in good enough condition to show the oval gonads situated proximally, leaving the distal parts of the radial canals free, as was the case in the *Albatross* specimens (Bigelow, 1909). And this corroborates Ranson's (1936, p. 168) observation that in his specimens (which had lost the gonads) the traces of the radial canals suggested proximal enlargements.

*General Distribution:* Previous records positively referable to *glabrum* + *album* are from the vicinity of the Azores (Ranson, 1936); and scattered along the route of the *Valdivia* in the eastern side of the Atlantic, from the offing of Morocco to Lat. 42° S., besides one locality record for the southern Indian Ocean (Vanhöffen, 1902a); several in the eastern tropical Pacific (Bigelow, 1909)<sup>11</sup>; and off California (Bigelow and Leslie, 1930). With the Bermuda records extending its known range to the western side of the North Atlantic, there seems no reason to doubt that the distribution of *H. glabrum* will eventually prove to be as wide as that of its better known relative, *H. minimum* (p. 122).

*Vertical Range:* It is not yet possible to make a final statement as to the vertical distribution of *H. glabrum*, as here defined, because it is combined with *H. racovitzae* and *H. conicum* in Thiel's (1935, 1936) discussions of the *Meteor* closing-net data. However, the fact that the *Valdivia*, *Albatross*, and Bermudian specimens all came from (open net) hauls from 550-0 meters, or deeper, suggests that it is chiefly bathypelagic in habit, though perhaps not exclusively so.

### ***Halitrephes.***

This genus, closely allied to *Halicreas* by the structure of the tentacles and of the sense organs, as well as by the simple circular mouth, without separate lips, but separated from it by the large number of radial canals, was first described from the collection made by the *Albatross* in the eastern tropical Pacific as *H. maasi* (Bigelow, 1909, p. 146, Pl. 33, Figs. 1-5, 7, 10, Pl. 45, Fig. 13). In the type specimen of the latter, 55 mm. in diameter, 28 canals were given off from the stomach, 5 of them branching dichotomously so that the number at the bell margin was 33; and there were about 70 tentacles of different sizes. Three years later, Vanhöffen (1912) described a second species, as *H. valdiviae*, from the collection of the German South Polar Expedition, with as many tentacles or even more, but separated from *maasi* by having only 16 canals. As the specimens examined by him ranged in diameter from 18 to 70 mm.—i.e., included full grown individuals as well as juveniles—the specific distinction seems well founded.

As the genus has not been seen since, the captures listed below from Bermuda are of interest, for although the specimens are extremely fragmentary, their identity seems reasonably certain.

### ***Halitrephes valdiviae* Vanhöffen.**

*Halitrephes valdiviae*, Vanhöffen, 1912, p. 384.

*Material:* Net Nos. 135, 154, 247, 357, 451, 562, 580, 614, 635, 709, 714, 745, 767, 778, 818, 830, 843, 967; hauls from 914-0 to 1,829-0 meters; 19 specimens about 30 to 80 mm. in diameter.

All the specimens are in poor condition. Even when much battered,

<sup>11</sup> Thiel's (1936, p. 36) chart of distribution also includes locality records for *racovitzae* and *conicum*.

however, the flat, lenticular form, but with central thickening, combined with numerous endodermal tentacular roots, (which are so resistant that they are recognizable even in the most fragmentary specimens), give a general aspect so characteristic as to make *Halitrephes* easily recognizable, even when the canals have been lost. And the two known species differ so widely in the number of tentacles that in most cases a specimen is referable either to the one or to the other, with reasonable certainty. All of the Bermudian specimens show the endodermal roots of some of the tentacles; and in one example, several tentacles are still sufficiently intact to show the contrast between stiff distal, and soft proximal, portions, characteristic of the *Halicreidae*. It was not possible to make certain of the total number of tentacles, in any specimen. But the minimum number (specimen of about 55 mm.) was certainly as great as 102. In another of 45 mm., there were at least 105, while in others of 60-80 mm., 145-170 tentacular roots were counted, total numbers being evidently somewhat greater. This corresponds well to the distribution with size recorded by Vanhöffen (1912) of 32 tentacles in a specimen of 12 mm.; 32-64 tentacles at a diameter of 18-20 mm.; 64-96 at a diameter of 30-40 mm.; and 200 at 70 mm. As pointed out for *H. maasi* (Bigelow, 1909, p. 146), the tentacular bases are of various sizes, indicating their successive development. But as no trace of canals is to be seen in the marginal zone of any of the Bermudian specimens, nothing can be said as to the order of development of tentacles relative to canals.

In one specimen, a sector of the margin still bears several rhopalia, alternating with the tentacular roots, as is the case in *H. maasi*, and agreeing closely with the rhopalia of the latter in structure and club-like appearance (Bigelow, 1909, Pl. 33, Fig. 10). The only example in which there is any trace of the gastrovascular system still to be seen, shows the circular lip characteristic of the genus and its allies, with the bases of about 8, at broad canals in about one-half the circumference, suggesting a total of about sixteen; or the same number described by Vanhöffen (1912) for the original series of *H. valdiviae*.

*General Distribution:* The original collections of *H. valdiviae* were from the tropical Atlantic between Lat. 6° N. and Lat. 20° S.; and from the Indian Ocean between Lat. 2° N. and Lat. 34° S. The Bermuda captures are thus the most northerly yet recorded, and the farthest extra-tropical for the Atlantic. Present indications are that this is a tropical and sub-tropical species, else it would probably have been picked up in some of the many deep towings that have been made farther north and east in the Atlantic.

*Vertical Range:* All the records for *H. valdiviae* have so far been from hauls that worked down to at least 500 meters; in most cases to at least 1,000 meters. Its bathypelagic status thus seems established.

More precise information as to the depth of its chief center of abundance would be of interest, because, while colorless, most of the captures, like those of *Halicreas minimum*, have been in nets working so deep as to indicate that the specimens were from levels inhabited also by the deeply pigmented groups of medusae, and by the black bathypelagic fishes.

#### GERYONIDAE.

##### *Liriope.*

Although this sharply defined genus is perhaps the most often encountered of Trachomedusae, there has been no agreement as to the specific relationships of its many described representatives, owing to the difficulty (I believe we may say "impossibility") of finding any differences, the gaps between which cannot be bridged by examination of sufficiently large series. Final decision that all known representatives of *Liriope* represent but a

single variable species was already foreshadowed in Browne's (1927) interesting exposition of the situation that faces every student of the genus. Thiel (1936, p. 45) has now definitely made this union of all the named forms under the oldest designation, *L. tetraphylla* Chamisso and Eysenhardt. And the reader is referred to his discussion for a clear exposition of the reasons justifying this procedure. Granting, however, that the various forms of *Liriope* cannot be considered "species," in the sense in which the term is generally employed in zoological nomenclature, it still remains an interesting question how they are to be interpreted, and how recorded in scientific literature. While it is now established that intergrades can be found with regard to every character which has been suggested as specific, we have still to recognize that the representatives of different swarms, or of different populations (seasonal or regional), often do differ so widely in many respects, as Browne (1927) has vividly described, that they would be referred without hesitation to different species had not the existence of intermediates been proved.

### ***Liriope tetraphylla* Chamisso and Eysenhardt.**

*Geryonia tetraphylla*, Chamisso and Eysenhardt, 1821, p. 357, Pl. 27, Fig. 2.

For lists of references to the named forms of *Liriope*, all of which, following Thiel (1936) are now referred to *L. tetraphylla*, see Mayer, 1910, p. 413-424; also, Thiel, 1936, p. 45.

**Material:** Net No. 51, Surface, April 29, 1929, 1 specimen about 5 mm. in diameter.

The gonads in this young specimen are of about the same form as in a 7 mm. specimen, already pictured from the eastern tropical Pacific (Bigelow, 1909, Pl. 4, Fig. 3), namely, squarish with rounded angles. This stage has already been proved preliminary to the triangular or rhomboid outlines often, but not always, attained by adult *L. tetraphylla*.

The most interesting thing about this record is that 974 hauls in various months from May to October, in two different years, yielded only the one specimen of a genus so widespread and frequently abundant in warm seas. Nor can the paucity be credited to the depths at which the hauls were made, for 108 of them were in the upper 200 meters; 86 right at the surface. This, added to the corresponding fact that the *Bache* hauls in the winter of 1914, yielded only 4 *Liriope* at 2 stations on lines run between Cape Hatteras, Bermuda, the Bahamas, and the Straits of Florida, can only mean that it was decidedly rare in this side of the Sargasso Sea area during the periods in question, which included both the warm and the cold months. This is the more astonishing, when one remembers that the Plankton Expedition (Maas, 1893) took *Liriope* regularly from Latitude about 40° N., southward to Bermuda; and thence eastward all along the track across the tropical Atlantic.

### ***Geryonia*.**

#### ***Geryonia proboscidalis* Forskål.**

*Medusa proboscidalis*, Forskål, 1775, p. 108.

For synonymy, see Bigelow, 1909, p. 116, and Mayer, 1910, p. 425.

**Material:** Net No. 613, 1,097-0 meters, 1 fragmentary specimen, diameter about 30 mm.

Net No. 621, 1,097-0 meters, 1 fragmentary specimen, diameter about 16 mm.



Net No. 850, 1,463-0 meters, 1 fragmentary specimen, diameter about, 25 mm.

These very fragmentary specimens (identified by the number of canals) add nothing to previous knowledge of the morphology of this well known species.

*Geryonia* had already been reported to the north and to the east of Bermuda (Maas, 1893) as well as at many other localities in the warm belt of the Atlantic.

#### NARCOMEDUSAE.

In the classification adopted by Broch (1929), by Ranson (1936), by Uchida (1928), and by me in earlier papers (Bigelow, 1909; 1913; 1918; 1919), the Narcomedusae that have gastric pockets are divided into two families, Cuninidae and Aeginidae, depending on whether the pockets are perradial, equal in number to the tentacles, and not extending out beyond the points of origin of the latter (Cuninidae), or whether the definitive pockets are interradial in location, and at least twice as numerous as the tentacles, with the tentacles arising in the notches between the pockets (Aeginidae). This scheme is followed here. Thiel (1936, p. 55), on the contrary, follows Mayer (1910), in referring all Narcomedusae with peripheral gastric pockets to one family, Aeginidae.

Such of the typical Narcomedusae as lack gastric pockets are now generally grouped in the family Solmaridae. If the curious sand-dwelling form, *Halammohydra*, actually is an aberrant Narcomedusa, as Remane (1927), Uchida (1928), and Leloup (1935) believe, it calls for a separate family (Halammohydriidae, Remane).

#### *Cunina*.

#### *Cunina* sp.?

*Material*: Net No. 242, 1,646-0 meters, 1 specimen, about 30 mm. in diameter.

Although this specimen is very much damaged, enough remains to show that it had perradial gastric pockets, and a well developed peronial canal system, a combination of characters locating it in the genus *Cunina*, as contrasted with *Solmissus*, which lacks canals. Unfortunately, the exumbrella is so much rubbed or macerated, that it is impossible to tell whether, or not, otoporopae were present. And all the otocysts have been destroyed. There are 23 large tentacles and one very small one. Identification of any specimen of *Cunina* with as many as 20 tentacles depends, in the first place, on decision whether the *Medusa mucilaginosa* of Chamisso and Eysenhardt (1821), with 21-24 tentacles, belonged to *Cunina*, to which Blainville (1834) referred it, or whether it actually was a *Solmissus* according to the definitions for these two genera now generally adopted. The name *mucilaginosa* was used by Vanhöffen (1908a, as "*Solmaris mucilaginosa*") for a series of Cuninidae of large size (25-60 mm. in diameter), with 21-24 tentacles. But since his specimens lacked peronial canals (he gave no information as to the presence or absence of otoporopae), they are more likely to have belonged to *Solmissus* than to *Cunina*.<sup>12</sup> And I have argued (Bigelow, 1909, p. 55; 1918, p. 392) that it was wisest to discard *mucilaginosa* as a nomen nudum, because it will never be possible to tell from Chamisso and Eysenhardt's account, to which of these two genera their original specimens did actually belong, lacking information on the critical points—canals and otoporopae. Ranson (1936, p. 200), however, has recently revived this name, for a *Cunina* of 55 mm. with 21 tentacles.

<sup>12</sup> See Bigelow, 1919, p. 327, for discussion of Vanhöffen's treatment of the genus *Solmissus*.



Without attempting to settle this question, I may point out that if *mucilaginosa* be finally accepted as a *Cunina*, it was the earliest named member of this genus. Hence, if it lies within the varietal range of the species commonly called *rubiginosa*, a possibility suggested by Thiel (1936), *mucilaginosa* must take precedence over *rubiginosa*, and the latter becomes a synonym of it.

### **Solmissus.**

#### **? *Solmissus incisa* Fewkes.**

*Solmissus incisa*, Fewkes, 1886, p. 954, Pl. 9; Bigelow, 1909, p. 67, Pl. 21, Figs. 1-3, 5; 1913, p. 57; Mayer, 1910, p. 483; Broch, 1929, p. 527; Uchida, 1928, p. 90; Bigelow and Leslie, 1930, p. 560; Ranson, 1936, p. 206.

*Solmissus faberi*, Haeckel, 1879, p. 350.

*Solmissus bleekii*, Haeckel, 1879, p. 351.

? *Solmaris rhodoloma*, Vanhöffen, 1908a, p. 60, Pl. 1, Fig. 5. [non *Aequorea rhodoloma* Brandt, 1838.]

*Material*: Net Nos. 599, 628, 632, 680, 700, 713, 735, 753, 765, 799, 848 885, 891; 914-0 to 1,829-0 meters; 13 specimens; those of which measurement is possible, range from about 50 mm. to about 75 mm. in diameter; also other fragments.

These specimens—all extremely fragmentary—are identifiable as *Solmissus* because they show indications of the presence of gastric pockets in the radii of the tentacles, but no signs of a canal system. In all cases, the free gastric wall has been destroyed, but persistent bands of subumbral tissue, around the outer margins of the pockets, and in the septal spaces between them, show the pockets to have been oval in outline and somewhat longer than broad. This fact, combined with the large number of tentacles (see below), warrant tentative reference to *S. incisa*. And this identification is rendered the more probable by the fact that even in their present state, they agree in thinness of the disc, in softness of the gelatinous substance, and generally in appearance, with the *incisa* collected by the *Albatross* in the Pacific, with which I have been able to compare them.

In no case was an exact count of the tentacles possible, but the presence of at least 23 in one specimen of about 55 mm., and of 25 to 30, in three others of, roughly, 60 and 75 mm., corresponds with earlier counts, which have shown a range of from 23-40 in specimens 50 mm. in diameter or larger. This contrasts with a maximum of 16 tentacles in *S. albescens* and in *S. marshalli*.

All specimens of *S. incisa* previously seen have lost all trace of the gonads, nor is the present series any better in this respect. They do, however, confirm Fewkes' original illustration of the marginal outline as straight or nearly so, from peronium to peronium. All the otocysts have been lost, and even the pads on which these organs stand.

*General Distribution*: *S. incisa* was to be expected in the vicinity of Bermuda, for it has been taken at several stations along the American continental slope, between the latitudes of Cape Hatteras and of Sable Island, Nova Scotia, on the one side, and mid-way between Bermuda and the Azores on the other. Other Atlantic records are off the coasts of France and of Spain. It has also been taken at a number of localities in the eastern tropical Pacific; off Monterey, California; between San Francisco and the Aleutians; in the Bering Sea region; off Kamchatka; and in Japanese waters.

*Vertical Range:* Most of the captures of this species have been from hauls made with open nets at considerable depths, but the list includes three captures from the surface, one from the northwestern Atlantic (Fewkes, 1886), the others from the eastern tropical Pacific (Bigelow, 1909).

#### AEGINIDAE.

##### *Aegina.*

Up to 1910, fourteen supposed "species" referable to *Aegina* had been described. Mayer's (1910) summary made it clear, however, that this list required drastic reduction. And as the result of subsequent studies, by various authors, evidence has gradually accumulated to the effect that all *Aeginas* yet described represent at most two species, the *Ae. rosea* and *Ae. citrea* of Eschscholtz (Bigelow, 1913; 1919; Broch, 1929; Ranson, 1936); or perhaps only one as Thiel (1936) has most recently argued. Decision here rests on whether the difference between the "*citrea*" type, in which the margin of each of the eight adradial gastric pockets is more or less indented in the mid-line, and the "*rosea*" type in which it is entire, is genetic, or is simply the result of sex or of age differences, of differing degrees of distention of the pockets, or of contraction, as Thiel (1936) maintains. The situation may be summarized as follows (see Thiel, 1936, p. 74, for details): Juveniles, up to perhaps 9 mm. in diameter, have undivided pockets, i. e., are, as a rule, of the "*rosea*" type; all very large specimens (35 mm. in diameter or larger), so far recorded, (of which adequate descriptions were given) have likewise been of the "*rosea*" type;<sup>13</sup> for example, Haeckel's (1879) *Ae. rhodina*, and the *rosea* reported by me (1913) from the northwest Pacific. Among middle-sized individuals, however, of, say, 9-25 mm. in diameter, both types have been recorded. Otherwise stated, all typical *citrea* have fallen within this size range, whereas the much more numerous records of the *rosea* type have covered the entire size range so far recorded for the genus. Furthermore, several specimens of 7-16 mm. in the present series show intermediate conditions, with some of the adradial pockets notched, others not, or showing a slightly sinuous outline. One point not previously stressed is that in specimens of the *citrea* type the gonads usually (but not always) form two swellings on the oral surface of each primarily adradial pocket, whereas in the *rosea* type, the swelling involves the oral surface of each of the 8 pockets as a whole. In oral view, that is to say, there are up to 16 very conspicuous swollen areas (sometimes only 14 or 15) in the *citrea* type, but only 8 in the *rosea* type. And this difference is much more conspicuous than is the difference in outline of the pockets, for even at its maximum, the latter is slight.

The question as to the relationship of the two types cannot be settled until a microscopic study is made to determine whether we may not be dealing here with a sexual dimorphism—nor would this be unique among Narcomedusae, for the gonads of the two sexes of *Aeginura* differ widely, in appearance. But the present series does not offer hopeful material for histological study. It is also possible that the very large representatives of the *rosea* type are spent individuals. Nor can the rôle played in this matter by contraction be determined without a study of living material.

Meantime it seems wisest to follow Thiel, at least provisionally, and to class *citrea* and *rosea* as forms (of undetermined significance) of one species. This, however, must be named *citrea*, not *rosea* as Thiel has called it, because the former has page priority in Eschscholtz's (1829) original accounts of the two.

<sup>13</sup> *Ae. alternans* (Bigelow, 1909) was probably a large damaged *rosea* (Bigelow, 1913, p. 59).

***Aegina citrea* Eschscholtz.**

*Aegina citrea*, Eschscholtz, 1829, p. 113, Pl. 10, Fig. 3.

It is probable, as explained above, that all the citations to supposed species of *Aegina*, listed by Mayer, 1910, p. 451-454, refer to one variety or another of this species. For a recent list of references, see Thiel, 1936, p. 73 ("*Ae. rosea*").

**Material:** Net Nos. 263, 292, 294, 296, 488, 564, 566, 576, 627, 649, 657, 666, 686, 692, 693, 708, 745, 762, 779, 800, 809, 857, 874, 882, 885, 971; hauls from 0 to 1,829-0 meters; 31 specimens, 5-20 mm. in diameter, in various stages of preservation.

Among the specimens that are well enough preserved to show the gastric pockets, 9 (ranging in diameter from 5-20 mm.) are definitely of the *rosea* type, i.e., the adradial pockets show no signs of additional subdivision. Two, of 15-16 mm., are as definitely of the *citrea* type. The most interesting specimens are nine others (7-16 mm. in diameter) which show various intermediate states as follows:

- A. Each adradial pocket shows but one swelling ("*rosea*" type); margins of some pockets entire ("*rosea*" type), of others notched ("*citrea*" type).
- B. Some pockets show "*citrea*" swellings, some "*rosea*"; margins of all pockets entire ("*rosea*" type).
- C. Swellings as above; margins of some pockets notched ("*citrea*" type), of others entire ("*rosea*" type).
- D. Each pocket with 2 swellings ("*citrea*"); but with margin entire ("*rosea*").

Obviously, these corroborate Thiel's (1936) view that it is not possible to segregate two groups (however named) on this basis. However, we are still faced with the fact that while a great majority of specimens of the "*citrea*" type show the normal metamerism, a large proportion of those of the "*rosea*" type that have been seen, have had 5 or more tentacles. This was, indeed, the case with Eschscholtz's original series of *rosea* (4 specimens, 3 with 5 tentacles, one with 6 tentacles), and has repeatedly been reported since; see especially Vanhöffen (1908a) and Uchida (1928). The present series again yields 3 pentamerous specimens among the 9 of *rosea* type just mentioned, the others having 4 tentacles each. A possible explanation is that variants of this sort are more frequent in one sex than in the other.

Reduction of the tentacles also occurs, though more rarely; the series includes one specimen of 9 mm. with only three tentacles. But it is too much contracted to allow classification, as to type.

While most authors who have written of *Aegina* have described it as having only a small number of otocysts, Vanhöffen (1908a) found about 20 per marginal sector in one of the "*rosea*" type, 16 in one of the "*citrea*" type. And while I have not been able to make a complete count of otocysts, even for a single sector, of any of the Bermuda specimens, the spacing of such of these organs as are still recognizable, or of their basal pads, is consonant with Vanhöffen's counts.

**General Distribution:** *Aegina citrea* is widespread in the warm belts of all oceans—this was already known to apply both to the *citrea* and *rosea* forms—also in the Mediterranean. Southward, it had been taken in the sub-Antarctic; and northward to the Bering Sea region in the Pacific; to Lat. 58° N. in the northeastern Atlantic. The present series is, however, interesting geographically because there was no previous record of *Aegina* in the western half of the north Atlantic except close to the coast (see Thiel, 1936, p. 76, Fig. 15, for a recent chart of this distribution).



*Vertical Range:* *Ae. citrea* has repeatedly been taken at the surface (the Bermuda series includes 2 surface hauls), but also in open nets lowered to various levels, and—more instructive—in closing nets from 1,000-700 meters (Vanhöffen, 1908a, as "*Ae. lactea*"); about 800 meters (Bigelow, 1909); 200-100, 600-400, 700-500, 800-600, and 1,030-830 meters (Thiel, 1936, "*Ae. rosea*"). Its bathic range is thus very wide.

Thiel (1935, p. 81) has also pointed out that the specimens taken deepest averaged the largest, those taken shoalest, the smallest; evidence that *Aegina*, like various other medusae, reproduces chiefly near the surface, tending to sink, with increasing age. This is corroborated by the Bermudian collection, the distribution of catches with depth being:

Depth in Meters.	Number of Specimens.
0	2
914-0	2
1,097-0	3
1,280-0	4
1,463-0	11
1,646-0	5
1,827-0	4

### *Aeginura.*

It is now generally agreed that all representatives of *Aeginura* that have been examined recently, are referable to the wide-ranging, bathypelagic species, named *Ae. grimaldii* by Maas (1904) from the collections of the Prince of Monaco. Thiel (1936), in his historical survey of the genus, goes still further, in definitely uniting *grimaldii*, and its more recent synonyms, with the *Aeginura myosura*, *Cunocotona nausithoe*, and *C. lanzerotae* of Haeckel (1879); hence he employs the latter name (it has page priority over *nausithoe* and *myosura*). This point is discussed in an earlier publication (Bigelow, 1913, p. 60). I need only repeat here, that (quite apart from the presence or absence of a peronial canal system), if we are to conclude that the *Aeginura* of modern students is identical with these older Haeckelian species we must assume (a) that the otoporopae so clearly shown in Haeckel's (1879, Pl. 20, Figs. 1-2) illustrations of his two species of "*Cunocotona*" were imaginary; and (b) that the absence of secondary tentacles and the small number of otocysts (16 indicated) in his *Ae. myosura* were the result of mutilation. As his descriptions were based on preserved (no doubt alcoholic) material, the second assumption is not unreasonable. But there is no way to establish the correctness of either of these assumptions; and it is possible that an *Aeginura* lacking secondary tentacles and with very few otocysts, may some day be found. It, therefore, seems to me wiser to treat Haeckel's old names as doubtful synonyms of *grimaldii*, rather than to select one of them as the name for the species in question.

I need only note farther that if Haeckel's accounts were to be taken at face value, *grimaldii* could not be referred to his genus *Aeginura* at all, because he described the latter as having a well-developed canal system. But as Maas (1905, p. 78) pointed out, what Haeckel (1881, Pl. 13, Fig. 7) pictured as canals were in reality parts of the gastric pouches.

### *Aeginura grimaldii* Maas.

*Aeginura grimaldii*, Maas, 1904, p. 38, Pl. 3, Figs. 19-28; Bigelow, 1909, p. 80, Pl. 9, Fig. 4; 1913, p. 61; Mayer, 1910, p. 470; Kramp, 1913,



p. 276; 1914, p. 436; 1920, p. 6; 1924, p. 37; Broch, 1929, p. 533, Fig. 37; Thiel, 1932a, p. 156; Ranson, 1936, p. 211.

*Aeginura weberi*, Maas, 1905, p. 77, Pl. 11, Fig. 73, Pl. 12, Fig. 76, Pl. 14, Figs. 90-99.

*Cunoctona grimaldi* var *munda*, Vanhöffen, 1908a, p. 53, Pl. 2, Fig. 6.

*Cunoctona guinensis*, Vanhöffen, 1908a, p. 53, Pl. 3, Fig. 29.

*Cunoctona obscura*, Vanhöffen, 1908a, p. 52, Pl. 2, Fig. 7, Pl. 3, Figs. 25-28, 30.

*Aeginura lanzerotae*, Thiel, 1936, p. 86.

? *Aeginura myosura*, Haeckel, 1879, p. 343, Pl. 19, Figs. 8-9; 1881, p. 41, Pl. 13-14; Mayer, 1910, p. 468.

? *Cunoctona lanzerotae*, Haeckel, 1879, p. 318, Pl. 20, Figs. 1-6.

? *Cunoctona nausithoe*, Haeckel, 1879, p. 318.

? *Aeginura lanzerotae*, Mayer, 1910, p. 469.

*Material*: Net Nos. 18, 22, 24, 36, 41, 48, 49, 52, 53, 64, 66, 67, 69, 73, 78, 111, 121, 122, 137, 270, 293, 295, 362, 400, 427, 442, 455, 468, 481, 539, 562, 582, 605, 606, 612, 620, 621, 627, 628, 631, 632, 635, 638, 639, 645, 646, 652, 654, 665, 680, 681, 685, 698, 700, 702, 708, 712, 715, 719, 720, 721, 724, 726, 732, 740, 742, 745, 746, 753, 759, 760, 761, 778, 779, 781, 793, 794, 804, 805, 810, 811, 812, 842, 849, 852, 861, 885, 894, 959; hauls from 540-0 to 1,829-0 meters; 184 specimens, 1-6 per haul. Also, Net Nos. 26, 42, 65, 76, 110, 143, 295, 360, 447, 488, 598, 716, 929, 949; 19 specimens, probably belonging here, but so fragmentary as to preclude positive identification.

In spite of its extent, the collection adds nothing to previous knowledge of the morphology of this species, for the specimens are all in such poor condition that it is only the very characteristic appearance of *Aeginura*—especially the large tentacle roots, the outlines of gastric pockets, and the dense pigmentation—that makes them recognizable at all. It was disappointing that the margins are in every case so battered that neither the secondary tentacles peculiar to the genus, nor the otocysts, are to be seen. The very large white eggs are, however, so resistant that they are still visible in specimens from Net Nos. 111, 122, 468, 606, 726, 761, 794, 810, and 959. These catches were made in the months of May, June, July, August, and September, evidence that in this region the breeding season of *Aeginura* covers spring, summer, and early autumn—very likely the entire year.

*General Distribution*: The wide distribution of previous records (Thiel, 1936, Fig. 18) had already established the cosmopolitan nature of this medusa in the ocean basins. The present captures are, however, interesting as the first for the eastern side of the North Atlantic; interesting also as showing that this is one of the most regularly occurring medusae at suitable depths in the Bermuda region, which may be taken as representative of the Sargasso Sea as a whole.

*Vertical Range*: Up to the present, there is no positive evidence that any *Aeginura* larger than 8-10 mm. has been taken from a depth less than 400-500 meters, for while the great majority of captures have been in open nets, those taking adults have in every case sampled the water down to at least this depth—in most cases much deeper. And there is record of closing net captures of adults from about 780 meters (Maas, 1904), as well as from 1,000-700 meters and deeper (Thiel, 1935, Table 16). Thus, when adult, *Aeginura* belongs to the same bathypelagic community as *Atolla* and *Periphylla*, as indeed, its dense pigmentation would indicate. The depth distribution of the Bermuda hauls yielding *Aeginura*, relative to the total number made at each depth, tabulated below, suggests a rather definite concentration between, say, 1,000 and 1,600 meters.

Depth in Meters.	Total Number Hauls.	Number Hauls with <i>Aeginura</i> .	% with <i>Aeginura</i> .
549-0	23	1	4
732-0	40	2	5
914-0	132	9	7
1,097-0	134	19	13
1,280-0	132	27	19
1,463-0	132	19	14
1,646-0	135	17	13
1,829-0	135	8	6
2,012-0	4	0	0

Thiel (1935), however, has recently made the interesting discovery that young stages of 1-5 mm. occur in the upper water layers, the *Meteor* having taken them on four occasions shoaler than 100 meters, once shoaler than 50 meters (Thiel, 1936, p. 86). From this, he suggests that the eggs rise to the surface, and that, as growth proceeds, the young medusae sink deeper and deeper, as seems commonly to be the case among bathyplanktonic animals.

#### SOLMARIDAE.

#### *Pegantha*.

#### ? *Pegantha clara* R. P. Bigelow.

*Pegantha clara*, R. P. Bigelow, 1909, p. 80; Mayer, 1910, p. 445; H. B. Bigelow, 1918, p. 397.

*Polycolpa forskali*, Vanhöffen, 1908a, p. 56; 1912, p. 391; 1912a, p. 32. [Non *P. forskalii* Haeckel, 1879; 1881.]

*Pegantha smaragdina*, H. B. Bigelow, 1909, p. 90, Pl. 14, Fig. 1, 2, Pl. 19, Figs. 1-9, Pl. 22-26.

*Material*: Net Nos. 50, 157, 271, 720, 812, 882, 902, 959; 914-0 to 1,463-0 meters; 8 fragmentary specimens, about 10-about 20 mm. in diameter.

Although damaged, having lost all trace of exumbrial sculpture, and with the stomach much battered, the specimens all show the peronial canals, and the outlines of the stomach without any trace of gastric pockets, that are characteristic of *Pegantha*. Owing to the obvious contraction of some specimens and the flattening of others, it is not possible to state the normal relationship of height to breadth: in the present state they suggest that at diameters of 10-20 mm., the bell of this species is from  $\frac{1}{4}$  to  $\frac{1}{2}$  as high as broad; perhaps still higher relatively in some cases.

The tentacles range in number from about 20 to about 24; the largest number being in a specimen of about 12 mm., while the largest specimen has only 22 tentacles. The small specimens (6 in number, 10-12 mm. in diameter) without gonads, are referred to this species chiefly because this is the only *Pegantha*, yet known, in which upwards of 18 tentacles have been found before the development of the gonads. This identification is strengthened, in the case of the 20 mm. specimen, by the fact that traces are to be seen of simple interradial swellings—forerunners of the gonads—at the margin of the stomach.

Most of the otocysts have been lost; but the spacing of those still visible suggests the presence of 3-5 per marginal lappet; or about the number to be expected in juveniles of *P. clara*, in adults of which there may be up to 8 per lappet. In only one specimen are traces of the otoporopae still to be seen.

*General Distribution:* The original record of *P. clara* was from the continental slope in the offing of Woods Hole, and young specimens were taken near the Bahamas by the *Bache* (Bigelow, H. B., 1918), so that it was to be expected at Bermuda. Other records referable to it are from the vicinity of the Cape Verde Islands (Vanhöffen, 1912, "*Polycolpa forskali*"), off Chile (Vanhöffen, 1912a, "*Polycolpa forskali*"), off Peru, (Bigelow, 1909, "*Pegantha smaragdina*"), and from the tropical Pacific between Hawaiian and Caroline Islands (Vanhöffen, 1912a, "*Polycolpa forskali*").

*Vertical Range:* Previous records include both the surface, and open net-hauls from considerable depths.

## SCYPHOMEDUSAE.

### Carybdeida.

Mayer (1910) grouped all known Carybdeida in a single family—Carybdeidae. For convenience, however,—even if for no other reason—it seems preferable to follow Krumbach (1925) and Uchida (1929) in limiting that family to forms which lack gastric pouches projecting from the manubrium into the subumbrella cavity, and in which there are only 8 (adradial) marginal pockets. The more complexly organized forms with free gastric pouches and more numerous (16) marginal pockets are divided by Krumbach (1925) into 2 families, but (I believe more logically) grouped by Uchida in one, Chirodropidae. The latter need not be discussed here, as it is not represented in the Bermuda collection.

### CARYBDEIDAE.

Few pelagic coelenterates came to scientific attention earlier than did the quadritentaculate members of this family, for the well known Mediterranean *Carybdea* was described by Linnaeus, (1758). Since that time, the number of named forms multiplied, until Mayer (1910) gave a list of twenty-one. It was already obvious, however, that the number of actual species represented was much smaller. And although insufficiency of most of the early descriptions precluded revision, Mayer (1910) tentatively classed all of them as varieties of four species at most. The carybdeids have subsequently been the subject of repeated discussion, notably by Stiasny (1919, 1926, 1929, 1930, 1934, 1935, 1937), by Uchida (1929), by Thiel (1928) and by Menon (1930). But views held, as to generic and specific characters, have been so divergent that a résumé is requisite, before the Bermudian specimens can be discussed even though these belong to forms known for many years.

Much of the confusion has resulted from uncertainty as to how much weight should be given (in classification) to the position of the groups of gastric filaments (phacellae); i. e., whether in clusters or horizontal bands at the 4 interradial corners of the stomach (*Carybdea* type), or extending as vertical bands along the interradial sides of the latter, as described by Müller (1858), for *Tamoya haplonema*. Unfortunately, Müller's illustration did not show the location of the filaments. And while his account of their location has repeatedly been quoted, or paraphrased, no first-hand description of this type of phacella appeared subsequently until Stiasny (1919, p. 40) found the phacellae forming "interradiale vertikale Fadenreihen längs der Magenseiten," in Sumatran specimens otherwise agreeing so closely with Müller's *Tamoya* that generic identity was assured. And in 1934 Stiasny (1934) was at last in the position to present a good illustration of a West African carybdeid, evidently referable to Müller's *T. haplonema*, clearly showing this same vertical arrangement, with phacellae extending along  $\frac{2}{3}$  of the length of the stomach. It is thus proved that the type species



of *Tamoya* differs from the type of *Carybdea* (*C. marsupialis*, Linné) not only in the larger stomach and in the presence of mesenteries (often used as the chief generic separation), but equally sharply in the arrangement of the phacellae.

Uchida (1929, p. 175), it is true, described the phacellae as "numerous short gastral filaments in the interradial crescentic area of the stomach," for a Japanese carybdeid agreeing otherwise with *Tamoya* (i.e., in the structure of the stomach, mesenteries, and canalization), hence, no doubt correctly, referred by him to that genus. But he did not illustrate the phacellae. And Stiasny (1930, p. 10) included their arrangement as one of the alternative characters for the genera, *Tamoya* and *Carybdea*, a course followed here, as well.

On the other hand, it proves necessary to abandon size and the prominence of the exumbrella sculpture, as generic characters—also included by Stiasny in his recent synopsis—because the Bermudian collection (p. 144) verifies Agassiz and Mayer's (1902) account of the existence of at least one species with the *Carybdea* type of stomach (i.e., flat and lacking mesenteries) and phacellae, but with weak sculpture and growing to a larger size than any other carybdeid yet seen. Thus, if the generic separation is to be based primarily on structural features—and that this is the more logical procedure need hardly be defended—we arrive at the following:

1. Stomach flat, without mesenteries: gastric cirri forming brush-like bundles at the interradial corners of the stomach, or (if expanded) crescentic areas extending horizontally.....*Carybdea*.
2. Stomach deep, connected with the subumbrella by well developed per-radial mesenteries: gastric cirri in bands, extending vertically along the walls of the stomach, in the interradia.....*Tamoya*.

This, the reader will observe, is a return to the scheme long ago proposed by Haeckel (1880); an instance where the latter's classic system has proved more prophetic of knowledge to come than it was justified by facts at hand at the time.

The family, Carybdeidae (as here defined), also includes one well known genus, *Tripedalia*, which shows a multiplication of tentacles, but otherwise resembles *Carybdea* and *Tamoya* in simplicity of organization.<sup>14</sup>

### **Carybdea.**

Among the Carybdeas that have yet come to light, one, recently described by Stiasny (1930), but unnamed, is set apart by the fact that its tentacles bear lateral branches. As the tentacles in all other members of the family—whether single or grouped—are simple, this form certainly deserves specific recognition. The new species, *Carybdea stiasnyi*, is therefore proposed for it. Stiasny (1930, p. 5) suggests that "auf Grund dieses einen Merkmals könnte ein neues Genus aufgestellt werden." But in this regard, we may well await the action of its discoverer.

Successive studies by different authors have brought cumulative evidence to support Mayer's (1910) contention that all other named forms of *Carybdea* in reality represent nothing more than varieties or races of a very small number of good species. But views have differed as to how many such deserve recognition, largely because of the uncertainty as to which, if any, of the supposed "Carybdeas," should actually be referred to its companion genus, *Tamoya*. A survey of recent literature, added to the specimens I have myself seen, corroborates Mayer's (1910) view that the great majority of Carybdeas, the generic identity of which is established by adequate descrip-

<sup>14</sup> Haeckel's (1879-80) problematical genera *Procharagma* (lacking velum) and *Procharybdis* (with velarium, but lacking velar canals) would also fall among the Carybdeidae, should it ever prove that any existing carybdeids show these primitive states when adult, i. e., that they were not founded either on mutilated specimens, or on juvenile stages.



tion or by illustration of the critical characters, fall in one or other of the following well differentiated groups:

*Group A.* Of small or moderate size (for the most part less than 50 mm. high); with strong exumbrel sculpture; with the gastric cirri in each cluster arising either from a single basal stalk or from stalks closely clustered at the four interradial corners of the base of the manubrium. The earliest named *Carybdea*, *C. marsupialis* Linné, of the Mediterranean, was of this type; so also two other well known forms, *C. xaymacana* Conant from the West Indian region, and *C. rastonii* Haacke of the Indo-Pacific—likewise *C. murrayana* Haeckel, from West Africa.

Mayer (1910, p. 508) in his tabular view classes *xaymacana* as a variety of *marsupialis* from which it differs only in somewhat smaller size, in having fewer and less complexly branched velar canals (4 per quadrant instead of up to 6 or 8), and phacellae arising from a single primary trunk, instead of from 8-10 primary branches.

The unity between *xaymacana* and *marsupialis* with respect to the phacellae is in fact, even closer than Mayer supposed. On the one hand, Claus (1878) long ago pointed out that in *marsupialis* each group of filaments arises from a single main trunk, while on the other, my own examination of Bermudian and Bahaman specimens of *xaymacana* described below (p. 139) shows that the basal trunk divides into several primary branches, each of which bears a cluster of filaments either simple, or showing further dendritic branching (Text-figs. 3, 4, 5), much as described for *marsupialis*. Nor are there any differences in the outline of gonads and of pedalia, in the shape of the rhopalar niches, or in exumbrel sculpture, that can not be explained as due to contraction, or—at most—to individual variation.

Comparison does, however, substantiate the supposed difference in canalization, for whereas in the *xaymacana* that I have seen, as well as in those described by Conant (1898), by Mayer (1910), and by Stiasny (1919), there have been at most four (sometimes three, according to Stiasny), unbranched or simply forked canals per quadrant, there may be 6 or even 8 in *marsupialis*, some of them complexly subdivided. In canalization, then, *xaymacana* corresponds to half-grown *marsupialis*; as it does in the fact that the largest so far seen (with large gonads) have been only  $\frac{1}{2}$  to  $\frac{2}{3}$  as high as mature *marsupialis*.

Present indications, therefore, are that *xaymacana* is a dwarf—perhaps paedogenetic—form of *marsupialis*; one, too, with a different geographic distribution, for the typical (*marsupialis*) form has never been seen in the western side of the Atlantic, nor the dwarf (*xaymacana*) form in the eastern. Furthermore, *C. murrayana* bears much the same relationship to *marsupialis* that the latter does to *xaymacana*, for while it agrees with *marsupialis* in sculpture and in the structure of its phacellae, its velar canals are not only more complexly branched than in typical *marsupialis*, but more numerous, i.e., 10-12 per quadrant. It is, indeed, doubtful whether a half-grown *murrayana* would be distinguishable from a full-grown *marsupialis*—except perhaps, by the state of development of the gonads—or a half-grown *marsupialis* from a fully-grown *xaymacana*, though there would be no danger of confusing full-grown specimens.

Forms bearing a relationship of this sort, one to the other, would unhesitatingly be named "subspecies" by students of molluscs, of crustacea, or of the higher vertebrates. And as they certainly require recognition in nomenclature, more precise than the vague designation "variety," it seems justifiable to introduce trinomials into the classification of pelagic coelenterates, also, to cover such cases.

The discussion must also touch on the status of *C. rastonii*, because if the latter be, in fact, indistinguishable from *xaymacana*, as Stiasny (1919) has suggested, the combined subspecies must be named *rastonii* Haacke

(1886), this being the older of the two names; or perhaps even *prototypus* or *cuboides*, if it finally prove that Haeckel's (1880) problematical *Procharybda prototypus* and *Procharybdis cuboides* are young *rastonii* as Mayer (1910, p. 509) has classed them.

Apart from geographic distribution, the only distinctions between *xaymacana* and *rastonii*, listed in Mayer's (1910) tabular view, are slight differences in shape and relative length of pedalia, and in length of tentacles, which certainly would not justify separation. Furthermore, the canalization of *rastonii* is intermediate, in type, between that of typical *marsupialis*, and of the subspecies, *xaymacana*.

On the other hand, *rastonii* does differ from *xaymacana* in the structure of its phacellae, for, whereas in *xaymacana* all, or most of the primary branches arise from a single basal trunk (p. 140), in *rastonii* they arise independently from the gastric wall, in a row, flanked on either side by several simple cirri, as long ago described by Haacke (1887, Pl. 35, Fig. 4), a state derived (in young medusae) from a row of simple cirri.<sup>15</sup> And this difference, by which specimens of *rastonii* can be recognized at any stage after the appearance of the gastric cirri, seems sufficient to warrant its continued recognition as a distinct species, to emphasize the fact that the Indo-Pacific representative of this group differs more widely from the Atlantic representatives, than do the latter, one from another.

*Group B.* This group includes much larger forms up to 230 mm. high; relatively narrower in outline than the *marsupialis* group; with weak exumbrel sculpture, if any; with the gastric cirri grouped along crescent-shaped rows centering at the interradial corners of the base of the gastric cavity. Recent collections have repeatedly yielded large *Carybdea* of this type, most frequently reported as *C. alata* Reynaud, as *C. grandis* Agassiz and Mayer, as *C. moseri* Mayer, or as one or other of the last two considered as a variety of the first. According to various accounts the group differs also from the *marsupialis* group, in the form of the pedalia, in the relative height of the rhopalia above the bell margin; in the outline of the rhopalar niches, and in the more numerous velar canals, as described below (p. 146, 147).

The earliest named form that can be positively referred to this group (because of the distinctive characters of bell and of phacellae) was *C. grandis* Agassiz and Mayer (1902) from the tropical Pacific, half-grown individuals (or a dwarf race) of which were redescribed shortly afterward by Mayer (1906) as *C. moseri*. But it seems probable that *C. alata* Reynaud (1830) was based on a young *Carybdea* of this same type, for the original illustration shows a rounded, non-sculptured bell, nor is there anything in Reynaud's illustration or account to argue to the contrary. Consequently, Vanhöffen (1908) revived the name *alata*, for *Carybdeas* from the Indian Ocean and Straits of Malacca, that agreed with *grandis* in canalization and in structure of phacellae. Mayer in his tabular view (1910, p. 508), followed Vanhöffen in classifying both *grandis* and *moseri* as varieties of *alata* Reynaud, as have subsequent authors, generally.<sup>16</sup> And while one must admit that it will never be possible to determine, with absolute certainty, the identity of the specimen pictured by Reynaud, because no description was given of the morphological features on which identification primarily depends, to follow Vanhöffen will tend toward stability of nomenclature. The situation is, however, confused by the fact that Uchida (1929), while agreeing that *grandis* and *moseri* belong in the synonymy of *alata* Reynaud, transferred the latter name to a species of *Tamoya*, on the supposition that Agassiz and Mayer's (1902) original figures of *grandis* referred to a member of that genus, not to a *Carybdea*. And this course has been followed by Stiasny (1929;

<sup>15</sup> I have been able to confirm Haacke's (1887) account of stages in development for small and middle-sized specimens from the tropical Pacific (Bigelow, 1909), and for a large series from Japan, in the collection of the Museum of Comparative Zoology.

<sup>16</sup> Thiel (1928) has revived the name *grandis*.



1930, 1935, 1937), likewise by Rao (1931). Successive examinations of specimens of the *alata-grandis* type have, however, proved that actually they have the shallow stomach and the arrangement of phacellae characteristic of *Carybdea*.

So far as can be judged, from published accounts, and by the specimens (Atlantic and Pacific) that I have myself examined, the members of the *alata-grandis* group, so far named, represent only one species, including *C. madrasputana* recently described by Menon (1930) which seems to represent an immature stage in development. It is even doubtful whether any of the named forms deserve the term variety.

Group *C. Mayer* (1900; 1910) described (as *C. aurifera*) a juvenile *Carybdea* from the Tortugas, differing from *C. xaymacana* in the facts that the velar canals next the tentacular radii were broadly palmate, and that the exumbrella was sprinkled with nematocyst warts, as well as in strong coloration. Recently, Stiasny (1926) has described a second species, *C. sivickisi*, from the Philippines, in which all the canals are of this palmate form, and with similarly warty exumbrella. Its rhopalar niches also differ from those either of the *marsupialis* group, or of the *alata* group, in lacking a well-developed covering scale. But it is separated from *aurifera* by the fact that its exumbrella is strongly sculptured; that it has large gonads though only slightly larger (10-12 mm. high, as against 7 mm.); and in the tentacles and sensory niches. Examination of a larger series alone can show how far these differences can be credited to different stages in growth; especially since Mayer's figures of *aurifera* are evidently somewhat diagrammatic and conflicting as regards the phacellae; meantime the two species are best retained.

Summation of the foregoing yields the following synopsis of *Carybdea*, as here recognized:

1. Tentacles simple.

A. Sensory niches overhung by well developed covering scales; exumbrella not warty.

a. With prominent exumbral sculpture; sensory niches with covering scale above, but entry open below.

(1). Phacellae dendritic, the filaments primarily arising from a single trunk.....

*marsupialis* (including *xaymacana* and *murrayana*).

(2). Phacellae more diffuse, of several trunks arranged in a row .....*rastonii*.

b. Exumbrella without prominent sculpture; sensory niches enclosed by a pair of scales below, as well as by one above. *alata*.

B. Sensory niches without well developed covering scale, exumbrella warty .....*sivickisi* (*aurifera*?).

2. Tentacles bearing lateral branches.....*stiasnyi*.

***Carybdea marsupialis xaymacana* Conant.**

*Charybdea xaymacana*, Conant, 1897, p. 8, Fig. 8; 1898, p. 4, Figs. 1-16, 31-34, 36-43, 57, 67, 69, 70, 72; Berger, 1898, p. 223; 1900, p. 1, 3 pls.; Mayer, 1904, Pl. 7, Fig. 60; 1910, p. 509, Pl. 56, Figs. 5-7, Pl. 57, Fig. 1; Stiasny, 1919, p. 34.

*Tamoya punctata*, Fewkes, 1883, p. 84, Pl. 1, Figs. 4-6.

**Material:** Net No. 745, Surface, June 29, 1930, 4 specimens, about 12-23 mm. high.

Net No. 840, Surface, September 3, 1930, 1 specimen, about 11 mm. high.

Dip net, Surface, October 16, 1930, 1 specimen about 15 mm. high.

Net. No. 935, 1,463-0 meters, September 23, 1930, 1 specimen, about 19 mm. high.

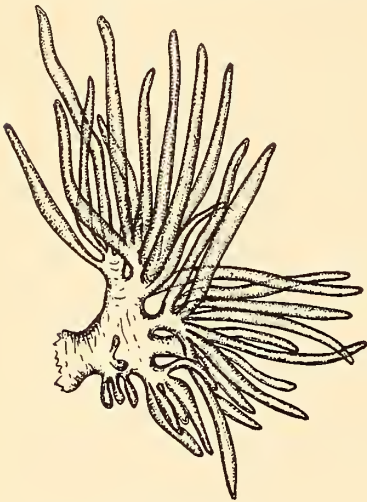
Net No. 977, Surface, May 12, 1931, 14 specimens, about 10-20 mm. high.

Net No. 978, Surface, May 15, 1931, 18 specimens, about 10-18 mm. high.

Net No. 979, Surface, May 16, 1931, 66 specimens, about 10-19 mm. high.

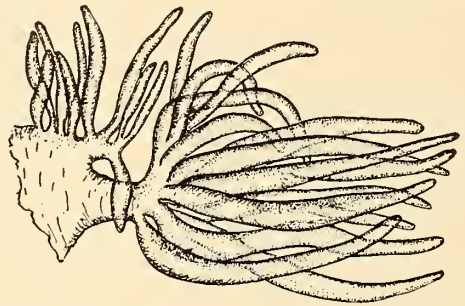
The general features of *xaymacana*, including exumbra sculpture, need no comment here, having been well described by Conant (1898) and by Mayer (1910); the phacellae, and rhopalar niches in more detail by Stiasny (1919). But notes are pertinent on the range of variation in these respects, and on the branching of the velar canals, questions bearing on the relationship of this form to typical *marsupialis* on the one hand, and to *rastonii* on the other.

*Phacellae*: Conant (1898) and Stiasny (1919) both describe the gastric cirri of each group as arising from a single trunk, as is likewise the case



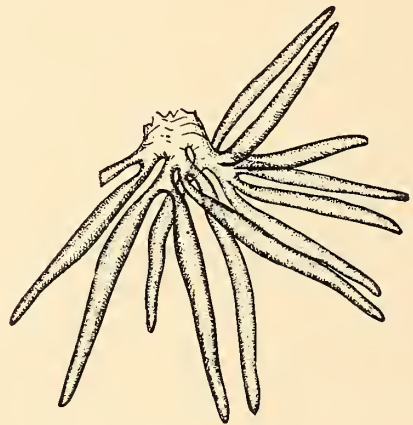
Text-fig. 3.

*Carybdea marsupialis xaymacana*. One of the groups of phacellae from a specimen 16 mm. high (Net No. 745), showing the typical state in which the filaments all arise from a single primary trunk. x 30.



Text-fig. 4.

*Carybdea marsupialis xaymacana*. One of the groups of phacellae from a specimen 23 mm. high (Net No. 745). x 30.



Text-fig. 5.

*Carybdea marsupialis xaymacana*. One of the primary branches, with terminal filaments, from the group of phacellae shown in Text-fig. 3.



in most of the Bermudian specimens (Text-fig. 3). And while in one of the clusters in the specimen from Net No. 745 (Text-fig. 4), there is a secondary cluster of filaments close beside the primary group (the other 3 phacellae are of the more usual type), the fact that the primary trunk invariably bears most, if not all of the cirri, is a ready distinction between *xaymacana* and juvenile *alata* of the same size (p. 147).

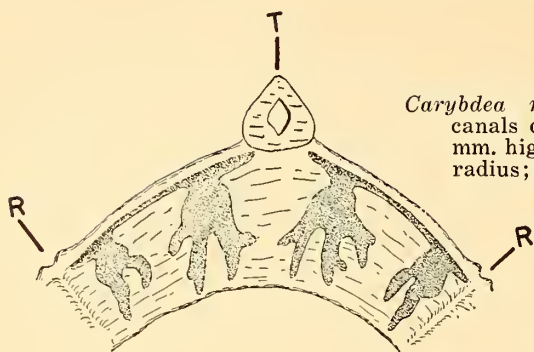
According to Stiasny (1919, p. 36), the filaments are not branched<sup>17</sup>; and they present this same appearance of simplicity when viewed through the bell wall. But when the groups are dissected out and the filaments teased apart (Text-figs. 3-5), it is seen that actually, the basal trunk gives rise to several primary branches, each of which in turn divides, close to the base, into a group of filaments, much as is the case in the typical *marsupialis* (p. 137). In one group, 5 such primary branches were detected, with a cluster of juvenile filaments at one side, apparently forecasting the development of a sixth; the total number of filaments being about 40 (Text-fig. 3).

*Canalization*: Up to the present time, Stiasny (1919) alone has reported any variation (3) from the number of velar canals per quadrant (4) originally reported by Conant; even when most deeply forked, the 4 primary trunks are identifiable as such in all specimens I have seen. However, the present series amplifies earlier accounts, in showing considerable variation in the degree and type of branching. Conant's (1898, Figs. 3-5) original figures pictured all of the canals, in adult medusae, as forked, either bifid or trifid. Mayer's (1910, Pl. 56, Fig. 7) illustration, however, shows each of the four canals in one quadrant as four-branched. And the present series proves that there may be as many as 5 terminal subdivisions, with indications even of a sixth (Text-fig. 6). On the other hand, Stiasny (1919) found most of the canals in Haitian specimens of large size (22-25 mm. high) to be unbranched, except for a tendency to dichotomous division at the tips. And the Bahaman specimens listed above are of this same type, the canals being simple (Text-fig. 7), though the specimens—evidently full-grown, or nearly so, judging from the large gonads (p. 144.)—are otherwise indistinguishable from the Bermudian series, and from the specimens originally described by Conant (1898) from Jamaica. Since both the simple types of canalization and the more complex have been found in the West Indian region (and exclusively one or the other at any one locality on a given occasion), it is likely that we have here to do with a case of what has been termed "swarm" variation.

The Bermudian series, added to earlier accounts, shows that when the canals are branched, there is much variation in the degree and type of subdivision, even from canal to canal in a given individual, though in most (if not all) cases, it is primarily a dendritic forking, very different from the lateral lobation such as characterizes *Tamoya* (p. 154, Text-fig. 22). And only a very rough correlation—if any—exists between the complexity of branching and the size of the medusa. Thus, the canals may already be bifid and trifid, in specimens not more than 10-14 mm. high as exemplified by the specimen from Net No. 745. One of 19 mm., shows much the same state, but one of 23 mm. (Text-fig. 6) shows a somewhat more complex branching. In most cases, the canals next the tentacular radii are somewhat more complexly branched than those next the rhopalar radii (Text-fig. 6); occasionally, however, one of the latter may have as many as four well developed branches.

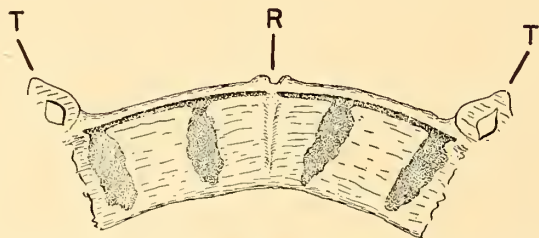
*Pedalia*: The only variations, worth mention, from the shape illustrated by Conant (1898) and by Mayer (1910) are slight individual differences in the precise outline of the fin-like basal expansion of the inner (oral) side

<sup>17</sup> Conant (1898, p. 14) was not explicit on this point.



Text-fig. 6.

*Carybdea marsupialis xaymacana*. Velar canals of one quadrant of specimen 22 mm. high (Net No. 745). T., Tentacular radius; R., Rhopalar radius. x about 6.



Text-fig. 7.

*Carybdea marsupialis xaymacana*. Velar canals of one quadrant of Bahaman specimen about 23 mm. high. x about 5.

(Text-fig. 8). And these are so slight as to be perhaps explicable as contraction phenomena (Text-fig. 8). The pedalia of all I have seen agree very closely with these structures in an excellent specimen of typical *marsupialis* from Naples with which I have been able to compare them; also with *rastonii* (Bigelow, 1909, Pl. 10, Fig. 1; Uchida, 1929, Fig. 60A). The lengths of the pedalia, in terms of bell height, in a series of 10 specimens ranging in height from 10 mm. to 23 mm., are as follows:

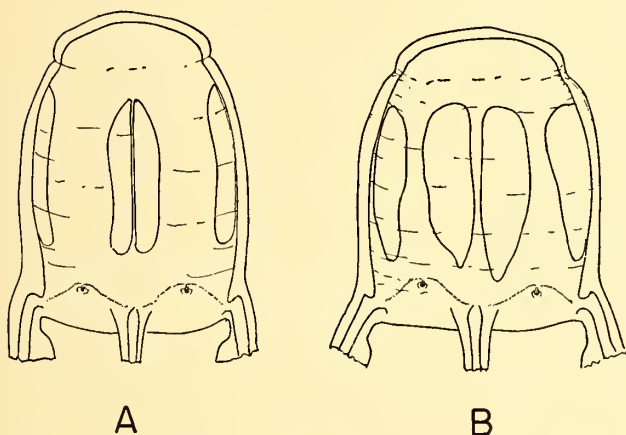
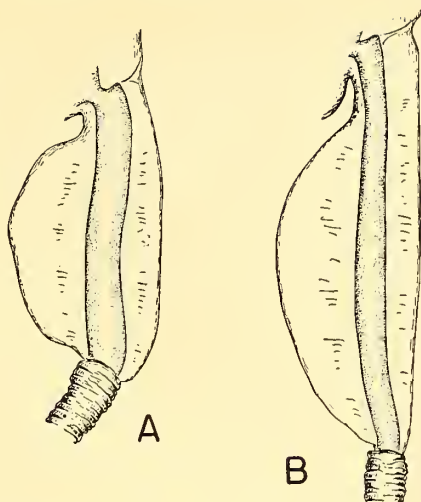
Net No.	Bell Height.	Length of Pedalia. <sup>18</sup>	Pedalia, % of Bell Height.
977	10	6	60
745	12	5	42
977	15	7	47
977	16	8	50
977	17	8	47
977	17	8	47
977	17	8	47
745	19	8	42
935	20	9	45
745	23	10	43

The foregoing shows some slight but irregular decrease in the relative length of the pedalia with the growth of the medusa; the average of 43% confirms Mayer's (1910) report of between  $\frac{1}{2}$  and  $\frac{1}{3}$  the bell height.

<sup>18</sup> Measured from the base of the fin-like expansion to the origin of the ringed portion of the tentacle.

Text-fig. 8.

*Carybdea marsupialis xaymacana*.  
Pedalia to show variations in  
outline. **A.**, From specimen 14  
mm. high from Jamaica; **B.**,  
From Bahaman specimen 23  
mm. high.



Text-fig. 9.

*Carybdea marsupialis xaymacana*. Outlines of two  
specimens about 20 mm. high to show variations  
in breadth and outlines of gonads. **A.**, From Net  
No. 979; **B.**, From Net No. 935.

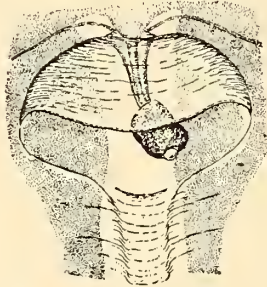
*Gonads*: The feature which shows most obvious variation, among preserved specimens of a given size, is the relative length and breadth of the gonads. In their final state (Conant, 1898, Pl. 1, Fig. 1), these extend distally, nearly to the margin of the bell. None of the Bermudian or Bahaman specimens are, however, as far advanced as this. In the largest of the former, the gonads reach only to about the level of the distal ends of the rhopalialia. In specimens 17-18 mm. high, i.e.,  $\frac{2}{3}$  grown, the gonads terminate about as high above the rhopalialia as are the latter above the bell margin. Among the Bermudian series, the gonads in specimens 18-23 mm. high vary from narrow-linear, to so wide that their free margins are close together (Text-fig. 9). Furthermore, the lamellae from which the sex organs arise, may be either so narrow that the gonads of each pair seem almost in union (Text-fig. 9A), or so wide that they are separated by a considerable space



(Text-fig. 9B). This last may mirror, simply, a flaccid condition. But the variation in length of the gonads, in specimens of equal size, is evidence that the growth of these organs does not necessarily parallel the growth rate of the medusa as a whole.

So far as can be determined in surface view, the Bermudian specimens are all males. Both sexes are, however, represented among the Bahaman series, the females being recognizable by the large eggs with which the leaf-like gonads are crowded, and which are easily visible with a hand lens.

*Rhopalar Nitches*: The present series confirms Stiasny's (1919) observation that the outlines of the pits in which the rhopalia are situated, and of the scales that partially cover the pits, offer specific characters in this genus. As Conant (1898, Pl. 1, Fig. 1) long ago showed (and Stiasny, 1919, Fig. 2 more recently), the covering scale of *xaymacana* (Text-fig. 10) has a simple undulatory outline, and the nitch is wide open toward the bell margin, i.e., there are no subsidiary scales such as characterize *C. alata* (p. 146). This is also true of typical *marsupialis*, as pictured by Claus (1878, Pl. 1, Figs. 1, 2), and as I have been able to verify on the specimen mentioned above; also in *C. rastonii* (Bigelow, 1909, Pl. 10, Fig. 1, 4; Uchida, 1929, Fig. 61).



Text-fig. 10.  
*Carybdea marsupialis xaymacana*. Sensory pit, with covering scale, of a Bahaman specimen. x about 10.

*General Distribution*: Previous records of *xaymacana*, under this name, are all from the West Indian region; Jamaica (Conant, 1898); Bahamas (Mayer, 1904; 1910); Haiti (Stiasny, 1919). But it is no surprise to find it near Bermuda, for it is probable that the *T. punctata* recorded thence by Fewkes (1883) was actually a young *xaymacana*.

*Vertical Range*: The list of captures (see above) confirms previous experience that the species occurs chiefly close to the surface.

### ***Carybdea alata* Reynaud.**

*Carybdea alata*, Reynaud, 1830, p. 95, Pl. 33, Fig. 1; Haeckel, 1880, p. 441; Vanhöffen, 1908, p. 34; Mayer, 1910, p. 510; Bigelow, 1918, p. 400.

*Marsupialis alata*, Lesson, 1843, p. 276.

*Tamoya alata*, L. Agassiz, 1862, p. 174; Rao, 1931, p. 27 [partim].

—, Semper, 1863, p. 561, Pl. 39, Figs. 8, 9.

*Charybdea pyramis*, Haeckel, 1879, Pl. 25, Fig. 5-8; 1880, p. 440.

*Charybdella alata*, Haeckel, 1880, p. 441.

*Charybdea grandis*, Agassiz and Mayer, 1902, p. 153, Pl. 6, Figs. 26-31; Bigelow, 1909, p. 19; Thiel, 1928, p. 4.

*Charybdea moseri*, Mayer, 1906, p. 1135, Pl. 1, Figs. 2-26.



*Carybdea alata* var. *pyramis*, Mayer, 1910, p. 511.

*Carybdea alata* var. *grandis*, Mayer, 1910, p. 511; 1915, p. 171; 1917, p. 189; Light, 1921, p. 26.

*Carybdea alata* var. *moseri*, Mayer, 1910, p. 512; Light, 1914, p. 196; Stiasny, 1919, p. 37.

*Carybdea madraspatana*, Menon, 1930, p. 3, Pl. 1, Fig. 3.

? —, Semper, 1863, p. 561, Pl. 39, Fig. 8.

? *Charybdella philippina*, Haeckel, 1877, No. 404.

? *Charybdea philippina*, Haeckel, 1880, p. 440.

? *Charybusa obeliscus*, Haeckel, 1877, No. 406.

? *Charybdea obeliscus*, Haeckel, 1880, p. 441.

? *Charybdea* sp? Browne, 1905, p. 157.

Non *Tamoya alata*, Uchida, 1929, p. 172; Stiasny, 1929, p. 196; 1930, p. 5; 1935, p. 10; 1937, p. 210.

*Material*: Net No. 448, 732-0 meters, September 9, 1929, 1 specimen, about 75 mm. high.

Net No. 459, 732-0 meters, September 11, 1929, 1 specimen, about 20 mm. high.

Net No. 663, 732-0 meters, June 4, 1930, 1 specimen, about 80 mm. high.

Net No. 979, Surface, May 16, 1931, 1 specimen, about 90 mm. high.

Also, 4 specimens, 55-63 mm. high, from Jamaica, in the collection of the Museum of Comparative Zoology.

For the reasons for the choice of *alata* Reynaud (1830) as the name for this species, see p. 138. Apparently, the next record of it was one of Semper's (1863, Pl. 39, Fig. 9) unnamed carybdeids from the Pacific; while a second of his unnamed forms (Semper, 1863, Pl. 39, Fig. 8), may have been a young stage of it, judging from the number (6) of canals in one quadrant.<sup>19</sup> It is for this same reason that *C. obeliscus* Haeckel is provisionally included here in the synonymy of *alata*. As Mayer (1910) has already decided, this seems certainly to apply to Haeckel's *C. pyramis*, for the latter had not only the number of canals now known to be characteristic of *alata*, but also the lunate groups of phacellae, while the relatively great length of its pedalia is explicable as associated with the small size of Haeckel's specimen (20 mm. high).

So far as I am aware, *alata* was not seen again until 1902, when Agassiz and Mayer gave the first adequate description of it (large adult), from the tropical Pacific, as *C. grandis*, followed by Mayer's (1906) account of half-grown (or dwarf) examples, from the Hawaiian Islands, as *C. moseri*. Browne (1905) had meantime reported, from Ceylon, a small *Carybdea* that may have been of this parentage, though its velar canals were less numerous. Soon thereafter it was reported from the South Seas (Bigelow, 1909, p. 20) and from Philippine waters (Mayer, 1915; 1917, "*C. alata* var. *grandis*").

Since that time, specimens definitely referable to *alata* have been reported from Sumatra (Stiasny, 1919) and from the west tropical Pacific (Mariana Islands, Thiel, 1928) in the one hemisphere, from the Florida-Bahamas region (Bigelow, 1918) and from unnamed Atlantic localities (Thiel, 1928) in the other. The figures by Menon (1930) of his *C. madraspatana* from India, also agree closely with *C. alata*, so far as general form and shape of pedalia are concerned, while the depression of the apex, thought by him to be distinctive, seems more likely to have been the result of contraction, or of distortion. And as the large number (up to 10) of canals

<sup>19</sup> This later formed the basis for Haeckel's (1880) *Charybdea philippina*.

per quadrant, reported (but not figured) by Menon may likely be derivable from the primary 6, characteristic of *alata*, it seems probable that *madras-patana* belongs in the synonymy of the latter. Some of the specimens recorded by Rao (1931) as *Tamoya alata* seem also to belong here, because of the number (6 per quadrant) and simplicity of their canals, whereas others (because of complexity of the latter) seem to have been true *Tamoya*.

As no account—other than Reynaud's (1830) original—of the Atlantic representatives of this species has ever appeared, details are added here, as warrant for definitely uniting it with its Indo-Pacific relative. The latter has been redescribed by Stiasny (1919).

*General Form*: The Atlantic series agrees with previous accounts in being not only of large size, and in the absence of any pronounced exumbral sculpture, but in the fact that the bell is relatively narrower than in any member of the *marsupialis* group; measurements are as follows:

Net No.	Approximate Height in mm.	Approximate Breadth in mm.	Pedalia, % of Bell Height.
459	20	14	70
663	80	43	56
979	85-90	42	50 (approx.)
Also, Jamaica	63	35	55
"	60	35	60
"	60	35	60
"	55	35	64
			62%, average

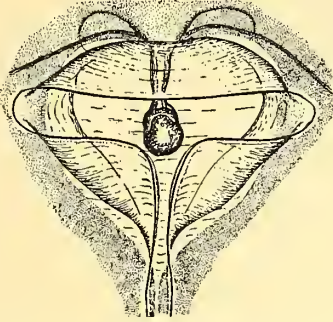
In the Indo-Pacific examples, measured by Agassiz and Mayer (1902), by Mayer (1906; 1915; 1917), and by Stiasny (1919), the width also averaged 50-60% of the height, contrasting with an average of about 80% in *xaymacana*, and in the *marsupialis* group generally. However, there is no specific discontinuity in this respect—not, at least, in preserved specimens—for Mayer (1915; 1917) has reported large *alata* (as var. *grandis*) from the Philippines, in which the height was 73% and 81% of the breadth. It should be noted, however, that preserved specimens are usually so much flattened that breadth is exaggerated. And the better preserved of the *alata* I have seen all taper toward the apex, which is not normally the case in *marsupialis* and its immediate allies.

In the specimens of *alata* I have seen, exumbral sculpture has been confined to a faint trace of a circumferential furrow, at the level of the base of the stomach, and to the prominences in which the rhopalar niches are situated; nor has any trace of the longitudinal ridges and furrows, so prominent in the *marsupialis* group, been reported by any observer for *alata*; neither have nettle warts.

*Rhopalia*: In the largest two of the Bermudian specimens, the distance of the rhopalia above the bell margin equals about 12% of the bell height; about 15% in the somewhat smaller Jamaican examples, about 15-20% in the smallest Bermudian, while in Indo-Pacific specimens, so far measured, it has ranged from 13-19% (Agassiz and Mayer, 1902; Mayer, 1906; 1915; 1917; Stiasny, 1919).

*Rhopalar Niches*: The series confirms Stiasny's observation that these differ from the niches of the *marsupialis* group, in being partially covered, on the side toward the bell margin, by scale-like projections of the umbrella on either hand, in addition to the roof-like scale that overhangs the nitch

from above; a difference illustrated by Text-fig. 10, compared with Text-fig. 11 (cf. also Text-fig. 20 of *Tamoya haplonema*).



Text-fig. 11.

*Carybdea alata*. Sensory pit, with covering scales, of specimen from Net No. 979. x about 6.

**Gonads:** No gonads are visible on the 20 mm. specimen, but as this is in poor condition, they may have been lost. In the 80 mm. specimen, they reach about to the level of the rhopalia; to a point about halfway between the latter and the bell margin in the 90 mm. specimen. Perhaps as the result of contraction of the bell, they overlap somewhat near their upper ends in the 80 mm. specimen (Text-fig. 12).

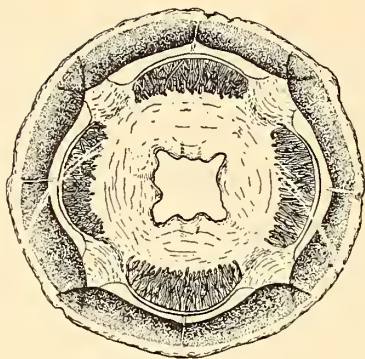
**Stomach:** As the name *alata* has also (but incorrectly) been applied to a *Tamoya* from the Indo-Pacific, it should be emphasized, as Stiasny (1919, p. 37) has pointed out, that in *Carybdea alata*, the stomach is flat and with very short lips, much as it is in *C. marsupialis*, and with no trace of mesenteries; indeed it is so shown in Agassiz and Mayer's (1902) and Mayer's (1906; 1910; 1915) illustrations.

**Phacellae:** Previous students have already shown that the numerous gastric cirri of each group, occupy crescentic areas extending horizontally, at the corners of the stomach (Text-fig. 12), an arrangement differing sharply from the dendritic phacellae of the *marsupialis* group (p. 140); but no detailed account of these structures in *alata* has yet appeared. In the best preserved of the Bermudian series, the 4 crescents occupy about  $\frac{2}{3}$  of the periphery of the stomach (Text-fig. 12) confirming Agassiz and Mayer's and Mayer's illustrations. Stiasny (1919, p. 37) has described the filaments as "einfach, unverzweigt." And in surface view, the Bermudian specimens presented this same appearance. But when one cluster (Text-fig. 13) was dissected, and its component filaments spread apart it proved that the latter are the terminal branches of numerous primary trunks, standing in a single row. In most cases, a primary trunk bears 2-8 such branches (Text-fig. 14). It is the fact that the end filaments are much longer than the (very short) primary trunks that gives the deceptive appearance of simplicity. In one group of phacellae examined, there were approximately 20 primary trunks, and more than 75 filaments. As Uchida (1929) has expressed doubt, whether Atlantic specimens earlier recorded by me (Bigelow, 1918, p. 400) as *alata* really belonged to this species, I may note that one of these in the collection of the Museum of Comparative Zoology, has phacellae of this same type, besides agreeing with the Bermudian series in other respects.

The fact that the small specimen, 20 mm. high, has only 6-8 primary trunks, in each crescentic cluster, contrasted with the much larger number in large specimens, gives a measure of the increase in number that takes place with growth.

**Canals:** All recent accounts credit this species with 6 velar canals per quadrant, as is also true of the Bermudian specimens (Text-fig. 15); evi-





Text-fig. 12.

*Carybdea alata*. Somewhat schematic apical view of specimen 75 mm. high, from Net No. 448, to show the location of the lunate groups of gastric filaments.



Text-fig. 13.

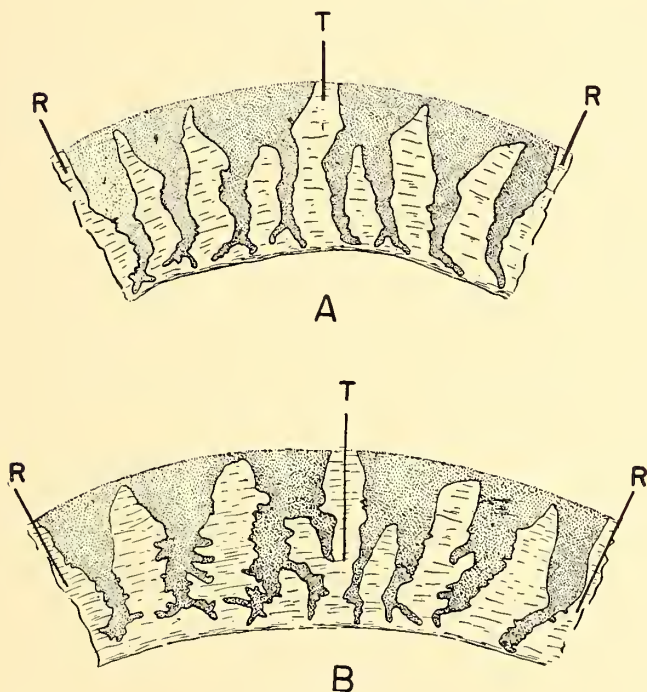
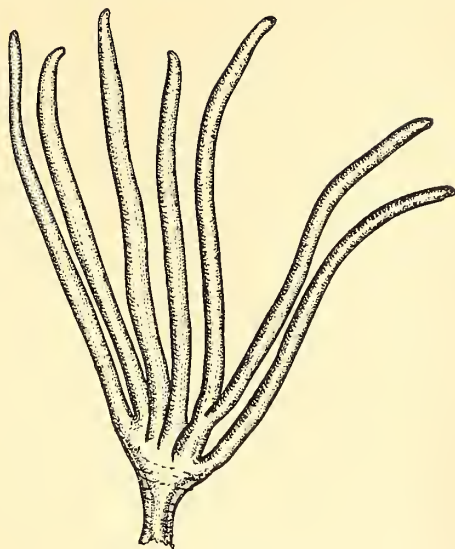
*Carybdea alata*. One cluster of gastric filaments, specimen from Net No. 448. x about 12.

dently, variants from this state are rare, except that a canal next one of the tentacular radii may be so deeply cleft that unless it be traced back to its proximal end, it might appear that the primary number was greater (Text-fig. 15B). Evidence thus accumulates to the effect that the number of canals is a dependable specific difference between *alata* and the *marsupialis* group (p. 141). Accounts have, however, differed widely as to the extent to which the canals branch. On the other hand, Mayer (1906) and Stiasny (1919) have described them as simple, or at most as showing the commencement of division. But Agassiz and Mayer (1902), copied by Mayer (1910), picture them as digitate, with short lateral lobes, while in Vanhöffen's (1908) two specimens, they were variously forked—those of the tentacular radii usually the most deeply. And the two large Bermudian specimens not only show forking, with similar contrasts between the perradial and the interradian pairs, and with complexity increasing with growth (cf. Text-fig. 15A with Text-fig. 15B), but also with wide variation from octant to octant even of



Text-fig. 14.

*Carybdea alata*. One primary branch with terminal filaments, from the group of phacellae in Text-fig. 13.



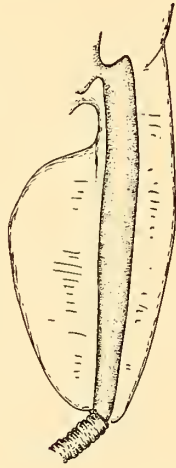
Text-fig. 15.

*Carybdea alata*. To show velar canals. **A.**, One quadrant of velarium of specimen about 75 mm. high from Net No. 448; **B.**, One quadrant of specimen about 90 mm. high, from Net No. 979. **T.**, Tentacular radii; **R.**, Rhopalar radii. x about 3.

a given specimen, in the precise degree of subdivision, and in the lateral lobing of the canal margins.

*Pedalia*: By earlier accounts, and in the Bermudian and Jamaican series, the length of the pedalia (measured along the inner edge) equals about 25-30% of the bell height, in medium-sized specimens of 60-90 mm. In larger specimens they are relatively shorter: 17% according to Agassiz and Mayer (1902) at a bell height of 230 mm. In young specimens they are relatively longer: 33% in the Bermudian example of 20 mm.; and shown as about 50% in a young medusa by Agassiz and Mayer (1902).

The fin-like expansions of the pedalia are relatively narrower in the Bermudian and Jamaican specimens (Text-fig. 16) than they are pictured by Agassiz and Mayer (1902, Pl. 6, Fig. 37) or by Mayer (1906, Pl. 1, Fig. 2; 1917, Fig. 3); their outlines less pronouncedly semi-lunar. But this may well be the result of different states of contraction, between preserved and fresh material.



Text-fig. 16.

*Carybdea alata*. Basal part of  
tentacle of specimen  
from Net No. 448.

*General Distribution*: The wide distribution, Atlantic and Pacific, of locality records for this species (listed above), suggests that it is cosmopolitan, in the warm belts of the oceans. But it probably does not occur in the Mediterranean (perhaps barred thence by low water temperatures), for it could hardly have been overlooked there.

### ***Tamoya*.**

If the *Bursarius cytherae* of Lesson (1830, p. 108, Pl. 14, Fig. 1) was, in fact, congeneric with the form later named *Tamoya* by F. Müller (1858), as Haeckel (1880) suggested, it would be necessary to substitute *Bursarius* as the generic name. However, as Haeckel pointed out, Lesson's account and illustration differ from all known carybdeids in showing only 2 tentacles (though 4 pedalia); nor do they give any indication as to the structural characters which determine generic position in this group. It is thus wisest to abandon the name *Bursarius* for good and all, on the ground that the type species of the genus is and must always remain unrecognizable. For this same reason the specific name *bursaria*, substituted by Haeckel (1880) for Lesson's *B. cytherae*, is likewise best regarded as a *nomen nudum*.

During the years that have elapsed since the type species of the genus *Tamoya* (*T. haplonema*) was described by Müller (1858), carybdeids that can be referred to this genus as here defined<sup>20</sup> have been described from the two sides of the Atlantic (Haeckel, 1880, as "*T. prismatica*"; Mayer, 1910; Stiasny, 1934); from Samoa (Haeckel, 1880); from Japan (Uchida, 1929); from the Malay Archipelago (Stiasny, 1919; 1930); and from India (Menon, 1930; Rao, 1931); showing a world wide distribution within the warm belt.

All Atlantic records undoubtedly belong to *T. haplonema*. And so far as can be judged from available information, all Indo-Pacific Tamoyas so far reported also represent a single species. But it is still an open question whether or not the Atlantic and Indo-Pacific forms are distinct. If so, the correct name for the Indo-Pacific species is *gargantua*, for the earliest named Indo-Pacific carybdeid that is definitely proved, by the description, to have been a *Tamoya*, is the *T. gargantua* of Haeckel (1880), for which he revived a name under which Lesson (1830) had long before reported a large carybdeid from New Guinea. And while neither Lesson's account, nor his illustration, gave any indication of the details needed to show whether his specimen was actually a *Tamoya*, or a large *Carybdea*, stability of nomenclature will be served by following Haeckel in this regard. Should the Atlantic and Pacific Tamoyas be finally united, *haplonema* would become a synonym of *gargantua*.

Reasons are given above for abandoning altogether the specific name *bursaria* which Haeckel (1880) substituted for Lesson's *Bursarius cytherae*, on the assumption that it also was a *Tamoya*.

### ***Tamoya haplonema* Müller.**

*Tamoya haplonema*, Müller, 1858, p. 1, Pl. 1, 2; L. Agassiz, 1862, p. 174; Haeckel, 1880, p. 443; Brooks, 1882, p. 138; Von Lendenfeld, 1884, p. 245; Mayer, 1904, p. 28, Pl. 7, Figs. 60-64; 1910, p. 513, Pl. 57, Fig. 2; Stiasny, 1934, p. 339.

*Tamoya prismatica*, Haeckel, 1880, p. 443.

*Charybdea (Tamoya) haplonema*, Fewkes, 1889, p. 526.

Non *Tamoya haplonema*, Boone, 1933, p. 39, Pl. 6.

*Material*: Surface, June 25, 1929, 1 specimen, height about 70 mm., breadth about 45-50 mm. (depending on the degree of flattening), length of pedalia along inner edge, about 22 mm., of fin-like expansion of latter, 15 mm., height of rhopalia above bell margin, 13 mm.

Although the Atlantic species of *Tamoya* has been mentioned repeatedly, by name, in the literature of medusae, few students have been fortunate enough to have seen specimens of it. First described by Müller (1858), it was next reported by Haeckel (1880) whose description (as "*T. prismatica*") of a West Indian specimen agreed so closely with the original account, both in arrangement of phacellae, in size of stomach, and in complexity of velar canals, as to make it certain that he was dealing with *haplonema*. As the next reports were by name only (Brooks, 1882; Fewkes, 1889), it is possible that they may actually have referred to some *Carybdea*. And the "*T. haplonema*" recorded from the Bahamas by Boone (1933, p. 39, Pl. 6) seem certainly to have been *Carybdea* (probably *C. xaymacana*), for her illustration shows a very flat stomach, with brush-like groups of phacellae at its corners.

Mayer (1904; 1910), however, had typical examples of *T. haplonema*, as had Stiasny (1934) more recently.

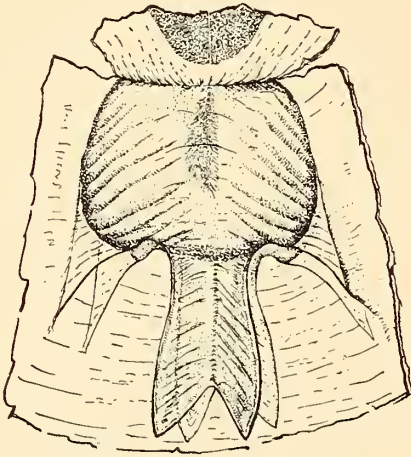
The single Bermudian specimen (considerably crumpled) agrees so

<sup>20</sup> Omitting references by name only.



closely in general form with Mayer's (1910, Pl. 57, Fig. 2) picture that illustration is not required.

In the preserved condition, the gelatinous substance is stiffer than in any other carybdeid I have seen. And the nematocyst warts described by previous students (see particularly, Stiasny, 1934) are still to be seen thickly strewn here and there on the exumbrella down to the bell margin, likewise on the outer faces of the pedalia, though the surface has been so badly rubbed that nothing can be said as to the regularity of their distribution. As the size of the stomach is a distinctive feature of the genus, I may note that this organ (Text-fig. 17) is about as long as shown by Müller (1858, Pl. 1, Fig. 1) and by Mayer (1910, Pl. 57, Fig. 2), i.e., with lips hanging to about the mid-level of the bell; this is somewhat shorter than in Stiasny's (1934) West African specimen—a difference perhaps due to the degree of contraction. The well differentiated, pointed lips are also much as pictured by Müller and by Stiasny. They are not shown clearly by Mayer (1910, Pl. 57, Fig. 2).



Text-fig. 17.

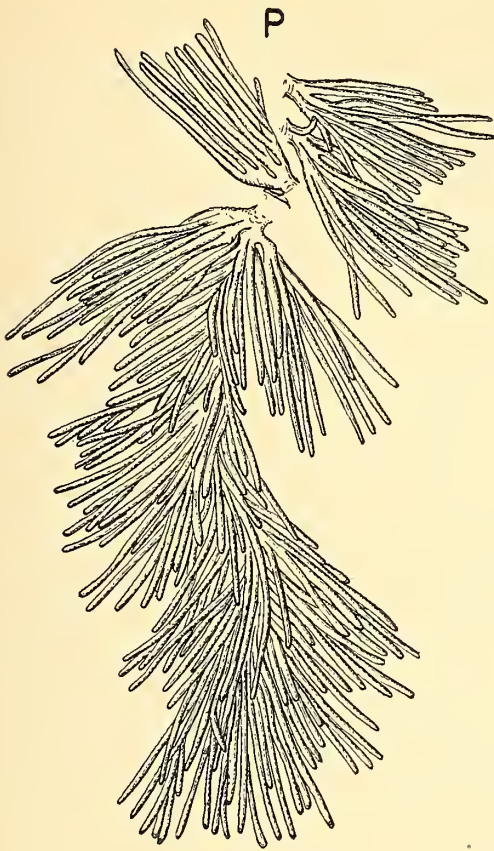
*Tamoya haplonema*. Dissection of upper part of bell of Bermudian specimen, to show outlines of stomach, lips, mesenteries, and area occupied by the phacellae. Somewhat schematic.

**Mesenteries:** Previous statements regarding mesenteries in *Tamoya* have been conflicting. According to Müller (1858) and to Haeckel (1880), the pendulous stomach is bound to the subumbrella by well developed mesenteries in the radii of the rhopalia, as Uchida (1929) also found for the Pacific *Tamoya*. Stiasny (1919, Fig. 6; 1934, Fig. 1), however, pictures the mesenteries as in the radii of the tentacles; while Mayer (1910, p. 512) states that the "so-called mesenteries . . . are merely the flattened perradial sides of the cruciform stomach."

It is therefore worth mention that the Bermudian specimen confirms early accounts, in the presence of mesenteries (Text-fig. 17), and that the latter are in the radii of the rhopalia (perradial). Structurally, they are thin, transparent plates (apparently ectodermic), their free margin crescentic, and by connecting the 4 sides of the stomach with the exumbrella, they subdivide the upper part of the bell cavity into as many blind pockets.

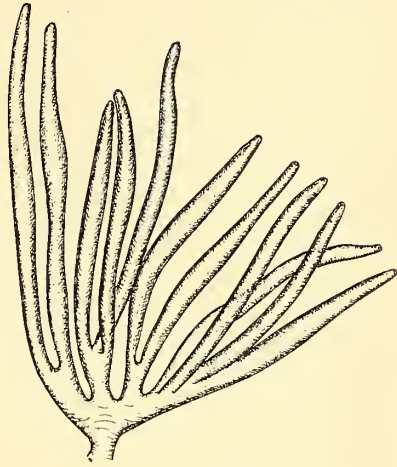
**Phacellae:** The gastric cirri agree with previous accounts, in being grouped in 4 bands extending vertically along the sides of the stomach, alternating with the lips, i.e., in the radii of the tentacles (thus interradianal, as is also the case in *Carybdea*). In Stiasny's (1934) illustration, these bands are shown extending as far as the distal end of of the dilated portion of the manubrium. In the present example, however, they reach only about





Text-fig. 18.

*Tamoya haplonema*. One of the groups of gastric filaments of the Bermudian specimen. P., Proximal end. x about 10.



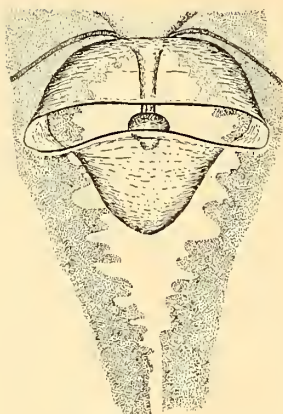
Text-fig. 19.

*Tamoya haplonema*. One of the primary trunks with terminal filaments, from the group illustrated in Text-fig. 18. x about 18.

to the mid-level of the latter (Text-fig. 17). As no detailed account has previously appeared, I should add that each group consists of a single row of about 40 primary trunks, arranged (but somewhat irregularly) in a single row, and each dividing, close to its base into several filaments (Text-figs. 18, 19).

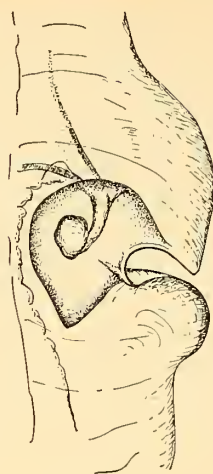
*Rhopalar Nitches*: Earlier accounts (Müller, 1858, Pl. 1, Fig. 1; Stiasny, 1919, p. 39, Fig. 7; 1934, p. 341, Fig. 1B; Uchida, 1929, Fig. 81B) had already shown that the shape of the rhopalar nitches is one of the minor characters separating *Tamoya* from *Carybdea*. In *T. haplonema* (and in its Pacific relative also), the nitches, situated on well marked, ovoid gelatinous prominences of the exumbrella (Text-figs. 20, 21), are continuously bounded, on the lower side as well as on the upper, by a rounded covering-scale, which gives the nitch a pit-like confirmation, very different in appearance, from the more open nitches of *Carybdea* (cf. Text-fig. 20, with Text-figs. 10, 11).

The edges of the marginal pouches, where they enclose the nitches, and for some distance beyond, are strongly lobate (Text-fig. 20); in *Carybdea* (Text-fig. 10), they are smooth.



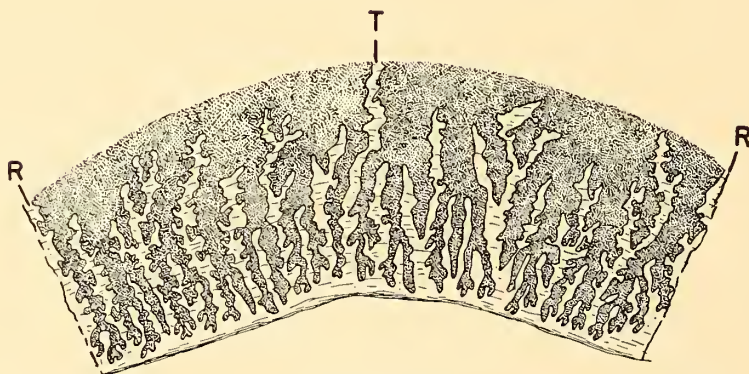
Text-fig. 20.

*Tamoya haplonema*. One of the sensory niches of the Bermudian specimen, to show covering scales and lobate outlines of the marginal pouches. x about 7.



Text-fig. 21.

*Tamoya haplonema*. Lateral view of sensory niche. x about 6.



Text-fig. 22.

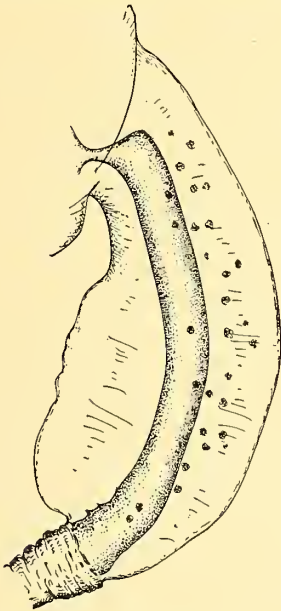
*Tamoya haplonema*. One quadrant of velarium of Bermudian specimen to show velar canals. T., Tentacular radius; R., Rhopalal radius.

*Canals*: The readiest field-mark to distinguish *Tamoya* from any *Carybdea* yet described is the lobing of the margins of its complexly forked velar canals (Text-fig. 22); this type of branching was long ago pictured by Müller (1858); more recently by Stiasny (1919, Figs. 8, 9; 1934, Fig. 1, C), and by Uchida (1929, Fig. 85).<sup>21</sup> Previous authors (Mayer, 1910; Stiasny, 1934) record 10 canals per quadrant for *T. haplonema*. In the Bermudian specimen, the number is less regular, there being only 3 primary canals in one octant (between tentacular and rhopalal radii); but so complexly subdivided that there are 33 terminal branches, whereas in the adjacent quad-

<sup>21</sup> Mayer's (1910, Pl. 57, Fig. 2) picture suggests a somewhat different type of subdivision, but it is evidently diagrammatic.

rant, the number of major trunks is 7 (some of which may have been derived by subdivision close to the base) with 30 terminal branches.

*Pedalia*: These (Text-fig. 23) are intermediate in outline between those figured by Mayer (1910, Pl. 57, Fig. 2) and by Stiasny (1934, Fig. 1a). According to Mayer's figure, the tentacular canals are widely dilated at the distal ends of the pedalia, whereas Stiasny shows them as of uniform bore. Here, again, the present specimen is intermediate, the canals showing only slight dilation distally, but with an irregularity of the margins suggesting that when the pedalia are relaxed, the dilation might be greater.



Text-fig. 23.  
*Tamoya haplonema*. Basal  
part of tentacle. x about  
2.

*Gonads*: These organs are somewhat farther advanced in development than those pictured by Mayer, not only reaching about to the level of the points of origin of the tentacular canals, but so broad that their free edges overlap slightly. In their present state, they are folded, but so irregularly as to suggest the effects of preservation.

*General Distribution*: Previous records of *T. haplonema* include Brazil (the type locality); West Indies; east coast of the United States, north to Latitude about 41° N., and to the offing of the French Congo.

### ***Periphylla*.**

#### ***Periphylla hyacinthina* Steenstrup.**

For early synonymy, see Mayer, 1910, p. 544, 546 ("*P. hyacinthina*" and "*P. hyacinthina forma regina*").

For subsequent discussions, see especially Broch, 1913, p. 4; Stiasny, 1934, p. 342.

*Material*: Net Nos. 13, 16, 17, 23, 26, 33, 34, 39, 43, 44, 45, 53, 83, 88, 89, 100, 103, 114, 116, 119, 121, 135, 141, 142, 144, 145, 154, 157, 178, 196, 221, 234, 235, 240, 241, 261, 267, 269, 270, 273, 274, 278, 279, 280,



291, 292, 293, 295, 296, 405, 434, 449, 543, 545, 546, 547, 548, 551, 552, 555, 562, 577, 581, 590, 595, 618, 619, 620, 621, 624, 625, 626, 631, 638, 644, 645, 646, 654, 674, 686, 688, 692, 699, 707, 709, 710, 712, 716, 721, 722, 723, 724, 726, 728, 730, 731, 732, 734, 736, 746, 750, 752, 756, 758, 759, 762, 766, 767, 772, 773, 774, 775, 778, 780, 785, 791, 795, 796, 797, 798, 799, 801, 804, 809, 818, 822, 825, 827, 832, 835, 836, 837, 838, 842, 846, 848, 850, 851, 852, 854, 855, 858, 860, 880, 882, 883, 885, 886, 895, 896, 898, 905, 916, 917, 918, 921, 925, 928, 930, 932, 933, 935, 937, 939, 940, 951, 963, 970; 317 specimens; 1-14 (in most cases, 1-3) per haul.

Successive studies (see especially Stiasny, 1934) have now definitely established that the two representatives of this genus most often reported—*dodecabostrycha* and *hyacinthina*—are nothing more than growth stages, contraction phases, or color variants of one species; and that this probably is equally true of the third, *regina*. Stiasny (1934, 1937), on the basis of the *Discovery* collection, has concluded that the three represent successive stages in growth, the *dodecabostrycha* form (small, with low rounded stomach and transparent peripheral zone) being the youngest, the *hyacinthina* form (with peripheral entodermal system also pigmented, and usually with high, pointed stomach), an intermediate stage—usually 75-80 mm. in diameter—while the *regina* form represents the largest, usually more than 80 mm. in diameter, with extensive and dense peripheral pigmentation, but again usually low-domed, as are the juveniles.

The Bermudian series (many of which are in excellent condition) corroborates this general growth relationship, so far as the *dodecabostrycha* and *hyacinthina* types of pigmentation are concerned, for among 38 small specimens taken at random, 5-12 mm. in diameter at the level of the coronal furrow, 37 have the peripheral zone so hyaline that the gonads are entirely visible, only one being so densely pigmented that they are concealed. Among 37 specimens of 15-20 mm. the gonads are completely visible in only 21; their upper portions are obscured by the spreading pigment in 7; and completely so obscured (*hyacinthina* form) in 9. And among 27 specimens of 25-40 mm., the gonads are entirely obscured in 18; partially so in 8; and completely visible only in 1. However, still larger specimens occasionally retain the restricted ("*dodecabostrycha*") type of pigmentation; this being true of one Bermudian example of 45 mm.; and of another of 55 mm. The series does not include any specimens larger than 60 mm., hence, throws no additional light on the *regina* form.

It seems that the very smallest specimens (smaller, say, than 8-9 mm. in diameter at the coronal furrow) usually, or always, have the gastric floor low-domed. It is already more or less definitely conical, however, in the majority of the Bermudian specimens of 10-12 mm., in several cases pronouncedly so (extreme *hyacinthina* type). It has already been sufficiently emphasized, by various students, that medium-sized specimens show wide variation in this respect, with complete integradation from the lowest and rounded, to the highest and most acutely conical—depending, I believe, entirely on phases of contraction.

Broch (1913, p. 7) and Stiasny (1934, p. 356) have both observed that the apical projection of the aboral gastric wall into the mesoglea, so often observed in *Periphylla* and frequently referred to as a "stiel canal," does not occur in very small specimens. This the Bermudian series corroborates, for while the gastric apex is acutely conical in some, even of the smaller (down to 11 mm. in diameter at the level of the coronal furrow), the smallest in which the apex shows anything that could be named a canalar elongation is about 17 mm. in diameter. We can, then, finally conclude that this struc-

ture has nothing whatever to do with a true stiel canal—i.e., does not indicate derivation from a Scyphistoma stage, but merely represents one extreme in the phases of contraction that govern the contour of the floor of the stomach in middle-sized individuals.

It is interesting that, in *Periphylla* (as in *Atolla*, p. 161), the gonads appear while the medusa is still not more than 5-8 mm. in diameter at the level of the coronal furrow<sup>22</sup>. By the time a diameter of 15-20 mm. is reached, the sexual organs may be proportionately about as large as they are in large specimens, the females with large eggs. But we have still to learn through how extensive a growth-phase any individual specimen may actually set free its sexual produce.

*General Distribution:* Enough records have now accumulated to prove that *Periphylla* is truly cosmopolitan in seas of appropriate depth and temperature<sup>23</sup>, Atlantic, Pacific, and Indian, right up to the polar fronts. Having been already taken in the Straits of Florida (Bigelow, 1918), and to the southeast of Bermuda (Bigelow, 1928), it was a foregone conclusion that any campaign of deep towing would yield it in the immediate vicinity of the latter.

*Seasonal and Annual Distribution:* The following tabulation of the percentage of the hauls, at 732-0 meters or deeper, that took *Periphylla* (the number taken shoaler was negligible) illustrates the relative frequency of occurrence, in different months, and as between the two years 1929 and 1930:

1929				1930			
Months.	Total Hauls.	Hauls with <i>P.</i>	% with <i>P.</i>	Months.	Total Hauls	Hauls. with <i>P.</i>	% with <i>P.</i>
April	47	13	29	April	.....	.....	.....
May	75	15	20	May	87	26	30
June	93	9	9	June	82	23	28
July	107	14	13	July	52	23	44
Aug.	51	0	0	Aug.	11	1	9
Sept.	106	3	3	Sept.	136	43	31

Thus it appears that *Periphylla*—like *Atolla* (p. 163)—occurred with much greater frequency in 1930 than in 1929. But the annual difference in actual abundance was not as great for *Periphylla* (180 specimens in 343 deep hauls, or 0.5 per haul in 1930; 127 specimens in 462 deep hauls, or 0.3 per haul in 1929) as for *Atolla* (p. 162). And the data for the two years agree in showing the greatest frequency in spring and early summer, with a decided decrease in late summer, followed by some recovery in early autumn, especially in 1930.

The 95 hauls that yielded juveniles of 15 mm. or smaller, were well distributed through the season, most numerous and in roughly comparable numbers (17-23) for May, July and September, evidence that *Periphylla*, near Bermuda, reproduces throughout the spring and summer. Probably it does so throughout the year there, as Kramp (1924) found to be the case in the Mediterranean.

*Vertical Range:* No *Periphylla* were caught in hauls from 366-0 meters or shoaler. The distribution of the catches in both years combined, in the deeper hauls, was as follows:

<sup>22</sup> The smallest individuals are in poor condition, but gonads are visible in several not more than 5 mm. in diameter, though still very small.

<sup>23</sup> It is not likely that it will ever be found in the Red Sea, for example.

Depth in Meters.	No. of Hauls Made.	No. of Specimens.	Av. No. Specimens per Haul.
366-0	12	0	0.0
549-0	23	2	0.08
732-0	40	4	0.1
914-0	132	53	0.4
1,097-0	134	85	0.6
1,280-0	132	29	0.2
1,463-0	135	28	0.2
1,646-0	135	60	0.4
1,829-0	135	48	0.4
2,012-0	4	2	0.5

From the foregoing, it appears that in the region in question, *Periphylla* regularly lives only deeper than about 600 meters and has its chief abundance considerably deeper (from about 900 meters downward) than in the Mediterranean, or off the coast of Spain and Portugal where the *Thor* (Kramp, 1924) found it most numerous in hauls from about 150-200 to 600-700 meters<sup>24</sup>, while one Mediterranean catch was made close to the surface. Farther north in the Atlantic, also, the upper limit to its most frequent occurrence was found to be between about 250 and 500 meters (occasional specimens as shoal as 50 meters) along the route of the *Michael Sars* Expedition (Broch, 1913); in the Sognefjord, Broch (1913) reports it as numerous as shoal as 150 meters—again with its upper limit a little above 50 meters. And in west Greenland waters the *Ingolf* found it about equally frequently at one level as at another, right up to the surface (Kramp, 1913). In high southern latitudes, also, *Periphylla* has been taken, not only in deep hauls, but in the superficial stratum, and at the surface as well, on several occasions (Browne, 1910; Stiasny, 1934, Table, p. 364, 365). The combined picture is thus of a species strictly bathypelagic throughout most of its range, but with the upper limit to its normal occurrence lying at a progressively higher level, toward high latitudes, until, in subpolar seas, it comes right up to the surface. Stiasny's (1934) observations show, too, that in upwelling regions it may frequently be brought up to the superficial strata, as well as casually elsewhere, as noted above.

So far as is yet known, it is in the Sargasso Sea region (typified by the vicinity of Bermuda) that the upper boundary to its regular occurrence lies deepest, at least for the Atlantic. On the basis of these data, it seems likely that the upper boundary for *Periphylla* is set by light combined with temperature. As to the latter, one can at least say that water of 12°-13° is not unfavorably warm for it, witness its regular occurrence in the deeps of the Mediterranean (Kramp, 1924). But, so far as I have been able to learn, it has never been found, more than casually, in temperatures much higher than that.

Recorded captures do not suggest any definite lower limit; like sundry siphonophores (Bigelow and Sears, 1937), however—and perhaps the majority of bathypelagic animals—its numbers decrease as truly abyssal depths are reached.

Segregation by sizes shows that the upper zone of concentration, near the 1,000-1,200 meter level, represents the zone of greatest abundance of juveniles, the depth distribution of specimens of 15 mm., or smaller, being as follows:

<sup>24</sup> Kramp (1924) estimates the depths of the *Thor* hauls as equalling about one-half the length of wire out. But it seems likely, from Jespersen's (1915) experiments, that the towing depths were actually somewhat greater, with 2/3 the wire length as perhaps maximal (Bigelow and Sears, 1937, p. 73).



Depth in Meters.	Number Juveniles.	Depth in Meters.	Number Juveniles.
366-0	0	1,463-0	6
549-0	4	1,646-0	18
914-0	41	1,829-0	8
1,097-0	44	2,012-0	1
1,280-0	9	2,195-0	1

The largest individuals were even more definitely concentrated in the deepest strata—responsible in part for the apparent concentration at the 1,400-1,800 meter level—for out of the 16 specimens, of 35 mm. or larger, 7 were from 1,646-0 meters<sup>25</sup>, 8 from 1,829-0 meters, one only from a shoaler haul (549-0 meters).

It is especially interesting that in West Greenland waters, Kramp (1913) found juveniles most abundant at about 600-700 meters<sup>26</sup>, i.e., but little shoaler than at Bermuda. This perhaps indicates that *Periphylla* is not permanently endemic in the Arctic water of the Greenland-Labrador sea region, but that the supply there is maintained by the deep indraft of Atlantic water, a hydrologic phenomenon now well recognized.

#### NAUSITHOIDAE.

##### *Nausithoe*.

##### *Nausithoe punctata* Kölliker.

*Nausithoe punctata*, Kölliker, 1853, p. 323.

For synonymy, see Bigelow, 1909, p. 35; 1928, p. 498; Mayer, 1910, p. 554; Thiel, 1928, p. 25.

*Material*: Net No. 627, 1,097-0 meters, May 23, 1930, 1 specimen.

Net No. 719, 1,280-0 meters, June 25, 1930, 2 specimens.

Net No. 773, 1,829-0 meters, July 4, 1930, 1 specimen.

Net No. 793, 1,280-0 meters, July 9, 1930, 1 specimen.

Net No. 967, 914-0 meters, September 30, 1930, 1 specimen.

The specimens, ranging from 5 to 9 mm. in diameter, are specifically recognizable, though fragmentary; one alone (Net No. 793) still shows the characteristic dark-pigmented ocellus on one of the rhopalia.

Earlier accounts have credited *N. punctata* with spherical gonads, as has been true of the specimens of it from the eastern tropical Pacific, from Japanese waters, from the Mediterranean, and from Florida and the West Indies that I have previously examined; likewise of the specimen from Net No. 793 (a ♀ with eggs of various sizes). A specimen from Net No. 719 and one from Net No. 967 seem at first sight to have horse-shoe shaped gonads, with concavities directed centripetally. But it appears from more careful examination that the pockets (globular in life) within which the sex products are developed, had been torn open on the centripetal sides by the rough treatment the specimens had received, correspondingly disrupting the sexual tissue still adhering to their inner walls. That is to say, their present resemblance to the horse-shoe shaped gonads pictured by Haeckel (1879, Pl. 27), for his genera, *Ephyra* and *Palephya*<sup>27</sup>, is purely accidental.

<sup>25</sup> This tends to corroborate Stiasny's (1934, p. 363) conclusion that, during its development, it tends to move slowly into the deeper layers.

<sup>26</sup> Recorded at 1,000 meters of wire out.

<sup>27</sup> In Vanhöffen's (1902, Pl. 3, Fig. 10) illustration of *Palephya indica*, they are kidney-shaped.

This being a neritic species, it is likely that the specimens here listed were the product of the Bermudian Bank. To find *N. punctata* a few miles out from the land is no surprise, for it has long been known that the free-living stage of *N. punctata* endures long enough for it to drift much greater distances. It had not been recorded previously from Bermudian waters, but was to be expected there, for it is common in the West Indies (Mayer, 1910), as well as widespread in warm seas generally. See Mayer (1910, p. 555), for a summary of the earlier accounts of its developmental stages.

As the attached stage is known to be commensal within certain sponges of the littoral zone, and as adults have commonly been taken close to the surface elsewhere, it is somewhat astonishing that the Bermudian specimens were all from deep hauls. But the numbers concerned are so small that no estimation is possible of the actual depths of capture.

#### ATOLLIDAE.

#### *Atolla*.

#### *Atolla wyvillei* Haeckel.

*Atolla wyvillei*, Haeckel, 1880, p. 488; 1881, p. 113, Pl. 29, Figs. 1-9.

For early synonymy, see Mayer, 1910, p. 563, 565, 567 ("*A. bairdii*" + "*A. valdiviae*" + "*A. gigantea*" + "*A. wyvillei*").

For subsequent discussions of relationships, see especially Broch (1913, p. 13), Browne (1916, p. 203), Bigelow (1928, p. 505), and Stiasny (1934, p. 365.).

*Material*: Net Nos. 23, 26, 29, 36, 39, 41, 53, 62, 66, 74, 78, 100, 102, 105, 111, 118, 122, 142, 154, 196, 221, 240, 247, 253, 292, 293, 295, 296, 368, 434, 539, 544, 545, 546, 552, 553, 556, 561, 562, 563, 565, 568, 574, 575, 582, 588, 596, 597, 598, 599, 601, 605, 606, 611, 618, 619, 625, 626, 631, 632, 633, 637, 639, 647, 648, 652, 657, 659, 666, 674, 676, 681, 682, 685, 687, 688, 691, 698, 701, 707, 719, 720, 721, 727, 739, 741, 745, 748, 767, 770, 774, 777, 778, 781, 787, 789, 798, 799, 800, 801, 804, 806, 808, 810, 812, 824, 826, 829, 831, 838, 846, 850, 860, 861, 863, 865, 875, 881, 882, 885, 892, 917, 926, 928, 937, 938, 943, 964; 549-0 to 1,829-0 meters; 232 specimens, 1-6 per haul, except for Net Nos. 565, 707, and 767, which captured 10, 8, and 9 specimens respectively. The specimens range from 7 to 100 mm. in diameter.

It now seems so thoroughly established that all known *Atollas*, that have smooth marginal lappets, belong to the one species *wyvillei*, that this viewpoint needs no further defence (see Kramp, 1924; Bigelow, 1928; and Stiasny, 1934, for recent pronouncements on this subject). Stiasny (1934, p. 366) has thought it possible from his study of the extensive *Discovery* series to divide the comprehensive species *wyvillei* into three forms, according as the margin of the central disc is indented with broad radial notches (*wyvillei* form), or with narrow notches (*verillii* form), or is entirely smooth (*bairdii* form). Conditions, however, in the Bermuda series and in the others I have studied suggest that these differences (so far studied only in preserved material), like the relative prominence of the annular zone, chiefly reflect the state of contraction, or relaxation of the animal when preserved. But individual variation may also enter into the case, to a degree that it is not yet possible to estimate. Certainly, we do not have to do with geographic variation, for the *Arcturus* and *Discovery* collections have already shown that it is not unusual for narrow-notched, broad-notched, and smooth disc'd individuals to be taken side by side in the same haul. In a given individual some of the notches may, furthermore, be broad, others narrow (Bigelow, 1909, p. 40); and it frequently happens that a

given individual may be equally well characterized as "broad-notched," or as "narrow," there being a complete inter-gradation between the two. The Bermuda collection now contributes at least one specimen (Net No. 221) about 65 mm. in diameter, in which the margin of the disc is entirely smooth on one side, but shows clear traces of broad notches on the other.

Recent collections have yielded the smooth and notched or furrowed forms in varying proportions, the relative counts being 112 notched (*verrilli*, *wyvillei*), and 92 smooth (*bairdii*), for the *Discovery* series (Stiasny, 1934, p. 370), 12 notched to 3 smooth, for the *Thor* series (Kramp, 1924), and 103 smooth (or nearly so) to 57 furrowed, for the *Michael Sars* collection (Broch, 1913). Among such of the Bermuda series as are in good enough condition to be significant in this respect, there are 25 smooth to 38 with the margin of the disc variously notched.

Previous collections had shown that in specimens upwards of, say, 30 mm. in total diameter, i.e., presumably with the final number of tentacles, there may be as many as 29 or as few as 14 of these; the majority of large specimens having from 22 to 28 (see Vanhöffen, 1902, Bigelow, 1909, and Kramp, 1924, for tabulations of tentacle numbers at different sizes). Eighteen to twenty-two tentacles have already been recorded in small specimens 8-10 mm. in diameter (Vanhöffen, 1902; Kramp, 1924). Among the smallest of the Bermudian specimens, of 7-12 mm., the tentacle number ranges from 19 to 24, most frequently 20, the smallest specimen (7 mm.) having the latter number.

The most interesting contribution by the Bermudian series to knowledge of *Atolla* is its confirmation of earlier observations (Maas, 1897; 1904, Vanhöffen, 1902) that the gonads regularly appear while the medusa is still very small, for these organs are already of moderate size in 11 out of 14 specimens of 7-9 mm., while all but two out of the 54 specimens of 15 mm. or smaller, that are in good enough condition for study, have gonads. And eggs of various sizes are clearly visible in one specimen of only 10 mm., in two of 11 mm., in one of 13 mm. and in one of 14 mm. But it seems that in occasional specimens these organs may not develop until much later, for in one of 30 mm., the gonads are still very small. At the other extreme, Maas (1904) has reported a 72 mm. *Atolla* as spent. Even the largest, however, of the Bermudian specimens, from 60-100 mm. in diameter, still have full, or partly full gonads, both sexes being represented.

In short, it appears that *Atolla*—like *Periphylla*—is sexually active throughout most of the growth period. But nothing is yet known as to how long, in point of time, this latter may continue.

Broch (1913) has argued, from the depth distribution of the extensive series collected by the *Michael Sars* in the North Atlantic, that the wide variations that occur in the characteristic pigmentation of *Atolla* are correlated with the depths at which given specimens live, those in which only the stomach is densely pigmented (Broch's group I) having been taken most numerous in hauls from 500 meters, those with more extensive pigmentation in hauls from 750 and 1,000 meters. Stiasny (1934) likewise found the *Discovery* captures at least compatible with this, except in the Antarctic and in the upwelling waters off West Africa. Unfortunately, the Bermudian series throws little light on this point, partly because the great majority of the hauls sampled the water to a depth of 900 meters or more, and partly, because the great majority of the specimens were so much rubbed in the nets, that it is impossible to tell how extensive their pigmentation was in life. The most that can be said is that 14 of the 16 specimens in which the ring muscle is strongly pigmented (or apparently was so in life), were from hauls from 1,097-0 meters, or deeper, whereas the genus was of most frequent occurrence in the 914-0 meter hauls, as noted below. But it is not safe to estimate the vertical distribution of the contrasting specimens in



which the pigment is now confined to the stomach (Broch's group I), because many of these still show some slight trace of peripheral pigment, as well.

*General Distribution:* *A. wyvillei* has already been reported close to Bermuda (Bigelow, 1928, p. 509), as well as at many other localities widespread in the North Atlantic from side to side; it is in fact now known to be one of the most cosmopolitan of bathypelagic medusae, to be expected anywhere in the basins of the open oceans. But like some other bathypelagic forms, it seems to be barred from access to the Mediterranean (Kramp, 1924; Bigelow and Sears, 1937).

To the northward, it has been taken to Lat. 64° N. in the western side of the Atlantic, north of the Faroe-Shetland ridge in the eastern (Kramp, 1914; Broch, 1913), to Bering Sea in the Pacific (Bigelow, 1913). To the southward, its recorded range extends right down to the Antarctic, namely to Lat. 63° S. in the Indian Ocean (Vanhöffen, 1902): to 68° S. in the Atlantic (Stiasny, 1934), to 70° 30' S. in the Pacific (Browne, 1910).

*Seasonal Distribution:* In 1930, *Atolla* was taken rather regularly right through the collecting season, from early May until late September. In 1929, however, when it occurred regularly from April through July, only one was taken in August, only 6 (in one net haul) in September, although 169 hauls to suitable depths (500-0 meters) were made during those two months. Similarly, the total number taken was only about  $\frac{1}{2}$  as great in 1929 (54 specimens) as in 1930 (171 specimens) although many more hauls were made to 900-0 meters or deeper, in the former year (462 hauls) than in the latter (343 hauls). In our present ignorance of the ecological relationships of this species, any attempt to explain this annual difference in its abundance would be pure guesswork. As elsewhere emphasized (Bigelow, 1918, p. 509) winter towing, in the Cape Hatteras-Bermuda-Bahamas triangle, did not yield it at all. But the interpretation of this seasonal periodicity must await a knowledge of whether it passes through a fixed stage in its development, or whether it is holoplanktonic as seems the more likely from its bathymetric range.

In 1929, so few very small specimens (of 12 mm. or less) were taken (3 in April, 1 in May, 1 in July, 1 in August) that no weight can be given to their seasonal distribution. In 1930, however, there was an unmistakable concentration of young stages in spring and autumn (24 were taken in May, 6 in June, 11 in September) contrasting with the comparative scarcity in July (5) and August (1). A combination of the data for the two years yields the picture of a species breeding at least from mid-spring to early August, but with a definite slackening of production in the late summer.

*Vertical Range:* The distribution of the specimens according to the depth of haul is as follows:

Depth in Meters.	No. of Specimens.	No. of Hauls.	Specimens. per Haul.
366-0	0	12	0.0
549-0	2	23	0.09
732-0	3	40	0.08
914-0	56	133	0.42
1,097-0	41	134	0.3
1,280-0	38	132	0.3
1,463-0	42	132	0.3
1,646-0	32	135	0.2
1,829-0	14	135	0.1
1,829-0	0	5	0.0

This indication of an upper limit not far from 500 meters, and of a preponderance between 1,000 and—perhaps—1,500 meters, is in line with the catches of the *Michael Sars* farther north in the Atlantic (Broch, 1913).

The catches of very small specimens (of 13 mm. or smaller) show even more definite concentration near the 1,000 meter level, with no indication whatever of any tendency on the part of the juveniles to live at any higher level in the water than do the adults; data are as follows:

Depth in Meters.	No. of Specimens.	No. of Hauls.	Specimens per Haul.
366-0	0	12	0.0
549-0	0	23	0.0
732-0	1	40	0.02
914-0	27	133	0.20
1,097-0	8	134	0.06
1,280-0	8	132	0.06
1,463-0	5	132	0.04
1,646-0	6	135	0.05
1,829-0	2	135	0.02

There is, however, some indication that as *Atollas* attain their full size they tend to sink, for no specimens of 50 mm. or larger were taken as shoal as 732-0 meters, only one from 914-0 meters, 3 at 1,097-0 meters, 2 at 1,280-0 meters, 7 at 1,463-0 meters, 6 at 1,646-0 meters (a preponderance at, say, 1,400 meters or deeper), and one at 1,829-0 meters.

#### LINUCHIDAE.

##### *Linuche.*

##### *Linuche unguiculata* Schwartz.

*Medusa unguiculata*, Schwartz, 1788, p. 195, Pl. 6, Fig. 1.

For synonymy, see Mayer, 1910, p. 558 ("*L. unguiculata*"), p. 560 ("*L. aquila*"); Vanhöffen, 1913, p. 429; Bigelow, 1928, p. 510; Stiasny, 1931, p. 30, 1935, p. 13; Darby, 1933, p. 268.

*Material*: Dip-net, surface, June 8, 1929, hundreds of specimens, about 1.5 mm. in diameter.

Dip-net, surface, July 23, 1929, 1 specimen, 5 mm. in diameter.

Net No. 293, 1,280-0 meters, July 12, 1930, 1 specimen, 6.5 mm. in diameter.

Net No. 690, 2,012-0 meters, June 9, 1930, 2 specimens, 4.5-11 mm. in diameter.

Net No. 694, 1,646-0 meters, June 12, 1930, 1 specimen, 5.5 mm. in diameter.

Reasons are given in an earlier paper (Bigelow, 1928) for including, under the old name *unguiculata*, the form *aquila*, first described by Haeckel (1880), which has at various times been regarded as a distinct Pacific species, or as a variety sufficiently well marked to deserve recognition in nomenclature. And this union has subsequently been accepted by Stiasny (1931).

Thiel (1928) has argued that *L. draco* Haeckel is a distinct species, separated from *unguiculata* by its large size (up to 20 mm. in diameter), by the arrangement of the subumbral pockets in two series, by the number

(48) of horse-shoe shaped gonads, and by green color (due to the infesting zooxanthellae). It is doubtful, however, whether these distinctions will stand the test of time. Size, in particular, is hardly likely to prove of specific significance. At most, a large variety might be indicated—whether regional, or seasonal—or representing the growth of the members of a particular brood under specially favorable surroundings. So far as the number of pockets and their arrangement is concerned, I may point out that while it is usual in typical *unguiculata* for these to be in 3 rows, 32 in the outer, 16 in the median, 4-8 in the inner, an occasional large specimen (12 mm.) may lack the inner row entirely. And the number in the intermediate row may even be as small as 8, reducing the total number to 40 (Bigelow, 1928, p. 512, Fig. 184). It has also been found in typical *unguiculata* that, while the gonads originate in pairs, the members of each pair may, with growth, either "come together in the perradii, resulting in four horse-shoe shaped figures" (Bigelow, 1928, p. 513, Fig. 184); i.e., attain the "*draco*" condition, or may still continue separate until the medusa is well grown (Bigelow, 1928, p. 513, Fig. 183).

Nor does color seem any more likely to prove an alternative character, Darby (1933) having recently found that *L. unguiculata*, at the Tortugas, contains 2 pigments<sup>28</sup>, which—depending on the degree of oxidation—give the subumbrella a yellowish brown color by day (the usual *unguiculata* color), but a spotted dark green pattern by night, i.e., the "*draco*" hue. In short, it now seems probable that specimens having the "*draco*" characteristics, represent variants of *unguiculata*, though we are still entirely in the dark, as what conditions—seasonal, environmental, or genetic—favor their appearance.

*General Distribution:* Previous records for the general region of Bermuda (Fewkes, 1883; Bigelow, 1928) had already made it likely that the Bermuda Bank is a center of production for *Linuche*, the farthest extra-tropical such center in the Atlantic. And this is corroborated by the catch of juveniles, listed above.

*Vertical Range:* *Linuche* commonly swarms at the surface. The few specimens listed above from deep hauls were probably picked up by the nets on their way down or up.

## DISCOPHORA.

### PELAGIDAE.

#### *Pelagia*.

#### *Pelagia noctiluca* Forskål.

*Medusa noctiluca*, Forskål, 1775, p. 109.

For synonymy, see Mayer, 1910, p. 572-576 ("*P. noctiluca*," "*P. noctiluca* var. *neglecta*," "*P. cyanella*," "*P. panopyra*," "*P. panopyra* var. *placenta*," "*P. flaveola*," "*P. perla*," "*P. phosphora*," "*P. crassa*,"); Stiasny, 1914, p. 529, p. 531 ("*P. purpuroviolacea*" and "*P. rosea*"); 1924, p. 83 ("*P. curaçaoensis*").

*Material:* Net No. 863, 1,646-0 meters, September 8, 1930, 1 specimen, about 26 mm. in diameter.

Surface, September 12, 1930, 1 specimen, about 45 mm. in diameter.

The several authors who have recently studied this wide-ranging and widely varying genus, have successively reduced the number of so-called species. On the basis of the *Arcturus* collection, I concluded that one species of *Pelagia* (*P. noctiluca*), at any rate, "occurs widespread, over the warmer

<sup>28</sup> Probably these are actually in the contained zooxanthellae.



parts of the Indian and Pacific and Atlantic oceans" (Bigelow, 1928, p. 519) and doubted whether any of the other named forms could be separated from it, specifically. Stiasny (1934, p. 388), in his most recent discussion of the genus, likewise makes equally drastic reduction, writing "there is most probably only a single species of *Pelagia* with a world wide distribution over all tropical and subtropical parts of the ocean." This species must bear the name that was earliest given to a medusa recognizable as *Pelagia*, the *P. noctiluca* of Forskål. Menon (1930) has likewise applied this name, without discussion, to *Pelagia* from the Indian Ocean.

Subsequently, however, Stiasny (1935) has maintained that *flaveola* is also a good species.

Whether any of the other named forms deserve recognition at all, as geographic or environmental races, or whether they merely represent individual or swarm variations, different stages in growth, or contraction phases, is still an open question, the solution of which is not aided by the present small series. I can only point out that, in the larger specimen, linear exumbral warts greatly predominate in the marginal zone, but are intermingled with round-oval warts in nearly equal numbers in the central zone. That is to say, the so-called *perla* and *pelagia* types are combined with the *noctiluca* type (narrow linear warts) on different parts of the bell. Menon (1930) also reports finding both long warts and rounded. This is additional evidence that specific distinctions cannot be based on the shape of these structures.

*General Distribution:* *Pelagia* was to be expected in the collection, having already been found near Bermuda (Fewkes, 1883; Bigelow, 1928). It is, however, interesting that so large a number of hauls, shoal as well as deep, made in so many different months, should have yielded so few specimens of a species which has now been encountered—often in swarms—at many stations, in the warm belts of all oceans, as well as in the Mediterranean.

### ***Poralia.***

#### **? *Poralia rufescens* Vanhöffen.**

*Poralia rufescens*, Vanhöffen, 1902, p. 41, Pl. 4, Fig. 15, 16; Bigelow, 1909, p. 45, Pl. 13, Figs. 1-5.

*Material:* Net Nos. 50, 247, and 726; hauls from 1,646-0, 1,829-0, and 1,463-0 meters; fragments of the central parts of 3 specimens; diameters of base of stomach, respectively about 30, about 35, and about 18 mm.

This species is one of the most interesting finds in the collection, for it is only the third record for the genus. *Poralia* was first described by Vanhöffen (1902) for a fragmentary specimen (marginal zone torn off) with very simple gonads consisting of outpocketings projecting direct from the gastric wall into the subumbral cavity, in seven groups of 3 or 4 pockets each. This type of symmetry, as Vanhöffen pointed out, was previously known (for Scyphomedusae) only as an abnormality of *Aurelia*. There were 21 or 22 narrow radial canals.

Two specimens in the *Albatross* collection (Bigelow, 1909), though likewise very fragmentary, allowed some amplification of Vanhöffen's original account. In the smaller, there were 8 groups of sexual folds, and 21 canals in about  $\frac{1}{2}$  the circumference, suggesting octoradial arrangement and about twice as many canals as Vanhöffen's example. In the larger and somewhat better preserved *Albatross* specimen, about 250 mm. in diameter, the sexual folds formed a practically continuous ring, surrounding the base of the stomach, but separated by gelatinous pillars, into 18 or 19 groups of 6 or 7 pockets each. And there were 41 canals. As already remarked (Bigelow, 1909, p. 46), a growth series is here indicated, with multiplication of canals,

and of sex folds, accompanied by a corresponding formation of additional pillars.

In the largest Bermudian specimen (so far as can be seen in the present fragmentary state), the sex folds are in five groups, separated by as many broad gelatinous pillars, corresponding to as many angles at the base of the manubrium. The number of folds per group is 5, 5, 6, 5(?), 5, while in most of the groups the larger central folds are flanked in addition by indications of very small folds, which (if they developed) would raise the number per group to 6-8. Several of the folds contain large eggs. But this cannot be taken as proof that the specimen had reached its full growth, for it is equally possible that the development of sex products may extend over a considerable period, allowing opportunity for subdivision of the primary groups of six folds by the development of additional pillars. The number of pillars is also apparently five in the smallest specimen (stomach, 18 mm. in diameter); the condition of the third specimen is too bad for counting.

The canals are very narrow, as in Vanhöffen's example of corresponding size, approximately 38 in number in the smallest specimen, about 40 in the example 30 mm. in diameter of stomach, but only about 30 in number in the largest.

These conditions of metamerism in the Bermudian specimens make it likely, not that *Poralia* is primarily octoradial as I formerly suggested, but that it is primarily quadriradial, but that with the growth of the medusa, the original state is obscured by the formation of additional canals, and by subdivision of the original groups of sex folds through the development of additional gelatinous pillars. Different specimens would then show different numbers of groups of sex folds—as is actually the case—if these developments take place at different rates, in different radial sectors, as may very well happen. Decision whether geographical races of the species exist in this respect, or whether it has been a matter of pure chance that different numerical conditions have been illustrated by the few specimens so far seen from the Indian, Pacific, and Atlantic oceans, must await a study of larger series.

In the Bermudian, as in the *Albatross* examples (Bigelow, 1909, Pl. 13, Figs. 1-3), the gastric cirri are arranged in a single fringe-like row, in as many groups as there are groups of sex folds, there being none on the gelatinous pillars.

Nothing can be said as to the form of the manubrium, all but the base having been destroyed.

The marginal zones have been torn off, as was also the case in Vanhöffen's and in the smaller of the *Albatross* specimens. And while the larger of the latter showed the distal terminations of the canals, and allowed a description of the rhopalial, the tentacles of this genus have yet to be seen.

The Bermudian specimens, like those previously seen, show the bathypelagic type of pigmentation, for they are given a reddish chocolate hue by pigment granules so large as to be individually visible under a magnification of only 3 diameters. Even the gelatinous substance is sparsely pigmented throughout; such of the subumbrella surface as is intact more densely so, likewise the surface of the sexual folds, though in places where the latter are torn, allowing the eggs to show through (specimen from Net No. 247), these are opaque white, as is also the case in *Aeginura*.

The depths of capture, listed above, added to preexisting records of 1,100-0 meters (Vanhöffen, 1902) and 549-0 meters (Bigelow, 1909), combined with the fact that a form so easily recognizable, and so striking in appearance has been taken on only 3 occasions, is sufficient proof that its habitat is exclusively bathypelagic.



## AURELLIIDAE.

*Aurellia*.<sup>29</sup>

The written history of *Aurellia* extends back nearly two centuries, during which period many descriptions of its members have appeared, and discussion of their interrelationships. It has been the object of much investigation, embryologic, physiologic, and varietal; and it is commonly used as material for biological teaching. None the less, we still await critical revision of the seventeen "species" of *Aurellia* that have been named.

It is, however, generally accepted that most of these represent nothing more than contraction-phases, growth stages, individual variants, or at most environmental races of a much smaller number. Thus, Mayer (1910, p. 620, 622), in his tabular view of the genus, grouped all the named forms as either "*aurita* and its varieties" or "*labiata* and its varieties." Comparison, a few years later, between specimens of the *aurita* group from various Atlantic and Pacific localities, lead me to the conclusion that they are not separable into varieties, by any of the characters previously suggested (Bigelow, 1913, p. 98). And Stiasny (1919a; 1922, p. 524, 525), after a preliminary survey of the genus, concluded that all known Aurellias fall in one or another of four "wohlunterscheidbare gruppen, nicht Varietäten" of the "grossen Species *aurita*" characterized by differences in the number of canals arising from each genital sinus.

The difficulty in defining the forms of *Aurellia* (whatever be the taxonomic rank of these) lies in the fact that the character chiefly involved, in recent discussions, is one in which differences are gradual, not discontinuous, namely, the complexity of branching of the canals, and the extent to which the branches anastomose. The extremes in this respect are far apart. The one is represented by the simple state illustrated by Mayer (1910, p. 624, Fig. 397) for a Mediterranean example, in which the main perradial canals show no branching between the subdivision that takes place close to their points of origin, and the immediate vicinity of the bell margin, and in which anastomosis is also confined to the latter region. The other extreme is represented by the form first reported by Brandt (1838) from Kamchatka, and subsequently by Uchida (1934) and by me (1913; 1920) from northern Japan, from the Sea of Okhotsk, and from the Bering Sea-Alaska region, in which the perradials give off numerous branches throughout the outer  $\frac{1}{2}$  of their lengths, and in which there is any extensive anastomosis between all the primary systems, perradial, interradial, and adradial. I have already argued (Bigelow, 1913; 1920) that this form differs so sharply from typical *aurita* in this respect, (also in the dense pigmentation of the margin) as to deserve specific recognition as *A. limbata* Brandt. However, it proves that the further difference reported by Uchida (1934), namely wrinkled exumbrellar sense pits in *limbata*, smooth in *aurita*, is not a dependable specific character (unless perhaps for full-grown specimens), for while the pits in a large example from the Kurile Islands agreed with Uchida's description in their wrinkling (Bigelow, 1913, p. 100, Pl. 5, Fig. 2), they are smooth in the smaller specimens with *limbata* canalization that I have seen. Neither have I been able to demonstrate, on any of the Aurellias of this type, the partial closure of the mouth by flaps from the oral arms, reported by Uchida (1934) and thought by him to suggest rhizostome affinities. This perhaps represents a contraction phase.

*Aurellia limbata*, in short, is very closely allied to *aurita* though differing enough from the latter (at least in its typical form) for specific recognition. It also has a much more circumscribed range, for all records of Aurellias, the canals of which have shown the extreme complexity and exten-

<sup>29</sup> This name has usually been spelled *Aurelia*. But Peron and Lesueur's (1809) original spelling was *Aurellia*, as Mayer (1910, p. 619) points out.



sive anastomosis characteristic of *limbata* have (so far as I am aware) been from the Arctic or Subarctic; namely, from northern Japan, Kamchatka, Sea of Okhotsk, the Bering Sea region (Brandt, 1838; Uchida, 1934; Bigelow, 1913; 1920), and Greenland (Kramp, 1913, as "*A. flavidula*"). Thus it is circumpolar, as I have previously pointed out (Bigelow, 1920, p. 14).

The status of *A. maldivensis* Bigelow, and of *A. solida* Browne—the former recently redescribed by Stiasny (1935), the latter by Menon (1930) and by Rao (1931)—still remains uncertain.

### *Aurellia aurita* Linné.

*Medusa aurita*, Linné, 1758, p. 660.

For early synonymy, see "*A. aurita*," Mayer, 1910, p. 623, 627, and "*A. labiata*," p. 628.

The more important subsequent discussions are listed above (p. 167).

*Material*: Net No. 296, 1,829-0 meters, July 12, 1929, 1 specimen, about 85 mm. in diameter.

Dip Net, Surface, October 16, 1930, 10 specimens, about 30-80 mm. in diameter.

Net No. 880, 914-0 meters, September 12, 1930, 1 specimen, fragmentary, about 85 mm. in diameter.

Also, 9 other Bermuda specimens, 25-90 mm. in diameter in the collection of the Museum of Comparative Zoology, collected in the summers of 1902, 1903, 1916, 1917.

The number of canal roots, arising from each genital sinus, shows the following range, in specimens of different sizes:

Diameter in mm.	Number of Specimens.	Number of Canals per Sinus.
25	2	3
30	1	3
33	1	3-4
35	1	3
37	1	3
40	2	3
45	1	3
50	1	3-4
52	1	3
55	1	1-3
75	2	3-5
80	2	3-5
90	1	4-5

Thus, most of the smaller examples would fall in the "*aurita*" group, according to Stiasny's (1922) subdivision, while the larger specimens bridge the gap between the latter and his "*colpota*" group. The first branching of the primary interradial canals is trichotomous, as Stiasny (1922) has emphasized, with further branching leading to the formation of what Mayer (1910, p. 624) has aptly named a "pitchfork-shaped system." In small *Aurellias*, the first branching of the interradial canals usually lies some distance distal to the boundary of each genital sinus. It is, in fact, probable that all *Aurellias* pass through this "*aurita*" stage in this respect, when

they are small. The outer boundaries of the sinuses spread centrifugally with growth. And it appears that the number of separate trunks that arise from a given sinus, in larger individuals, depends chiefly in how far outward the canal-system has become incorporated into the sinus, by the growth of the latter. With *Aurellia* proverbially variable and subject to abnormality, it is not astonishing that the number of canals often differs for the different sinuses of a given individual.

The Bermudian series gives evidence, in the foregoing tabulation, of the tendency toward an irregular increase in the number of canals, with growth, that is to be expected, on this basis. Failure of any of the specimens<sup>30</sup> to show a larger number of canal-roots than 5 per sinus is no doubt due to the fact that none of them was of large size. For example, the numbers per sinus in a large Cuban specimen, 250 mm. in diameter, are 6, 6, 8, 7.

I may note, in passing, that anastomosis of canals in the Bermudian specimens, is much as it has frequently been described for *A. aurita*.

*General Distribution:* It has long been known that *A. aurita* is one of the most abundant of medusae among the West Indies, and northward from Florida along the east coast of North America. It is also a familiar object at Bermuda, although no printed record of its presence seems to have appeared. Being strictly a neritic form, the specimens in the present collection were no doubt the product of the Bermuda Bank.

#### FAUNISTIC CONSIDERATIONS.

##### Neritic and Holoplanktonic Communities.

It is safe to conclude—from the geographic location of the station where the towing was done—that all the medusae taken, of species that pass through a fixed stage in their development, were the products of Bermuda. Hence, a comparison of this neritic element, in the catches, with the holoplanktonic species gives a good indication of the extent to which a small isolated Bank may be expected to contribute to the medusan fauna of the open ocean nearby.

In the case of the Hydromedusae, out of a total of 717 specimens, the number belonging to species that are either known to pass through an attached hydroid stage, or may reasonably be assumed to do so,<sup>31</sup> does not exceed 17. This, I may point out, does not include the small series of *Bougainvillia niobe*, which has a budding phase, hence is placed in the holoplanktonic category, so far as its dispersal is concerned. That is to say, the contribution made by the neighboring slopes and shallows of Bermuda, to a point not ten miles distant, was less than 3% of the total catch. And the numerical paucity of the neritic element is the more striking, when one recalls that it represents at least 9 species, the holoplanktonic element (Tracho- and Narcomedusae) only 14. It is probable that if the station had been located but a few miles further offshore, the neritic element in the medusa fauna would have been negligible, as Thiel (1935) has shown it to be for the Central and South Atlantic as a whole.

In the case of the Scyphomedusae, the situation was the reverse, if judged from the standpoint of total numbers only, for the number of neritic specimens was raised considerably above that of the holoplanktonic by one catch of several hundreds of juveniles of *Linuche*, a genus which almost certainly passes through a scyphistoma stage, though not yet actually proven to do so. And a second large catch (66) was also made of *Carybdea xaymacana*, which also probably has a polyp stage in coastal waters. How-

<sup>30</sup> Except for two abnormal tripartite specimens, each about 80 mm. in diameter, in which the number of canals per sinus were 9, 7, 9, and 9, 6, 7.

<sup>31</sup> *Zancleopsis*, *Pandea*, *Heterotiar*, *Calycopsis*, *Chromatonema*, *Aequorea*, *Olindias*.

ever, if the neritic and holoplanktonic groups of Scyphomedusae be judged, not by numbers of specimens, but by the frequency of occurrence, the latter group ranks far in advance, for 252 hauls yielded representatives of genera certainly or probably holoplanktonic (*Atolla*, *Periphylla*, *Pelagia*), while only 16 hauls and surface collections yielded genera which may be safely called neritic (*Carybdea*, *Tamoya*, *Nausithoe*, *Linuche*, *Aurellia*). And apart from the two species just mentioned, neritic (or probably neritic) Scyphomedusae numbered only 23 specimens, holoplanktonic Scyphomedusae 549.

Apart, then, from sporadic contributions of 2 species, produced on the Bermuda Bank, the regular population was as characteristically holoplanktonic for the Scyphomedusae as for the Hydromedusae. Why it is that the young of *Linuche* and *Carybdea* drift offshore more frequently, or in greater numbers, than do other medusae produced on the Bermuda Bank, is a problem for the future.

#### VERTICAL DISTRIBUTION OF MEDUSAE AS A WHOLE.

If we omit the few specimens, for which depth data are not available; fragments which may not have represented individual medusae; and also the swarm of juvenile *Linuche*, mentioned above, the distribution of all the medusae combined with respect to depth of haul, was as follows:

Depth in Meters.	Number of Hauls Made.	Number of Medusae Taken.	Specimens per Haul.
0	86	126	1.5
183-0	10	0	0
366-0	12	0	0
549-0	23	10	0.43
732-0	40	18	0.45
914-0	132	189	1.44
1,097-0	134	246	1.83
1,280-0	132	245	1.85
1,463-0	132	235	1.79
1,646-0	135	234	1.73
1,829-0	135	220	1.63
2,012-0	4	21	5.25

The fact that the yields of 85 hauls at depths of 183-0 to 732-0 meters was so trifling, is good evidence that catches made in the deeper hauls can have owed very little, if anything, to what the nets picked up while being lowered and hauled up again. Consequently, the tabulation indicates that, numerically, the immediate surface, on the one hand, and a stratum from about the 900 meter level downward, were about equally populated, but that the intervening zone, some 700 meters thick, was practically barren. And omission of the neritic specimens from the surface catches, shows that this barren zone extended right up to the surface, for only 4 specimens of the holoplanktonic group were taken at the surface, namely, 1 *Liriope*, 1 *Haliceas*, and 2 *Aegina*.

Consideration of the comparative regularity of occurrence at different depths leads to a similar conclusion, as appears from the following tabulation:



Depth in Meters.	Number of Hauls Made.	Number with Medusae.	% with Medusae.
0	86	10 (3)	11 (.3)
183-0	10	0	0
366-0	12	0	0
546-0	23	4	17
732-0	40	12	30
914-0	132	55	41
1,097-0	134	67	50
1,280-0	132	66	50
1,463-0	132	64	49
1,646-0	135	71	52
1,829-0	135	61	45
2,012-0	4	4	100

By this criterion, for all medusae combined, and even including the swarms of juvenile *Linuche*, the medusae occurred less regularly at the surface than from about 600-0 meters downward, not at all in the intervening strata. And omission of the neritic forms lowers the surface frequency to a very small fraction of that of the deep layers, for only 3 out of the 86 surface hauls yielded holoplanktonic medusae (about 3%), or 1 for 28 hauls.

If the foregoing tabulations were taken at face value, they would suggest that medusae were about equally abundant and equally frequent from about 800 meters, or thereabouts, downward, with a decided maximum as deep as 2,000 meters. But consideration of the method by which the hauls were made shows that such a conclusion would almost certainly be incorrect, because the catches from the deepest hauls were no doubt augmented, both in frequency and in numerical yield, by what the nets picked up as they were lowered through the comparatively rich 500-800 meter stratum, and then hauled up through it again. The data are not of a sort to allow numerical calculation of the probable contamination resulting from this. But it may be safely assumed that with depth, below, say, 800 meters, this increased significantly and rapidly. And it is not unlikely that all the specimens yielded by the 4 hauls at 2,012-0 meters actually came from much smaller depths. In short, the data yields no positive evidence that there were any medusae as deep as this.

Reasoning then from the collections actually made at Dr. Beebe's station, it seems safe to conclude for the part of the Sargasso Sea represented by the Bermuda region:

1. That the neritic element among the Hydromedusae is numerically negligible; and that this also applies to the Scyphomedusae, except on occasions when swarms of one species or another may drift out for a few miles from the Bermuda Bank.

2. That the whole upper 500 meters of water is practically barren of medusae from spring, through summer, to autumn, except when such events take place. On these occasions, the immediate surface may be the most thickly populated zone. But it appears that these periods are of brief duration; nor is it likely that they affect the situation on a broad scale more than a few miles out from Bermuda.

3. That medusae as a whole in this part of the ocean basin are usually most abundant and occur most regularly at about 500-800 meters, below which they decrease, in both these respects, with increasing depth.

## RELATIVE ABUNDANCE OF DIFFERENT SPECIES.

The relative abundance of the several species is shown in the following table:

Species.	Number.	Species.	Number.
<i>Zancleopsis dichotoma</i>	1	<i>Liriope tetraphylla</i>	1
<i>Bougainvillia niobe</i>	7	<i>Geryonia proboscidalis</i>	3
<i>Pandea conica</i>	1	<i>Cunina</i> sp?	1
<i>Pandea rubra</i>	4	<i>Solmissus incisa</i>	13
<i>Heterotiar anonyms</i>	2	<i>Aegina citrea</i>	31
<i>Calycopsis</i> sp?	2	<i>Aeginura grimaldii</i>	201
<i>Chromatonema rubrum</i>	2	? <i>Pegantha clara</i>	7
<i>Aequorea floridana</i>	2	<i>Carybdea xaymacana</i>	105
<i>Olindias tenuis</i>	3	<i>Carybdea alata</i>	3
<i>Rhopalonema velatum</i>	39	<i>Tamoya haplonema</i>	1
<i>Pantachogon haeckeli</i>	65	<i>Periphylla hyacinthina</i>	317
<i>Colobonema typicum</i>	47	<i>Nausithoe punctata</i>	6
? <i>Crossota brunnea</i>	50	<i>Atolla wyvillei</i>	232
Trachynemidae?	51	<i>Linuche unguiculata</i>	many
<i>Halicreas minimum</i>	186	<i>Pelagia noctiluca</i>	2
<i>Halicreas glabrum</i>	66	<i>Poralia rufescens</i>	3
<i>Halitrephes valdivii</i>	19	<i>Aurellia aurita</i>	12

## ABSOLUTE ABUNDANCE.

Some estimate of the absolute abundance has proved interesting. Since the neritic forms may be regarded as sporadic invaders of the offshore waters, they may be left out of account in this connection. The number of holoplanktonic medusae of all kinds taken in the hauls from 549-0 meters and deeper, i.e., in the most productive zone, was about 1,406; the number of hauls 869; the number of hours of towing was 3,276; or an average yield of only 1.6 specimens per tow, or 0.42 specimen per hour's towing. Divided into groups, the catch was approximately 0.23 Trachomedusae and Narcomedusae combined, and 0.16 of the bathypelagic Scyphomedusae (*Atolla* and *Periphylla*) per towing hour.

## QUANTITATIVE COMPARISON WITH OTHER REGIONS.

A quantitative comparison of the medusa population of the Bermuda region with that of the Mediterranean and of the Central and South Atlantic is interesting, as an indication of how the former—and its part of the Sargasso Sea as a whole—ranks as to productivity for this group, at different levels in the water, compared with other seas. Calculation of the Mediterranean catches made by the *Thor* as listed by Kramp (1924), but omitting one large catch of "many thousands" of *Liriope eurybia* in the Sea of Marmora (*Thor* Sta. 175, Kramp, 1924, p. 32), shows an average catch per hour's towing of about 41.5 medusae of all sorts, of about 36-37 Trachomedusae and Narcomedusae combined, and about 2.5 Scyphomedusae. Since the *Thor* collections were made with a net with a mouth area of 3 square meters, towing at a rate of about 2 sea miles an hour, the Bermudian collection with one of only about 0.78 square meters, towed at a rate of 2-2½ knots, a factor of about 3.8 must be introduced to make the catches comparable. So adjusted, it is obvious that the Mediterranean was many times the more productive region, both for the holoplanktonic Hydromedusae, and for the medusae as a whole. In the case of the bathypelagic Scyphomedusae, however—represented at Bermuda chiefly by *Atolla* and *Periphylla*,

but in the Mediterranean by the latter only—the two regions were about equally rich.

The Bermudian region is also poor in the holoplanktonic Hydromedusae, in general, as compared to the Central and South Atlantic as a whole, where the *Meteor* tows, with nets only half as large in diameter, yielded an average of about 5.4 specimens per 200 meters of towing at all depths and stations combined—a number that must be multiplied by a factor of perhaps 1.8 to correct for the size of the net alone, to be made comparable with the Bermuda average catch of only 0.23 per hour's towing. And the Atlantic figure would be much increased if the vertical *Meteor* tows were to be calculated on an hourly basis.

Reference to the foregoing discussion of vertical distribution (p. 170) makes it clear that this relative poverty of the Bermuda region results chiefly from the barrenness there of the upper 500 meters of water, in holoplanktonic medusae of any sort. In the Mediterranean, by contrast, most of the hauls from the upper 100 meters of water yielded considerable numbers of medusae, of one species or another (see Kramp's, 1924 lists), while most of the larger catches of the species most plentiful there, namely *Rhopalonema velatum* and *Liriope*, were from depths no greater than 300 meters. In the Central and South Atlantic also, the *Meteor* found Tracho- and Narcomedusae most abundant (10-11 individuals per 200 meters tow) between the surface and 200 meters, much less so in the deep underlying waters (Thiel, 1935, p. 43, Fig. 20, Table 3). And evidence in the same direction, in the Pacific, results from the rich catches of medusae of this category made in the Humboldt Current off northwestern South America, by the *Albatross* (Bigelow, 1909).

From the foregoing, it appears that the very warm superficial stratum of the Sargasso Sea is notably barren of medusae of the holoplanktonic category, but so far as the evidence goes, it suggests that the productivity of the deep waters in the more strictly bathypelagic types, represented by *Periphylla* and *Atolla*, is much more nearly of the same general order of magnitude there, as it is over the ocean basins as a whole<sup>32</sup>, or in the Mediterranean.

It is interesting as illustrating the relative numerical abundance of two allied groups of pelagic coelenterates that the average Mediterranean catch of about 41 medusae per hour's towing mentioned above (p. 172), contrasts with a corresponding average of between 200 and 300 calycephorid siphonophores, both in the Mediterranean and in the neighboring parts of the Atlantic (Bigelow and Sears, 1937, p. 137). Evidently, the latter group is much the more numerous in that particular region. But it is doubtful how far regionally this generalization would apply, for the average *Meteor* catches per 200 meters of towing, of siphonophores and of Tracho- plus Narcomedusae, for the Central and South Atlantic did not differ greatly one from the other (cf. Leloup and Hentschel, 1935, p. 24, Fig. 17 with Thiel, 1935, p. 43, Fig. 20, Table 3).

In the Bermuda region, we have no direct comparison between the two groups, as there are no published records of siphonophores for the years 1929-1930, and as the numbers captured are not recorded for the one year on record (1931, Totton, 1936). We may, however, point out that they were only taken in 55 out of 374 hauls (usually only one species in a haul), or 14% of the tows in 1931, whereas the medusae were taken at 41% of all hauls in the summers of 1929-1930. Hence assuming that the several summers were comparable, it appears that medusae are actually more frequently encountered in the Bermuda region than siphonophores. And this area may thus prove to be as barren of the latter as the former.

<sup>32</sup> Compare, for example, the catches of *Atolla* and *Periphylla* made in the North Atlantic by the *Michael Sars* (Broch, 1913).



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<sup>1</sup> This table does not include a number (less than 10) of specimens for which no Net Number was available at the time of compiling table.





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## 6.

## Classification of Carp-Like Fishes.

J. T. NICHOLS.

*The American Museum of Natural History.*

In attempting to classify the carp-like fishes (Eventognathi or Cyprinoidae) it is generally assumed that the suckers (Catostomidae) are the most primitive group. This is thoroughly in accord with the writer's views and he surmises that it is among ancestral bottom-feeding suckers that these fishes lost oral dentition, the lack of which is an outstanding feature with them all. Suckers are closely related to the true carps (Cyprinidae), but their recognition as a full family is at least convenient in this case. The comparatively few genera of suckers need no further subdivision. It may be noted that the northern genus *Catostomus* represents generalized or standardized forms, and that the single peculiar genus *Myxocyprinus* in China resembles one of the specialized genera in the lower Mississippi Valley. These peculiar suckers also have characters which are perhaps ancestral; and it may be questioned whether resemblance between Chinese and American genera is relationship or parallelism, whether these are specializations of more standard northern suckers or of some different ancestral forms.

More different in the main from the true carps are the loaches, a large varied group with characters generally spoken of as degenerate. It is the writer's view that the loaches are a recent specialization from the carps, perhaps more or less polyphylatic, but this may not be generally accepted. Classification of the loaches is very difficult. Two families are usually recognized, true loaches (Cobitidae), and flattened bottom forms (Homalopteridae). In the latter a series from *Crossostoma* to *Gastromyzon* is rather clear, its relationship to the others of which *Lepturichthys* seems to be a terminal specialization, obscure. It is probably impossible to divide the loaches on the basis of structural resemblances without violating relationships. To place the emphasis on apparent relationships the writer would recognize a single family for them (Cobitidae), consider the obvious groups or series central for four subfamilies, and tentatively place aberrant forms wherever they seem to fit least badly.

*Cobitis* and related genera (Cobitinae) are more or less elongate with erectile spine under the eye, a peculiar un-carp-like specialization. As their ancestors must have been without it we have some justification in considering *Misgurnus*, a widely distributed, abundant and somewhat aberrant eel-like genus which lacks the spine and otherwise resembles *Cobitis* in various ways, a primitive member of this series. *Botia* and related genera might be secondarily free-swimming standardized forms derived from *Cobitis*.

*Nemacheilus*, *Barbatula* and related genera lacking the erectile spine may be grouped in a subfamily (Nemacheilinae) very abundant in High Asia, also with a claim, which we do not recognize, to the genus *Misgurnus*.

The aberrant carp-like genus *Gobiobotia*, for lack of a better place, may go as a primitive Homalopterine; and the *Crossostoma*-*Gastromyzon* series stand as a subfamily (Gastromyzoninae).

The true carps are the most abundant family in this group, and represented by many genera. Their relationships to one another are sufficiently close and sufficiently confused to make their subdivision hardly worthwhile, but it is certainly a convenience. In so doing one may also give tangible expression to one's views on relationships. The carps are most differentiated in Asia; all the main groups are represented and most divergent there.

Weber and de Beaufort (Vol. III, 1916) recognize 3 subfamilies for Indo-Australian forms, Abramidinae, Rasborinae and Cyprininae, of which the last is the most composite. Turning to the list of species from China on the Asiatic continent we find various genera which fit into these subfamilies without much question, and others with northern affinities which do not. The keeled breams, *Megalobrama*, *Hemiculter*, *Erythroculter* and so forth obviously go into the Abramidinae, *Opsariichthys* which is related to *Rasbora* in the Rasborinae, *Cyprinus* and *Barbus* and their allies in the Cyprininae. One hesitates to place *Leuciscus* and *Phoxinus*, which with their allies are widely distributed northward, in the Rasborinae and may recognize a superficially somewhat parallel subfamily (Leuciscinae) for these. Though probably derived from this group *Schizothorax* and allied genera, abundant in High Asia, are sufficiently numerous and distinct to recognize as another subfamily (Schizothoracinae). The peculiar transverse mouth of the abundant Chinese genus *Xenocypris* is presumably derived from a more or less sucking mouth of bottom feeding forms, and this is perhaps the secondarily actively free swimming terminal member of a series (Chondrostomatinae) that runs from *Labeo*, through *Varicorhinus* to it, with various aberrant side specializations. The little fishes belonging to *Rhodeus* and allied genera form a uniform well differentiated group (Rhodeinae). The whole series of genera allied to *Gobio*, showing gradation from standard free-swimming to specialized bottom forms, may conveniently be considered a subfamily (Gobioninae), perhaps the most recently evolved, now replacing in the Chinese center of specialization earlier Chondrostomatinae, just as these or some other bottom Cyprinids presumably replaced the Catostomidae.

The standardized Leuciscinae may be the oldest group. Native American carps belong to it, with the exception of *Notemigonus*, an Abramidin. The Abramidinae and Schizothoracinae seem to be specializations of the Leuciscinae. Whence the Rhodeinae came is uncertain but one may suspect from the Abramidinae. The Cyprininae are now flowering in southern Asia, and *Cyprinus* itself is possibly a relict from an earlier period of differentiation in this group. The Gobioninae may be derived from the Cyprininae.

There are plenty of Cyprinid genera, aberrant or otherwise, to be assigned to this or that of these eight divisions according to one's idea of their relationships, but these eight as outlined can be considered to cover the group in all parts of the world, and afford a basis for discussion of the relationships of any genus.

#### TENTATIVE SUBDIVISION OF THE CYPRINOIDEA.

Suborder Cyprinoidea. Carp-like fishes.

Family Catostomidae. Suckers.

Family Cyprinidae. True Carps.

- (1) Subfamily Leuciscinae—*Leuciscus*, *Phoxinus*, *Richardsonius*, *Hybopsis*, etc.



- (2) Subfamily Rasborinae — *Rasbora*, *Danio*, *Opsariichthys*, *Barilius*, etc.
- (3) Subfamily Abramidinae. *Abramis*, *Erythroculter*, *Hemiculter*, *Notemigonus*, etc.
- (4) Subfamily Schizothoracinae. *Schizothorax*, *Schizopygopsis*, *Diptychus*, etc.
- (5) Subfamily Rhodeinae. *Rhodeus*, *Pseudoperilampus*, *Acanthorhodeus*, etc.
- (6) Subfamily Cyprininae. *Cyprinus*, *Osteochilus*, *Barbus*, *Labeo*, etc.
- (7) Subfamily Chondrostomatinae. (*Labeo*), *Varicorhinus*, *Chondrostoma*, *Xenocypris*, etc.
- (8) Subfamily Gobioninae. *Gnathopogon*, *Gobio*, *Pseudogobio*, *Saurogobio*, etc.

Family Cobitidae. Loaches.

- (1) Subfamily Cobitinae. *Misgurnus*, *Cobitis*, *Botia*, etc.
- (2) Subfamily Nemacheilinae. (*Misgurnus*), *Nemacheilus*, *Barbatula*, etc.
- (3) Subfamily Homalopterinae. (*Gobiobotia*), *Homaloptera*, *Lepeturichthys*, etc.
- (4) Subfamily Gastromyzoninae. *Crossostoma*, *Hemimyzon*, *Gastromyzon*, etc.

Dr. Y. T. Chu has recently (1935, *Biol. Bull.* St. John's Univ., Shanghai, No. 2, p. ix) listed Chinese genera of Cyprinidae in eight subfamilies. He does not differentiate Rasborinae from Leuciscinae, and recognizes a subfamily for the aberrant genus *Hypophthalmichthys* of uncertain relationships. There are presumably other aberrant Cyprinid genera which might be so treated. He confines the Chondrostomatinae to genera close to *Xenocypris*, leaving less terminal ones in the Cyprininae, a more conservative procedure especially as the phylaticy of the series from *Labeo* to *Xenocypris* is assumed rather than proved. Also the name Acheilognathinae is used by him in place of Rhodeinae.



## 7.

Tissue Responses of *Cyprinodon variegatus* to the Myxosporidian Parasite, *Myxobolus lintoni* Gurley.

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(Plates I-VII).

## INTRODUCTION.

Little is known about the histopathology of myxosporidian infections. The majority of these protozoan parasites are found in the gall-bladder and urinary bladder of fresh water and marine fishes but cause little or no damage to the host tissues. However, when the infections become localized in the epithelium of the intestine, in the liver, or in other organs, a considerable number of pathological changes may occur. If the fins, skin or musculature are invaded, the resulting lesions are very conspicuous, producing in many instances tumor-like growths.

One of the best known myxosporidian tumors is found on the European Barbel, *Barbus barbus*, and is called the "boil disease" or "Beulenkrankheit." This condition is caused by *Myxobolus pfeifferi* Thélohan and has been reported for other European fresh water fishes such as *Barbus fluviatilis* and *B. plebejus*. Keysellitz (1908) has found tumors on these fish varying in size from that of a millet grain to one as big as a hen's egg, and as many as twenty-three small ones on a single fish. According to Doflein (1928), the causative agent may be found in all organs of the body. When the musculature becomes infected tumor-like growths are formed. Microscopically, such structures show a hypertrophy of the "interfibrillares" connective tissues, Myxosporidia, degenerated muscle, and a secondary infection with bacteria.

Fiebiger and Kahls (1929) have also described the "boil disease" from certain Austrian fishes. In the Barbel, the typical nodules were found, showing the characteristic pathological picture. However, a similar infection in the Giant Perch (*Lucioperca sandra*) resulted in no pathological changes, except for some vascular congestion.

Plehn (1910) reported that *Myxobolus piriformis* Thélohan produced in a European minnow, *Leuciscus*, growths which resemble a papillary adenocystoma, but which were not regarded as true tumors. These are usually found in the tail and histologically show folds of the epithelium of the skin with the parasites within the folds.

Hahn (1913) described tumors from the common killifish, *Fundulus*

*heteroclitus*, resulting from an infection of *Myxobolus musculi* = *M. funduli* Kudo, 1919. The lesions, according to Hahn, are caused primarily by worm parasites or mechanical injury and only secondarily do they become infected with Myxosporidia. Microscopically, the tumors show an infiltration with small lymphocytes and a preponderance of vascular tissue and erythrocytes. Numerous non-staining granules of unknown nature and origin were found in infected epidermis, in connective tissue of the dermis and in atrophied muscle fibers. The latter were completely degenerated, showing but few fibers with normal fibrillae and cross striations. The entire tumor mass eventually becomes infected with bacteria. According to Hahn, the vegetative stages of the parasite are intracellular and found within the muscle fibers.

Kudo (1929, 1931) has noted tumor formation due to *Myxobolus* and related Myxosporidia in several species of fresh water fishes. One form, *Myxobolus notatus* Mavor, is found in the sub-dermal connective tissues of the tail muscles of the blunt-nosed minnow, *Pimephales notatus* (*Hyborhynchus notatus*) and *Leuciscus rutilus*. The tumor enclosing a trophozoite reaches a diameter of 7 mm. Histologically, the growths are composed of large cysts which are surrounded by the sub-dermal cells of the hosts. The tissue around the parasite becomes so highly changed that it appears as an "epithelium." The tissues not in contact with the cysts show no cytological changes. However, such areas have an abundance of blood capillaries. The nuclei of the cells in direct contact with the cysts become hypertrophied; the cells stain deeper than the normal cells, and lack the distinct membrane characteristic of epithelial cells. They vary considerably in size and shape, being columnar, club-shaped or irregularly rounded, and do not form a continuous layer. Kudo believed that these "epithelial cells" are modified connective tissue cells. Similar pathological pictures were described by Mavor (1916) and Debaisieux (1925).

There are other genera of Myxosporidia that produce definite responses of host tissues. In some cases such infections result in a complete degeneration of the invaded areas, often causing the death of the fish; other infections result in a simple hypertrophy of the connective tissue cells, enclosing the spores or vegetative stages of the parasite (Plehn, 1905; Kudo, 1919, 1926; Davis, 1923; Dunkerly, 1925).

Recently, the writers have encountered several specimens of *Cyprinodon variegatus* Lacépède with large myxosporidial tumors of the body. This has afforded the opportunity of making a study of various histological responses of the host resulting from such an infection. It is recalled that this disease was first noted by Linton (1889) in sheepshead minnows caught at Woods Hole, Massachusetts. Gurley (1891) definitely allocated the parasite causing the tumors and named it *Myxobolus lintoni*. In 1894, he gave a more detailed description of the species. Similar parasites and tumors were observed by Hahn (1913).

#### MATERIAL AND METHODS.

The infected *Cyprinodon* were caught at Sandy Hook Bay, New Jersey, and the Connecticut River. The tissues were fixed in 10% neutral formalin, and embedded in paraffin after decalcification. These were then sectioned at 3-10  $\mu$  thick and stained with Giemsa's, Wright's, hematoxylin-eosin and Masson's special connective tissue stain. An examination of the spores in these preparations showed them to be *Myxobolus lintoni* Gurley.

#### DESCRIPTION OF THE PARASITES.

*Vegetative Stages.* Histological examination of the tumors revealed many stages in the development of the parasite. Although an occasional



spore was found free in the lumen of the intestine, there was no evidence of sporoplasm or multiplicative stages in the gut-epithelium. The tumors themselves are composed of enormous numbers of spores and vegetative parasitic masses surrounded by host tissues (Figs. 4-7). These masses vary as to number. Thus in certain flat tumors (Fig. 1), there are only a few present and more or less widely scattered. In more rounded pendant types of tumors (Figs. 2 & 3), the vegetative groups are numerous but are situated mostly at the base or the periphery near the body wall. The parasites towards the surface of the growths are usually fully developed spores. The size and shape of the circumscribed vegetative masses also vary a great deal. A few are spherical, measuring from  $30\ \mu$  to  $66\ \mu$  in diameter. The majority of them, however, are oval and range in size from  $18 \times 29$  to  $62 \times 128.7\ \mu$ .

Each vegetative mass demonstrates clearly various stages in sporogenesis. In the larger groups may be found sporonts with two, four and six nuclei and minute basophilic staining granules in the cytoplasm, or young spores with a nucleus at the base of each polar capsule and two or four nuclei in the sporoplasm, depending upon whether or not the shell is developed. In these young spores, the polar filaments are in the form of basophilic granules aligned spirally. Scattered throughout the vegetative masses may be found nuclei of different forms together with degenerating host tissue. Other large circumscribed masses contain only matured spores (Fig. 7), many with but a single nucleus in the sporoplasm. In smaller masses ( $10$ - $15\ \mu$  in diameter) trophozoites with many nuclei are present. According to Kudo, and other investigators, the larger of the nuclei are vegetative, while the smaller become generative nuclei. The latter are "budded" off with a small bit of cytoplasm and become the sporonts. The nucleus of the sporont divides several times until, in this species at least, six nuclei are produced. Such cells have basophilic granules in the cytoplasm. These may be discarded nucleoli; a phenomenon previously reported for other Myxosporidia (see Kudo, 1926). In so far as could be determined, the sporont at this stage becomes transformed into the definitive spore. It is assumed that in the final stage of sporogenesis two nuclei are used in the formation of the polar capsule, two for the shell and two remain as the nuclei of the sporoplasm. Therefore, unlike the majority of forms belonging to the genus *Myxobolus* the pansporoblast of *M. lintoni* gives rise to a single spore, instead of two or more.

*Spore.* The present observations on the fully developed spores agree with those of Linton and Gurley, except in size. The measurements given by Gurley and also used by Kudo (1919) are as follows: length  $13.9\ \mu$ ; breadth  $11\ \mu$ ; thickness  $8\ \mu$ . Certain of our measurements agree with those given by Gurley, but the average size, for over 200 spores taken at random, is slightly smaller than those given above, measuring  $10.96 \times 7.47 \times 6.46\ \mu$ . The extreme measurements are as follows: length  $9.13$  to  $14.9$ ; width  $4.98$  to  $10.40$ ; thickness  $4.15$  to  $7.47\ \mu$ . However, the smaller size recorded here for *Myxobolus lintoni* is no doubt partly due to shrinkage following fixation.

The spores (Fig. 7) are oval in shape. The shell is more or less thick and with a fairly marked sutural ridge. There are two polar capsules, having an average measurement of  $4\ \mu$  in length and  $2\ \mu$  in width. The sporoplasm usually contains two nuclei and a large "iodinophilous" vacuole. The more mature spores have but a single nucleus which, according to Kudo (1931), is the result of a fusion of the two nuclei of the younger spore.

With Masson's stain the shell, capsule and vacuole of the sporoplasm are colored green; the polar filaments and sporoplasm are colored red; while the nuclei take on a deeper red color.

Although the organisms are usually localized in the tumor mass, an occasional spore was found in the lumen of the intestine, on the gills, in the liver, kidney and external to the meninges of the cord. None of these spores resemble the species reported by Davis (1917) as *Myxobolus*

*capsulatus* which was found in the visceral connective tissues of *Cyprinodon* from Beaufort, North Carolina. According to this investigator, *M. capsulatus* is present in a state of diffuse infiltration, and differs from *M. lintoni* mainly in having longer polar capsules, almost two-thirds the length of the spore.

#### DESCRIPTION OF THE TUMORS.

As was previously mentioned, two types of tumors were encountered. Fig. 1 shows the flattened type with the overlying skin slightly ulcerating and pigmented. Figs. 2 and 3 demonstrate the large pendant types of tumors. The fish in Fig. 2 measures about 4 cm. in length. The tumor is situated on the dorsal surface of the body and measures 8 x 10 mm., the upper border extending above the surface of the body. The fish in Fig. 3 is 4.24 cm. in length and the tumor, irregular in shape, measures approximately 1 x 1.2 cm. This is situated behind the left pectoral fin and extends dorsally for about one-half the body width. The ventral border of the tumor reaches about 4 mm. below the surface of the body. In the last two fish, the skin appears to be sloughed off, while the tumor of the fish in Fig. 3, is beginning to show signs of ulceration.

In most of the microscopic preparations the loss of the epithelium covering the surface of the growths is apparent. The external boundary of the tumors consists of a single layer of elongated flattened melanophores (Fig. 6, p). These pigment cells are of the usual corial type found in this fish, normally lying under the transparent epithelium. It is immediately below this narrow outer layer of pigment cells that characteristic changes of host tissue occur (Figs. 4-15). The diffusely scattered spores and vegetative masses of varying sizes are embedded in a meshwork of delicate fibroblasts of the host. As was previously mentioned, the diffuse arrangement of the spores is more frequently encountered near the free surface of the tumor, whereas the circumscribed collections of spores or vegetative stages are more numerous near the base or the mesial aspect of the tumor. It is in the deeper parts of the growth that the fibroblastic response of the host is most marked. Many delicate spindle-shaped, irregular or often stellate forms of fibroblasts are loosely arranged between the parasitic masses forming a stroma of the tumor which separates and supports the circumscribed collections of the organisms (Fig. 6, fi). It is only rarely that the connective tissue stroma takes on a denser appearance (Fig. 8). Lying in the stroma are occasional polynuclear cells, lymphocytes, eosinophiles and mast cells. This leucocytic inflammatory reaction is a very mild one, and there is practically no evidence of necrosis. The connective tissue stroma contains also a few melanophores which perhaps have migrated into the mass of Myxosporidia (Figs. 8 and 10, p). Bacteria, bacilli and a few cocci, may be seen near the surface of some of the myxosporidial tumors. These doubtless represent a secondary infection.

In most microscopic fields there co-exists with the fibrous stroma, a serous or albuminous substance staining faintly pinkish with eosin in which Myxosporidia lie scattered (Fig. 9).

The vascular supply of myxosporidial growths consists of a very fine network of capillary blood vessels, very often only wide enough to permit the passage of a single file of red blood cells. In some fields a few erythrocytes lie in the tissue spaces outside the lumen of the capillaries. These cells are normal in appearance, and indicate a mild form of extravasation of blood. No hemorrhages of importance were noted. A few small nerve trunks were found in areas involved in myxosporidial infection, but these did not seem to be affected by the diseased conditions.

The tumors of *Cyprinodon* are not encapsulated, as an irregular infiltration by the organisms into adjacent structures occurs along the margins of



these growths. Myxosporidia gain access to the deeper lying muscular structure by penetrating through the relatively dense external limiting fascia which normally separates muscles from the layers of the skin (Fig. 10, f). The fibers of this fascial structure become fragmented and split in the longitudinal direction into finer bundles between which Myxosporidia in small groups are found. Organisms which collect below the level of the external limiting membrane spread out along the fibrous septa which separates muscle bundles. This streaming infiltration along intermuscular septa is shown in Fig. 11. In some places the vegetative masses were found well organized in the fibrous tissue separating groups of muscle fibers (Fig. 12). Where the diseased process is advanced, atrophy, loss of striation, hyalin degeneration and necrosis of muscle fibers may occur (Fig. 12, n). In the sections examined we have found no evidence of spores or vegetative stages lying directly in the individual muscle cells as reported by Hahn (1913).

In microscopic sections prepared in the region of the body cavity of one fish, there were found certain areas where a penetration of organisms through the pigmented peritoneal lining had occurred (Fig. 13). This was usually only a slight involvement of the peritoneum, and interestingly enough, was not associated with an inflammatory exudate. The normally densely massed pigmented cells of the peritoneum were disarranged so that groups of melanophores were seen separated by collections of Myxosporidia. Although this penetration of myxosporidial tumor had occurred immediately in the region of the liver, an infiltration of liver substance had not taken place to any extent, as only a very few spores could be identified in the liver tissue.

Partial destruction of scales in the diseased regions was not uncommon. Bony tissue and cartilage, when lying in a myxosporidial growth, were found surrounded and infiltrated by spores (Fig. 14). This was particularly true in the case of spongy bone, where the meshes between the bony spicules were filled with varying numbers of spores (Fig. 15). Here and there the bony spicules appeared degenerated and necrotic.

#### DISCUSSION.

Microscopic tissue changes caused by myxosporidial infections have been described by previous investigators, and have been referred to in the introduction. The present studies are restricted to material obtained from Sandy Hook Bay, New Jersey, and the mouth of the Connecticut River. These fish were caught during August and the early part of September, 1937, in the two locations about 100 miles apart. The lesions in the fish from both localities were similarly advanced and much the same in character and distribution. It became apparent, after microscopic studies, that there was a mild general infestation in each fish examined, as indicated by the occurrence of spores in the liver, kidney, on the gills and in the lumen of the intestine. In these organs no histological lesions were evoked. Contrasting with this, the skin and subcutaneous lesions were most extensive, as there resulted in these regions relatively large tumor masses. Here the Myxosporidia were seen as diffuse spores or as circumscribed vegetative masses in various phases of development and embedded in a delicate meshwork of fibroblastic tissue varying somewhat in density. This meshwork of fibroblasts, with its rich capillary blood supply, represents one of the major responses of the host to the myxosporidial infection. Associated with it there occurs a wide-spread exudate which stains a light pinkish color with eosin and thus resembles a serous or albuminous material. In certain areas, the exudate exists as a homogenous substance in which spores and vegetative masses lie free. In other places, it is granular or appears to contain fine threads not unlike fibrin. The exudate accompanies fibrous tissue organization. It is least conspicuous where the fibro-

blastic network is most highly developed and condensed. The fact that the exudate is present at sites without fibroblastic development suggests the possibility that it precedes the fibrous organization of the tumors.

The spread of the myxosporidial parasites from the subcutaneous region to the muscles of the body wall is accomplished by their passing between the loosened fibers of the external limiting fascia. Intermuscular fibrous septa form pathways for the parasites to reach the deep seated musculature and the peritoneum. In one specimen a limited involvement of the peritoneum had occurred.

Myxosporidia infecting intermuscular fascia may result in the degeneration of muscle tissue itself. This is evidenced by the loss of striation, hyalinization and atrophy of the fibers.

Bony and cartilaginous structures, interposed in the spread of the infection, are surrounded and infiltrated by spores and may become necrotic.

A secondary invasion of bacteria, which frequently occurs, may contribute to bring about destruction of various tissues infected by Myxosporidia.

#### SUMMARY.

1. Several specimens of *Cyprinodon variegatus* were found showing tumors caused by the Myxosporidian, *Myxobolus lintoni* Gurley.

2. Certain stages in sporogenesis are reported and the morphology of the spore redescribed.

3. In so far as could be determined, the sporont of *M. lintoni* gives rise to a single spore.

4. This sporont has six nuclei and several discarded nucleoli in the cytoplasm. As in many Myxosporidia, two of the nuclei probably give rise to the polar capsules, two to the shell and two remain as the nuclei of the sporoplasm.

5. With Masson's special connective tissue stain the shell, capsule and vacuole of the sporoplasm are colored green; the polar filaments and sporoplasm are colored red; while the nuclei take on a deeper red color.

6. Various histological changes in the host tissue due to the infection with *Myxobolus lintoni* are described.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Live *Cyprinodon* taken at Sandy Hook, N. J. This fish shows flat myxosporidian tumors.
- Figs. 2 & 3. *Cyprinodon* with large pendant types of myxosporidian tumors. Killed and fixed specimens taken from Sandy Hook.

## PLATE II.

- Fig. 4. Low power photomicrograph through the myxosporidian tumor of the skin. x 40. Stained with Giemsa.
- Fig. 5. A slightly higher magnification of the tumor shown in Fig. 4. Note the vegetative parasitic masses in the deeper parts of the tumor. x 75.

## PLATE III.

- Fig. 6. Tumor showing circumscribed vegetative parasites and spores. Note the fine network of fibroblasts (fi) between the parasitic masses. Outer surface lined by pigment cells (p); the epidermis has disappeared. About x 250.
- Fig. 7. Fully developed spores of *Myxobolus lintoni*. x 1500.

## PLATE IV.

- Fig. 8. Fibroblastic response of the host supporting vegetative, parasitic masses. Note that in this section the fibroblasts (fi) are denser than those shown in Fig. 6. A large single melanophore (p) with its dendrites may be seen in the center. No albuminous exudate present. x 375.
- Fig. 9. Section showing a single vegetative mass with developing spores. A few solitary spores are present in the adjacent albuminous or serous exudate. About x 500.

## PLATE V.

- Fig. 10. Low power photomicrograph showing extension of the myxosporidian parasites through the loosened external limiting fascia (f). (m), muscle layer. (p), pigment cells. x 90.
- Fig. 11. Section showing spores scattered along the intermuscular fibrous tissue. (m) muscle. x 375.

## PLATE VI.

- Fig. 12. Section showing infiltration of intermuscular connective tissue by the myxosporidian parasites. (n) necrotic muscle fibers. x 90.
- Fig. 13. Fragmentation of the pigmented peritoneum by Myxosporidia. About x 375.

## PLATE VII.

- Fig. 14. Myxosporidia surrounding bony spicules (b). x 100.
- Fig. 15. Infiltration of spongy bone by the spores of *Myxobolus lintoni*. x 750.



FIG. 1.



FIG. 2.



FIG. 3.

TISSUE RESPONSES OF *CYPRINODON VARIEGATUS* TO THE MYXOSPORIDIAN  
PARASITE, *MYXOBOLUS LINTONI* GURLEY.





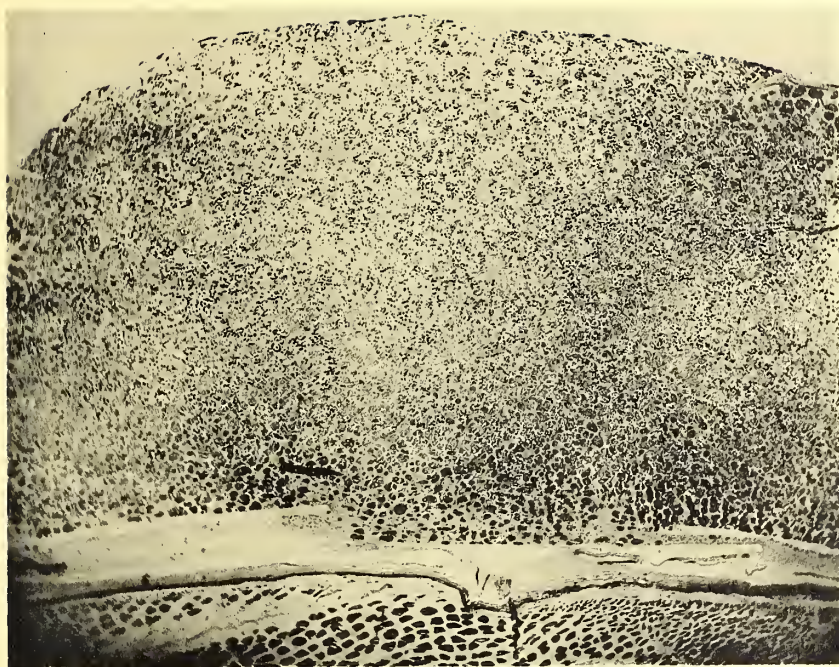


FIG. 4.

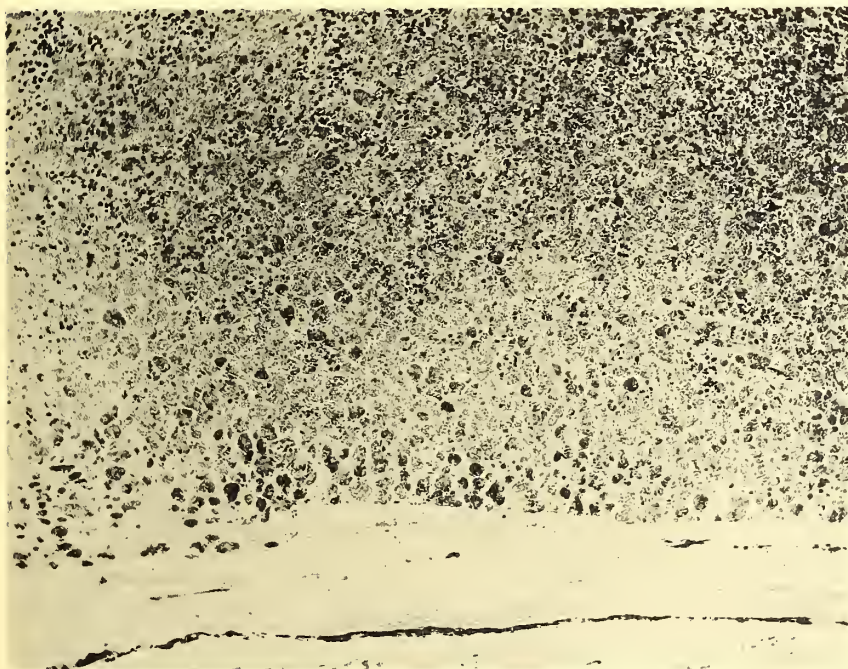


FIG. 5.

TISSUE RESPONSES OF *CYPRINODON VARIEGATUS* TO THE MYXOSPORIDIAN  
PARASITE, *MYXOBOLUS LINTONI* GURLEY.



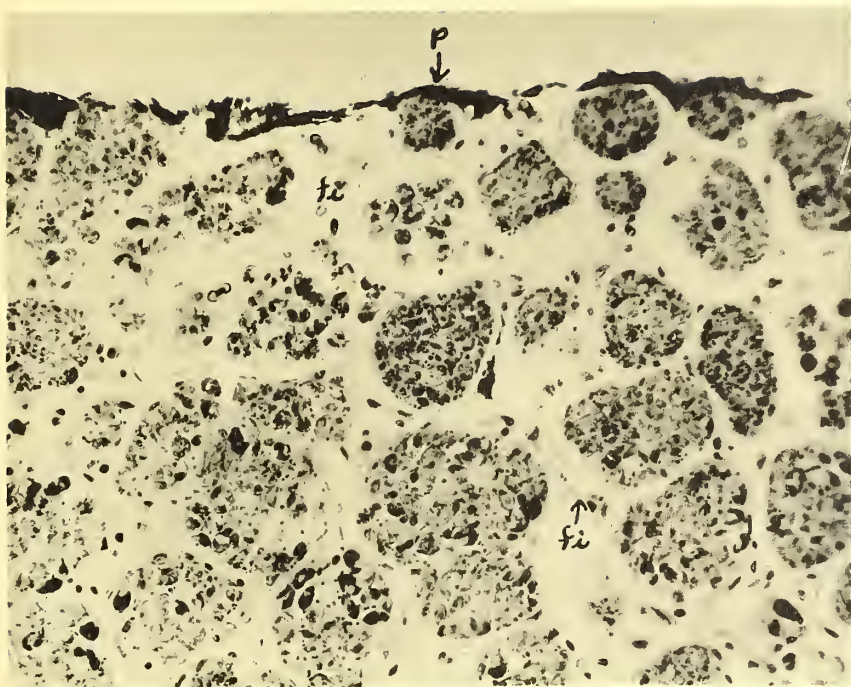


FIG. 6.

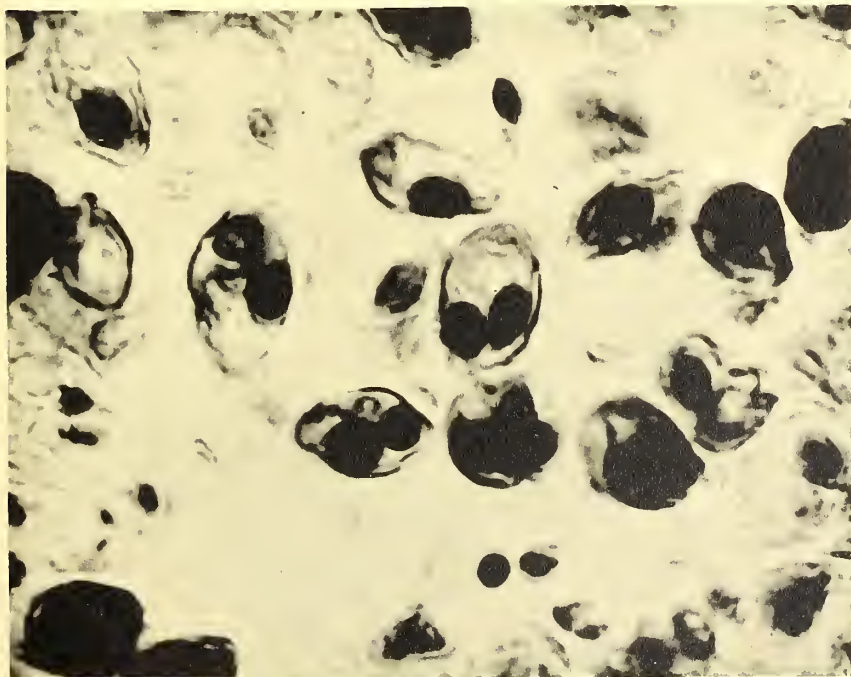


FIG. 7.

TISSUE RESPONSES OF *CYPRINODON VARIEGATUS* TO THE MYXOSPORIDIAN  
PARASITE, *MYXOBOLUS LINTONI* GURLEY.





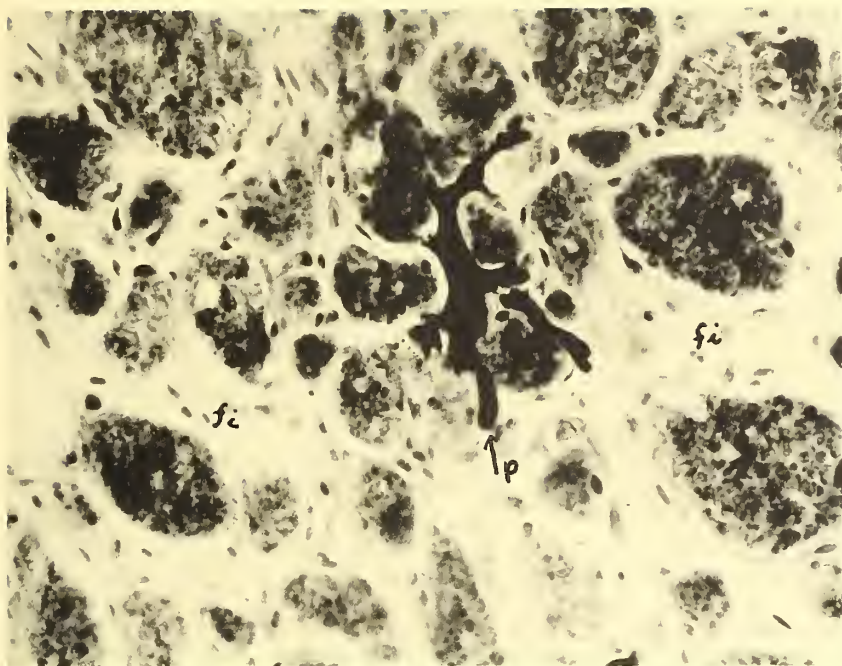


FIG. 8.

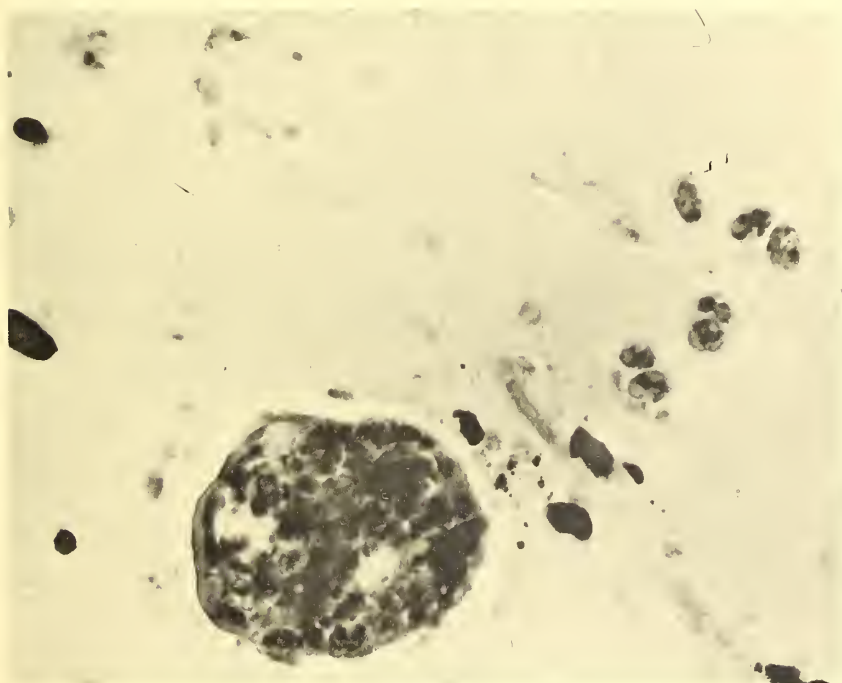


FIG. 9.

TISSUE RESPONSES OF CYPRINODON VARIEGATUS TO THE MYXOSPORIDIAN  
PARASITE, MYXOBOLUS LINTONI GURLEY.



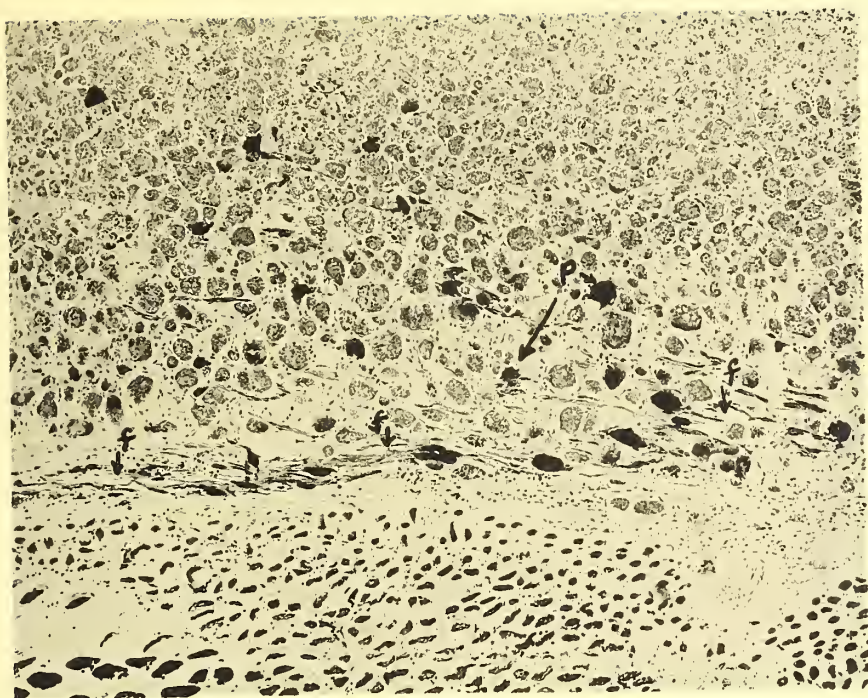


FIG. 10.

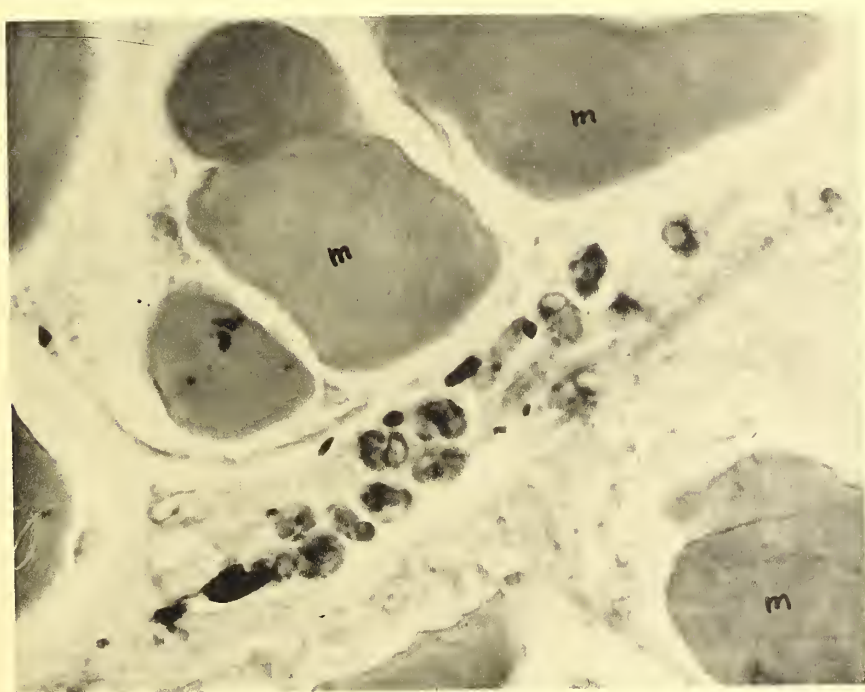


FIG. 11.

TISSUE RESPONSES OF *CYPRINODON VARIEGATUS* TO THE MYXOSPORIDIAN  
PARASITE, *MYXOBOLUS LINTONI* GURLEY.





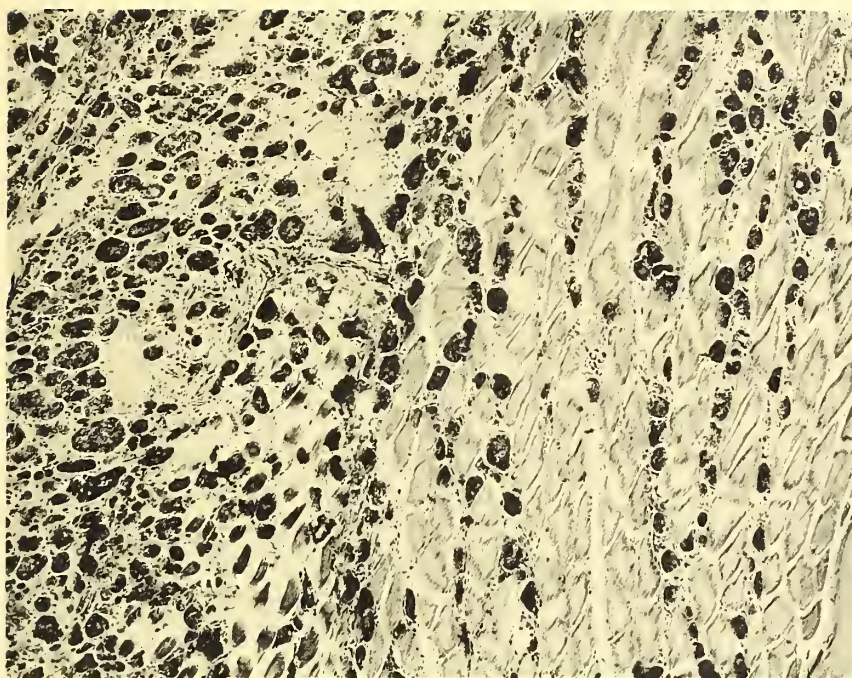


FIG. 12.

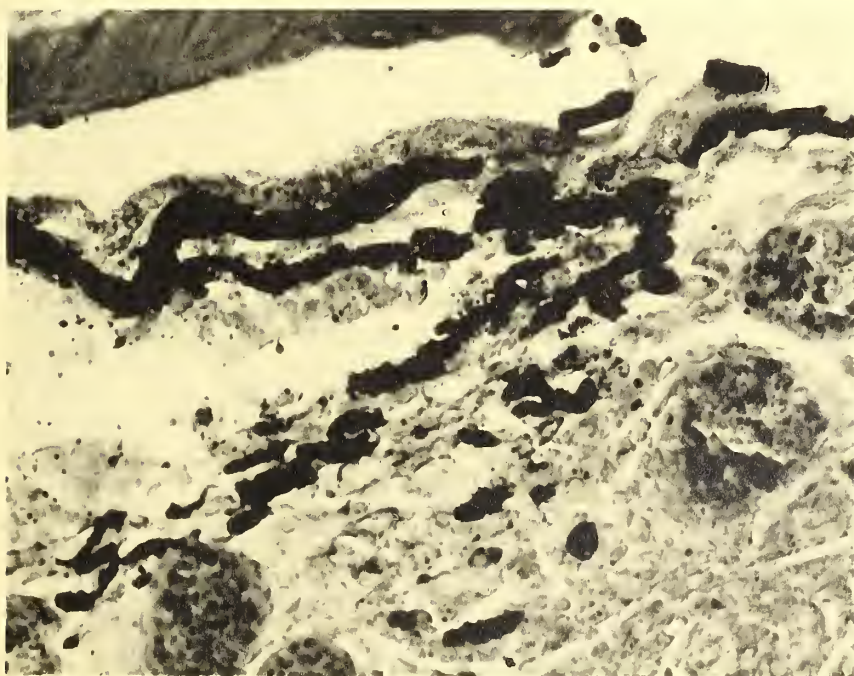


FIG. 13.

TISSUE RESPONSES OF *CYPRINODON VARIEGATUS* TO THE MYXOSPORIDIAN  
PARASITE, *MYXOBOLUS LINTONI* GURLEY.



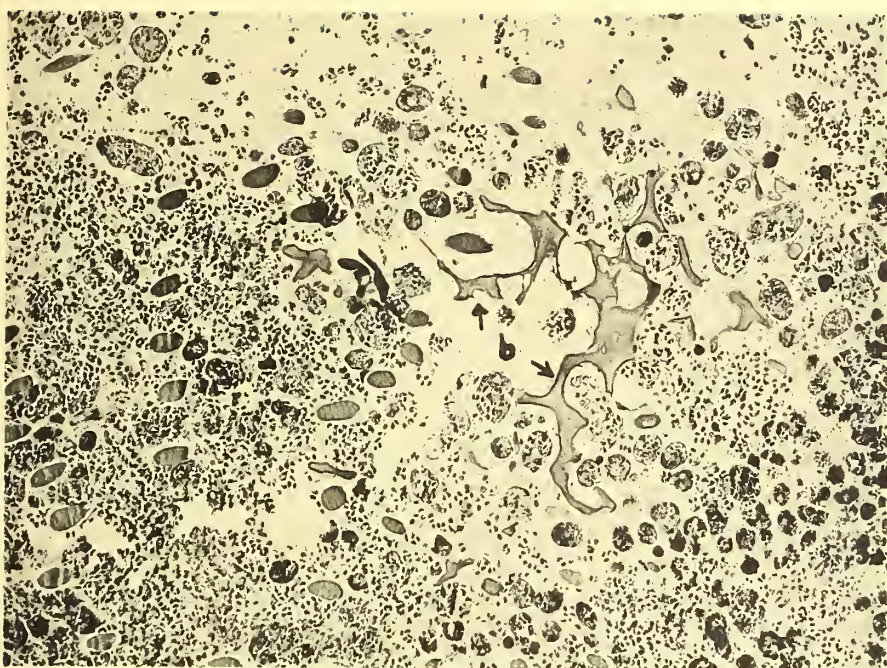


FIG. 14.

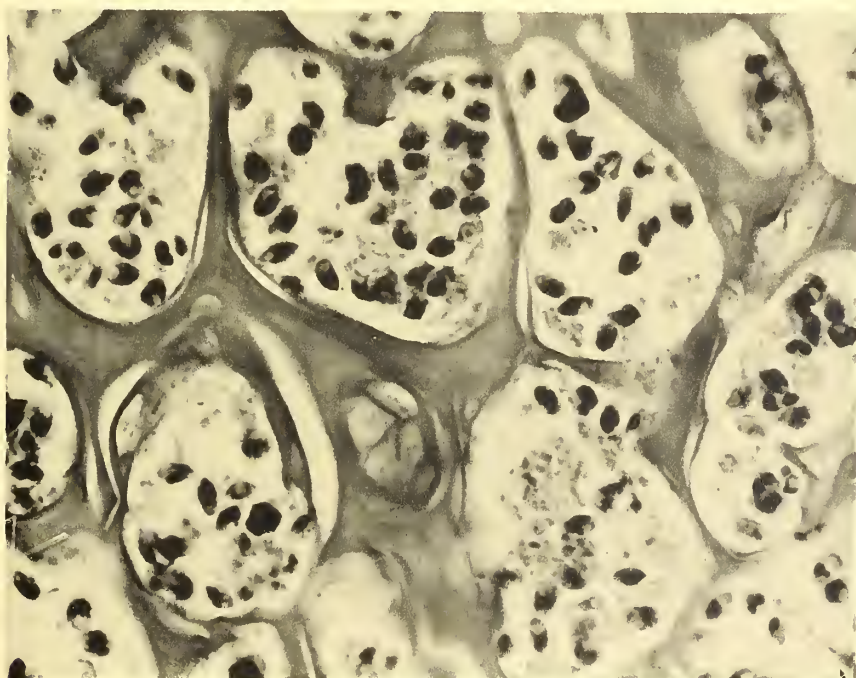


FIG. 15.

TISSUE RESPONSES OF *CYPRINODON VARIEGATUS* TO THE MYXOSPORIDIAN  
PARASITE, *MYXOBOLUS LINTONI* GURLEY.







## 8.

Electrical Characteristics of the Electric Tissue of the Electric Eel,  
*Electrophorus electricus* (Linnaeus).

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*New York Aquarium*

(Plate I; Text-figures 1 &amp; 2).

A previous paper<sup>1</sup> by the present authors jointly with L. P. Granath described observations made with a cathode-ray oscillograph of the discharge of the electric eel. In that work two types of discharge, the "major" and "minor," characterized by repeatable peak voltages, were identified as the discharges of the large organs and the organs of Sachs respectively. Other discharges, of indefinite peak voltage but identified by their occurrence only between a minor and an ensuing train of major discharges, were assigned to a third type under the name "intermediate," and were tentatively associated with the organs of Hunter. Observations made with external electrodes on the skin of the eel out of water showed that the major discharge runs along the large organ as a pulse of potential gradient at a speed of the order of 500 to 1,000 meters per second.

On the completion of this part of the work it was considered advisable to carry the research for a time to a place where the electric eel was plentiful and could be observed in the wild state or at least under nearly natural conditions. Accordingly an expedition was organized by New York University and the New York Aquarium. Its expenses were met by a generous grant from the Doctor Simon Baruch Foundation, for which we wish to express our gratitude. To the Goeldi Museum of Para, Brazil, we are indebted for a laboratory and facilities for the work, and to Dr. Haggmann and Snhr. Pira of the staff of the Museum we are particularly obliged for their constant kind assistance. Specimens for observation were supplied by Mr. Karl Griem. He and his associates, Messrs. Hory, and Weber, were most helpful. We should like to give our thanks also to the Brazilian Embassy in Washington, to Mr. George E. Seltzer and Mr. Reginald S. Kazanjian of the U. S. Consulate at Para, and to Dr. Eladio da Cruz Lima and a number of other residents of Para for facilitating arrangements for the expedition. To Mr. Robert S. Mathews and Miss Shelby Shackelford, members of the expedition, we are indebted for a great deal of varied assistance.

<sup>1</sup> Coates, C. W., R. T. Cox & L. P. Granath. The Electric Discharge of the Electric Eel, *Electrophorus electricus* (Linnaeus). *Zoologica*, Vol. XXII (Part 1), No. 1, April 5, 1937.

The observations made at the Goeldi Museum confirmed in general and extended those made earlier in New York. A report of them has been published in abstract.<sup>2</sup> In the present paper some of these observations are combined with others made later at the New York Aquarium. Whereas our first observations at the Aquarium were almost wholly concerned with the variation in the external voltage along the electric organs at different instants during the discharge, the present work undertakes to determine some of the electrical characteristics of the electric tissue and to make some inferences concerning the process of electric discharge.

It has long been surmised that the electric organ of electric fish is in some sort a battery of cells. Thus Faraday remarked of the torpedo:

"In concluding this summary of the powers of torpedinal electricity, I cannot refrain from pointing out the enormous absolute quantity of electricity which the animal must put in circulation at each effort. . . . These circumstances indicate that the torpedo has power (in the way probably that Cavendish describes) to continue the evolution for a sensible time, so that its successive discharges rather resemble those of a voltaic arrangement, intermitting in its action, than those of a Leyden apparatus, charged and discharged many times in succession."<sup>3</sup>

There is a variety of other evidence pointing to the same conclusion. The possibility of generation of electromotive force by the conversion of mechanical energy, as in an electrostatic or an electromagnetic generator, is precluded by the absence of any structure in the organ suitable to this conversion and by the observation that no muscular action is required for the discharge. The possibility that the discharge is generated by the thermoelectric effect is similarly ruled out by the lack of suitable structure and of the requisite differences in temperature.

There remain to be considered only electrochemical processes, and their consideration here is rendered reasonable by the fact that the minute electrical effects observed in nerve and muscle tissue have been convincingly ascribed by recent research to such processes. The voltages observed in nerves and muscles have been identified as concentration potentials. The theory of their production is that the cell membrane is permeable to one ion of an electrolyte and impermeable to the other ion. If then the electrolyte is present in different concentrations on the two sides of the membrane, there will be a migration through the cell membrane of the ions to which it is permeable. The region on the side of lower concentration will thus acquire an electric charge of the sign of these ions and an equal charge of the opposite sign will be left on the other side. The ions which pass through the membrane will hinder the migration of other like ions by the electrostatic repulsion they exert on charges of their own sign, and in time an equilibrium will be reached characterized by a definite voltage across the membrane. This voltage is determined by the chemical valence of the diffusing ion, by the relative concentrations of the electrolyte on the two sides of the membrane, and by the temperature. These conditions being known, the voltage is calculable. In the case of the boundary of a nerve fiber, the relative concentration of potassium on the inside and outside of the fiber, as found by Fenn, Cobb, Hegnauer and Marsh,<sup>4</sup> would give rise at room temperature to a concentration voltage of 118 millivolts. This is much greater than the voltages actually observed in experiments with nerve, but the means of observation are not such as to reveal the maximum voltage.

The voltages observed in the discharge of the electric eel, on the other hand, are very much greater than the concentration voltage found across any single membrane. We have observed voltages as high as 500 between the anterior and posterior ends of the large electric organ, and voltages

<sup>2</sup> Cox, R. T. & R. S. Mathews. *Journal of Applied Physics*, Feb., 1938. (Abstract).

<sup>3</sup> Experimental Researches in Electricity. Everyman's Library Edition, London, 1922. Page 26.

<sup>4</sup> Cited by Erlanger & Gasser. *Electrical Signs of Nervous Activity*, Philadelphia, 1937. Page 134.

above 300 are common. Such voltages as these must be the sums of many concentration voltages. Each unit or electroplax of the electric tissue is divided by a vertical partition, and we suppose this partition is the boundary across which the concentration voltage is developed, so that each electroplax is a single concentration cell. E. du Bois-Reymond<sup>5</sup> gives the dimension of one electroplax of the large organ in the direction in which the electric polarity is developed as 0.1 mm., so that there would be about 100 cells to the centimeter. If the cells in line along the organ are all joined in series, the electromotive force (which is the voltage measured when no appreciable current is flowing) of the whole series is the sum of the electromotive forces of the separate cells. With 100 cells to the centimeter and 100 millivolts to the cell, an electromotive force of 10 volts would be developed in one centimeter. This is approximately what we measure near the anterior end of the large organs.

It seems then altogether probable that the electromotive force of the electric organs is that of a series of cells, in each of which there is developed a concentration voltage by the selective diffusion of ions through a boundary. The cells in any cross-section of the electric organ we suppose act in parallel. The electromotive force is not thereby increased, since a number of similar cells in parallel have only the electromotive force of each one of them. But when a parallel array of cells is joined to an external conductor, so that a circuit is made and a current flows, the total current in the external conductor is the sum of the currents in the cells. Thus we suppose that the parallel action of the cells of the electric organ serves to produce the large currents (of the order of one ampere at maximum) which we have observed.

We have now to account for the release of energy by the electric organ in brief transient discharges. Evidently the electromotive forces of the cells and their connection in series cannot both be maintained all the time, for if it were so, there would not be transient discharges, but at all times an electric current would flow in the water around the fish. Hence either the electromotive forces of the cells, or their connection in series, or possibly both, must be transient, existing only for the duration of the discharge.

The structure of the electric tissue seems adapted to a transient series connection rather than to a transient generation of electromotive force. The discharge at any part of the organ is evidently governed by the nerve branching to that part, for transection of the nerve cord stops the progress of the discharge down the organ at the point of transection. On the other hand, transection of the electric organ without injury to the nerve cord makes no appreciable difference in either the open circuit voltage or the rate of propagation of the discharge. There is an ending of a nerve fiber on the posterior face of each cell of the electric tissue. A fall of the resistance of the sheath of a nerve fiber during the nervous impulse is well established. It seems reasonable to suppose that, except during the discharge of the organ, cells adjacent along its axis are effectively insulated from each other by the high resistance of the nerve sheath, but when a nervous impulse reaches the end of a fiber the drop in this resistance makes an electrical connection between the posterior (electrically negative) face of each cell and the anterior (electrically positive) face of the cell next behind, so that there follows a progressive connection in series of the cells all along the organ.

Several observations on the discharge give qualitative evidence that the discharge is produced by a transient connection in series of cells with constant electromotive force rather than by the transient generation of electromotive force in cells permanently connected in series. If two points on the large organ are connected to the oscillograph with the circuit open,

<sup>5</sup> du Bois-Reymond, Emil. Dr. Carl Sachs Untersuchungen am Zitteraal *Gymnotus electricus*, Leipzig, 1881. Page 49.



so that no current flows except that which makes a circuit within the tissue of the eel, one of the most striking features of the oscillographic trace is the uniformity of the peak voltage throughout a long series of discharges. In this case, since the current flowing in the electric tissue must be rather small, the observed peak voltage must be near the full electromotive force. Thus it appears that the electromotive force, at least at the peak, is nearly the same in successive discharges. But when a circuit is made through the organ and an external conductor of low resistance, so that a large current flows, the peak voltages are observed to be less uniform. In this case, the peak voltage is the electromotive force less the drop in voltage caused by the dissipation of energy in maintaining a current through the internal resistance of the tissue. It appears then that, while the electromotive force is nearly uniform at the peaks of successive discharges, the internal resistance is somewhat variable. This would seem to lend some support to the hypothesis that the electromotive force is uniform not only at the peaks of discharges but also during and between them, the discharge being produced by a variation in the internal resistance such as would occur in the transient series connection of the cells.

Another evidence, more convincing than this, is obtained when the oscillograph is connected to two points near the posterior end of the large organ and the two ends of the whole organ are short-circuited by a low resistance. The voltage recorded by the oscillograph is the electromotive force of the segment included between the points of contact less the drop in voltage caused by the current which the electromotive force of the entire organ sends through this segment. The electromotive force of this segment alone would make the anterior end of the segment positive with respect to the posterior. The current flowing through the resistance of the segment would cause by itself a voltage in the opposite sense. Under the action of these two opposing voltages, the net voltage of the anterior end of the segment with respect to the posterior end will be positive or negative as the electromotive force in the segment is greater or less than the voltage drop caused there by the current. Moreover, since the discharge runs along the organ from anterior to posterior, the relation between these two opposing voltages may be different at different instants during the discharge, and the voltage recorded by the oscillograph may change sign, i.e., it may be diphasic. If so, the order in which the two phases occur will be just opposite according to whether it is the electromotive force or the resistance of the electric tissue which varies to produce the discharge. If the electromotive force varies progressively from anterior to posterior while the resistance remains constant, then, before the pulse of electromotive force has reached this segment near the posterior end, the current caused by the electromotive force of the anterior parts will have started in the entire organ and the negative phase of the discharge will be observed in the segment. Only later, when the electromotive force has been generated in the segment and has declined in the anterior parts, will the positive phase occur. On the other hand, if it is the resistance which varies progressively from anterior to posterior, the electromotive force remaining constant, no large current will flow until the resistance of the whole organ, including that of the entire posterior segment, has fallen to a low value. In this case, the voltage across the posterior segment will first become positive, as its cells are thrown into series by the falling resistance, and afterward will become negative, as the impulse reaches the posterior end of the organ, dropping the resistance there and so completing the circuit to allow the passage of a large current. When the observation is made, it is found that the voltage across the segment is first positive, rising sharply for a very brief time, then sharply falling and reversing. Consequently the hypothesis that the discharge is produced by a drop in the internal resistance is favored.





A circuit for the discharge was completed through a resistor and a battery, which could be connected either to reinforce or oppose the discharge of the eel through the resistor. It was necessary in making observations to connect the resistor and battery only briefly in the circuit. The repeated discharge of the eel through a low resistance not only produces the injury to the skin already mentioned but also, of course, exhausts the electric organs. The exhaustion shows itself, at least in eels of large size, not in an appreciable reduction of the peak voltage on open circuit but in a reluctance of the eel to discharge. The effects of connection to a battery are more striking. On being connected through a low resistance to a battery of voltage even considerably less than its own and with either polarity of connection, the eel becomes restive. If the connection is maintained, the peak voltage on open circuit declines and the form of the oscillographic trace is markedly altered, the peak becoming much sharper. The alteration persists for some time after the eel is disconnected from the battery. To avoid it in these observations, our procedure was as follows: The eel was made to discharge by gentle prodding. When it was discharging with some regularity, the resistor was thrown into the circuit by a button switch and the camera shutter was opened to photograph the screen of the oscillograph. As soon as traces of the discharge were obtained, the shutter was closed and the button switch released. Since the shutter was always open for the interval of several discharges, the traces of these discharges overlap on the photographs.

In Plate I, Figs. 1, 2 and 3, the resistance was 1,000 ohms. In Fig. 1 the battery voltage was 90 reinforcing the discharge of the eel. In Fig. 2 there was no battery voltage. In Fig. 3 the battery voltage was 90 opposing the discharge of the eel. A constant voltage between the terminals of the oscillograph does not show on the oscillographic trace. If the resistance of the electric tissue were constant during the discharge, the battery would add only a steady voltage to that of the electric tissue. If then the electromotive force of the electric tissue varied during the discharge in the same way for each of the three connections, the same trace would be obtained each time. On the other hand, if the internal resistance of the electric tissue varies during the discharge, the current produced in it by the battery will vary and also the contribution of the battery to the recorded voltage. Thus different traces will be obtained with the three connections. It will be seen that the traces in Plate I are different, the voltage being raised when the battery reinforces the electric organ and lowered when the battery opposes the electric organ. Hence we infer that the resistance varies in the discharge.

In Plate I, Figs. 4 and 5, as in Fig. 2, there was no battery voltage. Plate I, Fig. 4, is the trace of the discharge on open circuit, so that the external resistance was effectively infinite. In Fig. 2 the resistance was 1,000 ohms and in Fig. 5 it was 300 ohms. The current flowing in the organ is increased as the external resistance is lowered, and the drop of the observed peak voltage below the electromotive force is consequently also increased.

Using various battery voltages and external resistances, we have obtained traces of a large number of discharges, and from measurements on these we have undertaken to calculate for different instants during the discharge the values of the internal resistance of the segment of the electric organ employed in the observations, assuming the resistance changing and the electromotive force constant. For this calculation it was necessary to make some assumption concerning the leaking of current through the tissue of the eel adjacent to the electric organ. The paths followed by this current could doubtless be accurately represented in diagram only by a complicated network, but for purposes of rough reckoning we have employed the simple scheme shown in Text fig. 1(b). In this figure, E denotes the elec-

tromotive force of the electric tissue and  $R$  its resistance, which we assume changing throughout the discharge. The leakage path is represented by a single resistance  $r$ , shunting the electric organ. The electromotive force of the battery is denoted by  $E'$  and the external resistance by  $R'$ .

At the junction of the three resistances, the current,  $I$ , in the electric tissue unites with the current,  $I'$ , in the external part of the circuit to produce the current,  $i$ , in the leakage path, and we have:

$$i = I + I'$$

In the circuit comprising  $E'$ ,  $R'$ , and  $r$ , there is a drop in voltage  $I'R'$  through the resistance  $R'$  and a drop  $ir$  through the resistance  $r$ . These must together be equal to the electromotive force  $E'$  of the battery, for around the whole circuit the net drop in voltage must be zero. Hence we have:

$$I'R' + ir = E'$$

Similarly for the circuit comprising  $E$ ,  $R$ , and  $r$ , we have:

$$IR + ir = E$$

With these three equations we can eliminate the two currents,  $I$  and  $I'$ , and obtain for the third current,  $i$ , an expression in terms of the electromotive forces and resistances alone. This expression is:

$$i = \frac{ER' + E'R}{RR' + rR + rR'}$$

Except during the discharge, we suppose that  $R$  is very large. If this is so, the only appreciable current flowing when the organ is not discharging is that produced by the battery in a circuit closed through the external resistance  $R'$  and the leakage resistance  $r$ . If we denote by  $i_0$  the current flowing in  $r$  when the organ is not discharging, we have:

$$i_0 = \frac{E'}{r + R'}$$

The voltage between the terminals of the oscillograph is  $ir - E'$  during the discharge and  $i_0r - E'$  between discharges. (The resistance of the battery is low enough that the voltage between its terminals may be regarded as constant and equal to  $E'$ .) Hence the variable part of this voltage is  $ir - i_0r$ . This is the voltage as recorded on the oscillographic trace. If we denote this voltage by  $V$ , we obtain from the two preceding equations:

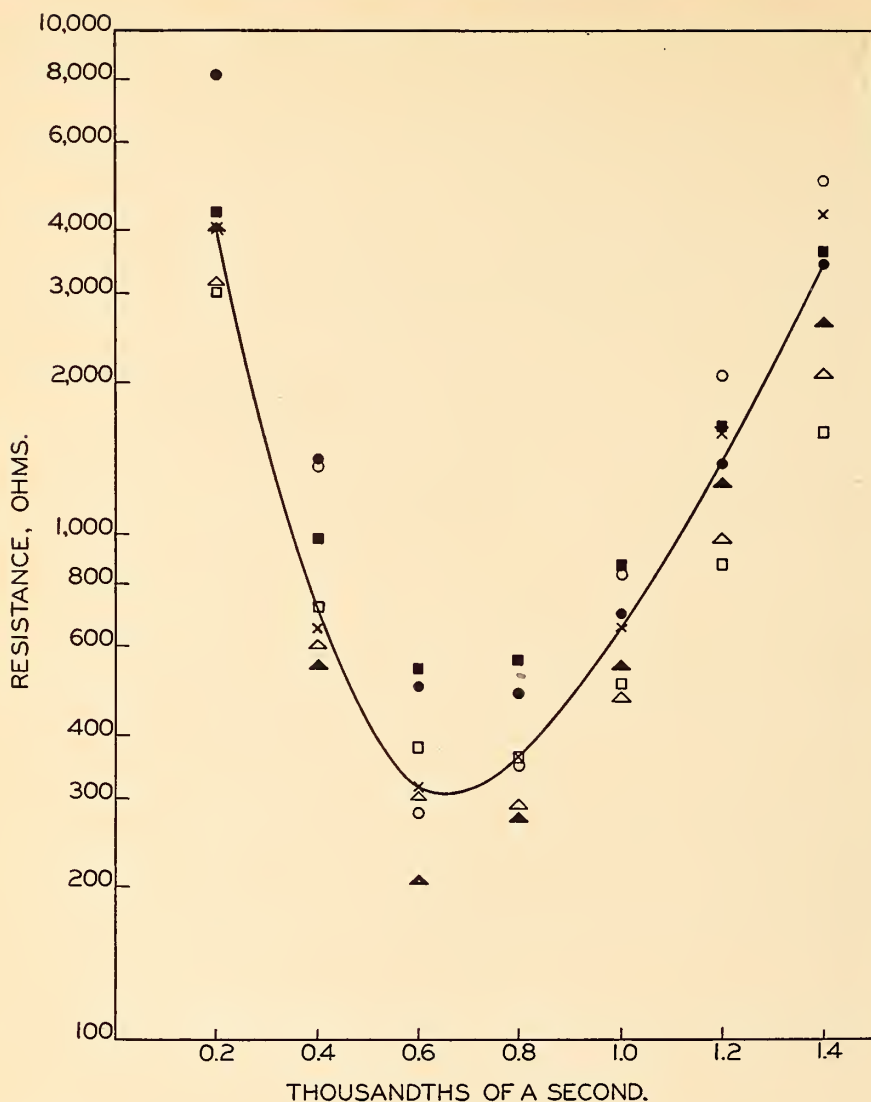
$$V = r \left\{ \frac{ER' + E'R}{RR' + rR + rR'} - \frac{E'}{R' + r} \right\}$$

Finally, if we solve this last equation for  $R$ , we obtain:

$$R = \frac{rR'}{r + R'} \left\{ \frac{E - V}{V} - \frac{E'}{V} \frac{r}{r + R'} \right\}$$

In this expression,  $E'$  and  $R'$  are known, being chosen at will by the connection of different batteries and resistors in the circuit, and  $V$  is the voltage measured on the oscillographic trace for any instant during the discharge.  $E$ , the electromotive force of the segment of the electric organ, and  $r$ , the leakage resistance of the adjacent tissue, are not directly given and values must be sought which will bring into the best possible agreement the values of  $R$  calculated for the same instant from different traces. In the calculations  $E$  was taken as 260 volts and  $r$  as 3,600 ohms.

The values of  $R$  calculated from a number of traces obtained with widely varying electrical connections are shown in Text-fig. 2. Each plotted point denotes an average of measurements made on the traces of from four to thirteen discharges. The traces of discharges obtained with the same connections are sometimes rather widely variant. Moreover the measurements could not be made with accuracy, by reason of the lack of high preci-



Text-fig. 2.

Resistance of a segment of the large electric organ at different instants during the discharge, calculated from voltages observed when the organ discharges through various circuits.

Open circles	.....	open circuit
Crosses	.....	external resistance, 1,000 ohms
Open triangles	.....	300 ohms
Open squares	.....	100 ohms
Solid circles	.....	battery voltage, 90 volts reinforcing discharge
Solid triangles	.....	157.5 volts opposing discharge
Solid squares	.....	202.5 volts opposing discharge
		External resistance, 1,000 ohms.

sion of the apparatus and also of the impossibility of finding at all closely on the trace the point corresponding to the instant at which the discharge



began. It will be observed that the extreme values of the resistance calculated for any instant during the discharge differ in most cases by a factor somewhat greater than two. On the other hand, in the observations from which the calculations were made, the net electromotive force acting was varied by a factor of about six and the effective resistance through which it acted was varied by a factor of about forty. Considering these wide variations in the experimental conditions, the inaccuracy of the observations, and the extreme crudity of the schematic representation in assuming the leakage current as flowing through a single resistance, we think the discrepancies in the results are not significant and we consider that the results confirm the general hypothesis from which the calculations were made. Our conclusion is then that the electromotive force of the electric tissue is almost certainly that of a series of concentration cells, that the discharge is very probably produced by a transient drop in the internal resistance of the electric tissue, and that this drop is probably an action of the nervous impulse at the ends of the nerve fibers which changes a virtual insulation between adjacent cells into an effective connection.

Two other observations seem worth noting. One of these is that the electric tissue is rectifying, that is, during the discharge, when its resistance to an electromotive force in the same direction as its own falls markedly, its resistance to an electromotive force in the opposite direction remains high. As the opposing electromotive force of the battery shown in Text-fig. 1 is increased, the discharge diminishes in voltage and at a certain value of the opposing electromotive force disappears altogether. A further increase in the opposing electromotive force, up to some 90 volts at least, produces no additional effect; discharge is not reversed.

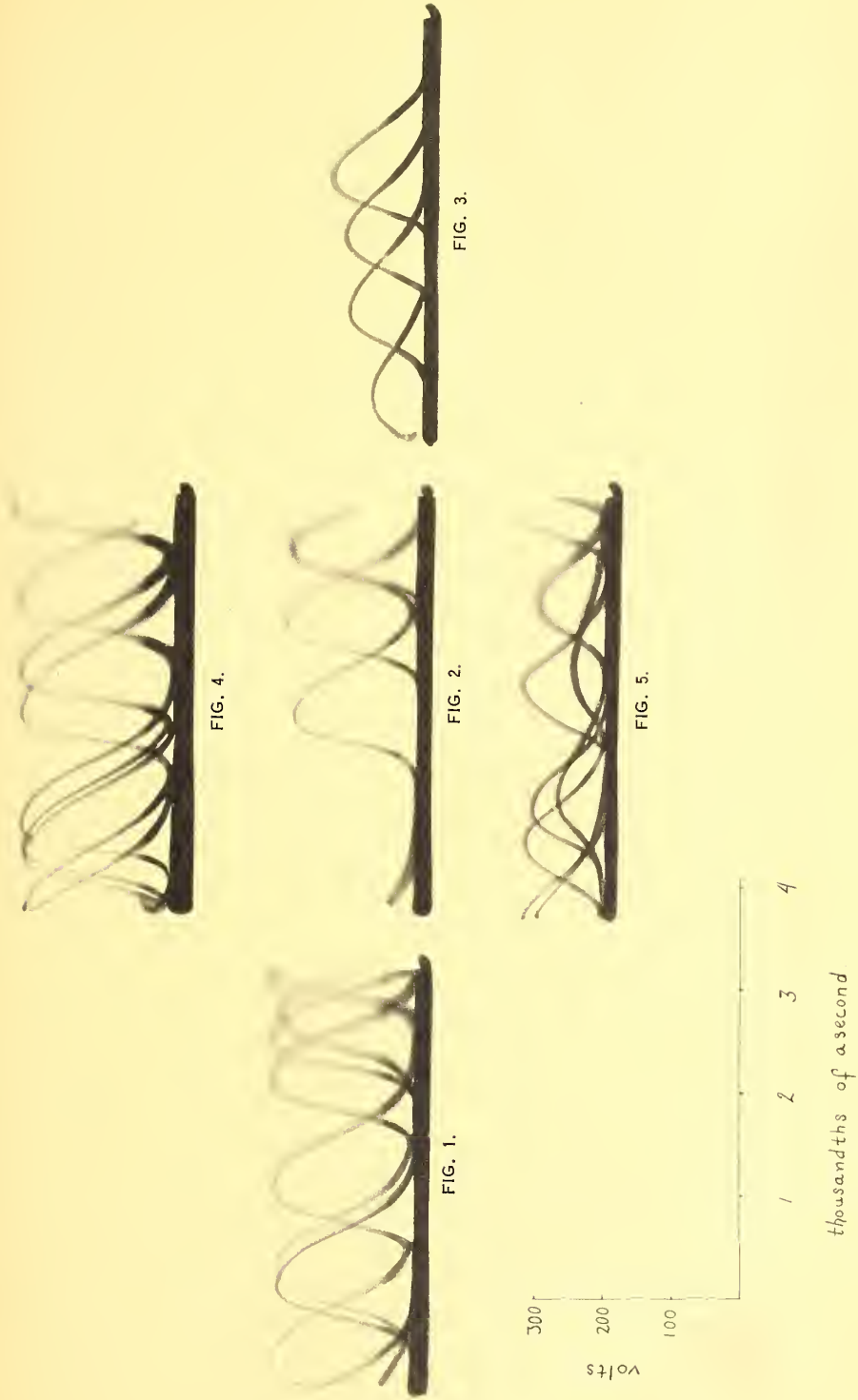
The other observation concerns the intermediate discharge. Since the major and minor discharges can be definitely attributed to the large organs and the organs of Sachs, and since the only other electric organs are those of Hunter, it seems natural to associate the third type of discharge with these. However, our observations on the discharge through various resistances indicate that this discharge has a power altogether out of proportion to the bulk of Hunter's organs. These organs, while nearly as long as the large organs, have a very much smaller cross-section. Consequently their internal resistance should be much higher and the voltage they could develop externally across a low resistance should be only a very small fraction of that developed in the major discharge. Plate I, Fig. 3, shows one and probably two intermediate discharges, those of the lowest and next lowest peak voltages. (They are distinguished from the major discharge by their more gradual fall as well as by their lower peak voltage.) The peak voltages of these two discharges, while definitely lower than those of the major discharges, are still relatively about as large as on open circuit. Consequently it would seem that only the large organs would have enough power to produce the intermediate discharge. It may be that the intermediate discharge is a discharge of the large organs modified, in some way of which as yet we have only a very vague idea, by the simultaneous discharge of Hunter's organs. On open circuit, the intermediate discharge has sometimes a spur before the main peak. This spur may show the discharge of Hunter's organs.

## EXPLANATION OF THE PLATE.

## PLATE I.

Oscillographic traces of the major discharge of a segment of the large organ with various electrical connections.

- |   |  |
|---|--|
| Fig. 1. Battery voltage, 90 volts reinforcing discharge   | } External<br>resistance,<br>1,000 ohms. |
| Fig. 2. No battery voltage                                |  |
| Fig. 3. Battery voltage, 90 volts opposing discharge      |  |
| Fig. 4. Open circuit.                                     |  |
| Fig. 5. External resistance 300 ohms, no battery voltage. |  |



ELECTRICAL CHARACTERISTICS OF THE ELECTRIC  
TISSUE OF THE ELECTRIC EEL.  
ELECTROPHORUS ELECTRICUS (LINNAEUS).





## 9.

## Colonial Rattlesnake Lore, 1714.

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The subjoined document,<sup>1</sup> here printed for the first time, is in all likelihood the fullest account before the Nineteenth Century of the characteristics and habits of rattlesnakes. The author was a Captain Walduck (probably Thomas Walduck<sup>2</sup>), who at an earlier time had sent to his friend James Petiver,<sup>3</sup> apothecary and Fellow of the Royal Society of London, eight letters concerning the trade, government, society, and natural curiosities of Barbados.<sup>4</sup> While at Barbados he had made wistful efforts to bring himself to the attention of the Royal Society; and in his "Account of the Rattlesnake," read before the Society January 7, 1714, he achieved his ambition. From a reference in the manuscript it appears likely that Walduck sent it to Petiver from New England.

The whole paper, presented with due solemnity before the most distinguished scientific society of the time, is an extraordinary collection of folklore pertaining to a creature almost as fictitious as the basilisk, the hydra, or the unicorn. One can imagine the honest Captain, full of inquiry and thirsty for scientific glory, noting down for the Royal Society of London the mendacities of Indians and fur traders. He displays no less assiduity in this task than his distinguished contemporary, the Reverend Cotton Mather, D.D., who in 1712 had contributed snake lore to the archives of the Royal Society. Why Captain Walduck's letter was not similarly honored by inclusion in the Society's *Philosophical Transactions* is not clear; perhaps the editors doubted the authenticity of the Captain's information.

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Capt Walducks Acct of y<sup>e</sup> Rattle Snake Read before  
y<sup>e</sup> Royall Society [word illegible] Jan: 7<sup>th</sup>. 171 $\frac{3}{4}$

The most pernicious Creature in y<sup>e</sup> English Empire upon y<sup>e</sup> Main of America is the Rattle Snake, as well for their Number as Effect, whose bite is as mortall as Fate, unless y<sup>e</sup> part be immediately cut out: beleiving it may not be unpleasant to you, I will describe as many of it's Qualities as I can,

<sup>1</sup> The MS. forms Number 21 (ff. 113b-116b) in Sloane MS. 3339 (British Museum), which is Volume VIII of the collections of James Petiver from 1691 to 1717, entitled *Adversaria*. See Samuel Ayscough, *A Catalogue of the Manuscripts Preserved in the British Museum* (London, 1782), II, 653; E. J. L. Scott, *Index to the Sloane Manuscripts in the British Museum* (London, 1904), p. 556.

<sup>2</sup> Tho. Waldock was appointed Register of the Court of Admiralty for the Bahamas, February 25, 1697 (*Calendar of State Papers, Colonial Series: America and West Indies*, 15 May, 1696-31 Oct., 1697, ed. J. W. Fortescue [London, 1904], p. 383). The Minutes of the Council of Barbados, March 16, 1703, refer to a lawsuit of Thomas Walduck (*Calendar of State Papers, Colonial Series: America and West Indies*, Dec. 1, 1702-1703, ed. Cecil Headlam [London, 1913], pp. 265, 771).

<sup>3</sup> Petiver's name appears frequently in *Philosophical Transactions* (see particularly XXII, 795). Regarding his collections see Sir Hans Sloane, *A Voyage to . . . Jamaica* (London), II (1725), iv-v.

<sup>4</sup> Of these the first appears to have been lost; the remaining seven are preserved in Sloane MS. 2302. The fourth is dated October 29, 1710, and the last September 17, 1712. In a letter from Barbados dated November 12, 1710, Walduck speaks of himself as having passed fourteen years in the West Indies, "and I support my self with the hopes of Seeing England once More" (Sloane MS. 2302, f. 16).

leaving y<sup>e</sup> Descriptions of its Parts to Surgeons & Anatomists. He is bred from an Egg an Inch & half long, & about y<sup>e</sup> bigness of a Mans little finger; y<sup>e</sup> Shell is of y<sup>e</sup> Colour of Parchment, & when first laid near as Tuff, & what surprized me, I found some of these Eggs once, & they hapned to be near Maturity to hatch, & I brake them with a Stick, & out ran a Snake all perfect, att least 7. inches long, & as big as a Goose-Quill, for they are quoil'd oblong in y<sup>e</sup> Shell, their head in y<sup>e</sup> middle & their Tayl on y<sup>e</sup> outside, & when they hatch y<sup>e</sup> Shell groweth dry, & they break it with their heads & come out: In Carolina & Virginia they engender in y<sup>e</sup> Month of Aprill (when y<sup>e</sup> Sun is near y<sup>e</sup> Tropick of Cancer, & warms y<sup>e</sup> Earth, & vivifies those dead Animalls buried in y<sup>e</sup> Winter) for a fortnight or 3 weeks together: In New-England & Pensylvania not untill May, or June; when they [*folio* 114] engender some Thousands of them gott together (I heard a man say he saw a heap as big as a hhd) some flying about others hissing & making a horrible noise, in a strange permiscuous manner—And this to me obviates a vulgar Opinion that there is a king among y<sup>e</sup> Snakes, in whose head is a Carbuncle that shines in y<sup>e</sup> night with wonderfull Lustre, & this is only y<sup>e</sup> Agrigation of their Eyes, by such a number getting together, their Spirits being high & volatile & full of venom, that by y<sup>e</sup> Reflection of water, or some such Accident gives such a light in y<sup>e</sup> Night as Travellers love to report) a little time after they lay their Eggs at y<sup>e</sup> Roots of dry Trees, amongst leaves & dry moss, where y<sup>e</sup> heat of y<sup>e</sup> Sun & Earth vivifies & hatches them, & in August young Snakes have been seen; their Eggs are laid like a chain 8. 10. 12. together if they lay but once or oftner is uncertain: at a year old they have a Rattle in their Tayls, & about 2 foot long & as bigg as a Mans thumb, & then they come to be deadly poysonous, so they shall grow to be 8. 10. 12 foot long & as bigg as a Mans thigh, & every year increases a Rattle (some belive they grow like y<sup>e</sup> Alligator as long as they live) there have been some kill'd with 24 Rattles in them, & it is beleived they do not exceed that age, they live upon Squirrells & all sorts of Birds that they can catch, & by a wonderfull Facination they shall charm them, both Squirrells & Birds into their mouths, from y<sup>e</sup> Top of a Tree 50 foot high, for they are a Slothfull heavy Creature (to other Snakes) otherways they could not gett their prey, they swallow all whole, for their bite is as deadly to themselves as to those they bite, as soon as they bite they apply themselves to a certain Root w:<sup>ch</sup> they eat & is an Antidote to their own poyson, by y<sup>e</sup> want of which they shall dye in an houres time by their own poyson [y<sup>e</sup> Indians [*folio* 114*b*] & some of y<sup>e</sup> English that trade amongst y<sup>e</sup> Indians know this Root & keep it always about them, & when they are bitt, they chew this Root & apply it to y<sup>e</sup> wound, by w:<sup>ch</sup> means y<sup>e</sup> Poyson will be expelled: y<sup>e</sup> Indians likewise have another Notion, or rather a peice of superstition as a Remedy ag.<sup>t</sup> y<sup>e</sup> bite of y<sup>e</sup> R: Snake that by painting a R: Snake upon their Bodies, they beleive y<sup>e</sup> Rattle Snake will not bite them, & several both Indians, & White men have Snakes drawn with black strokes most curiously upon their bodies: We may Quest:<sup>n</sup> whither this might not be taken from y<sup>e</sup> brazen serpent in y<sup>e</sup> Wilderness, & handed down to them by Tradition, or whither there might not be some Magick in it, for all Diabolical Magick came from Natural Magick (as all Idolatry is a Corruption of y<sup>e</sup> true Religion), as soon as they bite they run away, & they never bite but once, y<sup>e</sup> Experiment of their killing themselves by their own bite hath been tryed thus: An Indian hath been hired to bring in a Rattle snake (for there be some of them, & white men too, that will take up a Rattle snake as one would take up an Eel, & it hath been put into a Cask standing up with one head out, & y<sup>e</sup> Snake hath been provok'd by a stick to bite y<sup>e</sup> Stick, which it hath done, but could not be provoked to bite y<sup>e</sup> 2d time, & in an hour after hath died for want of this Root. Another Experiment of y<sup>e</sup> virulence of its Poyson hath been this a Snake hath been confined as above & by green switches their Rind being pealed off, y<sup>e</sup> Snake hath been provoked to bite y<sup>e</sup>



end of y<sup>e</sup> switch, & y<sup>e</sup> poyson hath been observed to run up y<sup>e</sup> switch, & turned y<sup>e</sup> green of y<sup>e</sup> switch [*folio* 115] to a blackness all y<sup>e</sup> way up to y<sup>e</sup> Top, this hath been tryed some score of times by several hands, & it is y<sup>e</sup> Nature of y<sup>e</sup> Poyson to ascend; for if a man be bitt by y<sup>e</sup> Snake in y<sup>e</sup> Arm, or Leg, lett him hold that part up higher than his body he shall live some days, but if it be below he shall not live 2 houres, but their body shall break full of large Chapps, & Crakks as if their Skinn had been roasted by y<sup>e</sup> Fire. The R. Snake cannot bite running, he must be quoiled round with his head in y<sup>e</sup> middle & then he will rise as high as his navel, & no higher & so chop to bite, Dogs that are used to them shall make them kill themselves by running round & baying at them, that by chopping att y<sup>e</sup> Dogg they have bitt themselves. Their Poyson lieth in som little bladder att y<sup>e</sup> Root of their two lower Tusks, which when they bite breaks & is squeaz'd out, & their is two socketts in their upper jaw to receive them, they never make use of them in their ordinary feeding but swallow all whole, their Stomach's are of a large Capacity young Fauns being taken out whole. The Indians never are in fear of them, nor will they be perswaded to kill any of them. The Indians believe that y<sup>e</sup> R. Snakes are y<sup>e</sup> Executors of y<sup>e</sup> Divine Vengeance, & that he that is bitt by them hath been a Murrderer, w:<sup>ch</sup> likewise was the Opinion of y<sup>e</sup> Inhabitants of Maltha when S:<sup>t</sup> Paul was shipwrek'd there according to y<sup>e</sup> sacred Text. Indeed they never do bite but when provoked, & a Man may as securely sleep in y<sup>e</sup> wood for them as in a feather bed. [*folio* 115b] They never bite but first make a Rattling with their tayls, & they may be heard 20 yards of. Those Men y<sup>t</sup> use y<sup>e</sup> Woods say they never come near a R. Snake but they are aprised of it before they either hear or see them, & they are in a fright as tho' a Spectre was near them, & that their breath inflames y<sup>e</sup> Air & before they either hear or see them they are seized with sorrow. So that y<sup>e</sup> Fiction of Phyton is verifys'd in y<sup>e</sup> Rattle Snake, or they are all one Creature, they are locked up all y<sup>e</sup> Winter in y<sup>e</sup> Earth, & when they first come forth in y<sup>e</sup> Spring they are weak & have lost all their Stock of poyson, & their bite is of no danger, untill by feeding & warm weather they are supply'd with fresh venom, & in a Month's time their bite shall become Mortall, & their venom is deadly lett it be lodg'd any where so long as y<sup>e</sup> Snake lives but not longer Experienced by y<sup>e</sup> Following History: A Man in Virginia being in y<sup>e</sup> Woods having a pair of boots on was bitt by a RSnake thro' his boot came home to his wife & dyed, his Boots were hung up in y<sup>e</sup> house, & his widdow married a second husband, who putt on those Boots, & by rideing a Small Journey complain'd with a pain in his Leg & likewise dyed, the Boots were hung up again, & y<sup>e</sup> Woman married y<sup>e</sup> third Husband, who made use of y<sup>e</sup> same Boots, & y<sup>e</sup> first time of wearing them complained as y<sup>e</sup> former of a small tumor in his legg & likewise died; Upon this y<sup>e</sup> Surgeon cutts y<sup>e</sup> boot in peices & found y<sup>e</sup> Tooth of y<sup>e</sup> Rattle Snake that bitt y<sup>e</sup> first Husband, & did all y<sup>e</sup> Execution since as small as a hair, they took it out with a [*folio* 116] pair of Forceps, & prick'd a dog with it that within few hours dyed, y<sup>e</sup> Surgeon took y<sup>e</sup> tooth some time after tryed it upon another Dog & it did him no hurt, & it was supposed then y<sup>e</sup> Snake was dead. Wherever y<sup>e</sup> English come & settle y<sup>e</sup> Snakes leave y<sup>e</sup> place in a little time, which keeps up y<sup>e</sup> superstition of y<sup>e</sup> Indians that there is some extraordinary virtue in y<sup>e</sup> English, when I can conceive no other Reason in it but by planting & weeding y<sup>e</sup> Earth, plowing & breaking up y<sup>e</sup> glebe, they eradicate y<sup>e</sup> Root out of y<sup>e</sup> Ground that is y<sup>e</sup> Antidote & self preservation to y<sup>e</sup> Snake against his own poyson, & therefore they are forced to leave y<sup>e</sup> place & go where it is to be found. They are not all over America, not to y<sup>e</sup> Southward of y<sup>e</sup> Tropick & to y<sup>e</sup> Norward of 55°, whither y<sup>e</sup> heat destroys them in one & y<sup>e</sup> Cold in y<sup>e</sup> other I am not Judge, there is none in y<sup>e</sup> Kingdom of Mexico amongst y<sup>e</sup> Spaniards, but they say they were once all over there & drove away by y<sup>e</sup> prayers of one of their Fryers; this is one of their Legends. We may say y<sup>e</sup>

same thing 100 years hence in N. England, a Man may live there 20 Years now & not see one, & in some Ages a RSnake will be as great a Rarity in N. England as a Wolf is now in Old England, tho' they were once very populous in each Country. There be Water R. Snakes as well as Land & as deadly in some Rivers in Virginia they shall creep up y<sup>e</sup> Calles of Shipps, & assault a boat when near y<sup>e</sup> Shore. there's abundance of Strange Reptiles in y<sup>e</sup> Woods in Virginia & Carolina Viper about 2 foot long more deadly than y<sup>e</sup> R. S. [*folio 116b*] but not so Common, & for whose bite y<sup>e</sup> Indians themselves know no remedy, & of which they stand very much in fear, there be likewise in y<sup>e</sup> Woods of Carolina Snakes made like a Coach whip as long & as small, that will twist their head round a horse's Leg, & with their Tayl Lash a horse with great Violence untill y<sup>e</sup> blood comes, there is like wise a Glass Snake about 2 foot long, & as green & as brittle as Glass, that if they happen to fall off a bough they will break as short as glass, & with a little switch it is more easye to break one of them than a Tobacco pipe, & what adds to y<sup>e</sup> Wonder they never bleed.

This is what I have learned (having particularly enquired) of y<sup>e</sup> Indians, & white Men conversant & Tradeing amongst y<sup>e</sup> Indians, & beleive most of this is Matter of Fact.



## NOTES

**External Parasites of the Electric Eel, *Electrophorus electricus* (Linnaeus).**

Two external parasites have been found so far on the electric eel, *Electrophorus electricus*. On one eel, measuring about five feet in length, numerous "anchor" parasites (copepods) were found embedded in the thick skin along the dorsal surface of the body. The copepods were identified as *Lernaecocera cyprinacea* L. and have been previously reported by many investigators from several species of cyprinid fishes. On September 30, 1937, five of the smaller eels (ranging in size from 18" to 2'6") were found to be heavily infected with leeches. More than 2,375 parasites were removed from one eel measuring 24½ inches in length. These leeches are the common *Placobdella parasitica* (Say) which are usually found on the soft parts of turtles, but which also have been reported on other fishes. When bearing eggs or young, the leeches often leave the host for a time and lead a free life underneath stones, and feed on worms and larvae.

The interesting thing about these infections is that the parasites were able to withstand the electric discharges of the eels. These discharges, according to Coates, Cox and Granath (1937)<sup>1</sup> may reach a voltage of 300 in eels exceeding 50 cm. in length. One 11½" eel gave off about 200 volts (Coates and Cox, 1936)<sup>2</sup>.

It is definitely known that the eels were discharging at the time the parasites were present.—ROSS F. NIGRELLI, New York Aquarium.

<sup>1</sup> C. W. Coates, R. T. Cox, and L. P. Granath (1937). *Zoologica* 22: 1-32.

<sup>2</sup> C. W. Coates and R. T. Cox (1936). *Zoologica* 21: 125-128.



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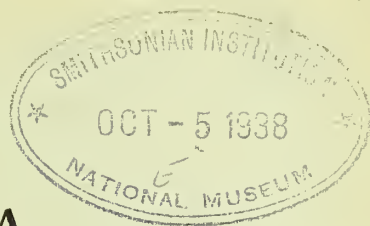
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## 10.

Morphology of the Hypophysis of the Common Goldfish  
(*Carassius auratus* L.).<sup>1</sup>

W. RANDAL BELL

Washington Square College, New York University

(Plates I &amp; II; Text-figures 1 &amp; 2).

There is much speculation concerning the possibility of pituitary-gonadal relationships in fish similar to those found in mammals. Implants and extracts of fish pituitaries have been found to cause a premature ovulation in fish, (Houssay, 1930, von Ihring, 1935) and an increase in gonad size (Cardoso, 1934). Noble, Kumpf and Billings (1936) have induced brooding behavior in the Jewel fish (*Hemichromis bimaculatus*) with injections not only of fish pituitary extracts but of sheep extracts and prolactin as well. Wunder (1931), Fleischman and Kann (1932), and Kanter (1934), have found the color and ovipositor length of the bitterling (*Rhodeus amarus*) to be affected by hormones from the fish pituitary but not by gonad stimulating hormones from the pituitary of mammals. Smith (1931), Zondek and Krohn (1932), Matthews (1933), Parker (1934), Zondek (1935), Hoggben (1936), and numerous other workers have studied the pigmentation effects caused by changes in the amounts of intermedin and other "chromatophorotropic" hormones. The effects of the physiological removal of the pituitary have been observed by Lundstrom and Bard (1932), Matthews (1933), Parker (1935), and Smith, Burr and Ferguson (1935). Recently Abramowitz (1937) has reported the successful removal of the pituitary of the catfish and the killifish, using an opercular approach. Examination of the goldfish gives reason to believe that such an approach would be efficacious in its hypophysectomy. However, an improved technique for this operation, especially one which would make possible a partial ablation, would be highly desirable.

It is the purpose of this investigation to demonstrate the anatomy and histology of the pituitary and its surrounding structures in a form of fish<sup>2</sup> well adapted to experimentation. *Carassius auratus* (the goldfish) was selected because it is highly adaptable to laboratory conditions and has an exceptional resistance to surgical shock. Also, its compact pituitary is suspended by a stalk which passes through a connective tissue membrane, covering a foramen in the brain-case floor. These protective structures should make it quite feasible to remove the gland without injury to the brain. It is hoped that the observations presented here will provide an adequate foundation for future investigations.

At this time, I wish to acknowledge the thoughtful guidance of Dr. Harry A. Charipper in the accomplishment of this work. I would also like

<sup>1</sup> Accepted in partial fulfillment of the requirements for the degree of Master of Science, New York University.

<sup>2</sup> A résumé and key references on the pituitary of various teleosts may be found in the symposium report of H. A. Charipper (1937).

to thank Mr. C. M. Breder, Jr., of the New York Aquarium for providing the laboratory facilities and for his helpful advice on the ichthyological aspects of the problem.

#### MATERIALS AND METHODS.

The specimens of *Carassius auratus* were obtained from commercial fisheries in Saddle River, New Jersey. Their over-all length varied from seven to eight inches, while their body length from the tip of the snout to the proximal border of the tail fin averaged five inches. Material for histological preparations was fixed between the end of December and the latter part of March. Most of this was from female animals.

For convenience, the fish were removed from the large main tank into small individual tanks before being used. All tanks were supplied with actively flowing tap water, which maintained a temperature of about 8° Centigrade. This water was cold enough to prevent any active maturation of the eggs in the ovaries.

The fish were taken from the water and rapidly anaesthetized by flooding the gills with chloroform. The roof of the cranium was removed first by cutting transversely through the dermal bone between the eyes, and continuing the incision through the dorso-lateral angles of the neurocranium. The entire roof was then lifted and broken away at its posterior margin. The neurocranium was then freed posteriorly by a transverse incision in the region of the medulla, and anteriorly by another incision midway between the olfactory lobes and the olfactory bulbs. Finally the entire neurocranium was separated from the rest of the animal by cutting through the opercular attachments and separating the gill bars from their cartilaginous attachments on the neurocranium. The optic nerves and muscles were carefully cut to avoid altering their relation to the pituitary. The neurocranium with the brain and pituitary were removed to the fixative. The whole procedure was accomplished in about three minutes.

Helly's, Bouin's and Zenker's fluids were employed for fixation. At first the crania from anesthetized fish were immersed in these for about seven-teen hours. Later it was found more desirable to kill the animals directly by injecting the fixing fluid through the thin medial wall of the olfactory pit into the cavity above the brain. The neurocranium was then rapidly removed as before and more fluid injected into the myodome near the gland before immersion. The fixation time was reduced to six hours by this procedure.

When the pituitary was to be sectioned alone, it was carefully removed from the cranium after fixation. All attempts to remove the brain and the pituitary together were unsuccessful, due to the fragile nature of the pituitary stalk and to the intimate relation of the endocranial membranes and the bone floor to the pituitary body. Specimens designed for sectioning of the neurocranium were decalcified for four hours in 10% solution of nitric acid in 70% alcohol. Sections of the pituitary were cut from 5-7 micra in thickness and those of the neurocranium at 10-15 micra. Serial sections, longitudinal, horizontal and transverse, were made of the pituitary in situ in the neurocranium and also of the gland alone. The Masson stains were used for cytoplasmic differentiation and Delafield's haematoxylin and eosin as a routine procedure. The latter technique was used for the anatomical preparations.

#### RELATION OF THE PITUITARY GLAND TO SURROUNDING STRUCTURES.

The pituitary body of *Carassius auratus* lies deeply embedded in the neurocranium. It does not occupy a sella turcica in the basisphenoid bone of the cranial floor as is the case in higher vertebrates. Instead, it lies in a tunnel-like cavity, the myodome, below the floor of the brain case (Plate I,



Fig. 1). This space is enclosed in the apex of the V-shaped neurocranial floor, just above the prominent parasphenoid or "keel bone" (Plate I, Fig. 4). The myodome extends posteriorly from the optic foramina to the region of the medulla, the pituitary lying near its anterior end.

The lateral walls of the teleost neurocranium in the region of the pituitary are formed by the proötic and alisphenoid bones. The alisphenoid bones extend forward and medially to form the walls and floor of the brain case proper in the region of the orbit. Posterior to the pituitary, the roof of the myodome forms the floor of the brain case. This is made up of two horizontal plate-like processes, extending medially from the proötic bones and fusing in the midline, forming the "proötische Brücke" of Holmgren and Stenzio (1936).

When viewed from above, a large oval optic-pituitary foramen may be observed in the floor of the brain case. The posterior rim of this is formed by the proötic bridge and the anterior, more dorsal rim by the alisphenoid bones (Plate I, Fig. 1). Its lateral edges are formed by delicate bony processes projecting from the lateral walls. A thin, tough extension of the endocranial membrane completely covers the foramen except where it surrounds the optic nerves and pituitary stalk as they enter the brain case (Plate I, Fig. 3). A sac-like fold of this membrane is reflected over the pituitary body, which lies immediately below the posterior half of the foramen. The optic nerves enter the myodome through the optic foramina, and then pass through the anterior half of the optic-pituitary foramen to reach the brain.

The pituitary body is placed dorsally in the myodome (Plate I, Fig. 4) above the rectus externus muscles of the eye, which enter this bony chamber ventral to the optic nerves. In transverse section, the muscles appear as two oval masses ventro-lateral to the pituitary. A medial bony septum rises from the parasphenoid a short distance between them.

The pituitary lies with its dorsally flattened surface pressed against the membrane covering the optic-pituitary foramen. Its posterolateral edge is enclosed by a cupping of the rim of the proötic bridge (Plate I, Fig. 3). Likewise the lateral edges of the foramen project past the sides of the gland. (Plate I, Fig. 2). The above three structures effectively separate the pituitary from the cavity of the brain case.

As a result of this separation, the pituitary is suspended from the brain by a short and heavy stalk. This solid process is about twice as wide as it is long in a transverse section (Plate I, Fig. 2). It rises in the midline from the floor of the hypothalamus at the posterior end of the lobus medialis. The latter is a small eminence of the lamina post-optica lying between the anterior ends of two large, oval lateral lobes, the lobi inferior (or mammillary lobes). These latter bodies are over-shadowed dorsally by the larger optic lobes (Plate I, Fig. 4). In a transverse section, the narrow, medial, slit-like cavity of the third ventricle may be seen to penetrate the ventral infundibular region for a short distance but it does not extend into the pituitary stalk.

No large blood vessels were observed entering the pituitary body, although a large vein occupies the angle formed by the posterior indentation of the pars intermedia (Plate I, Fig. 3). The membranes surrounding the gland contain a profusion of small vessels, which were frequently observed to penetrate the pituitary, especially in the region of the pars anterior. The gland, as well as the brain itself, lies in a semi-fluid fatty mass.

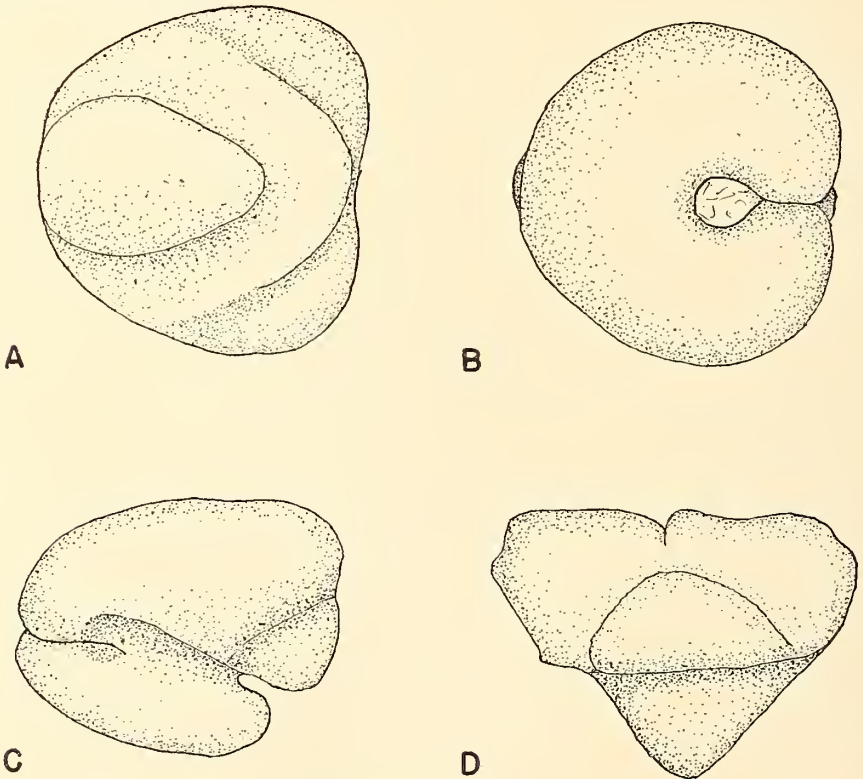
#### ANATOMY OF THE GLAND.

The pituitary in *Carassius* is an irregular, solid, rounded mass about 1.3 millimeters in length. Its form can best be appreciated by consulting

Text-fig. 1 showing sketches of its various aspects. From above (Text-fig. 1, B) it is almost circular with a flattened posterior side. A slight crevice connects the stalk with the posterior extremity. Ventrally and laterally (Text-fig. 1, A and C), it shows a rounded cone-shaped body projecting from the main mass of the gland. The apex of this cone-like portion of the intermedia points posteriorly and somewhat ventrally. The separation of this portion from the remainder of the pars intermedia is not always so pronounced.

The posterior aspect (Text-fig. 1, D) is almost triangular with the apex being formed by the cone just described. The dorsal, more massive, rectangular portion represents the übergangsteil and the remainder of the intermedia. This latter is faintly outlined as a central triangular portion.

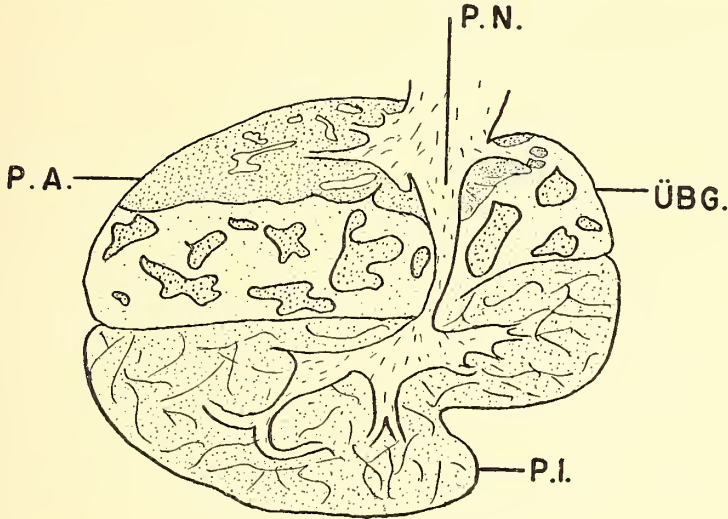
The pars intermedia is the most ventral portion and occupies somewhat less than one-half the volume of the gland. A crevice may be seen to separate this lobe from the übergangsteil everywhere except at the very core of the gland. In addition to the cone-shaped, antero-ventral portion the intermedia is made up of a more dorsal plate (Text-fig. 2, and Plate I, Fig. 3), lying intimately in contact with nearly the whole ventral surface of the übergangsteil. Anteriorly this plate has a flat dorsal surface, but posterior to the center it rises medially to form a triangular cross section. In some cases the plate disappears entirely from transverse sections taken near the posterior extremity.



Text-figure 1.

Drawings of various aspects of the hypophysis. (A) Ventral aspect, (B) Dorsal aspect, (C) Lateral view and (D) Caudal view. In A, B, and C the nasal end is to the left. Approximately x 12.

The *übergangsteil* is formed by a deep plate of cells, indented antero-dorsally by the pars anterior and postero-ventrally by the ridge of the intermedia. The pars nervosa forms a solid core-like mass in this lobe posterior to the midpoint (Text-fig. 2, and Plate I, Fig. 3). Branching root-like processes extended from this into all the other lobes but especially into the pars anterior and the intermedia. A heavy process curves ventrally toward this latter portion in the median plane and on reaching it, broadens out into a mass which sends processes radiating throughout the lobe.



Text-figure 2.

A diagrammatic reconstruction of a median sagittal section of the pituitary body showing the anatomical and area relationships of the various portions. P.A.—Pars anterior; P.N.—Pars nervosa; P.I.—Pars intermedia; Übg.—Übergangsteil. Approximately x 15.

The pars anterior (Text-fig. 2, and Plate I, Fig. 3) may be considered to consist of two portions; first, a flat plate-like region anterior to the pituitary stalk and dorsal to the *übergangsteil*—the pars anterior proper; and second, a layer of peculiar cells enveloping the dorsal nervosa mass and the roots of the processes which radiate from it (Plate I, Fig. 5).

#### HISTOLOGY OF THE PITUITARY GLAND.

*Pars Nervosa.* This tissue appears as a loose fibrous mass with scattered neuroglia nuclei and occasional glandular cells (Plate I, Figs. 2, 3, 5). The coarse basophilic fibers run lengthwise in the cords, as do the nuclei of the neuroglia cells. These latter are fusiform or irregularly elongate in shape and are characterized by scattered coarse granules. They are stained red with the Masson technique. Occasionally an area appears around the nuclei which stains as would cytoplasm, but no cell borders are visible. Numerous large basophilic glandular cells, resembling those of the *übergangsteil*, are found in the nervosa masses but not in the cords. These are always degenerate and often appear as irregular blue masses. Eosinophilic colloid material was observed in rare cases only. Numerous blood vessels penetrate the cords of the nervosa and occasional large vessels appear in the dorsal mass.



*Pars Intermedia.* A compact irregular cord-like arrangement is characteristic of the pars intermedia (Plate I, Fig. 6). The cords are separated from each other and from the processes of the nervosa by thin connective tissue membranes. The lobe appears as a typical epithelial gland, and the roots of the nervosa occupy only a small portion of its volume.

Two cell types were observed—a large, rounded one, flattened by adjoining cells, and a smaller, more polygonal type (Plate II, Fig. 7). The rounded cells are predominant and are responsible for the faintly basophilic staining reaction of this lobe. They occupy the center of the cords and much of the periphery, while the polygonal cells are always located adjacent to the connective tissue membrane.

The vesicular nuclei of the basophils are large and oval and occasionally indented. They are made prominent with the Masson stains, by a deep red-staining rim, scattered large red granules, and often a round, central nucleolus. The cytoplasm is marked by numerous faint blue granules.

The polygonal cells are smaller than the basophils, although their nuclei are identical in size as well as staining reaction. The cytoplasm of the former is dense and finely granular. It takes both acid and basic stains better than that of the basophilic cells and stains a reddish purple with the Masson technique. These may be called amphiphils.

The goldfish intermedia is moderately well supplied with blood vessels. The largest vessel observed in the pituitary appears in the region adjacent to the lower nervosa mass (Plate I, Fig. 3). Numerous other smaller vessels are associated with the connective tissue elements throughout the intermedia and between this lobe and the übergangsteil.

*Übergangsteil.* The übergangsteil is the largest portion of the pituitary body, occupying about one-half of its volume (Plate I, Fig. 3). Although connective membranes separate it from the pars intermedia and the pars nervosa, no similar structure lies between its cells and those of the pars anterior. The übergangsteil is quite homogeneous in structure; there are no connective tissue elements within it and nervosa processes extend into it for only a short distance. Strongly contrasting areas appear, however, as a result of differential staining. Small irregular masses of deep-staining acidophils are characteristically distributed throughout a deeply basophilic background (Plate I, Fig. 3, and Plate II, Fig. 8). These masses increase somewhat in number, as one proceeds posteriorly. The transition from acidophilic to basophilic areas is strikingly sharp and is visible even in unstained sections.

The acidophilic areas (Plate II, Fig. 8) are made up of large, polygonal cells, having a finely granular cytoplasm, which takes an intense red color with the Masson stains. The cell borders are exceptionally sharp and distinct while the nuclei are very prominent and about the size of those of the pars intermedia. The round or oval vesicular nuclei possess a few large granules and frequently a large central nucleolus. Like the nuclei of the intermedia, these take a deep red stain and have a dense rim. Scattered among the acidophils are occasional polygonal cells with the typical red nuclei but whose cytoplasm is vesicular, containing large faintly violet granules. These are chromophobic cells, presumably degranulated eosinophils.

The basophilic background (Plate II, Fig. 8) is composed of large polygonal cells, having indistinct borders and spherical or picnotic nuclei, that are more granular than those of the acidophils. The nuclei of most of the cells appear degenerate and many are missing entirely. With the Masson stains, several differentiated areas may be distinguished. The cells of all regions possess large red cytoplasmic globules which are usually located near the cell borders. The cells of the central region have relatively few globules in a pure blue cytoplasm in which individual granules cannot be



distinguished. Those of the posterior region are similar but have more numerous globules. The most anterior region and also an area of cells lying below the pars anterior present a different picture. Here the number of globules is greatly increased so that they may occupy a large portion of the volume of the cells. The cytoplasm is not deep blue but shows a coarse violet or violet and blue granulation. These cells appear to be largely degranulated although they have not lost their red globules.

The vascular supply of the *übergangsteil* is poor. Only small capillaries have been observed, and rarely do more than several of these appear in any one field.

*Pars Anterior.* The characteristic cellular arrangement in the pars anterior is due to the presence of a large number of cords of the nervosa which course through the lobe in an anterior-posterior direction (Plate I, Fig. 5, and Plate II, Figs. 10, 11). In tranverse section, the lobe has a perforated appearance, while in a sagittal section, the cells seem to be divided into horizontal cords several cells in depth.

The cells are small as compared with those of the *übergangsteil* and the *intermedia* (Plate II, Figs. 9, 10). They are rounded or polygonal and have distinct borders and large typically ovoid nuclei. Many indented or folded nuclei are also present. The majority of the nuclei are vesicular, having large, deep red granules and a smooth prominent red rim outlined against a yellowish nucleoplasm. On the basis of cytoplasmic staining reactions, three cell types may be distinguished; e.g., purplish-red amphiphilic cells, basophils, and chromophobes. The lobe is composed predominantly of the amphiphils, which have considerably less affinity for acid fuchsin than the amphiphils of the pars *intermedia*. The chromophobes (Plate II, Fig. 10) are relatively scarce and are distributed uniformly throughout the lobe. They have normal nuclei but appear pale violet in color like the degranulated cells of the *übergangsteil*. The basophils (Plate II, Fig. 10) are smaller than the other cells but have nuclei which are identical in size and staining reaction. Their cytoplasm is filled with fine deep blue granules.

A transition from a predominantly basophilic condition next to the *übergangsteil* to an acidophilic one at the dorsal free border, occurs in this lobe. Most of this is due to the depth of staining of the amphiphilic cells. At the ventral border, the majority of these assume a deep purple color and have a dense cytoplasm without visible granulation, while those at the dorsal border are more red than purple and have varying numbers of coarse granules. Some of the transition is also due to the increase in the number of basophils toward the ventral border. At most, however, these cells account for only a small fraction of the change.

A few of the amphiphilic cells possess nuclei unlike the vesicular acidophilic nuclei of the remainder of the cells of the pars anterior. They are uniformly filled with fine basophilic granules, are without nucleoli, and have a deep blue rim (Plate II, Fig. 9).

The processes of the nervosa that penetrate the pars anterior are highly fibrous and especially loose in consistency (Plate II, Figs. 10, 11). Associated with most of them are blood vessels of various sizes; these always lie within the connective tissue membranes separating the processes from the surrounding cells (Plate II, Fig. 11). A few vessels lie in the parenchyma itself, and occasionally one of these near the free border may be seen to connect with a vessel in the connective tissue capsule of the gland. The pars anterior is the most vascular lobe of the goldfish pituitary; nevertheless, its vascular supply is relatively poor as compared with that lobe in the mammal and most higher vertebrates.

The layer of cells, enveloping the dorsal mass of the pars nervosa (Plate I, Fig. 5) is considered part of the pars anterior, because of their resemblance to the cells found in that part of the gland and should be

confirmed further by morphogenic studies. The layer is thickest next to the mass and thins down to a few cells as it follows the processes a short way. Some nesting of the cells is evident. A few cells follow the main stalk all the way to the pars intermedia. The cells are small and polygonal with large vesicular nuclei and a scanty rim of cytoplasm. When stained with Delafield's hematoxylin and eosin, the nuclei are deep blue and the cytoplasm is a faint blue. Masson staining produces a pale violet coloration of the fine cytoplasmic granules. The nuclei are pale yellowish-red with deep red rims and a few scattered large red granules.

#### DISCUSSION.

The anatomical relationships of the pituitary in *Carassius auratus* to the neurocranium and brain resemble those found in higher vertebrates more than in most other teleosts. Matthews (1936) found the pituitary of *Fundulus heteroclitus* to be closely applied to the floor of the brain and merely covered ventrally by the parasphenoid bone. This condition is characteristic of most of the teleost pituitaries that have been described, e.g., *Anguilla vulgaris* and the Mormyridae (Stendell, 1914), *Anguilla anguilla* (Florentin and Weiss, 1931, and v. Hallerstein, 1934), *Gasterosteus aculeatus* (Bock, 1928), *Gadus morrhua* (Herring, 1908 and 1913) and the haddock (de Beer, 1926).

In *Carassius*, on the other hand, the gland is separated from the brain by the shelf-like cranial floor and the extension of the endocranial membrane over the optic-pituitary foramen. As a result of this change, the pituitary is attached to the lobus medialis by a relatively long stalk, which penetrates the foramen. Two teleost pituitaries, those of *Cyprinus carpio*, the carp, and of *Esox lucius*, the pike, as described by Stendell (1914), are very similar in structure to the gland of the goldfish. Whether they also have similar anatomic relationships is unknown. In fact, previous accounts of teleost pituitaries have included only brief comments on this subject. The only available literature dealing with it is that provided in anatomical discussions by Jordan (1905), Gregory (1933), von Hallerstein (1934) and Holmgren and Stenzio (1936).

Four main divisions were differentiated in the goldfish pituitary: pars nervosa, pars intermedia, übergangsteil, and pars anterior. These terms have been used by de Beer (1926) and other recent workers in describing the teleost pituitary. The configuration and structure of these divisions show a marked similarity to those in *Esox* and especially in *Cyprinus*.

Certain changes in the orientation of the various lobes have taken place as a result of the development of the pituitary stalk. The glands have assumed a compact ovoid form with a somewhat variable orientation of the lobes. The pars anterior of *Carassius* and *Esox* are antero-dorsal in position while the pars intermedia is ventral and ventro-caudal respectively. In the acorn-shaped gland in *Cyprinus*, the pars anterior is dorsal and the intermedia is directed antero-ventrally. The change in the position of the gland in *Cyprinus* has been associated by Stendell (1914) with its greater anterior rotation as a result of a more extensive stalk formation. These glands represent a considerable advance over the condition in other teleosts, in which the lobes are serially extended in an anterior-posterior direction, i.e., pars anterior, übergangsteil, and pars intermedia.

The goldfish has a typical teleost pars nervosa, which is composed of a mass of tissue in the postero-dorsal region, from which root-like processes radiate in all directions into the glandular tissue. Like *Cyprinus*, however, it has an additional long internal process leading to the distant, compact, lobe-like pars intermedia. Here the process ends in an additional mass of nervosa tissue from which processes radiate throughout the intermedia. The fine structure of the nervosa is very similar to that described by other work-



ers. Numerous acidophilic colloid droplets have been noted in the nervosa adjacent to the pars intermedia by Herring (1908), Stendell (1914), Bock (1928), and Matthews (1936). Some such strongly acidophilic material was observed in the pars intermedia and occasionally in the adjacent nervosa in *Carassius*. This material was missing, however, in the dorsal mass of the nervosa. Stendell (1914) and Bock (1928) noted glandular cells distributed throughout the nervosa and stated that these had migrated there from the pars intermedia and the pars anterior. These cells are present in *Carassius* but they definitely resemble the basophils of the übergangsteil.

The pars intermedia of the goldfish forms a distinct lobe and, like that of the carp, it is separated from the übergangsteil by a partial cleft and a connective tissue membrane. In most other teleosts it consists of a region, occupying the posterior or postero-ventral extremity and enveloping the roots of the nervosa. This is the case in *Anguilla*, *Mormyrus*, *Mugil*, *Salmo*, *Chrysops* and *Esox* (Stendell, 1914) and in *Gasterosteus* (Bock, 1928). In *Fundulus* it takes the form of a layer, several cells in thickness, following the contours of the nervosa (Matthews, 1936).

Stendell (1914) found no pattern of cell arrangement and no blood vessels in the intermedia of the teleosts he studied. The only vascular supply in this lobe was that carried into it by the roots of the nervosa. The condition is strikingly different in *Carassius*. Here the parenchyma is broken up into irregular cords by a connective tissue network which extends throughout the lobe. Moreover, blood vessels are more numerous in this lobe than are free in the parenchyma of all the pituitary regions. The cord-like arrangement resembles that seen in the intermedia of some of the mammals.

As in all vertebrates, the intermedia of the goldfish is predominantly basophilic in staining reaction. The cells in the center of the cords are basophilic while many of those next to the nervosa and connective membranes are amphiphilic in reaction. The latter take both acid and basic stains better than the basophilic cells. Matthews (1936) noted large intensely staining acidophiles adjacent to the nervosa cords in *Fundulus* and Stendell found a similar condition in *Esox*. It seems likely that these cells are identical with the amphiphils in *Carassius*. As in Matthews' description in *Fundulus*, many of the nuclei in this lobe of the goldfish pituitary are folded or indented.

A marked similarity also exists between the übergangsteil of *Carassius* and that of *Cyprinus* (Stendell, 1914). In both it is the largest portion of the complex; that of *Carassius* is central in position while it is central and posterior in *Cyprinus*. The position of this lobe in other teleosts is highly variable. The simple pituitaries, lacking hypophyseal stalks, have a mass of differentiated cells occupying a central position between the pars anterior and the pars intermedia. Bock (1928) found it to be located centrally in *Gasterosteus* and to be covered ventrally by the pars anterior and the pars intermedia. In *Esox*, it is a compact mass in the anterior region while in *Fundulus* (Matthews, 1936), it is composed of an anterior mass and a layer which covers the periphery of the gland everywhere except at the posterior extremity.

Many irregular patches of large polygonal acidophils lying in a background of similar basophilic cells have been described in the übergangsteil of the goldfish. Stendell (1914) found acinar groups of acidophils lying in a chromophobic background in the closely related *Cyprinus* and in a basophilic area in *Esox*. The basophils of the goldfish appear degenerate, at least in the late Winter and Spring, but nevertheless they take a much stronger basophilic stain than the basophils of the intermedia.

The staining reactions of the übergangsteil of the various other teleost pituitaries are variable and widely divergent from these. Tilney (1911) described columns of acidophils, separated by blood vessels in *Anguilla vulgaris*, while Stendell (1914) found the cells to be predominantly basophilic in this

form and in *Mormyrus*. This lobe is predominantly acidophilic in *Fundulus* (Matthews, 1936) and *Gadus* (Herring, 1908) and equally acidophilic and basophilic in *Esox* (Stendell, 1914). Usually the cells of the other teleost übergangsteils are smaller and more rounded than those of *Cyprinus*, *Esox* and *Carassius*.

Stendell (1914) held that there is a progressive increase in the number of basophils and a decrease in acidophils from the region adjacent to the pars anterior to that next to the pars intermedia in the teleost übergangsteil. Bock (1928) could not confirm this in *Gasterosteus* nor does it occur in *Carassius*. In the latter, an increase in the number of acidophilic masses occurs toward the caudal extremity.

Few nervosa cords penetrate the teleost übergangsteil. Connective tissue has not been reported in it, and there is no sharp boundary separating it from the pars anterior. In *Gasterosteus* there is a partial separation (Bock, 1928).

A pars anterior, very similar to that described by Stendell (1914) in *Cyprinus* and *Esox*, is present in *Carassius*. Matthews (1936) was unable to distinguish such a differentiated portion in *Fundulus*. However, all other descriptions in teleosts have included such a portion in an anterior or antero-dorsal region of the pituitary.

A characteristic cellular arrangement in the form of cords, separated by processes of the nervosa was noted in *Carassius*. Stendell (1914) noted a similar cord-like arrangement of the cells in *Cyprinus* and *Esox*, but found them to be separated by blood sinusoids. Many large blood vessels were found enclosed within the nervosa cords in the goldfish and it seems possible that Stendell mistook such cords for blood sinuses.

Most of the cells of the goldfish pars anterior stain purple or a purplish-red with the Masson stains and have been described as amphiphilic. Some basophils and chromophobes are also present. The cells of *Cyprinus* and *Esox* (Stendell, 1914) and *Anguilla vulgaris* (Tilney, 1911) are reported to be basophilic. Stendell (1914) also described large acidophils next to the blood sinusoids in *Esox*. He and Bock (1928) have found the pars anterior to be acidophilic in the primitive *Mormyrus* and *Gasterosteus*, respectively. It is interesting to note that an antero-dorsal chromophobic zone was found in the pars anterior of *Gasterosteus* (Bock, 1928) and in *Gadus morhua* (Herring, 1908). In the former, the nuclei are closely packed and surrounded by a small ring of basophilic granules.

A small specialized region has been included in the discussion of the pars anterior of *Carassius* although its significance is uncertain. This is the area of small polygonal cells surrounding the pars nervosa and fusing with the posterior end of the pars anterior proper. The cells resemble those of the pars anterior in size but have less cytoplasm and are nearly chromophobic. On the other hand, its position and form, as a layer surrounding the nervosa, immediately recalls the descriptions of the pars intermedia in *Fundulus* (Matthews, 1936), in the haddock and the cod (Butcher, 1936) and in other teleosts. It seemed advisable to classify this region with one of the other lobes of the gland until more is known about it rather than further confuse the pituitary terminology.

No large blood vessels were found entering the pituitary body in *Carassius*. Occasionally capillaries were observed, however, leaving the rich network in the pituitary capsule and entering the pars anterior. The blood supply of the gland is poor as compared with those of most higher vertebrates; this is true in general of all teleosts. The pars anterior is most vascular of the teleost lobes with the exception of that in *Gasterosteus* (Bock, 1928). In *Carassius*, the vessels are located in the nervosa cords while in *Anguilla* (Tilney, 1911) and *Esox* and *Cyprinus* (Stendell, 1914) numerous blood sinusoids are reported. The pars nervosa carries numerous vessels



throughout the gland. Few vessels are present in the übergangsteil in *Carassius*, *Anguilla* and *Cyprinus* (Stendell, 1914) while *Mormyrus*, and *Esox* (Stendell, 1914) and *Fundulus* (Matthews, 1936) are somewhat better supplied. Blood vessels are reportedly absent in the parenchyma of the pars intermedia, nevertheless they are present in considerable number in *Carassius*.

In the accounts of the pituitary of the teleosts, most investigators have included a thin-walled, folded pouch, the saccus vasculosus. This lies posterior to the gland and is a separate outgrowth of the posterior hypothalamus. It is not present in all Teleostei; von Hallerstein (1934) reported the presence of one in *Cyprinus* but there is none in *Carassius*. The saccus vasculosus is related in no way to the pituitary body. According to von Hallerstein (1934), its thin epithelial wall contains numerous characteristic sensory cells, as well as nerves, which is evidence for its being a special sense organ. For these reasons, it is suggested that this organ should be omitted from discussions of the teleost pituitary.

If granulation and regranulation, as evidenced by the presence of the similar cells with varying numbers of granules can be taken as evidence of secretory activity, as is usually done, and if certain changes in the form and staining reaction of the nuclei may also be taken as such evidence (as Severinghaus (1938) believes valid for the rat at least) then the cells of the pituitary of the goldfish may be considered to be in a state of active secretion in the late Winter and early Spring. Such variations in granulation occur in *Carassius* both in the pars anterior and in the übergangsteil. Scattered about the pars anterior, cells have been observed the nuclei of which stain uniformly with basic stains instead of the usual vesicular manner with acid ones. Otherwise these cells cannot be differentiated from the normal amphiphilic cells.

In this discussion of the pituitary, the terminology developed by Stendell (1914), Herring (1908), Tilney (1911) and de Beer (1926) and used as such by de Beer, has been adopted. This is based on Stendell's homology of the various portions of the teleost pituitary with those of this gland in higher vertebrates. The suitability of this terminology has been questioned. Indeed, Stendell himself stated that the übergangsteil of the Teleostei suggests the pars anterior more than it does the pars intermedia. He thought it not impossible that the anterior lobe of higher vertebrates arose from the übergangsteil of fish.

Bock (1928) carried this idea to a positive conclusion as a result of his study in *Gasterosteus*. He said that the anterior lobe of Teleostei is thus to be regarded as a structure typical of this group, to which there is no homology in amniotes and amphibia.

In the absence of detailed embryological evidence Stendell, (1914), preferred to retain a homology based largely on relative position. It seems to the author, however, that a modification of this type of "homology" to include histological and cytological similarities, such as Bock (1928) suggested with respect to the übergangsteil, would be of definite value. Such a homology would undoubtedly approach closer to a fundamental physiological analogy. Such an analogy and the simplification it might bring should be the goal of comparative physiological experimentation. Very little has been accomplished in this direction as yet, with the exception of the work on the pars intermedia. The functions of the other portions of the pituitary in vertebrates below the mammals are almost completely unknown.

Both the evidence of secretory activity and the cytological structure of the cells of the pars anterior and the übergangsteil in the goldfish pituitary, suggest that these two portions ought to be considered as a glandular complex, which is equivalent to the pars anterior of higher vertebrates. Although no attempt has been made here to study the embryological origin of

the various portions and thus arrive at a true homology, if such a thing is possible, the lack of separation of the übergangsteil from the pars anterior suggests a common embryological origin. In contrast to this, there is a very definite separation of the übergangsteil from the pars intermedia.

The pars anterior (Hauptlappen) in teleosts was considered by Stendell (1914) to be homologous to the lobe of that name in higher forms, while Bock (1928) thought it was distinctive of this group. Certain facts suggest another possibility, which would afford a definite simplification in terminology. This lobe is strikingly similar to the pars tuberalis in reptiles, birds and mammals in various morphological respects. The lobe is typically composed of small polygonal basophils with a few acidophils in some forms. Only the primitive pituitaries of *Mormyrus* and *Gasterosteus* are acidophilic. The acinar, vesicular, cord-like or columnar arrangement of the cells found in the tuberalis of various higher vertebrates can all be duplicated in the teleost pars anterior. Stendell (1914) has reported the presence of intercellular colloid in *Esox lucius*.

The position and relationships of the pars anterior may also be equated to the tuberalis. It is dorsal or antero-dorsal in the more complex teleost pituitaries and anterior in the lower forms. The position of the pars tuberalis in amphibians is antero-ventral, in reptiles it is antero-dorsal, and in birds and mammals it is dorsal. The tuberalis usually fuses with the pars anterior without a line of separation much as the teleost pars anterior does with the übergangsteil. In the stalked pituitaries, the pars anterior lies in contact with the infundibular stalk much as does the tuberalis in the birds and mammals.

It seems desirable to simplify the pituitary terminology in the teleosts and to correlate it with that applied to higher vertebrates. The morphological similarity of the teleost übergangsteil and pars anterior with the pars anterior and pars tuberalis respectively of higher forms suggests that the latter terms might well be substituted for the former in referring to the teleost.

No thorough cytological investigation has been attempted in this paper. An elaboration of this material with information of that type, secured throughout the year and including seasonal variations would allow a more critical examination of the above question. At best, however, this can only elaborate on the morphological similarities. By combining this method with physiological experiments, an analogy with the functions of the lobes of the pituitary of higher vertebrates might be established.

#### SUMMARY.

1. The anatomical relationship and position of the pituitary gland in the teleost fish, *Carassius auratus*, are distinctive not only in the vertebrate group as a whole but also in the teleost group itself. It is well below the floor of the brain in the region of the diencephalon, above the prominent parasphenoid and surrounded by the proötic and alisphenoid bones. Its dorsal surface is separated from the floor of the brain by a tough membrane.
2. The pituitary body is attached to the brain in the infundibular region of the hypothalamis by a cylindrical stalk, which penetrates this membrane.
3. Only a few small blood vessels were observed entering the gland from the vascular network in its connective tissue sac. As in most teleosts the gland is poorly vascularized as compared with those of higher vertebrates.
4. The pituitary is made up of the following four main divisions.  
(A) A pars nervosa made up of two irregular masses connected by a

heavy process. Root-like processes ramify throughout the pituitary from these regions.

(B) A pars intermedia which is a large compact ventral lobe almost completely separated from the übergangsteil by a narrow cleft.

(C) An übergangsteil in the form of a large thick plate-like region dorsal to the pars intermedia. Its structure resembles most closely the pars anterior of higher vertebrates.

(D) A small plate-like pars anterior in the antero-dorsal region. In structure it is very similar to the pars tuberalis of many of the higher vertebrates.

5. Evidence is offered to confirm Bock (1928) in the suggestion that the übergangsteil in Teleostei is really the pars anterior in the sense that this term has been applied to higher vertebrates.
6. Similarly evidence is presented and the suggestion is made that the "pars anterior" in Teleostei is in fact the pars tuberalis of higher forms. Cell type, arrangement, and the position and relationships of the lobe as a whole were used as criteria.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Median sagittal section of a portion of the neurocranium with the brain and pituitary in situ. Nasal end at the right. The section shows the pituitary (**P**) lying in the myodome (**MY**) below the floor of the brain case. The cerebrum (**CB**), cerebellum (**CBL**), lobus viscerosensibilis (**L.V.S**), parasphenoid (**PS**) and optic nerve (**O.V.**) are also indicated. Zenker's; Delafield's haematoxylin-eosin. x 4.
- Fig. 2. Transverse section of the pituitary near the posterior end and of adjacent structures, further magnified from Fig. 4. Note the cavity of the third ventricle above the pituitary stalk and the thin lateral bone shelves between the gland and the brain. **P.N.**, pars nervosa; **UBG**, Übergangsteil; **P.I.**, pars intermedia. x 13.
- Fig. 3. An area from Fig. 1 under higher magnification, showing the attachment of the pituitary to the brain, the cupped anterior rim of the proötic bridge, the connective tissue capsule of the gland, and the large blood vessel lying in the posterior indentation of the intermedia. Nasal end at the right. **P.A.**, pars anterior. x 13.
- Fig. 4. Transverse section of a portion of the neurocranium with the brain and pituitary in situ. The section shows the attachment of the pituitary to the floor of the hypothalamus and the bony shelves that separate them laterally. **B.S.**, bony shelf; **L.In.**, lobus inferior; **L.M.**, lobus medialis; **O.L.**, optic lobe; **P.**, pituitary; **R.M.**, rectus muscle. Bouin's; Delafield's haematoxylin-eosin. x 4.
- Fig. 5. Dorsal mass of the pars nervosa and the adjacent specialized region of the pars anterior (the group of cells above the arrows). The dark cells in the nervosa are glandular cells similar to the basophils of the Übergangsteil. Zenker's; Masson stains. x 160.
- Fig. 6. Transverse section of epithelial portions of the pituitary showing histological structure of the (**P.I.**) pars intermedia; (**UBG**) Übergangsteil and (**P.A.**) pars anterior. The dark areas in the Übergangsteil represent acidophils and the light areas in the pars anterior are nervosa cords. Zenker's; Masson stains. x 200.

## PLATE II.

- Fig. 7. Pars intermedia showing amphiphilic cells adjacent to the nervosa cord at left. Remaining cells are weakly basophilic. Zenker's; Masson stains. x 1080.
- Fig. 8. Übergangsteil area. Acidophils appear dark while the basophils appear chromophobic with haematoxylin. Several chromophobes may be noted among the acidophils. Bouin's; Delafield's haematoxylin and Masson A. x 1800.
- Fig. 9. Pars anterior at the dorsal border, showing typical amphiphilic cells, three with dark basophilic nuclei, also occasional chromophobes. Zenker's; Masson stains. x 1800.
- Fig. 10. Pars anterior near the ventral border with deeper-staining amphiphils than in the more dorsal region. **C.**, chromophobe; **B.**, basophil; **A.**, amphiphil. Zenker's; Masson stains. x 1800.
- Fig. 11. Section of an area from the pars anterior showing cords of the nervosa with blood vessels typically enclosed within them. Zenker's; Masson stains. x 1800.

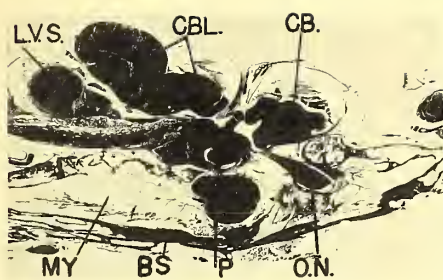


FIG. 1.

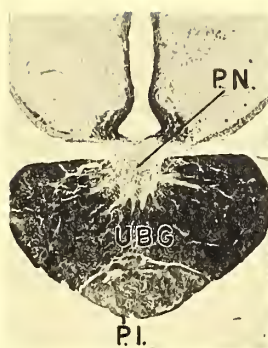


FIG. 2.

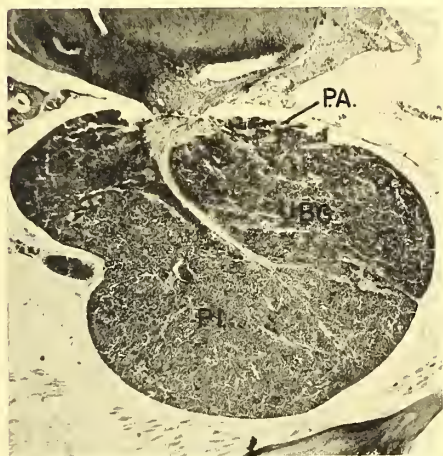


FIG. 3.

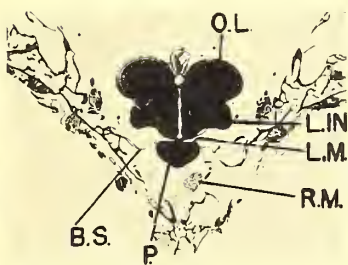


FIG. 4.

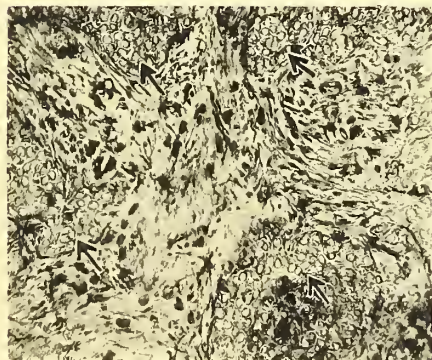


FIG. 5.

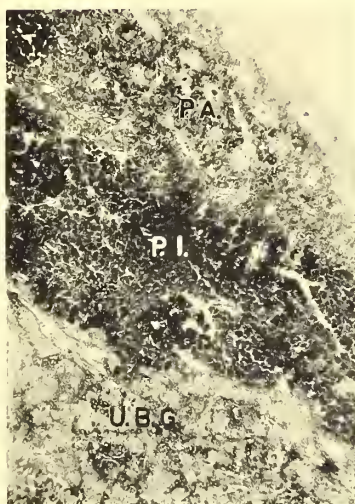


FIG. 6.

MORPHOLOGY OF THE HYPOPHYSIS OF THE  
COMMON GOLDFISH (*CARASSIUS AURATUS* L.).





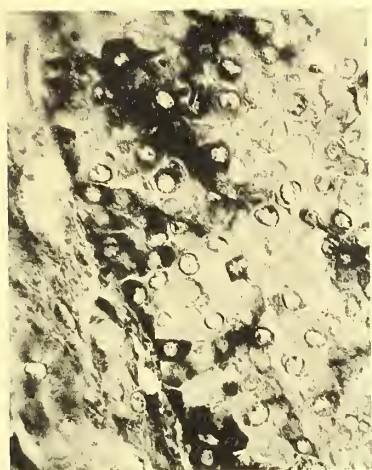


FIG. 7.

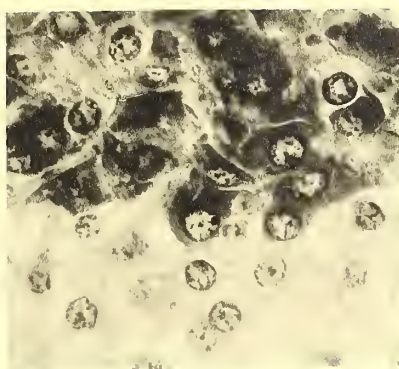


FIG. 8.

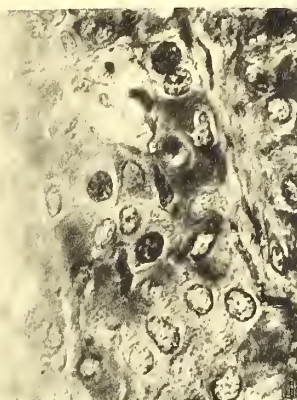


FIG. 9.

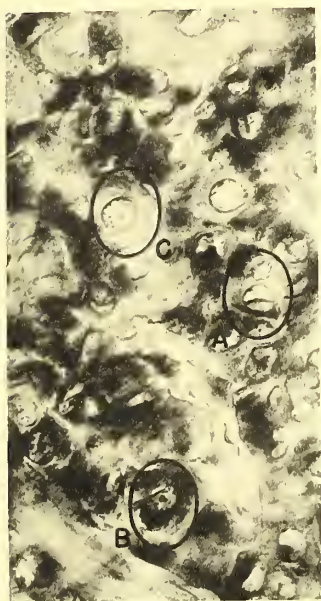


FIG. 10.

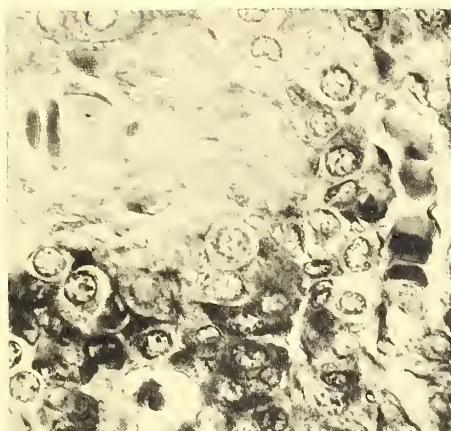


FIG. 11.

MORPHOLOGY OF THE HYPOPHYSIS OF THE  
COMMON GOLDFISH (*CARASSIUS AURATUS* L.).



## 11.

Pathology of *Dirofilaria* Infestation.<sup>1</sup>

Report of a case with chronic pulmonary arteritis.

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Mt. Sinai Hospital, New York City.

(Plates I-V).

The prominent increase in the recognition of *Dirofilaria immitis* infestation among dogs in the United States during recent years has made this a subject of some importance. Anatomic reports, although plentiful, have been generally incomplete and inconclusive. A case of extensive *Dirofilaria immitis* infestation in a gray wolf has recently come under our observation, the study of which forms the basis of this report. In view of the gaining importance of the disease it is of value to review briefly the literature on the subject and to discuss its various features.

The occurrence of this type of parasitism in the gray wolf, as far as we can determine, has not been reported in detail although there are frequent records of its appearance in dogs. Textbooks, however, refer to the occurrence of *Dirofilaria* in foxes, wolves, muskrats, raccoons, and occasionally other animals. Infestation with *Dirofilaria immitis* does not occur in man and conversely *Filaria bancrofti* is not observed in animals except perhaps in primates.

The presence of worms in the heart of the dog was first reported by Peysson in 1806 and by Von Gruby and Delafond in 1843. Leidy named the parasite *Filaria immitis*. Raillet and Henry in 1911 established the genus *Dirofilaria*, the most common species of which is *Dirofilaria immitis* (*dirus*, meaning cruel), a designation which has remained to the present. The members of the group besides *D. immitis* are: *D. magalhaes* and *D. repens*. The genus *Dirofilaria* is characterized by the absence of oral labia and by the possession of very inconspicuous cephalic papillae.

Shattock in 1881 observed worms in the cardiac chambers of a dog in Japan and found many parasites partly embedded in a post-mortem blood clot, which extended into the pulmonary artery and its larger branches.

In 1886, J. R. Figueira de Saboia described the presence of male and adult filaria in the chamber of the left ventricle of the heart of a child and referred them to De Magalhaes for study. A statement of the illness of the child was not given; the blood was not known to have been examined for larvae. The role of the parasite in the child's illness is therefore unknown. These were designated *D. magalhaes*. This occurrence in the child plus one case of *D. repens* found in man by Skrjbin, Althausen and Schulman (1930), represent the only recorded instances of infestation in man by a related species of *Dirofilaria*.

<sup>1</sup> From the laboratories of the Mt. Sinai Hospital and the New York Zoological Park.



Woods, in 1885, observed that *Dirofilaria* infestation was a common disease throughout the coastal cities of China. In one of his cases a continuous coil of filaria was found extending from the right hepatic vein, through to the inferior vena cava, into the right auricle, through the tricuspid valve orifice into the chamber of the right ventricle. The left auricular chamber was packed with the nematodes connected with a mass fourteen inches long extending into both lungs through the pulmonary arteries. He was of the opinion that the ova were introduced into the animal by drinking from stagnant pools. F. Fullerborn and others, however, definitely established the fact that the disease is transmitted by means of the mosquito which functions as the intermediate host.

De Magalhaes (1892) emphasized the difference between *Dirofilaria immitis* and *Filaria bancrofti*. This investigator felt that whereas *Dirofilaria immitis* was generally found in the chamber of the right heart and in its great vessels, *Filaria bancrofti* was constantly encountered within the lymphatics. The recent studies of Augustine and his co-workers demonstrated, on the other hand, that the microfilaria of *D. immitis* could occasionally also be found within the lymphatic channels.

The first comprehensive articles on *Dirofilaria immitis* appeared in 1889 with the reports by Janson of post-mortem findings in 41 dogs. The parasites were most frequently found in the right cardiac chambers and its great vessels but only rarely within the cavity of the left ventricle, aorta or femoral artery. Pulmonary emboli were found in the branches of the pulmonary artery with infarction, necrosis and even abscess formation of the pulmonary parenchyma. The adult parasites were found in the inferior vena cava, extending into the hepatic vein, producing thereby congestion of the liver with secondary congestion of the portal vein and subsequent ascites. In one heart a worm was seen passing through a patent foramen ovale with one half of its body located in each auricle. This offers a ready explanation, at least in some instances, of a mechanism for the entrance of the parasite into the general systemic circulation. Janson further described 26 cases of hypertrophy of the right ventricle and in some specimens marked dilatation, 5 of obstruction of the pulmonary artery, 2 examples of aneurism of the pulmonary artery without thrombosis, 9 of aneurism of the pulmonary artery with thrombosis, 13 of "interstitial hepatitis," 19 instances of hydrothorax and ascites, 1 of edema of the subcutaneous tissues, 5 examples of worms entangled in the chordae tendinae. He referred to the presence of chronic endocarditis which he felt had proceeded the filariasis, and was aggravated by the presence of the nematodes. In the lungs of acute cases he found "anemia and atelectasis with and without edema." A "nut-meg liver" was not infrequently observed. The kidney exhibited "parenchymatous, catarrhal and interstitial changes." On the basis of these anatomical findings Janson believed that the embryos of *Dirofilaria immitis* escaped from the body mostly in the urine. This concept has been subsequently shown to be erroneous, for although microfilaria are known to pass through the kidneys, the renal lesions, described by Janson, correspond to the so-called spontaneous interstitial nephritis, so commonly observed in animals (Horn, 1937). However the possibility of any exaggeration of this process by the toxins elaborated by the parasite cannot be negated.

Van Meter (1892) reported the gross finding of a case which included chronic endocarditis of the tricuspid valve, attributed to the presence of the parasite. The inter-auricular septum was perforated (foramen ovale?) and the nematodes were also found in the pulmonary vein. French (1899) reported the gross findings of a case in a bitch whose litter of pups three months previously died with diarrhea. He found some small worms in the intestines of the offsprings and raised the question of the possibility of the placental transmission of the disease. Riesman (1903) described an animal with dyspnea, who fell to the ground while trotting and on examina-



tion revealed markedly accentuated heart sounds, a murmur (type not described), cyanosis and ascites. Necropsy disclosed a "white thrombus" in the right heart enmeshing a parasite and slightly hypertrophied right cardiac chambers. The left branch of the pulmonary artery was completely occluded with an ante-mortem thrombus. Larvae were not demonstrated. He stated that 50% of the canine population of China and Japan harbored the worm and that the embryos were found more easily during the night than the day. The attention of Hopkins three years afterwards was drawn to this disease when three of his dogs being used for experimental purposes died under anesthesia. These and three additional animals showed gross findings typical of *immitis* infestation. In one case, the wall of the pulmonary artery two centimeters above the valve was studded with fine granules which on section proved to be subendothelial fibrous nodules.

In 1919 Lynch anesthetized an infected dog in whose blood he had demonstrated many larvae and proceeded to observe the vessels of the omentum drawn over the stage of a microscope. He observed the microfilaria moving about in the capillaries but found no evidence of plugging of the vessels. In the same year Ryan reported the case of a dog which had contracted the disease in the northern temperate zone of the United States. Kowakami, in 1919, studied the distribution of the microfilaria in the body and found them to be most commonly within the lungs, heart and respiratory muscles. Yano (1927) gave the order of frequency of the involved organs as heart, lung, kidney and asserted that 20% of the dogs about Tokio were infected. Histological studies of the kidneys of his animals disclosed the typical lesion found in the so-called interstitial nephritis of dogs. In one instance, however, the author found multiple hemorrhages and in another, multiple zones of infarction. Microfilaria were found in scattered capillaries of the cortex. In advanced cases there was renal atrophy. It was Yano's opinion that the microfilaria did not form glomerular emboli but suggested that the renal changes might be of toxic origin. A few of the vitally stained microfilaria injected into healthy dogs were recovered in the urine and were at times associated with renal hemorrhage. Blood eosinophilia was not observed. His attitude concerning the toxic origin of renal changes was strengthened by the fact that when a centrifuged extract of female *Dirofilaria immitis* was injected into mice, distinct changes, resembling those found in dogs, were elicited in the kidneys.

Yamanouchi (1928) attempted to study the distribution of experimentally introduced larvae in the kidneys of mice. When he injected living larvae into mice both intravenously and into the renal artery, he found the embryos in the capillaries of the cortex located, for the most part, in the capillaries of the glomeruli. Heat-killed larvae were distributed mostly in the afferent vessels of the glomeruli but none in the excretory tubular system, the kidney, ureters or bladder. Blackberg and Ashman (1930) emphasized the pronounced effect of filarial infestation upon cardiac function. Electrocardiographic tracings taken on dogs during exercise disclosed an inversion of the T wave in lead I and almost complete disappearance of the T wave in lead II. In view of the similarity of the tracings to those seen during attacks of angina pectoris in man the changes were attributed to an inadequate blood supply resulting in a deficient oxygen supply to the cardiac muscle.

Hayes (1933) reported that 80% of the dogs in Florida that he examined had *Dirofilaria immitis* infestation. Hayes asserted that in 1931-1933 this disease caused more loss than canine distemper. He referred to the increase of the disorder in recent years throughout the southern tiers of the United States. It was panzootic in 1932, throughout Georgia, Florida, Alabama, Mississippi and Louisiana. The most common symptoms were poor general condition, a rough coat, lack of endurance, a lazy attitude developing into extreme weakness, progressive anemia, often chronic in-

digestion, accompanied by ascites and generalized dropsical swellings. Mild infestations produced less marked symptomatology and with good care the animals could go on indefinitely without any apparent discomfort.

In recent years Augustine and his co-workers studied the question of the filtration of microfilaria by lymph nodes. They found that the larvae were not phagocytosed, as were the erythrocytes, and that they could pass through the lymph nodes with slight hindrance. In another experiment, after exsanguinating a normal dog and substituting the blood of a heavily infested dog, they were able to collect living embryos in the lymphatic channels and in the spinal fluid. Thus, they demonstrated that the larvae may escape from the blood vessels, traverse tissues and enter the lymphatic system. The histological findings were the same in both donor and recipient. Microfilaria were disseminated in every part of the body. Great numbers were present in the lungs, liver and kidney. None was found in the stomach or intestines. In the lungs many were discovered in the large arteries, veins, capillaries and occasionally in the alveoli. Many lay in the veins and sinusoids of the liver. The kidneys manifested the microfilaria most frequently in the glomeruli, some edema was present but no pathological changes. They usually followed the course of the capillaries. Very few were recovered in 40 cc. of urine of a heavily infected dog. Evidence that they passed through the glomeruli to the efferent vessels was offered by the presence of the organisms in the renal veins. Few existed in the capsule of the spleen but many were in the pulp. The lymph nodes likewise showed few and those were mostly in the intermediary sinuses in the depths of the node. Great numbers were embedded in the myocardium, particularly the left ventricle. They were mostly in the capillaries but in some instances lay outside the capillaries parallel to the fibers. A tremendous number rested in the blood vessels of the pericardium. No cellular reaction to the microfilaria was evident anywhere.

To settle the question of the behavior of the larvae in the capillaries and the reason for the absence of embolic phenomena these workers injected the microfilaria into bats and observed their behavior in the capillaries of the bat's wing. This was a superior method to that of Lynch, who examined the exposed mesentery of a dog, because it did not disturb the normal physiological conditions of the host. "The anterior end of the microfilaria were constantly active in searching movements. As the blood vessels branch and become smaller the organisms may eventually enter capillaries which are obviously somewhat contracted and proceed into them until the lumen gets too small, when they never were observed to escape or make permanent plugs. They simply backed out. That is the reason why microfilaria do not form emboli. Whenever these active organisms became stuck in a capillary they merely moved backwards against the current until they were safely on their way elsewhere."

Joyeux and Cabassu (1935) found microfilaria in the blood of 19 out of 26 dogs examined in the area known as Camargue. They identified the adult *Dirofilaria* in one of two foxes they studied. Yamamoto (1936) described microfilaria in the uterus and detected their escape in the menstrual flow. However, he did not regard this fact as definite proof of passage through the placenta. Ohashi, in the same year, established the fact that the larvae could be found in the skin of the eyelids, bulbar conjunctivae and membrana nictitans. A few embryos were present in the lacrimal secretion. He occasionally found that they worked their way into the vitreous body or produced hemorrhage about the optic nerve.

Hinman and Baker (1936) made a helminthic survey of 1,305 dogs from New Orleans and found 321, or 24.4%, infected with *Dirofilaria immitis*. They recovered the embryos in immature dogs and concluded that they may pass through the placenta. Diagnostic serological and intradermal tests in filaria were introduced independently by Taliaferro and



Hoffman, and also by N. H. Farley (cited by Manson-Bahr 1935). The antigen was obtained from *Dirofilaria immitis*.

Nematodes have been found in the hearts of the harbor seal. According to Ross Nigrelli of the New York Aquarium this species belongs to the genus *Halocercus*, the members of which are common parasites of the lungs of other species of seals, dolphins and porpoises. This parasite not infrequently is mistaken for *Dirofilaria immitis*.

#### REPORT OF A CASE.

On December 12, 1937, a male wolf (*Canis nubilus*) died in the New York Zoological Park. He was observed to have had a distended abdomen during the previous four years.

*Post-mortem Examination:* The body was well developed and in fairly good condition. The dentition was good. The abdomen was moderately distended. The wall of the right heart was strikingly hypertrophied and the chambers tremendously dilated so that it appeared to be about twice the size of the left ventricle (Plate I, Fig. 1). The pulmonary ring was dilated and measured 6.5 cm. in circumference whereas the aortic ring measured 5.5 cm. A thrombus filled the right ventricle in which many adult round worms were enmeshed. These were identified by Luckner and McIntosh in E. W. Price's laboratory of the Bureau of Animal Industry, Washington, D. C., as *Dirofilaria immitis*. A reddish-brown, rough, irregular, endocardial nodule, 3 mm. in diameter, was found in the outflow tract of the right ventricle. A thrombus, with entrapped *Dirofilaria*, extended into the lumen of the pulmonary artery and of many of its branches. Many of the branches of the right pulmonary artery and some of the left showed aneurysmal dilatations and some were thrombosed. In the branches the thrombi were, for the most part, firmly adherent. Some were reddish-brown and others grayish-white, fibrotic and evidently organized (Plate I, Fig. 2). Some of the nematodes were still motile. The intima of the main stem of the pulmonary artery was roughened, due to shallow, fine, pit-like, closely grouped depressions. Along the intimal surfaces of the branches of the pulmonary arteries there was longitudinal and transverse bridging. Transversing the lumina of some branches, in secant-like fashion was a network of slender, fibrous bands, strings and thin membranes, originating in the intima at one point and inserting at another (Plate I, Fig. 2), (Safir, 1932). The lungs weighed 1,370 grams together and presented many infarcted areas with associated areas of pneumonitis (Plate II, Fig. 1). The pulmonary veins exhibited no pathological changes. The larger radicles of the tracheo-bronchial tree were clear throughout. The hilar lymph nodes were large and succulent.

The peritoneal cavity was filled with 2,000 cc. of clear amber fluid. The liver was enlarged, weighed 1,900 grams and displayed evidence of marked acute and chronic passive congestion. Some areas manifested pseudo-adenomatous formation. There was one large cyst 4 cm. in diameter in the right lobe. A large thrombus containing *Dirofilaria* filled the right main branch of the hepatic vein and its smaller branches (Plate II, Fig. 2). The gall bladder and biliary system were normal. The spleen did not appear enlarged. A firm hemangioma, about 1 cm. in diameter, arose from the mid-portion. The gastro-intestinal tract showed evidence of severe passive congestion. Multiple minute mucosal hemorrhages were present. In addition many small, yellow, hard nodules 2 mm. in diameter were disseminated over the serosa of the small intestine. The kidneys were markedly congested. The spinal fluid was cloudy and on smear disclosed many gram positive cocci. The meninges had a dull fibrinous appearance. Pure cultures of staphylococcus were grown from the heart's blood and the spinal fluid. The or-

ganisms produced yellowish to light orange pigment but could not be definitely classified by fermentation tests.

*Microscopic Findings:* The myocardium revealed only degenerative changes. The intima of the main stem of the pulmonary artery was markedly thickened and showed pit formation. The adventitia was thickened and showed numerous perivascular infiltrations consisting chiefly of lymphocytes but also plasma cells and polymorphonuclear cells. The pericardium in this region revealed a membrane composed of fibrin with entrapped necrotic cells lying on the surface. The elastica Van Gieson stain disclosed marked reduplication and fragmentation of the elastic fibres. The elastic lamellae were of irregular thickness and often their continuity was interrupted.

The walls of the intra-pulmonic branches of the pulmonary artery were thickened and exhibited frequently a striking destruction with replacement of the elastic and muscle fibres of the media by connective tissue. The elastica was markedly fragmented (Plate III, Fig. 1). There was excessive thickening of the adventitia. The intima manifested a conspicuous focal thickening. In one place there was necrosis of the wall with inflammatory cell infiltration (Plate IV). The lumina of these vessels displayed thrombi in all stages of organization. The adjacent alveolar septa were very strikingly thickened and infiltrated with inflammatory cells. This interstitial reaction extended into the finer ramifications. The lung tissue in the immediate vicinity of the larger branches of the pulmonary artery showed collapsed alveoli, frequently containing polymorphonuclear cells and macrophages. Many of the smaller branches of the pulmonary artery were surrounded by a mantle of inflammatory cells and display a marked thickening of the wall and narrowing of the lumen (Plate III, Fig. 2). Some vessels disclosed entire replacement with fibrous tissue. There was also evidence of purulent bronchitis, obliterating bronchiolitis, pneumonia and edema. Organizing pneumonia was in evidence. One wide patch of lung tissue was completely fibrotic, suggesting a completely organized infarct. The ghost-like remains of its vessel of supply was present in its center (Plate III, Fig. 1). The lumen of this artery was completely filled with scar tissue indicating an organization of the original thrombus. A gram stain showed a small number of gram positive cocci in the lung tissue while an iron stain revealed large amounts of iron pigment in the walls of the larger arteries and in the macrophages (heart failure cells) which occupied the alveolar spaces. In the lumen of one bronchus an adult *Dirofilaria* was seen (Plate V, Figs. 1 and 2). The hilar lymph nodes revealed evidence of hyperplasia. A gram stain disclosed only an occasional gram positive coccus.

The capsule of the liver was slightly thickened. The hepatic architecture was severely distorted. There was marked central congestion and marked secondary atrophy of liver cells. In some places entire patches were devoid of liver cells and were replaced by cavernous sinusoids. Disse's spaces were widened and filled with granular material. The Kupfer cells were markedly swollen and some showed erythrophagocytosis. The biliary ducts were not increased. A large branch of the hepatic vein contained an organizing thrombus. An adult worm lay within the lumen next to the thrombus. An iron stain disclosed very little iron and the gram stain only occasional gram positive cocci.

The spleen was markedly congested. The pancreas displayed vascular congestion. The adrenals presented slight hemorrhage in the zone reticularis. The kidneys were the seat of marked congestion, edema and degeneration of the tubular epithelium. There was slight interstitial focal infiltrations of plasma cells.

Unfortunately the brain and spinal cord were lost and could not be examined microscopically. No larvae were detected in any of the tissues. All tissues were fixed in formalin.



The final diagnosis was: *Dirofilaria immitis* infestation of the right heart with thrombosis in the right heart, pulmonary artery and its branches, and the right branch of the hepatic vein; chronic arteritis of the pulmonary artery and its branches with aneurism formation of many of the branches and pulmonary arteriosclerosis; marked hypertrophy of the right ventricle and auricle with tremendous dilatation; chronic endocarditis of the out-flow tract of the right ventricle; multiple pulmonary infarcts; chronic purulent bronchiolitis; chronic pneumonitis of all lobes; staphylococcus sepsis; severe acute and chronic passive congestion of the liver with atrophy and pseudoadenomatous formation; acute purulent meningitis; large cyst of the liver; and slight interstitial nephritis.

#### COMMENT.

A review of the reported cases, including the instance herein described, indicates that the usual cause of death in dirofilariasis of the pulmonary arterial tree is congestive right heart failure. Anatomically, it was evidenced in this case by right cardiac hypertrophy and excessive dilatation, an extreme degree of chronic passive congestion of the liver and ascites. From the character of the arterial lesions observed there is indication that one of the earliest effects on the pulmonary arteries may be a toxic degeneration of the pulmonary arterial wall caused by the humoral products of the adult parasites. This arteritis in turn may have caused the thrombosis in the pulmonary vessels, followed by the development of marked chronic changes in the vessel walls and organization of the thrombi. The hypertension of the pulmonary circuit thus engendered by the presence of such an occluding mechanism, caused dilation of the right ventricle and subsequent hypertrophy. The pulmonary hypertension may in turn be a contributing factor in the causation of the thickening of the intima and the endocardium. The endocarditis may well be a change de novo or possibly an exaggeration of a preceeding endocarditis which is so commonly found in animals of the older age group. Thrombus formation may also be provoked by this endocardial lesion. As the right heart fails, the slowing of the circulation produced in the great veins leading to the right heart, plus the presence of the adult parasites, would tend to foster further thrombosis in these places. We have then, four factors that may have a causative relationship to thrombus formation, namely: toxic arteritis, chronic endocarditis, slowing of the venous circulation, and the adult *Dirofilaria* acting as foreign bodies. The pulmonary arteriosclerosis in the case herein reported may be considered as secondary to the pulmonary hypertension.

The presence of this obstructing mechanism, together with the associated infarcts, whatever the pathogenesis of the latter may be, causes generalized anoxemia, as a result of the interference with the pulmonary circulation. This readily accounts for part of the symptom-complex that the diseased animals present, such as, dyspnea, cyanosis and weakness.

It is interesting in connection with the arterial lesions encountered to briefly mention the report of Clark and Graef of a case of Schistosomiasis mansoni in a twenty-one year old Puerto Rican girl who died of congestive failure. Post-mortem examination revealed a markedly dilated right heart. Evidence of arteritis and dilatation of the branches of the pulmonary artery with associated severe arteriosclerosis was noted. The authors were able to demonstrate the ova in the media and concluded that the arteritis was a specific response to the parasite, while the arteriosclerotic thickening was assumed to be secondary to the increased tension within the pulmonary arterial tree. We do not feel that the arteritis observed by us was caused by the presence of adult or embryonic parasites in the wall of the vessels. We could not demonstrate such a lesion as did Clark and Graef. On the

contrary, we are inclined to the view that the toxins elaborated by the adult *Dirofilaria* and their larvae may have caused the arteritis. The work of Yano, referred to above, in which he produced renal changes after injection of a centrifuged extract of female *Dirofilaria*, gives some support to this concept.

In the case reported here, the additional factor of severe infection must be held accountable as the immediate cause of the animal's death.

We failed to detect any microfilaria in the tissues we examined. This is not surprising when one considers the life cycle of the *Dirofilaria*. For it is known that the larvae produced by the adult filaria are not capable of maturing in the host and tend to disappear. They must pass through an intermediate host (mosquito) and be inoculated into a dog or other susceptible animal before they are capable of reaching an adult, sexually mature state. In our case, where the adult nematodes were apparently dying as they were entrapped in thrombi, fewer and fewer embryos were produced and thus none was seen in the tissues. The blood of the wolf was not examined before death.

It is apparent from what has been said that in infested animals with cardiac embarrassment, the additional toxic effect of an anesthetic on the cardiac muscle readily explains the cases of death ensuing during anesthesia reported in the literature.

#### SUMMARY.

1. A review of the literature on the morbid anatomy of *Dirofilaria immitis* infestation in mammals is presented.

2. An instance of such infestation in a gray wolf dying of congestive heart failure and superimposed sepsis is described.

3. An unusual feature of arteritis with associated aneurysmal dilatation of the branches of the pulmonary artery is reported.

The author is indebted to Dr. Charles R. Schroeder for his kind cooperation and permission to publish the case; and to Drs. Paul Klemperer and Sadao Otani for their valuable aid in the preparation of this report.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Markedly dilated and hypertrophied right cardiac chamber.  
Fig. 2. Right lung with pulmonary arteries opened to show old and fresh thrombi (A) and adult *Dirofilaria* (B). Note organizing network over intima (C).

## PLATE II.

- Fig. 1. Right lower lobe (larger) and right upper lobe (smaller) showing areas of infarction and pneumonitis. Note aneurysmal dilation of pulmonary artery (A).  
Fig. 2. Liver with hepatic vein containing thrombus and adult *Dirofilaria*.

## PLATE III.

- Fig. 1. Cross section of a branch of the pulmonary artery showing complete organization of a thrombus. Elastica exhibits marked fragmentation and destruction. (Section taken from an infarcted area. Elastica-carmin stain).  
Fig. 2. Smaller branch of pulmonary artery showing markedly thickened intima and narrowed lumen. (Elastica-carmin stain).

## PLATE IV.

- Fig. 1. Wall of large branch of pulmonary artery showing purulent inflammation of intima (A) and thrombus in lumen (B).

## PLATE V.

- Fig. 1. Low power view of lung showing longitudinal section of an adult *Dirofilaria* (A) lying within the bronchus, thickened wall of main branch of pulmonary artery revealing fibrosis (B) and a thrombus in lumen (C).  
Fig. 2. Enlarged photograph of right lower corner of Fig. 1 showing portion of *Dirofilaria* lying within bronchus, and purulent bronchitis.



FIG. 1.



FIG. 2.

PATHOLOGY OF DIROFILARIA INFESTATION.







FIG. 1.



FIG. 2.

PATHOLOGY OF DIROFILARIA INFESTATION.





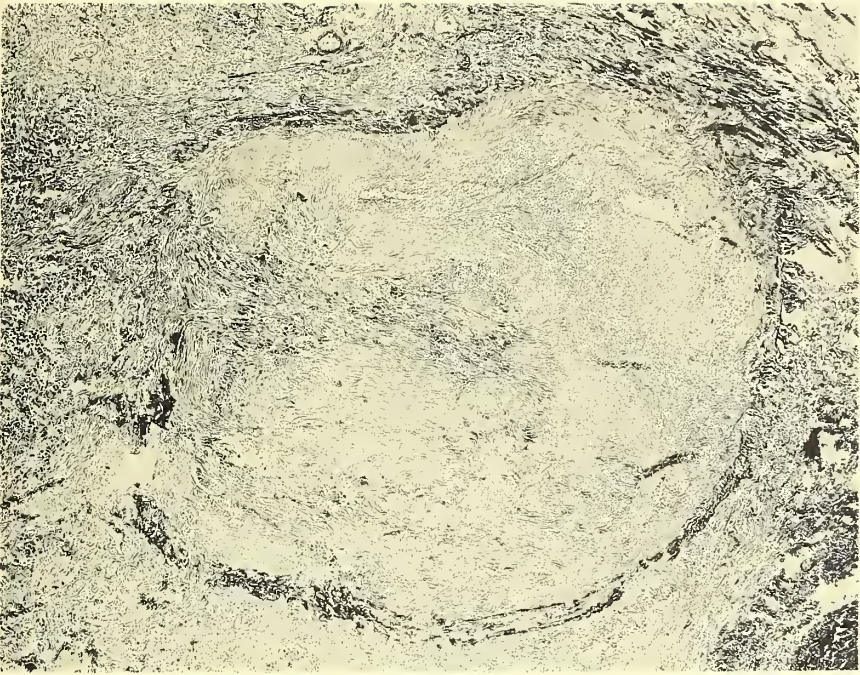


FIG. 1.

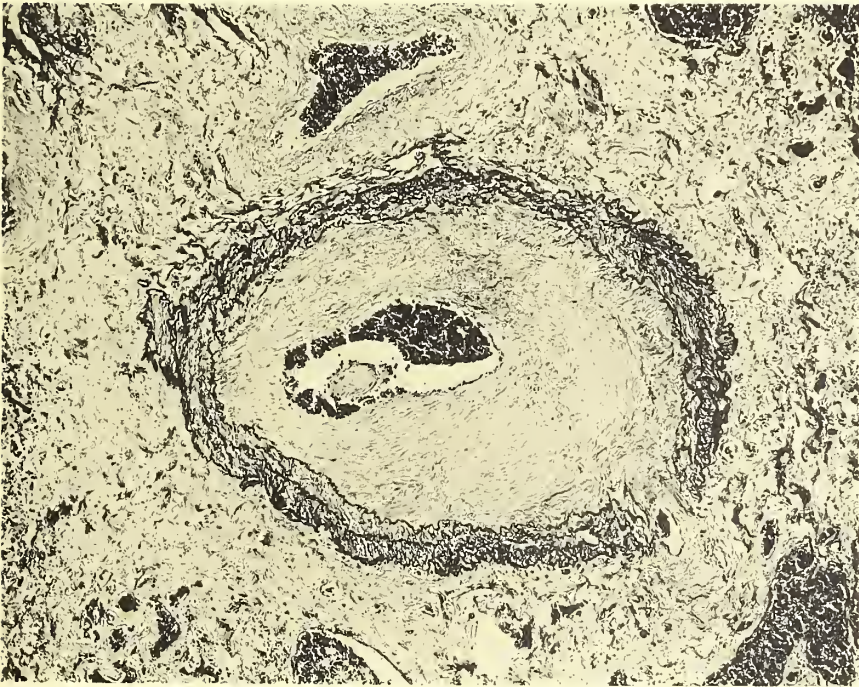


FIG. 2.

PATHOLOGY OF DIROFILARIA INFESTATION.





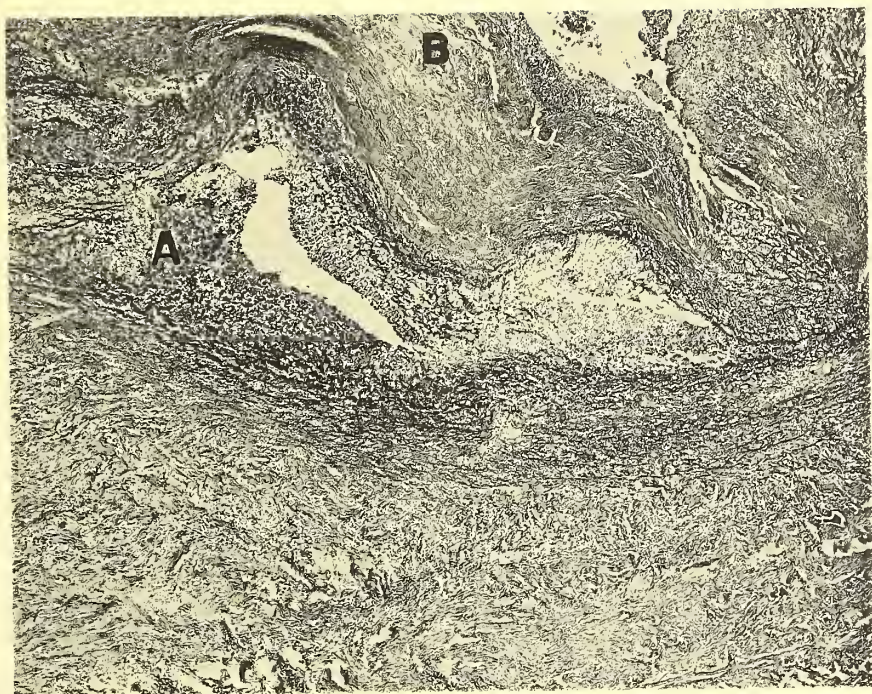


FIG. 1.

PATHOLOGY OF DIROFILARIA INFESTATION.





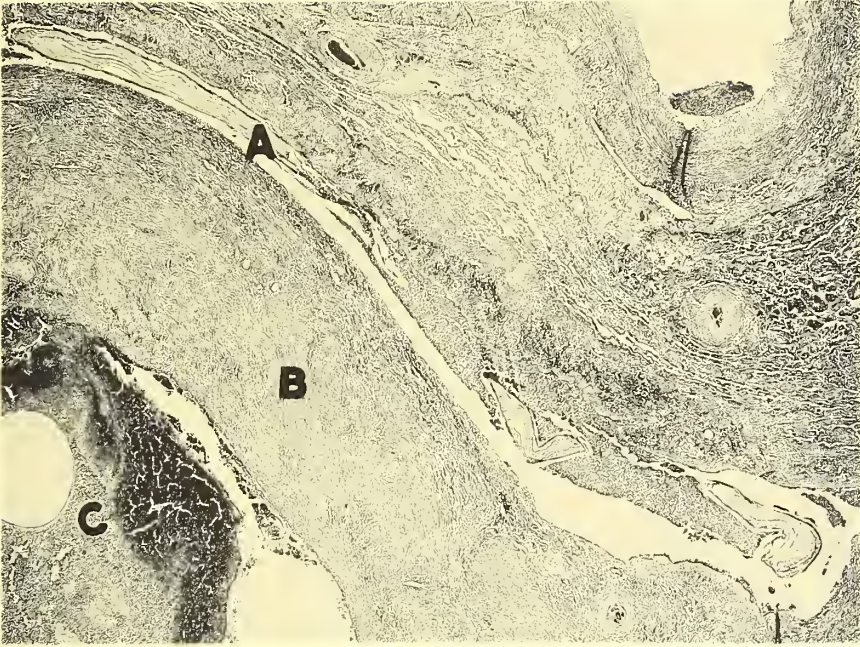


FIG. 1.

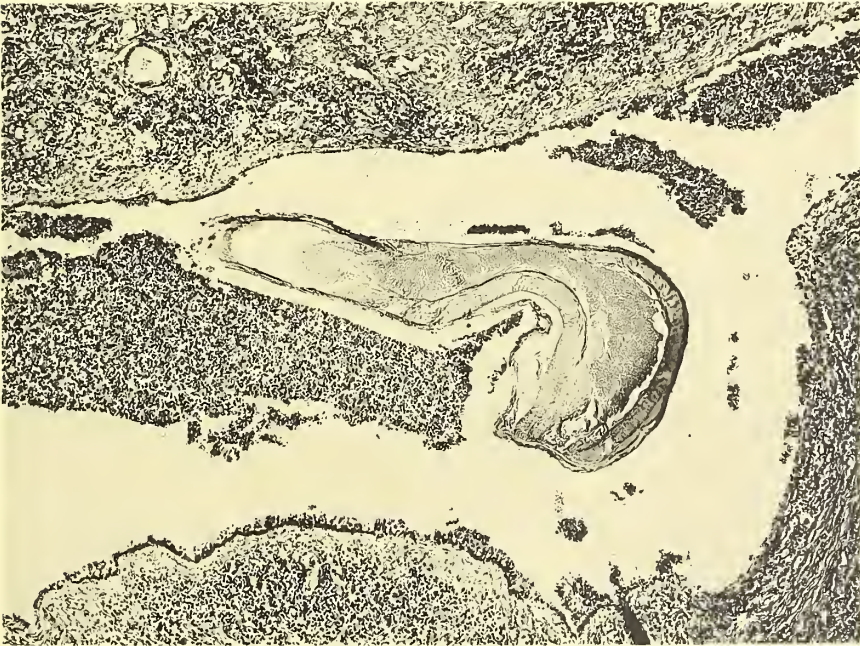


FIG. 2.

PATHOLOGY OF DIROFILARIA INFESTATION.





## 12.

Papilloma of the Skin Occurring in an  
Electric Eel, *Electrophorus electricus* (Linnaeus).

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(Plates I-VI).

With the increase in the reported instances of abnormal growths occurring in fishes, it has become apparent that cutaneous tumors of teleosts are more frequently encountered than are the visceral neoplasms affecting deeper-lying organs. Among the skin tumors of fishes those arising in the connective tissue of the derma or corium seem to be more common than those growths composed of the squamous and mucus cells of the epidermis. There are, finally, a group of papillary tumors of the skin in which the hyperplastic epithelium is heavily supported by a stroma of connective tissue carrying blood and lymphatic vessels and occasionally nerves to the tumor. These growths represent both an epithelial and mesodermal response with both types of cells about equally distributed. Such tumors may be classified as fibro-epithelial growths of the skin. Unlike neoplastic growths in mammals, teleost tumors which are composed principally of epidermal cells appear to be exceedingly rare. Even when they occur in a malignant form (epithelioma), their rate of growth is a relatively slow one, and the tumor, although involving adjacent tissues, usually remains localized in the region where it has its origin, rarely giving rise to the secondary growths in distant tissues or organs so frequently found in mammalian and avian tumors.

Of the few benign epithelial tumors in fishes which have been reported in the literature, the following instance described by Takahashi (1929) may be mentioned as an example. The growth was 3 x 2 x 0.5 cm., grayish-white in color, and occurred in a Crucian carp, *Carassius carassius*, occupying the region of the left operculum. It was sharply circumscribed and showed on its surface dilated blood vessels. The tumor was composed histologically of epidermal cells which were flattened near the surface and exhibited some cornification. Along the deep surface of the tumor there was an active proliferation of epithelial cells into the derma. Interstitial connective tissue

was scanty but fairly well supplied with blood vessels. There was no necrosis, nor were there metastases. Attempts to transplant small pieces of tissue into other fishes of the same species were unsuccessful.

There are no tumors reported up to the present time occurring in the electric eel, *Electrophorus electricus* (Linnaeus). The small cutaneous growth here described developed in the right mid-dorsal region of a large adult electric eel, caught in the Amazon river basin and maintained in good health in a fresh water tank at the New York Aquarium for a period of more than four years. This particular eel, measuring 6 feet in length and 18 inches in largest circumference, had been tested frequently for electrical discharges estimated by measurement to be approximately 350 volts and 40 watts (Coates, Cox & Granath, 1937). Such electrical discharges were repeated at intervals of about 2/1,000 of a second when the eel was disturbed. Other eels subjected to the treatment in measuring electrical discharges for approximately the same period showed no similar growths. The growth began as a small elevation of the skin, pinkish-gray in color, and a few millimeters in diameter. Its maximum growth of 2 x 2.5 cm. was reached in about ten weeks, at which time it was excised for purposes of histological study. No recurrence took place during the remaining year and a half of life.

The growth was a grape-like pedunculated mass (Plate I, Figs. 1 and 2) and was attached to the skin by a narrow short stalk above the lateral line. It did not appear to have its origin in the skin overlying the usual distribution of the electric organs. It was of considerable interest, therefore, when the microscopic study disclosed evidences of nerve trunks and nerve terminations in the epithelium of the growth itself (Plates, IV & V, Figs. 7 and 10).

The epithelial tumor, regarded as a benign papilloma, was composed of solid masses of squamous epithelium commingled with very numerous mucous cells, in an arrangement far more irregular than that exhibited by the normal skin (Plate II, Figs. 3 and 4). The epithelium composing the various lobes of the grape-like mass was supported by a central narrow fibrous core of connective tissue containing many small blood vessels along the course of which existed dendritic melanophores. The linear distribution of pigmented cells external to the thin walls of blood vessels gave to the interior of the tumor the peculiar branching or tree-like effect seen by transillumination in the gross specimen cleared in cedar oil (Plate I, Fig. 2). It will be noted that pigmented lines identifying the various ramifications of the connective tissue stroma extended outward nearly to the free surface of the growth.

It is not the purpose of the present paper to refer in detail to the rather complicated structure of the skin of the electric eel. It may be stated briefly, that the normal epidermis (Plate VI, Figs. 11 and 12) approximately 20-30 cells in depth, rests upon a well developed basement membrane which in its turn separates epithelium (E) from the corium (C). The latter is composed of dense connective tissue fibers supporting the blood capillaries, lymphatic vessels, small nerve trunks and branches and numerous melanophores. The pigment cells are spread out in horizontal arrangement, at times in several layers, immediately below the hyaline basement membrane. In the normal skin, extending outward at right angles to the surface of the body, are found at short regular intervals numerous prolongations of the fibrous tissue of the corium, passing as supporting septa (T) outward into the epithelium (Plate VI, Fig. 11). These supporting septa of connective tissue are somewhat conical in shape with the broader base continuous with the corium while externally they taper off to form finely pointed or club-shaped tips of delicate connective tissue which in this way carry the terminal branches of blood capillaries with closely lying melanophores to points near the extreme outer limits of the epithelial surface. Such sup-

porting septal strands, single or branching, form a region of attachment for narrow elongated closely packed palisade-like epithelial cells (T) (Plate VI, Fig. 12). In contrast with these the epidermal cells springing from the basement membrane between the supporting septa form a system of low cuboidal and small round epithelial cells several layers in density which in all probability represent matrix cells that give rise to predominant squamous and mucous cells of the many-layered epidermis. Relatively few elongated or fusiform cells are found resting on the basement membrane between septa.

Since both the above-mentioned prolongations of connective tissue from the basement membrane and the tuft-like arrangement of narrow epithelial cells covering their tips are very conspicuous features in the skin of the electric eel, it seems rather reasonable to suppose that they are somehow involved in the conduction of the electric discharge from the tissue of the fish into the surrounding water. If these structures differ in electric conductivity from the surrounding epithelial tissue, their presence must modify the distribution of electric current through the epithelium. If they are markedly more conducting than the surrounding tissue, their effect will be to concentrate the current in their own structure through the layers of cells near the basement membrane. The branching of the prolongations near the outer boundary of the epithelium would diffuse the current again where it passes through the outer layers. If such a distribution of current in the epithelium exists, its advantage may be to by-pass the discharge around the matrix cells and so to confine any injurious effect it may have on the epithelial tissue to the outer layers of cells which are constantly replenished.

In our preparations, the extreme outer layer of cells of the normal epidermis in contact with aquatic environment is composed of mucous cells.

In the papillomatous growth all forms and shapes of epithelial cells already mentioned were present, but did not give the appearance of having the precise and regular arrangement which is seen so well in the normal skin. Besides mucous cells there was a great irregular commingling of squamous cells with variations in shape and size, also with irregularities in the size of the nucleus. In many places epithelial cells were transversely arranged running parallel with the surface. For the most part the cells forming the outer boundary of the various lobules composing the tumor were of the mucous type. (Plate III, Fig. 5).

The entire tumor after excision was fixed in 10% formalin, embedded in paraffin, sectioned serially and stained with both hematoxylin and eosin and Masson's Light Green stain. An opportunity was afforded therefore to examine in sequence the stalk-like attachment of the growth to the skin in order to determine the presence of nerve tissues.

Several small nerve trunks were found entering the growth via the narrow stalk. One of these was composed of six separate bundles of myelinated nerves, while another consisted of two nerve bundles. The enveloping connective tissue of each nerve trunk was well developed. Of particular interest was the appearance of the perineurium immediately surrounding the smaller separate groups of nerve fibers. The perineurium was conspicuous by the lamellated appearance of its cells arranged circularly in several layers (Plate IV, Figs. 7 and 8). The two primary nerve trunks which could be traced in detail entered the same lobule of the tumor at different levels by penetration of the basement membrane and were unaccompanied by blood or lymphatic vessels. On reaching the epithelium the perineural cells were still further increased in number and rested in contact with flattened adjacent epithelial cells, from which they were clearly distinguished, particularly in sections stained by the Masson technique. The lamellated arrangement of cells about the several groups of nerve fibers persisted as the nerve bundles coursed through the hyperplastic



epithelium (Plate V, Fig. 9) to reach positions near the outer surface of the tumor. Here individual nerve fibers terminated with lamellated cells still visible (Plate V, Fig. 10). Terminal modifications of nerve fibers were thus formed resembling in many respects Pacinian bodies.

In numerous areas of the growth considerable oedema was noted. This affected principally the region near the surface representing the terminal branches of the small capillaries coursing along the fibrous septa. The tips of connective tissue septa here formed a delicate reticulum in whose meshes an oedematous or albuminous material existed.

Neither necrosis nor signs of inflammation were found in the papilloma. There was no evidence that parasites were present in the abnormal tissue. No intracellular inclusion bodies could be demonstrated. Collections of monocytes with ingested particles of pigment detritus were encountered at intervals (Plate III, Fig. 6).

#### SUMMARY.

The histological features of a papilloma arising in the skin of *Electrophorus electricus* (Linnaeus), containing certain terminal modifications of nerve fibers, are described, and the electrical possibilities of the regions containing palisade-like epithelial cells in the normal skin are briefly discussed.

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## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. Gross specimen of lobulated papilloma excised from the skin of an electric eel, *Electrophorus electricus* (Linnaeus). Fixed in formalin.
- Fig. 2. Gross specimen of papilloma, cleared in cedar oil, photographed by transillumination to show the pigmentation of the supporting stroma caused by melanophores which accompany small blood vessels.  $\times 4$ .

## PLATE II.

- Figs. 3 & 4. Photomicrographs of papilloma, composed of hyperplastic epithelium formed by commingling of squamous and mucous cells. The outer lining cells are columnar-shaped mucous cells. The supporting stroma of the papilloma is fibrous tissue containing pigment cells along the course of small blood vessels.  $\times 65, 85$ .

## PLATE III.

- Fig. 5. Mucous cells, columnar in form, covering the outer surface of the epithelial growth.  $\times 275$ .
- Fig. 6. Collections of monocytic cells containing ingested pigment detritus.  $\times 325$ .

## PLATE IV.

- Figs. 7 & 8. Bundles of nerve fibers with thickened lamellated perineurium lying in fibrous stroma of the growth.  $\times 150, 250$ .

## PLATE V.

- Figs. 9 & 10. Terminal modifications of nerve fibers resembling Pacinian bodies lying in the hyperplastic epithelium of the growth.  $\times 250$ .

## PLATE VI.

- Fig. 11. Normal skin of *Electrophorus electricus* (Linnaeus). Many layers of squamous epithelial cells with numerous distended mucous cells, rest upon a dense fibrous corium (C) containing pigment cells. Supporting the epithelium are connective tissue septa (T) arising from the corium and extending into the epithelium (E). The outer lining of the epithelium is formed by columnar shaped mucous cells.  $\times 95$ .
- Fig. 12. Normal epithelium of the skin of electric eel showing septa attached to which are narrow elongated epithelial cells giving a tuft-like appearance (T). (C) = corium, (M) = matrix cells, (S) = squamous cells, (X) = mucous cells.  $\times 250$ .



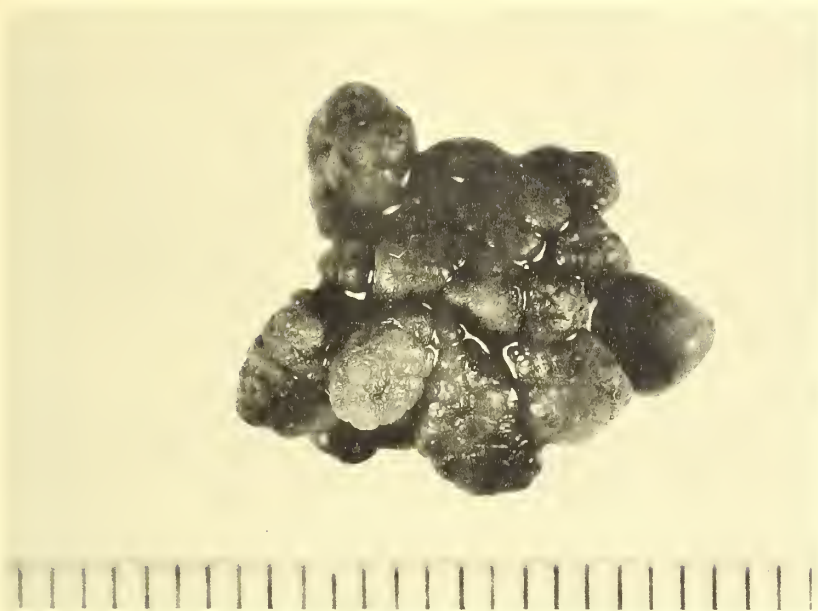


FIG. 1.

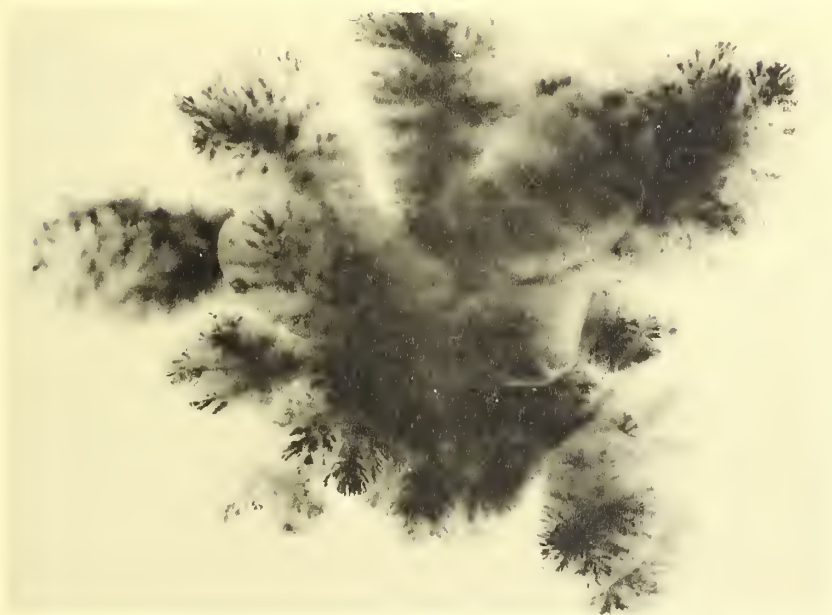


FIG. 2.

PAPILLOMA OF THE SKIN OCCURRING IN AN  
ELECTRIC EEL, *ELECTROPHORUS ELECTRICUS* (LINNAEUS).





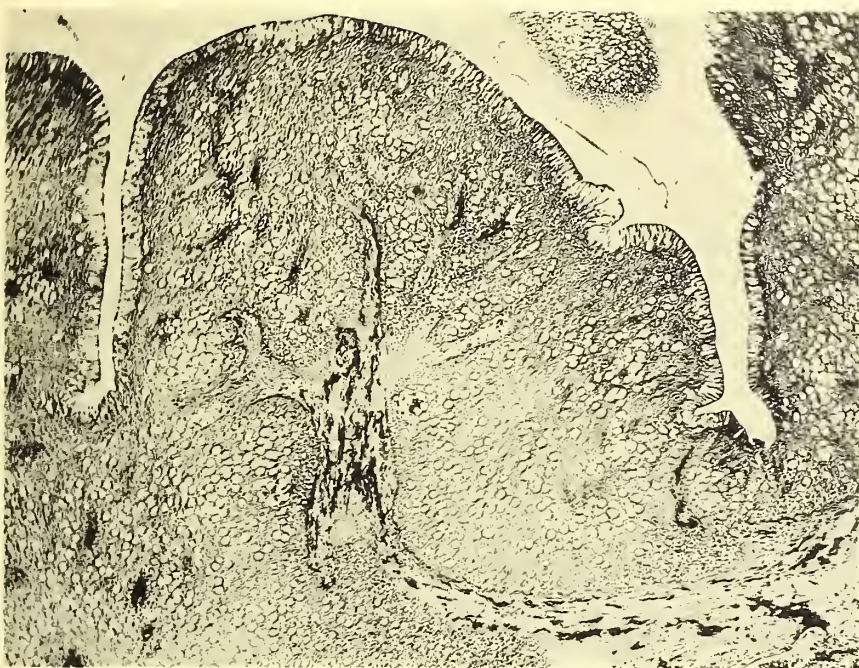


FIG. 3.

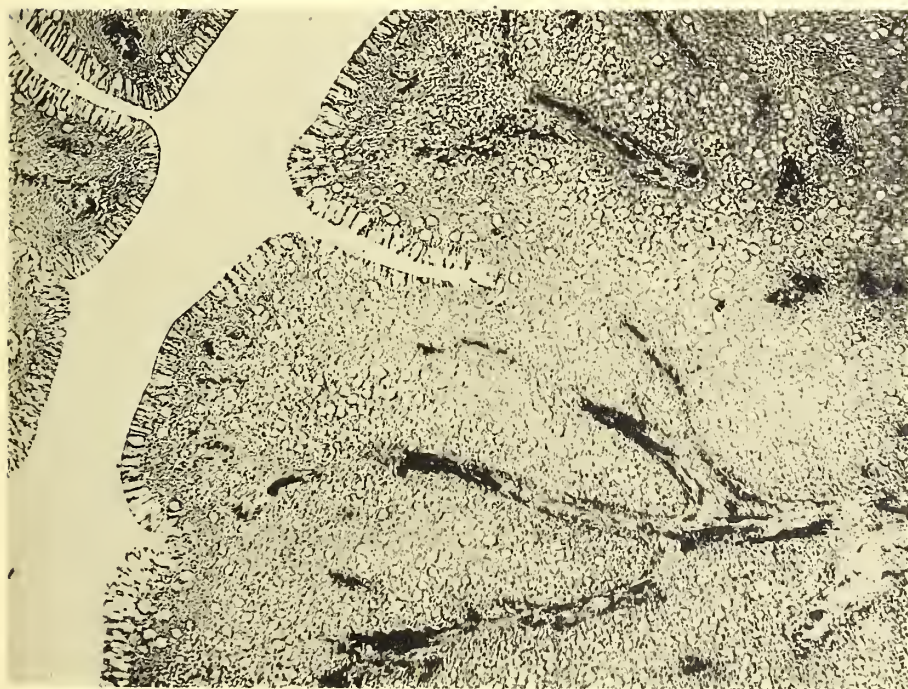


FIG. 4.

PAPILLOMA OF THE SKIN OCCURRING IN AN  
ELECTRIC EEL, *ELECTROPHORUS ELECTRICUS* (LINNAEUS).





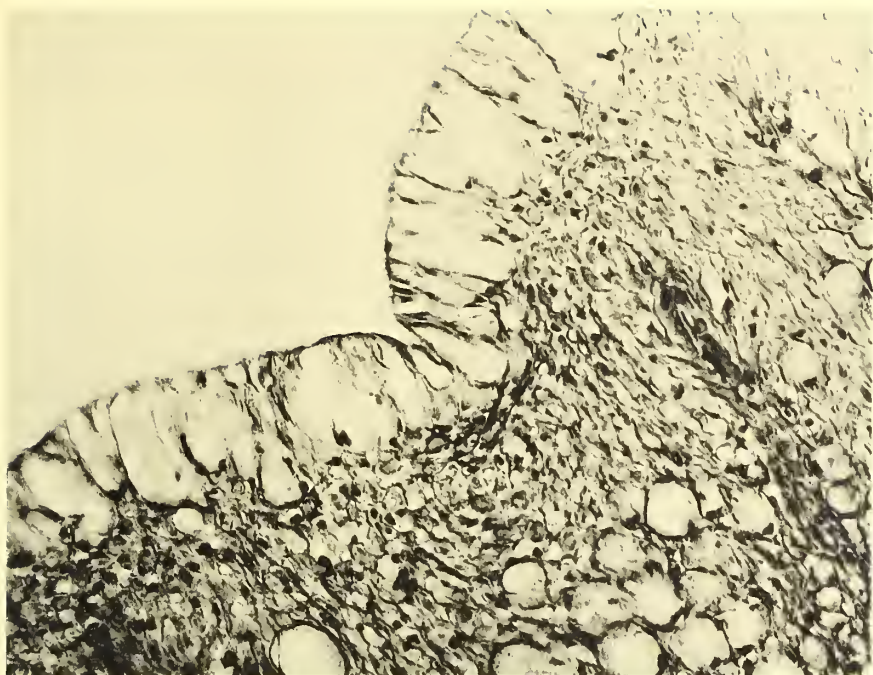


FIG. 5.

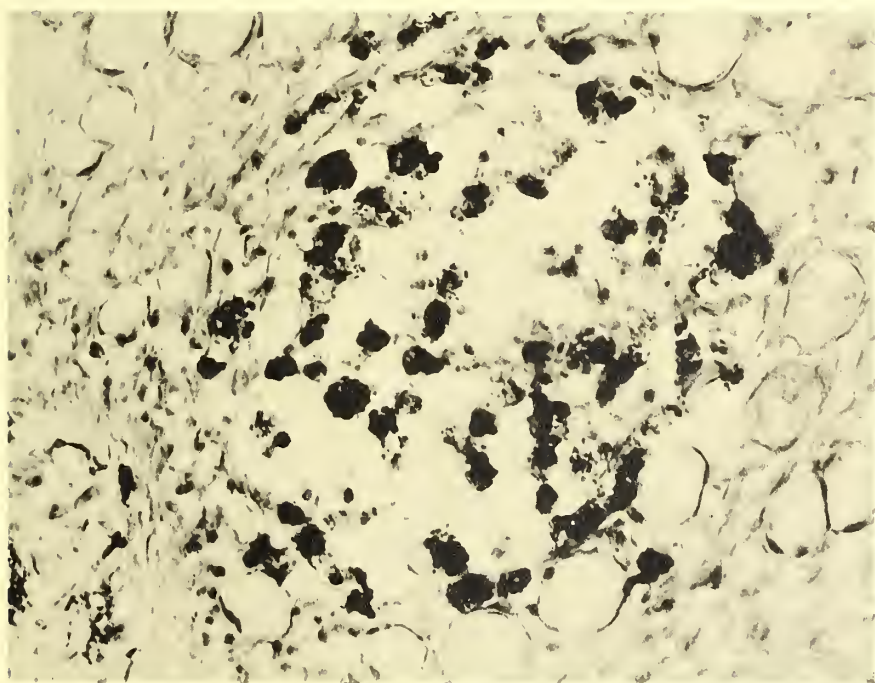


FIG. 6.

PAPILLOMA OF THE SKIN OCCURRING IN AN  
ELECTRIC EEL, *ELECTROPHORUS ELECTRICUS* (LINNAEUS).





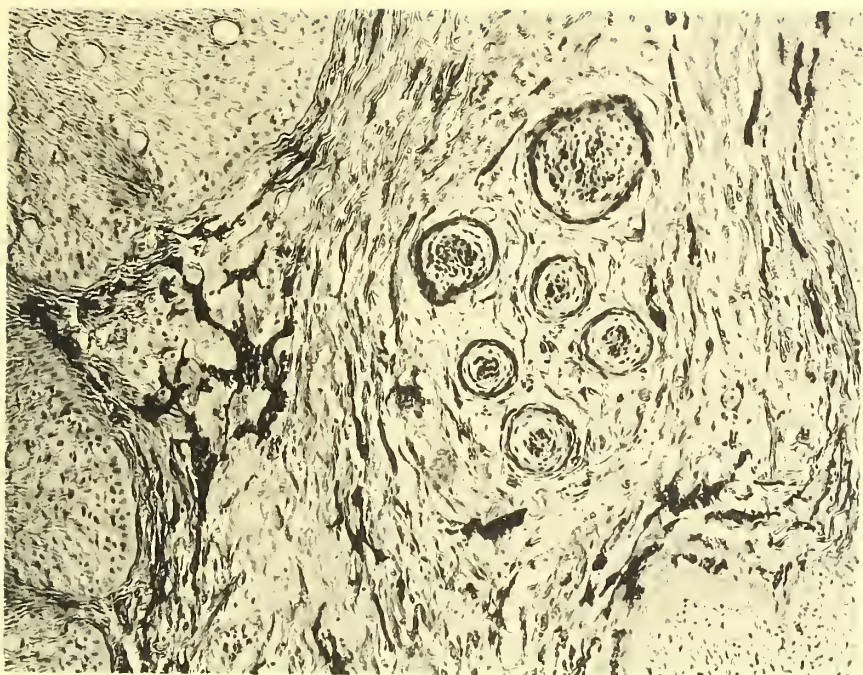


FIG. 7.

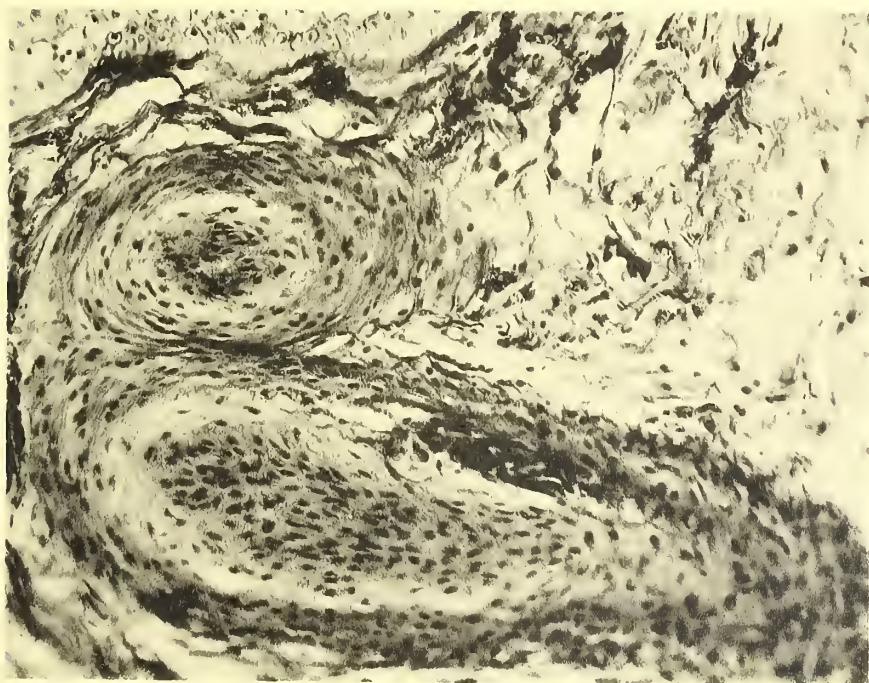


FIG. 8.

PAPILLOMA OF THE SKIN OCCURRING IN AN  
ELECTRIC EEL, *ELECTROPHORUS ELECTRICUS* (LINNAEUS).





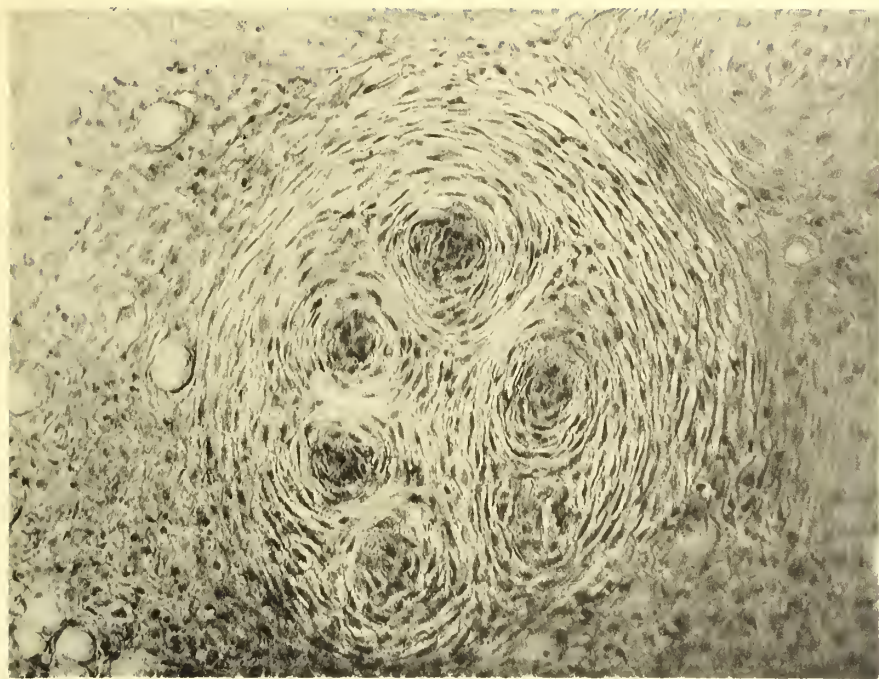


FIG. 9.

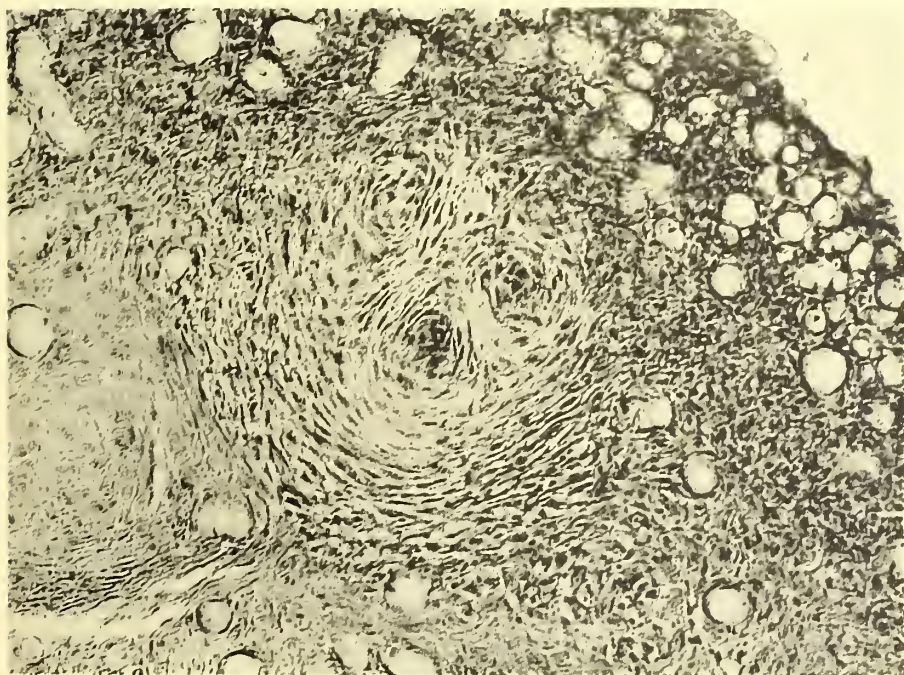


FIG. 10.

PAPILLOMA OF THE SKIN OCCURRING IN AN  
ELECTRIC EEL, *ELECTROPHORUS ELECTRICUS* (LINNAEUS).





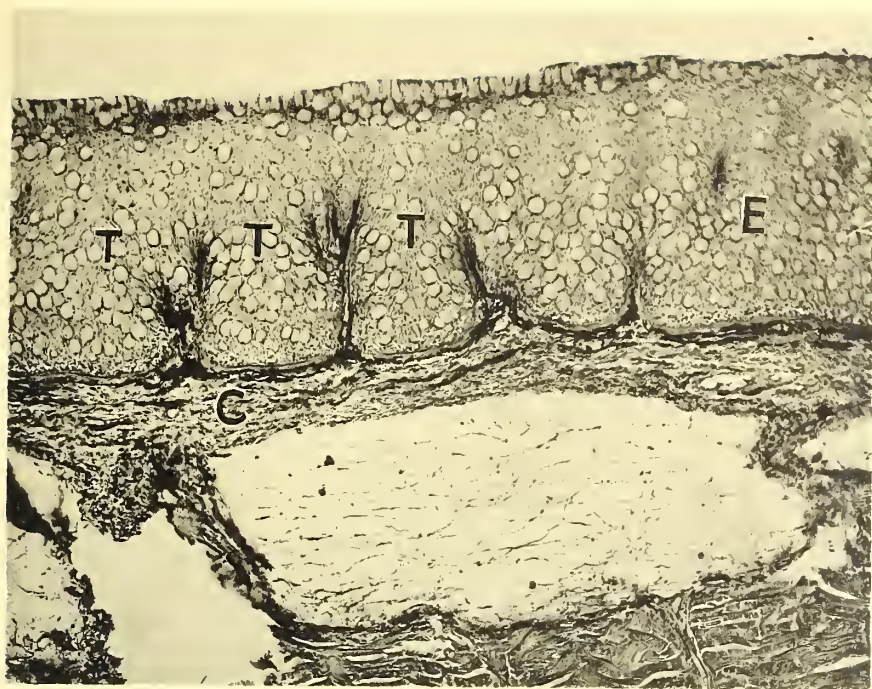


FIG. 11.

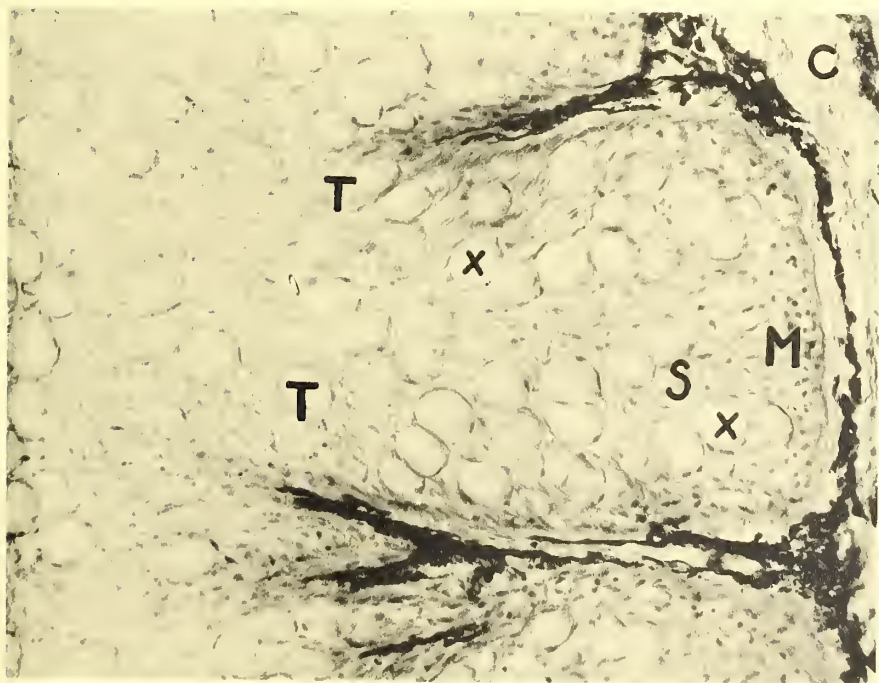


FIG. 12.

PAPILLOMA OF THE SKIN OCCURRING IN AN  
ELECTRIC EEL, *ELECTROPHORUS ELECTRICUS* (LINNAEUS).



## 13.

Arithmetical Definition of the Species, Subspecies and Race  
Concept, with a Proposal for a Modified Nomenclature.

Containing a simple method for the comparison of related populations.<sup>1</sup>

ISAAC GINSBURG.

(Text-figures 1-4).

## INTRODUCTION.

Ever since naturalists began to doubt the special creation of species, in consequence of the accumulating incontrovertible evidence proving the descent of species from preexisting forms of life, the question of what constitutes a species became bothersome. The acuteness of the problem was intensified when biologists ceased to be satisfied with describing and cataloging species of plants and animals by a study of one or but a few specimens, and began to study in detail the individuals comprising a species *en masse*. The great individual variability of the characters employed for specific distinctions and the consequent difficulty of drawing sharp lines of demarcation between closely related species was thus revealed.

This fundamental problem in biology engaged the attention of students and a considerable literature has grown up dealing with the question of what constitutes a species. A good deal of what has been written has reference to its speculative aspects. It is not the aim of this article to add anything to the purely abstract discussions of the problem. Instead, it represents an attempt to solve this problem and determine definitely just what is a species by reference to a series of actual data. It is my intention to consider in detail a number of concrete cases showing the facts of speciation as they occur in nature and an attempt is made to correlate the facts and draw the proper conclusions therefrom.

The data employed to support the propositions advanced in the present paper are entirely taken from populations of fishes. The data were not specially collected for this paper, but have been gathered in connection with my revisional studies of American fishes. Some of the data have been published in reports on these studies; others are here published for the first time, or previously published data are amplified. As far as the included evidence is concerned this paper may be said to be a sort of a by-product of my revisional studies of the genera of American fishes, and the supporting data presented below have been only casually selected to prove the propositions advanced. While the examples cited have been taken entirely from the class of fishes, the same method no doubt will be found applicable to other groups of animals, and plants as well.

All the examples included below are based on quantitative characters. The method developed here is most strikingly applicable to such characters

<sup>1</sup> Published by permission of the U. S. Commissioner of Fisheries.



which thus serve best for the purpose of illustration. For some specific characters this method will be applied with greater difficulty and a lesser degree of precision, and cases may be encountered in which it is inapplicable, especially in cases in which differences are based on qualitative characters (see below). However, this is a problem in practical usage. Such cases must be considered by themselves, and special means of expressing particular characters in the form of frequency distributions, may be devised. The fact that this method may be inapplicable practically in some cases does not detract from the pertinence of the general principles evolved as a result of its application in the great number of cases in which it may be used with ease and precision.

The question of what constitutes a species cannot be considered by itself. To solve this problem consistently it must be broadened to include the subdivisions of the species, since, as will be shown definitely hereafter, the different categories which may be established imperceptibly grade into one another. This paper, therefore, goes into the whole problem of the species and its subdivisions. In connection with this study the question of the nomenclature of taxonomic categories below specific rank is examined and a modification of the method now in general use, is proposed. A simple method for the comparison of closely related populations is employed in this paper, which may prove to be a useful tool in the taxonomic study of populations of specific or lower rank.

#### FAILURE OF PREVIOUS ATTEMPTS TO ESTABLISH ABSOLUTE LIMITS TO THE SPECIES CONCEPT.

A number of criteria have been used by previous writers for the purpose of defining and establishing absolute boundaries to limit the species concept. The literature on the subject is quite voluminous, and it is not my present purpose to give a complete review of such previous attempts. This has been done by a number of writers in greater or lesser detail, and the reader may be referred to one of these writers, such as Robson (1928) who also gives an extensive bibliography of the subject. In general, it may be stated that all criteria which have been proposed for establishing absolute boundaries by which we may definitely determine just what constitutes a species, have been found wanting. One of these criteria, the morphological, may be considered here briefly because the definitions proposed herewith are based solely on that criterion. It is the only criterion which is most generally useful in the practice of taxonomy.

A population of variable individuals was considered to be fully distinct specifically from another population differing in at least one structural or color character in such manner that no intergrading individuals occur, but that every single individual may be referred either to one or the other of the two populations. Such populations have been regarded as fully distinct species. Even at the present time some systematists hold to this as a criterion for distinguishing species, or as the most important criterion. However, absolute lack of intergradation in nature is far from being the usual condition. On the contrary, intergradation of related populations is so general that it would not be far fetched to make the statement that it is the rule rather than the exception. Certainly most closely related species of fishes, in my experience, have been found to intergrade more or less.

Specific characters are roughly divisible into two classes: (1) quantitative characters, such as the number of fin rays, scales or vertebrae, proportional measurements, etc.; (2) qualitative, such as differences in color, or the presence or absence of certain structures or color marks, or differences in their form. Among fishes the former is predominant. Qualitative structural characters which are absolute, that is, they practically do not show any intergradation, are in many cases considered to be of



generic or subgeneric, rather than specific, importance. Also, two groups of related species between which a comparatively wide gap exists with respect to a given quantitative character are often placed in separate genera or subgenera. Characters which are considered to be of specific importance only, by general consent, more likely than not, will be found to intergrade between two closely related populations when a sufficiently large number of individuals are studied in detail. This is true not only of quantitative characters, but frequently an imperceptibly gradual intergradation occurs also in the case of qualitative characters, although in the latter case it may be difficult to measure and express in terms of precise figures the degree of intergradation.

The general existence of intergradation is not duly reflected at present in taxonomic works. The reason taxonomists have been able to describe species generally in such manner as to make it appear that no intergrading individuals are present, is that these descriptions are usually based on but a few individuals. Consequently, by the law of chance, such few individuals were apt to fall, in most cases, near the center, and away from the extremes, of a regular frequency distribution. Occasional bothersome specimens may have been explained away as being abnormalities, sports or hybrids. However, such border line specimens will be found in most closely related species if a sufficient number of individuals are studied in detail. Except for possible occasional hybrids, or atypical individuals for various reasons, such specimens are normal individuals, but they fall in at the extreme of the frequency distribution, and as far as any given single character is concerned they may as well belong to one species as to another closely related one.

#### THE TRUE MORPHOLOGICAL CRITERION IS THE DEGREE OF INTERGRADATION, OR DIVERGENCE.

The intergradation between natural populations varies in degree. When a sufficient number of pairs of closely related populations are compared and the several intergradations, or divergences, are arranged in order of magnitude, we obtain a series that is graduated by virtually infinitesimal steps. It follows, therefore, that the determination of whether a given pair of populations constitute two species or belong to a category of lower rank depends on the *degree* of intergradation; or, to view it from another angle, the *degree* of divergence. As a further consequence, it follows that species as well as subspecies and races are not absolute entities. The lines drawn to limit these classificatory units must be arbitrary. That this is not merely a theory but the actual condition which exists in nature is attempted to be proved in the paragraphs which follow. (I discussed this proposition in another paper (1937a). Data to prove it are presented here.) After adopting a measure by which the degree of intergradation is expressed in terms of a definite figure, a series of data obtained by the study of pairs of closely related populations of fishes is presented and the figure expressing the degree of intergradation for each pair is calculated by the method employed. The figures thus obtained form a gradual series which may be arranged in ascending or descending order and there are no breaks in the gradual continuity of the series where sharp lines may be drawn to limit absolutely our concept of species, subspecies or race.

#### MEASURE OF INTERGRADATION, OR DIVERGENCE.

Our next step in the solution of the problem is to adopt a definite and uniform measure by which the degree of intergradation, or divergence, between any two closely related populations may be expressed in terms of a *single* figure. Several methods of measuring intergradation or divergence may be employed. For instance, Davenport (1898) proposes what are essen-

tially two methods of measuring precisely the difference between two closely related populations. Davenport represents the two related populations, in every instance cited by him, in the form of a single bimodal curve. One measure which he designates as the "index of divergence" represents "the ratio of the distance between the modes to the half-range . . . of the broader curve." The other measure, designated by the author as the "index of isolation," represents "the ratio of the depression [between the two parts of the bimodal curve] to the length of the shorter mode." (The "depression" is the vertical distance between the apex of the smaller curve and the lowest point of the depression). Both measures are expressed as percentages. A measure which is often employed to indicate the difference or divergence between two populations may be represented by the formula

$$\frac{M_1 - M_2}{\sqrt{E_1^2 + E_2^2}}$$

in which  $M_1$  and  $M_2$  represent the means of the two respective populations, and  $E_1$  and  $E_2$  represent the probable errors of the two means, respectively. This expression represents the ratio of the difference between the means to the probable error of this difference (see Pearl, 1930, pp. 282-287). In treatises dealing with the application of statistical methods to biological problems the statement is often made that when the numerical value of this ratio is 3 or 4, it is "significant." Other methods may be suggested. For our present purpose a simple method of expressing the degree of intergradation, or divergence, between two related populations is proposed to be used as indicated below.

For the present I am not going to discuss in detail the advantages and disadvantages of the various methods which have been proposed or which may be suggested with the method employed herein. This is a problem by itself, a full discussion of which would lead us astray from our main thesis. If any consistent method be adopted and a number of closely related pairs of populations be compared by it, the results quite likely will form a gradual series going to prove the continuity of intergradations, *inter se*, in nature; but the relative position of the pairs of populations compared, in the series, will no doubt change somewhat according to the method used, and some methods will more nearly represent the facts of nature than others. A brief comparison is made below (p. 279) between the method employed herein and the standard method, and it is shown that the latter is not well adapted for our purpose. Besides the fitness of the measure employed to represent the facts more nearly in their true light, it has two salient advantages which may be mentioned briefly. (1) It may be determined easily and quickly, a very desirable consideration, especially from the point of view of the busy taxonomist. (2) Because of its simple character its pertinence in explaining the facts of nature is strikingly evident and the relationship of variable and closely related populations may be appreciated readily when this measure is used.

Our simple measure may be illustrated by the following hypothetical examples. Let us assume two species of fishes, A and B, the chief differentiating character of which is represented by the number of scales in the lateral line, a character which is frequently employed in distinguishing closely related species of fishes. Let us suppose further that the scales of a hundred specimens of each species have been counted, and the figures obtained were as follows:

Number of scales (class)	24	25	26
Species A (frequencies)	92	8	
Species B (frequencies)		97	3

It may be said then that species A intergrades with species B to the extent of 8% and this figure may be suggested as our measure of intergradation.

While this figure obviously suggests itself, it is not the figure finally adopted. The measure of intergradation for the above hypothetical case, by the method employed, is 4%, for reasons which will become clear presently.

In nature examples similar to the above simple hypothetical case may be encountered; but the variability and relationship of closely related natural populations is much more often not as simple. Let us, therefore, take the next step and assume a hypothetical case where the dispersion of the frequency distributions and the overlap are a little more pronounced; while at the same time the frequency distributions are perfectly regular, as follows:

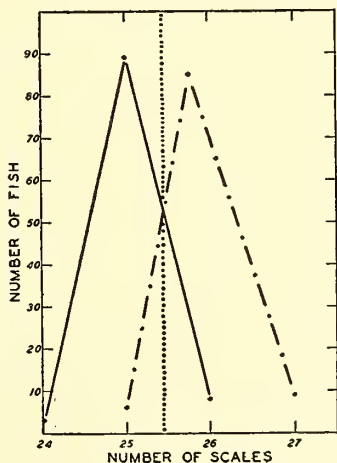
Number of scales (class)	24	25	26	27
Species A (frequencies)	5	90	5	
Species B (frequencies)		5	90	5

In this perfectly regular hypothetical case each species overlaps the other by 5% and this figure may be taken as our measure of intergradation.

Again it may be stated that perfectly regular frequency distributions such as the foregoing hypothetical case are seldom encountered in practice. Frequency distributions are usually irregular or, to use the technical expression, skewed. Part of the irregularity encountered in practice is no doubt due to incomplete sampling of the populations; but it is evident that skewness in the frequency distributions of populations is the more usual and normal condition in nature. Let us then assume a hypothetical case where the frequency distribution is irregular while the overlap is more pronounced than in the simple hypothetical case cited first, as follows:

Number of scales (class)	24	25	26	27
Species A (frequencies)	3	89	8	
Species B (frequencies)		6	85	9

This case is a little more complicated and is nearer the majority of examples encountered in actual practice. How are we to measure intergradation in this case?



Text-figure 1.

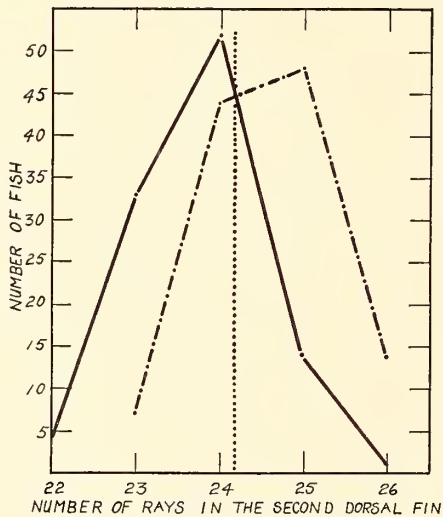
Frequency polygons of the number of scales of two hypothetical species; see discussion in text. Solid line represents species A, broken line represents species B.

If two frequency polygons be constructed to represent graphically the foregoing hypothetical data (Text-fig. 1), the polygons will intersect at a point over the abscissal axis between the points representing 25 and 26



scales. If a vertical line be drawn from the point of intersection of the two polygons, it will be found that 8 specimens of species A cross over to the right of the dividing line, and 6 specimens of species B cross over to the left. The specimens thus crossing over may be said to intergrade. Species A therefore intergrades with respect to species B to the extent of 8%; while species B intergrades with species A in 6% of the individuals. The intergradation is thus not the same in both species. This is a result of the skewness of the frequency distributions and is the usual condition encountered in practice, as stated. However, we want a single figure which will represent the intergradation between two species. This is obtained by taking the simple average of the two figures. The intergradation of species A and B in this hypothetical case is therefore 7%.

We will now take up an actual case and see how this measure works in practice. Let us take the case of *Sciaenops ocellatus*, the northern Atlantic and Gulf coast populations of which diverge sufficiently to place them well up in the following gradated series of examples. The two populations diverge chiefly in the frequency distribution of the number of rays in the second dorsal fin for which the data are given in Table VII, p. 267. These data are



Text-figure 2.

Frequency polygons of the number of articulate rays in the second dorsal fin of two populations of *Sciaenops ocellatus*, based on data given in Table VII, the actual number of specimens being represented. The solid line represents the Chesapeake Bay population; the broken line represents the Texas population. The dotted vertical line represents the dividing line between the two polygons as used throughout the present discussion for the purpose of determining and measuring the degree of intergradation.

represented graphically by Text-fig. 2 which illustrates the frequency polygons of the two populations and the dividing line that forms the basis of determining the measure of intergradation as used throughout the present discussion. Of the northern population 15 specimens cross over to the right of the dividing line, or 14.42% of the composite sample studied comprising 104 specimens; and 50 specimens of the Gulf coast population cross over to the left of the line, or 44.64% of the sample which comprises 112 fish. The simple average of these two percentages, in round figures, is 30, which rep-



resents the measure of intergradation of those two populations. In practice, it is usually not necessary actually to construct the polygons; but the point where the dividing line is to be drawn may be determined by inspection after arranging the data in a frequency distribution table, preferably in the form of percentages (see Table I).

This measure of intergradation, which is uniformly employed in this paper, has the following statistical basis. If the histograms representing the two populations compared be constructed on a percentage basis, the area enclosed by the two overlapping histograms, expressed as a percentage of the sum of their separate areas, equals the measure of intergradation determined as indicated above. In other words, the measure of intergradation as employed for our present purpose represents the measure of the area enclosed by the two overlapping histograms expressed as a percentage. This may be illustrated graphically by the pair of intergrading populations of *Sciaenops ocellatus*.

TABLE I.

Frequency distribution of the number of articulate fin rays in the second dorsal of two races of *Sciaenops ocellatus*, expressed as percentages of the total number of specimens counted of each race, respectively.

Locality	Number of dorsal rays (percentages) :					Totals
	22	23	24	25	26	
Chesapeake Bay	3.85	31.73	50.00	13.46	.96	100
Texas coast		6.25	38.39	42.86	12.50	100
The smaller of the overlapping percentages		6.25	38.39	13.46	.96	59.06

Table I gives in percentage form the data represented in Table VII, p. 267. This is necessary for the purpose of constructing the graphs because the number of specimens in the two samples is not the same, the usual condition in practice; whereas, in order to show the normal amount of overlap of the two populations it is necessary to have two samples containing the same number of individuals. Text-figs. 3 and 4 illustrate graphically the data presented in Table I. Text-fig. 3 shows the overlapping histograms of the two populations, the part of each histogram which overlaps the other being distinctively shaded. In Text-fig. 4, drawn to the same scale, the two histograms are shown side by side with the shaded areas the same as in Text-fig. 3. Text-fig. 4 shows at a glance the approximate relation of the sum of the two shaded areas, or the area enclosed by the overlapping histograms, to the sum of the areas of the two histograms. Precisely, this area equals 30%, in round figures, of the sum of the areas of the two histograms. The measure of intergradation is therefore 30% in this particular case. This result may be obtained by adding the smaller of the overlapping frequencies, as shown in Table I, and dividing the sum by 2 in order to get the percentage of the area overlapped to the sum of the two histograms; or by the simple arithmetical calculation as indicated above.

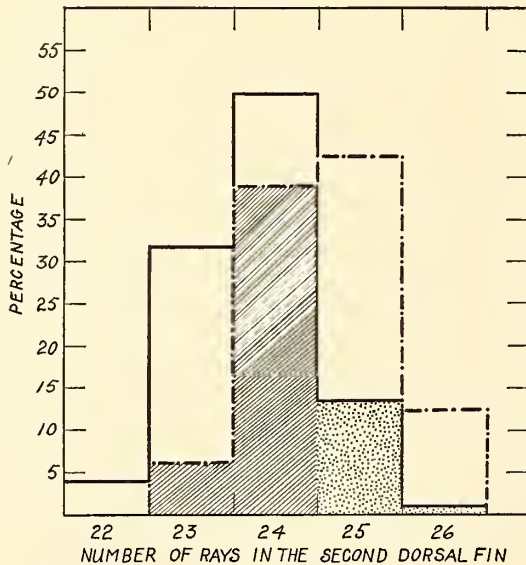
The measure of divergence may be indicated as a percentage also, by subtracting the measure of intergradation as determined above from 100.

The calculation, and hence the number denoting intergradation, or divergence, is always based on the character showing the greatest degree of divergence. There may be some question as to the adequacy of the use of a single character, since we know that populations usually differ in several characters, some of which such as color differences are not readily expressible in definite figures. Some attempts have been made to combine several characters and express the hypothetical sum of their differences by a single fig-

ure. However, I am not at all satisfied that such attempts have succeeded in producing a measure which will more satisfactorily express for our purpose the essential biological facts. Besides, in studying and combining the data for several characters the question will always come up as to just where to draw a line since practically it would be almost impossible to study them all. While not entirely adequate the present measure should prove sufficient for practical purposes, and conclusions arrived at as a result of studies by the standard statistical formulae have been based on a single character. Certainly in the determination of the differences between species or subspecies it is the character which shows the greatest divergence that is the important one to consider. In the method here employed provision is made for taking into consideration other differentiating characters besides the one showing the greatest divergence (see p. 276); although such characters are considered in a general way and not expressed in terms of definite figures. This is probably the best that may be done for the present.

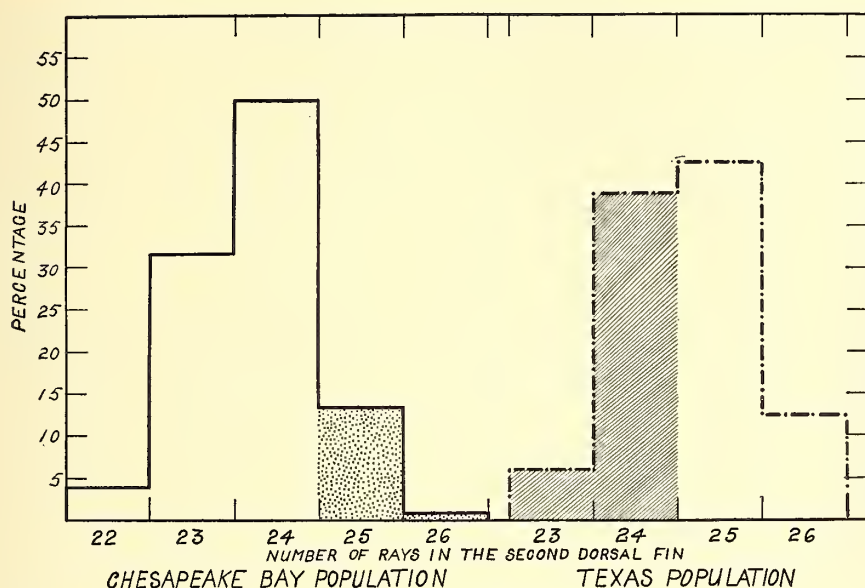
#### ARITHMETICAL DEFINITION OF SPECIES, SUBSPECIES AND RACE.

Using the above measure, it is proposed tentatively to limit the designation of species and its subdivisions as follows: Other things being equal, a given population is to be considered a race with respect to another closely related population when the average intergradation of the character showing the greatest divergence is between 30% and 40%; a subspecies constitutes a population intergrading between 15% and 25%; it is to be considered a full species when the degree of intergradation is not more than 10%. Con-



Text-figure 3.

Overlapping histograms of the number of articulate rays in the second dorsal fin of two populations of *Sciaenops ocellatus*; based on the same data as Text-figure 2, but the number of specimens in each class expressed as a percentage of the entire sample studied. The solid line represents the Chesapeake Bay population; the broken line represents the Texas population; the hatched space represents the area by which the latter histogram overlaps the former, and the stippled space represents the area by which the former histogram overlaps the latter.



Text-figure 4.

The same two histograms represented in Text-figure 3, separated and placed side by side to give a better picture of the relation of the shaded areas to the sum of the areas of the two histograms. In this particular case the sum of the two shaded areas is 30%, in round figures, of the sum of the areas of the two histograms, and this number represents the measure of intergradation in this particular case. The series of three Text-figures are graphic illustrations showing, by reference to a particular example, how the measure of intergradation as employed for our present purpose, is derived.

comitantly, the divergence between races is 60% to 70%; between subspecies 75% to 85%; and full species diverge to an extent of 90% or more.

For the benefit of those who are used to thinking in terms of graphs the above definition may be paraphrased as follows: When the area enclosed by the two overlapping histograms, constructed on a percentage basis, equals 30 to 40% of the sum of their separate areas, the two populations are to be considered as races; they are considered subspecies when the overlap is 15 to 25%; they are full species when the overlap is 10% or less.

The above proposed boundary lines are discussed on page 275.

#### THE VARIETY AND FURTHER POSSIBLE SUBDIVISION OF THE SPECIES.

In the above definition of the two principal subdivisions of a species, namely, the subspecies and the race, the maximum intergradation allowed for any population to be included under the latter category is 40%. All pairs of populations which intergrade to a greater extent than 40% are proposed to be grouped under the general category of "variety" and are not further analyzed in our present preliminary study.

In addition to the subdivisions of a species proposed herewith it is evident that the number of such subdivisions may be readily increased by simply narrowing the boundary lines, which are arbitrary anyway, in this completely gradated series. More extensive studies may indicate the de-



sirability of increasing the subdivisions, such as inserting a category between the subspecies and the race, and further subdividing the inclusive category here designated as the variety and consisting of populations which intergrade by more than 40%. The number of categories which may be found desirable to recognize may differ with particular genera or groups. Any such further subdivision should be based not on the rule of the thumb, but on the study and correlation of a sufficient number of actual cases. Most likely in the majority of cases the subdivisions of a species proposed herewith will be found sufficient.

#### SAMPLING.

The present study would be incomplete without a consideration of the question of sampling. Although I have tried to avoid the use of complex statistical formulae, it will be noted that the present study is largely statistical in its nature. Indeed, if taxonomy is ever to be placed on a high scientific plane it will perforce have to become to a large extent statistical in its methods; although, quite likely, simple statistical deductions will be found sufficient in most cases. One sometimes comes across the statement in taxonomic works that a certain species is a "statistical species," sometimes stated in a rather disparaging manner, as though such a species is not of much account. However, probably the majority of closely related species of fishes are "statistical species." The reason taxonomists were able to make this distinction between "statistical species" and those supposedly not statistical, is because their studies were largely based on but a few specimens, as noted above (p. 255). A "statistical species" is simply one which diverges from a closely related species to a comparatively low degree so that even the study of a few specimens shows the close approach or even intergradation of the frequency distributions of the differentiating characters.

The importance of proper sampling in statistical studies in general is universally appreciated, and it is not necessary to consider the subject here at any length. It will be sufficient here to state that, except in a few cases such as the complete enumeration of the population of a country during a census, the description of certain attributes of a population is in reality a description of the attributes of the sample which has been studied, and the value of the description is dependent on how nearly the sample is representative of the population as a whole.

The same is true of the description of species, subspecies, races or varieties. If a species is described from a single specimen or from a few specimens, the account in reality represents a description of those specimens. While in many cases such a description is sufficient for practical purposes to identify and distinguish the species, in many other cases such an account will be found entirely inadequate. Related species may be so close that it takes the detailed study of many specimens to establish their divergence. In such cases proper sampling becomes of importance; although in the case of populations which reach a sufficiently high degree of divergence to be regarded as full species, sampling is not of as transcendent importance as in populations showing a relatively higher degree of intergradation.

In my own studies during which the data presented below were obtained, I was impressed time and again with the importance of proper sampling. It was noted frequently that specimens in the same lot bearing the same data, evidently having been obtained in one or but a few drags of the net in the same place at the same time, and consequently, most likely having a common, immediate genotypic origin, would tend to group themselves, in a predominant manner, within a narrowly circumscribed space, sometimes even near either end of the frequency distribution of their species or race as a whole. This was noted especially in cases where the specimens in the lot were



of nearly the same size. Consequently, it may be readily appreciated that if the sample studied be obtained in one, or but a few drags of the net made at the same time in the same place, it is quite likely that it would not give a true picture of the population in many cases.

In obtaining the data presented below due attention was paid to the question of sampling. As stated above, the data were obtained incidentally in the course of taxonomic studies of the fishes. They were taken from lots of specimens obtained at different times by various collectors. In no case was a definite plan of sampling the particular population devised and carried out. Under the circumstances, the method of sampling which I adopted was as follows.

For the sake of brevity and clarity it is proposed to designate all the specimens from which the final data in a Table are drawn, as the *composite sample* and the smaller samples which go to make up the composite sample, as *constituent samples*. It has been stated that if the composite sample is obtained in one drag of the net, that is, it has but one constituent sample, it will quite likely not give a true picture of the population. The greater the number of constituent samples the more nearly will the data approach the true distribution of the population as a whole. As a consequence of these premises, it was my aim to include as many constituent samples as it was possible to obtain from the available material. If, for instance, I had 25 containers of specimens representing as many lots of fish taken on different dates, in different places, and 20 containers had but 1, 2, or 3 specimens each, while the other 5 containers had much larger numbers, the 20 smaller lots were included in the study, and only part of the specimens of each of the larger lots. Of course, my sampling was limited by the material available, but in every case I tried to come as near to my aim as was possible. The number of constituent samples will be stated hereafter under each example cited, so that the reader may judge as to the adequacy of the sampling. (For the meaning of the notation adopted see footnote on p. 264). I am confident that in most cases at least the given distributions represented by the composite samples are more or less fairly representative of their populations for practical purposes.

In some cases the number of specimens studied were too few to constitute a satisfactory composite sample, such as in case of the two races of *Hippocampus zosterae*, in *H. punctulatus*,<sup>2</sup> and in *Gobiosoma bosci* and *G. robustum*. Since it is my hope that the method adopted herein will serve as a useful guide for taxonomists who frequently and of necessity have to work with quite small samples, these examples are included in our series. Further remarks regarding sampling in the above three cases are given under their accounts.

#### EXAMPLES OF VARIETIES.

*Cynoscion regalis*. This species is discussed below in another connection and the frequency distributions of the number of dorsal rays are given in Table IX, p. 269. Turning to that Table and comparing the population of Chesapeake Bay with that from the east coast of Florida, it will be noted that the dividing line to be drawn according to the simple method outlined above, is between the columns representing 27 and 28 rays. Of the Chesapeake Bay population 21 specimens of a total of 40, or 52.50% of the composite sample, cross over to the left of the dividing line. The percentage of intergradation of the Chesapeake Bay population as compared with that of Florida is therefore 52.50. Likewise, of the Florida population

<sup>2</sup> The notation for subspecies employed in this paper is in accordance with the suggestion made on p. 284.

43 specimens out of a composite sample of 110, cross over to the right of the dividing line, representing an intergradation of 39.09%. The simple average of these two intergradations, 46 in round figures, represents our measure of intergradation. The measure of divergence in this case is 100 minus 46, or 54%. Constitution of composite samples: Chesapeake Bay 1 (4)<sup>3</sup>, 2 (4), 7 (1), 8 (1), 13 (1); Florida 5 (1), 28 (1), 77 (1). The two larger constituent samples from Florida do not bear any more definite data than the locality and month and each one possibly contains more than one constituent.

*Cynoscion nebulosus*. The well known spotted sea trout of the southern states is a common food and game fish from Chesapeake Bay to Texas, ranging northward, in diminishing numbers, to New York. For an account of the species the reader may be referred to any general work dealing with the fishes of the region where it occurs, such as the "Fishes of Chesapeake Bay" by Hildebrand and Schroeder (1928). No extensive study has been made as yet of its racial differentiation; but there is found a statistically measurable difference in the number of dorsal fin rays in fish from the Gulf coast as compared with those from Chesapeake Bay on the Atlantic Coast. It is possible that a more extensive study will reveal other characters showing a greater degree of divergence, but this is quite doubtful. At any rate, the dorsal fin ray count evidently shows sufficient divergence to be useful as an illustration in the present study.

TABLE II.

Frequency distribution of the number of articulate rays in the second dorsal of *Cynoscion nebulosus*.

Locality	Number of rays in second dorsal				
	23	24	25	26	27
Chesapeake Bay	1	17	53	31	6
Texas coast	1	12	38	48	5

The dividing line in this case is drawn between the columns representing 25 and 26 rays. The Texas population intergrades by 49.04%, while the Chesapeake Bay population intergrades 34.26%. The average intergradation in this case is 42% and the divergence 58%. Constitution of composite samples: Chesapeake Bay 1 (15), 2 (3), 3 (2), 5 (2), 6 (2), 16 (1), 43 (1); Texas 1 (2), 2 (4), 3 (2), 4 (2), 5 (3), 6 (1), 7 (2), 10 (1), 17 (1), 18 (1).

Although this example does not form a happy choice for the purpose of illustration, it is included in our series because similar cases no doubt will be encountered in practice. It will be noted that if the polygons representing the above data be constructed they will overlap at three points. Consequently, our method of drawing the dividing line and calculating the intergradation

<sup>3</sup> For the sake of brevity the sampling of every case cited in this paper is indicated by figures which have the following meaning. As suggested above (p. 263), the entire number of specimens of a given population, on which the final distribution in any one Table is based, is designated as the composite sample, while each lot of specimens bearing the same data is known as a constituent sample, a variable number of constituents going to make up the composite sample, depending on the particular population used as an example. In the notation adopted a figure outside a parenthesis indicates the number of specimens in one or more constituent samples, while a figure within a parenthesis gives the number of constituent samples each one of which contained the number of specimens indicated by the preceding figure. Thus, the composite sample of *C. regalis* from Chesapeake Bay was made up of 11 constituent samples, four of which had 1 specimen each, four constituents had 2 specimens each, while the remaining three had 7, 8 and 13 specimens, respectively.

does not apply strictly to the present case. However, it will be noted also that if one specimen from the Texas population be dropped at one extreme end and two specimens from the Chesapeake Bay population be dropped at the other end, the two polygons will overlap at one point as usual. This small irregularity caused by one and two specimens out of a little over a hundred in either composite sample, very likely is caused by the imperfection of sampling, and any such irregularity at either extreme where the number of specimens are few, is not likely to be compensated readily. At any rate, whatever the cause, for the purpose of computing the degree of intergradation by our present method, this small irregularity is disregarded. It is to be noted that computing by the standard formula (see Table XVII) the degree of difference between these two distributions almost reaches a "significant" figure.

#### EXAMPLES OF RACES.

*Bairdiella chrysura*. This is a very common fish on the east coast of the United States. A recent and quite extensive account of the life history of the species has been published by Hildebrand and Cable (1930). Like the preceding species its races have not been studied extensively as yet, but there is a difference in the frequency distributions of the dorsal fin rays between southern and northern fish, as follows.

TABLE III.

Frequency distribution of the number of articulate rays in the second dorsal of *Bairdiella chrysura*.

Locality	Number of rays in second dorsal				
	19	20	21	22	23
Chesapeake Bay	2	11	26	28	3
Texas coast	3	19	37	12	

If a line be drawn between the columns representing 21 and 22 rays, it will be found that the Chesapeake Bay population intergrades with that of the Texas coast to the extent of 55.71%, while the Texas population intergrades 16.9%, giving an average intergradation of 36% and a divergence of 64%. Sampling: Chesapeake Bay 1 (14), 2 (8), 3 (6), 4 (3), 5 (2); Texas 1 (6), 2 (1), 4 (2), 5 (1), 6 (1), 19 (1), 25 (1).

*Fundulus confluentus*. This is a rather common, small, cyprinodont fish originally described from Lake Monroe, Florida, by Goode and Bean (in Goode 1879, p. 118). The original description is in error in some important details, and the species has been confused with related species by all later authors which I consulted. However, it is a well marked species which may be distinguished without undue difficulty from its congeners occurring with it through a greater part of its range. An account of the species will be included in a revision of the genus which is under preparation. The Chesapeake Bay population of this species differs racially from that of Florida. In addition to a rather slight and variable difference in the color pattern, the structural character showing the greatest divergence is found in the number of rays in the anal fin as follows.



TABLE IV.

Frequency distribution of the number of anal rays in *Fundulus confluentus*.

Locality	Anal rays		
	9	10	11
Norfolk, Va.	23	35	
Beaufort, N. C.		19	1
Florida	2	21	2

It will be noted that the Chesapeake Bay population tends to have a markedly lower anal fin ray count. The population from North Carolina nearly agrees with that of Florida in the number of fin rays, but the color pattern is more nearly like that of the Chesapeake Bay population. Drawing the dividing line between the columns representing 9 and 10 rays and comparing the Chesapeake Bay population with that of Florida, it will be found that the former population intergrades by 60.34% and the latter by 8%; or an average intergradation of 34%. Sampling: Norfolk 3 (1), 9 (1), 14 (1), 32 (1); Florida 1 (6), 2 (1), 5 (1), 12 (1). This is the only example, of all those cited here, in which the well marked modes of both populations fall on the same side of the dividing line.

*Hippocampus zosterae*. In reviewing the species of its genus found in American waters I (1937) studied material of this species from Pensacola, Captiva Pass and Key West, and the data presented herewith are taken from my paper, where the question of racial differentiation is taken up in greater detail. The populations from the three localities differ, on the average, in the number of trunk segments and the number of rays in the pectoral fin, the former character showing the greatest divergence as follows.

TABLE V.

Frequency distribution of the number of trunk segments of *Hippocampus zosterae*.

Locality	Trunk segments		
	9	10	11
Key West <sup>4</sup>	4	16	1
Captiva Pass	5	12	1
Pensacola <sup>5</sup>	7	6	

It is to be noted that the greatest divergence exists between the Pensacola and Key West populations, while the Captiva Pass population is somewhat intermediate but nearer to that of Key West. This gradual differentiation with latitude is a frequently recurring phenomenon which is well known to students of fishes. In a case of this kind and in the absence of a more elaborate study of the species, we may compare the extremes. If a line be drawn between the columns representing 9 and 10 segments, it will be found that the Key West population intergrades with that from Pensacola to the extent of 19.05%, while the latter intergrades with the former by 46.15%, giving an average intergradation of 33%. Sampling: Pensacola 1 (2), 11 (1); Key West 1 (6), 2 (1), 3 (1), 4 (1), 6 (1).

<sup>4</sup> Including 4 specimens from Newfound Harbor.

<sup>5</sup> Including 1 specimen from Apalachicola.



The available material of this species is not sufficient to constitute a satisfactory sample; but the difference between the populations is significant, especially when considered in connection with the small spread of the frequency distribution, and approximately this difference very likely will be found to exist after a more satisfactory sampling (see also remarks on p. 263).

*Leiostomus xanthurus*. This species is the well known spot, a common market fish on the east coast of the United States. The most comprehensive account of its life history published so far is that by Hildebrand and Cable (1930). Almost nothing is known now regarding the racial differentiation of the species; but I found a significant difference in the number of rays in the second dorsal on comparing fish from Chesapeake Bay with those from the coast of Texas, as follows.

TABLE VI.

Frequency distribution of the number of articulate rays in the second dorsal of *Leiostomus xanthurus*.

Locality	Number of rays in second dorsal					
	28	29	30	31	32	33
Chesapeake Bay		5	25	33	18	
Texas coast	1	25	50	20	6	1

The dividing line is drawn between the columns representing 30 and 31 rays. The Chesapeake Bay population intergrades 37.04% and that of the Texas coast 26.21% giving an average intergradation of 32%. Sampling: Chesapeake Bay 1 (3), 2 (2), 3 (5), 4 (1), 5 (1), 10 (1), 20 (2); Texas 1 (5), 2 (2), 3 (1), 4 (1), 5 (1), 6 (1), 17 (1), 19 (1), 20 (2).

*Sciaenops ocellatus*. This species is the well known redfish in the markets of the Gulf coast, the celebrated channel bass of sportsmen. For an account of the species the reader may again be referred to Hildebrand and Schroeder (1928). The racial differentiation of this species likewise has not been studied to any extent, but there is a significant difference in the number of rays in the second dorsal when the Chesapeake Bay population is compared with that of the Gulf coast as follows.

TABLE VII.

Frequency distribution of the number of articulate rays in the second dorsal of *Sciaenops ocellatus*.

Locality	Number of rays in second dorsal				
	22	23	24	25	26
Chesapeake Bay	4	33	52	14	1
Texas coast		7	43	48	14

The dividing line in this case is drawn between the columns representing 24 and 25 rays. The intergradation of the Texas coast population is 44.64%, that of the Chesapeake Bay population 14.42%, or an average intergradation of 30%. Sampling: Chesapeake Bay 1 (1), 2 (1), 3 (1), 5 (1),

6 (1), 22 (1), 28 (1), 37 (1); Texas 1 (5), 2 (1), 4 (2), 5 (1), 8 (1), 10 (1), 12 (2), 21 (1), 29 (1).

#### EXAMPLES OF SUBSPECIES.

*Hippocampus punctulatus*<sub>2</sub> and *H. hudsonius*<sub>2</sub>. These seahorses from the east coast of the United States and the coast of Cuba have been generally recognized as independent species by American ichthyologists. However, they have been badly confused, and their structural characters have been stated incorrectly in most current accounts. A discussion of their morphological and geographical limits is given in my review of the species of *Hippocampus* (1937) where it is determined that the character showing the greatest divergence between them is found in the number of caudal segments, as follows.

TABLE VIII.

Frequency distributions of the numbers of caudal segments of *Hippocampus hudsonius*<sub>2</sub> and *H. punctulatus*<sub>2</sub>.

Locality and subspecies	Number of caudal segments						
	33	34	35	36	37	38	39
<i>H. hudsonius</i> <sub>2</sub>							
Chesapeake Bay to Maine			3	7	15	7	4
North and South Carolina			1	7	8	1	
Mississippi to Texas			1	5	10	2	
<i>H. punctulatus</i> <sub>2</sub>							
Florida and Cuba	1		8	10	7		

As in *H. zosterae* (see p. 266), the greatest divergence is found between the northern population, Chesapeake Bay to Maine, and the southern, Florida and Cuba. The population from the Carolinas and that from Mississippi to Texas are somewhat intermediate but nearer to the northern population. Other characters as well gradually differ with latitude. Although there is a gradual change in morphology with latitude, it nevertheless seems desirable to recognize two subspecies as discussed on page 277.

In this case the dividing line is drawn between the columns representing 36 and 37 caudal segments. Comparing the extreme northern population of *hudsonius*<sub>2</sub> with the extreme southern population, *punctulatus*<sub>2</sub>, the former intergrades the latter by 27.78%, and the latter intergrades the former by 26.92%, or an average intergradation of 27%. Also, in order to show the normal morphological range of *hudsonius*<sub>2</sub> as a whole, the data from North and South Carolina and Mississippi to Texas are combined with those from Chesapeake Bay and northward. Combining the data as indicated, the northern *H. hudsonius*<sub>2</sub> intergrades with the southern *H. punctulatus*<sub>2</sub>, to the extent of 33.80%, while the latter intergrades by 26.92%, giving an average intergradation of 30%. The composite sample of *H. hudsonius*<sub>2</sub> consists of 54 constituent samples as follows: 1 (43), 2 (7), 3 (3), 5 (1). Some of the constituents having more than one fish do not have the data any more specific than the name of the state on the coast of which they were captured, and they quite likely represent more than one constituent. At any rate, the number of constituents in the composite sample is not less than 54. The composite sample of *H. punctulatus*<sub>2</sub> consists of 23 constituent samples, as follows: 1 (21), 2 (1), 3 (1). The specimens in the composite sample of

*punctulatus*<sub>2</sub>, are very few, but they represent the limit of my available material. While lacking in numbers it consists of many constituents and possibly fairly represents its population (see also remarks on p. 263).

*Cynoscion arenarius*<sub>2</sub> and *C. regalis*<sub>2</sub>. The differences between these two common subspecies from the east coast of the United States have been discussed by me (1929) and the reader is referred to that paper for details. In grown specimens the character showing the greatest divergence seems to be found in the number of gill rakers on the outer gill arch; while the number of dorsal rays shows the next greatest divergence. However, the number of gill rakers is not susceptible of precise determination for reasons stated in the paper cited. Should it be found possible to discount the difficulties inherent in a precise determination of that character, it is doubtful whether it would prove to show greater divergence than the number of dorsal rays. On the other hand, the latter character is susceptible of absolutely precise determination at all stages of growth, soon after the fin rays have developed in the young fry. For the purpose of the present discussion it may be assumed that that character shows the greatest divergence.

TABLE IX.

Frequency distribution of the number of articulate dorsal rays in *Cynoscion regalis*<sub>2</sub> and *C. arenarius*<sub>2</sub>.

Locality and subspecies	Number of dorsal rays					
	24	25	26	27	28	29
<i>C. regalis</i> <sub>2</sub>						
Chesapeake Bay		1	5	15	16	3
North and South Carolina		1	6	21	12	
Cape Canaveral and Fernandina, Fla.		3	15	49	35	8
<i>C. arenarius</i> <sub>2</sub>						
Louisiana and Texas	2	35	59	22	1	

The dividing line in this case falls between 26 and 27 rays; *C. arenarius*<sub>2</sub> intergrading 19.33% and *C. regalis*<sub>2</sub> 16.32%, resulting in an average intergradation of 18%. The sampling of the populations of *regalis*<sub>2</sub> from Chesapeake Bay and from the coast of Florida has been indicated above (p. 264); while that from the Carolinas is as follows: 3 (2), 4 (1), 7 (1), 8 (1), 15 (1). Of *arenarius*<sub>2</sub> 69 specimens do not have any specific data by which the number of constituent samples could be determined; the rest consists of 14 constituents as follows: 1 (9), 2 (1), 5 (1), 6 (2), 22 (1).

#### EXAMPLES OF SPECIES.

*Hippocampus regulus* and *H. zosterae*. The former species is closely related to the latter, the races of which have been discussed above. More extensive accounts of the two species and a discussion of their relationship are given in my (1937) review. It will be sufficient to state here that besides its somewhat smaller size, and a slightly greater average number of trunk segments, *H. regulus* differs chiefly from *H. zosterae* in having a smaller number of caudal segments and fewer dorsal rays, the greatest divergence occurring in the latter character, as follows:



TABLE X.

Frequency distribution of the number of dorsal rays in *Hippocampus regulus* and *H. zosterae*.

Locality and species	Number of dorsal rays				
	10	11	12	13	14
<i>H. regulus</i>					
Mississippi and Texas	2	15	1		
Campeche, Mexico		5			
<i>H. zosterae</i>					
Key West, Fla. <sup>6</sup>		4	13	5	
Captiva Pass, Fla.			16	2	
Pensacola, Fla. <sup>7</sup>		2	9		1

An inspection of the foregoing Table shows that this character tends to be fairly constant within the limits of each species, there being no pronounced racial divergence as was found above for the number of trunk segments of *H. zosterae*. The Key West population shows a tendency to have a slightly smaller average—thus surprisingly more nearly approaching *regulus* from Mississippi and Texas than the Pensacola race of *zosterae* approaches *regulus*—but the difference is slight. The divergence of the two species in this case is measured by drawing a dividing line between the columns representing 11 and 12 rays. *H. zosterae* is thus found to intergrade to the extent of 11.54%; *H. regulus* intergrades 4.35%; giving an average intergradation of 8%. Sampling: *H. regulus* 1 (3), 2 (5), 5 (2); *H. zosterae* 1 (7), 2 (2), 3 (2), 6 (1), 11 (1), 18 (1).

*Gobionellus boleosoma* and *G. shufeldti*. Accounts of these two species of gobies and a discussion of their relationship will be found in my (1932) revision of the genus. Briefly, the two species differ in the maximum size to which they attain, in their color pattern, in the relative length of the ventral fin, in the extent of squamation in front of the dorsal, and in the number of dorsal and anal rays. However, none of these differences is absolutely decisive when each one is considered by itself, and individual fish often can not be distinguished and identified with assurance by any one single character, although there is usually no trouble in referring individual fish to their proper species when all the differentiating characters are taken in consideration. The greatest divergence between the two species is shown by the number of anal rays, as follows.

TABLE XI.

Frequency distribution of the number of anal rays in *Gobionellus boleosoma* and *G. shufeldti*.

Species	Number of anal rays			
	11	12	13	14
<i>G. boleosoma</i>	3	74	4	
<i>G. shufeldti</i>		3	33	1

<sup>6</sup> Including 3 specimens from Newfound Harbor and 2 from Biscayne Bay.

<sup>7</sup> Including 1 specimen from Apalachicola.



The dividing line in this case is between 12 and 13; the intergradation calculated for *G. shufeldti* is 8.11%, and for *G. boleosoma* 4.94%, resulting in an average intergradation of 7%. The counts of the fin rays in these two species are fairly constant throughout their ranges, there being no pronounced racial differences in this respect. Sampling: *G. boleosoma* 1 (13), 2 (8), 3 (1), 4 (1), 6 (1), 39 (1); *G. shufeldti* 1 (2), 8 (1), 13 (1), 14 (1).

*Paralichthys lethostigma* and *P. albigutta*. Some recent investigators have expressed doubt in regard to the distinctness of these two common species of flounders. This doubt is apparently caused by the fact that the chief differentiating characters are of a meristic nature, that is, quantitative, and vary within rather wide limits. Consequently, when specimens near the beginning or near the end of the two frequency distributions of the two species, respectively, are encountered, they may be referred to either species when any single character is considered. However, after preparing tables for the several characters showing the normal frequency distributions of each species, it becomes an easy matter, with the aid of such tables, to refer individual fish to their proper species. An extensive discussion of the differences between these two species, among others, is included in a revision of the genus which I now have completed in manuscript form. In connection with that study, I examined over 500 specimens representing both species, and out of this large number I encountered only one specimen the status of which was in doubt. Besides the structural differences the two species differ also in their color pattern. Without going here into details, it may be stated that the least intergradation is found in the number of anal rays, as follows.

TABLE XII.

Frequency distribution of the number of rays in the anal fin of *Paralichthys albigutta* and *P. lethostigma*.

SPECIES	NUMBER OF RAYS IN ANAL FIN																								
	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
<i>P. albigutta</i>	1	1	4	10	15	16	26	17	11	5	5														
<i>P. lethostigma</i>											2	5	10	15	25	27	31	13	14	9	1				1

Drawing the dividing line between 63 and 64 rays, it is found that *P. lethostigma* intergrades 1.31%; but no specimens of *P. albigutta* cross over to the left of the line, the intergradation of the latter thus being 0. The average intergradation is then 1% in round numbers. The composite sample of *P. albigutta* includes 70 specimens from the vicinity of Beaufort, N. C., and 16 from the vicinity of Corpus Christi, Texas, for which no detailed data are available, probably containing a number of constituents. The rest are from the Gulf of Mexico, except two specimens from the Atlantic coast, and altogether consist of 16 constituents as follows: 1 (9), 2 (6), 4 (1). The composite sample of *P. lethostigma* contains 13 specimens from Beaufort, N. C., without any further data, but probably obtained on different dates; 7 other specimens from the Atlantic coast and 133 from the Gulf coast. The sampling of all except the 13 is as follows: 1 (11), 2 (4), 3 (2), 4 (3), 5 (1), 6 (1), 7 (1), 8 (1), 9 (1), 10 (1), 12 (2), 13 (1), 21 (1).

*Gobiosoma bosci* and *G. robustum*. An extensive discussion of the relationship between these two species of gobies was published in my (1933) revision of the genus. Besides a difference in the color pattern which, however, is not always distinctive, the chief structural characters differentiating the two species are: the number of dorsal and anal rays and the length of the ventral. The numbers of fin rays intergrade in the two species; but the length of the ventral expressed as the number of times it enters into the distance between the ventral and anal origins, does not show any intergradation in the specimens measured, as follows.

TABLE XIII.

Frequency distribution of the length of the ventral in *Gobiosoma bosci* and *G. robustum*, expressed as the numerical value of the ratio of the distance from base of ventral to origin of anal, to the length of the ventral.

Species	Length of ventral in the distance from its base to origin of anal								
	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0
<i>G. bosci</i>					2	4	8	2	1
<i>G. robustum</i>	3	7	2	4					

In this case then intergradation is zero and divergence 100%. The heading numbers for the classes in the above table represent the mid-values, this example being an illustration of a character the measurements of which form a continuous series. Sampling: *G. bosci* 1 (9), 2 (4); *G. robustum* 1 (5), 2 (1), 4 (1), 5 (1). The composite samples are entirely inadequate but there is no question in regard to the specific distinctness of the populations compared (see also remarks on p. 263).

It should be stated also that the chief differentiating character which distinguishes these two species is not susceptible of determination with a high degree of accuracy. Although proportional measurements are widely employed for separating closely related populations of fishes, of specific or lower rank, such measurements can be determined only by a rather rough approximation to their true value. The values of the measurements, more likely than not, are apt to vary with the state and method of preservation of the specimens and also with the observer making the measurements. Even the same observer measuring the same specimens with the same instruments is apt to obtain somewhat different results by successive trials; although when sufficient care is exercised and a vernier caliper employed for taking the measurements, the results usually are sufficiently accurate for practical purposes even in the case of quite small specimens. Anyway, since the data represented in the above Table are not entirely satisfactory we may cite the following case which occupies the same position in our series, and which is based on a character that is susceptible of being determined with almost absolute accuracy.

*Lepidogobius y-cauda* and *L. guaymasiae*. These two gobies were described originally by Jenkins and Evermann (1888) from the Gulf of California. The two species are very closely related, and all later authors considered the above two names as synonymous. Indeed, the original descriptions are not sufficient to distinguish the two species, are erroneous in some important details, and it is very doubtful whether even the original describers separated all of their material properly. Nevertheless, the two

species are quite distinct. The differences distinguishing these two species will be taken up in greater detail in a revision of their genus which is now in process of preparation. It will suffice for our present purpose to state that the greatest divergence is shown by the number of pectoral rays as follows.

TABLE XIV.

Frequency distribution of the number of pectoral rays in *Lepidogobius y-cauda* and *L. guaymasiae*.

Species	Number of pectoral rays							
	20	21	22	23	24	25	26	27
<i>L. y-cauda</i>	6	23	11					
<i>L. guaymasiae</i>				7	51	42	5	1

In this case also intergradation is zero and divergence 100%, as far as the samples studied are concerned. Sampling: *G. y-cauda* 1 (1), 2 (2), 5 (1), 6 (1), 24 (1); *G. guaymasiae* 2 (2), 14 (1), 34 (1), 54 (1).

*Paralichthys dentatus* and *P. lethostigma*. The latter species was compared above with *P. albigutta*, with which it showed a slight amount of intergradation. When compared with another species of its genus, with *dentatus*, it does not show any intergradation. *P. dentatus* has a more northern distribution. It is the well-known summer flounder or fluke and is an important commercial species. Its range extends from Cape Cod to northern Florida. On the coast of North Carolina and southward its geographical range overlaps with its two common congeners which were discussed above. An extensive account of this species is included in my manuscript referred to above. For a published account of the species the reader is referred to "Fishes of Chesapeake Bay" by Hildebrand and Schroeder (1928), this being the only species of *Paralichthys* occurring in that body of water. For the purpose of the present discussion it may be stated that *P. dentatus* has nearly the same frequency distribution of the number of fin rays as *P. lethostigma*, but it differs decidedly in the number of gill rakers, as follows.

TABLE XV.

Frequency distribution of the number of gill rakers on the lower limb of the first gill arch of *Paralichthys dentatus* and *P. lethostigma*.

Species	Number of gill rakers on lower limb										
	8	9	10	11	12	13	14	15	16	17	18
<i>P. lethostigma</i>	7	67	66	6							
<i>P. dentatus</i>						4	3	18	44	35	11

The foregoing is an illustration of a case where a gap exists between two species with reference to a given character. The composite sample of *lethostigma* consists of 24 specimens from localities ranging from Albemarle Sound, N. C., to St. John's River, Florida, on the Atlantic coast, and 122 from the coasts of Texas and Louisiana (including 1 specimen from Apalachicola, Fla.). The Atlantic coast specimens include 13 from Beaufort, N. C., without any more detailed data, probably a mixed lot, and 7 other constituents as follows: 1 (3), 2 (4). The composite sample from the



TABLE XVI.

Summary of the preceding data showing the gradual continuity of intergradation and divergence arranged in order of decreasing intergradation, or increasing divergence.

Population showing greatest degree of intergradation	As compared with	Family	Percentage intergradation of first population	Percentage intergradation of 2nd population	Measure of intergradation	Measure of divergence	$\frac{sM_1 - M_2}{\sqrt{E_1^2 + E_2^2}}$	Taxonomic rank of the population
<i>Cynoscion regalis</i> Chesapeake Bay	<i>C. regalis</i> Florida Coast	Sciaenidae	52.50	39.09	46	54	.9	variety
<i>Cynoscion nebulosus</i> Texas coast	<i>C. nebulosus</i> Chesapeake Bay	"	49.04	34.26	42	58	2.7	"
<i>Bairdiella chrysura</i> Chesapeake Bay	<i>B. chrysura</i> Texas coast	"	55.71	16.90	36	64	4.9	race
<i>Fundulus confluentus</i> Chesapeake Bay	<i>F. confluentus</i> Florida	Cyprinodontidae	60.34	8.00	34	66	5.7	"
<i>Hippocampus zosterae</i> Pensacola	<i>H. zosterae</i> Key West	Syngnathidae	46.15	19.05	33	67	3.4	"
<i>Leiostomus xanthurus</i> Chesapeake Bay	<i>L. xanthurus</i> Texas coast	Sciaenidae	37.04	26.21	32	68	8.2	"
<i>Sciaenops ocellatus</i> Texas coast	<i>S. ocellatus</i> Chesapeake Bay	"	44.64	14.42	30 <sup>a</sup>	70	12.0	"
<i>Hippocampus hudsonius</i> <sub>2</sub> North of Florida	<i>H. punctulatus</i> <sub>2</sub> Florida and Cuba	Syngnathidae	33.80	26.92	30 <sup>a</sup>	70	6.8	subspecies
<i>Cynoscion arenarius</i> <sub>2</sub> Gulf coast	<i>C. regalis</i> <sub>2</sub> Atlantic coast	Sciaenidae	19.33	16.32	18	82	22.1	"
<i>Hippocampus zosterae</i>	<i>H. regalis</i>	Syngnathidae	11.54	4.35	8	92	15.0	species
<i>Gobionellus shufeldti</i>	<i>G. bolcosoma</i>	Gobiidae	8.11	4.94	7	93	22.1	"
<i>Paralichthys lethostigma</i>	<i>P. albignata</i>	Pleuronectidae	1.31	0	1	99	53.0	"
<i>Gobiosoma robustum</i>	<i>G. bosci</i>	Gobiidae	0	0	0	100	17.8	"
<i>Lepidogobius y-cauda</i>	<i>L. guaymasiae</i>	"	0	0	0	100	40.0	"
<i>Paralichthys lethostigma</i>	<i>P. dentatus</i>	Pleuronectidae			minus	gap	85.1	"



Gulf coast is constituted as follows: 1 (6), 2 (4), 3 (4), 5 (1), 6 (1), 8 (1), 9 (1), 10 (1), 12 (2), 13 (1), 21 (1). The composite sample of *P. dentatus* consists of 71 specimens from Chesapeake Bay constituted as follows: 1 (28), 2 (8), 3 (5), 5 (1), 7 (1); 37 specimens from Beaufort, N. C., for which no further data are available, probably a mixed lot; 7 specimens comprising 6 constituent samples from North Carolina to Georgia.

#### RECAPITULATION.

The data presented above of a series of actual cases in widely dissimilar groups of fishes, arranged to show the degree of divergence in a gradually ascending series, are recapitulated in tabular form on page 274, in order to give a birdseye view of the gradual continuity of the series. Table XVI shows the gradualness of divergence or intergradation and that any line drawn between the species concept and its subdivisions must be arbitrary. The continuity of the series is not as gradual as may be desired. A more evenly gradual continuity will no doubt be obtained by studying and citing a greater number of examples. However, those cited seem sufficient for this preliminary study to establish in a definite manner the gradualness of divergence in nature. Beside their number, the kinds of examples cited are not as well chosen as I would have liked them to be. I have now under study other populations which show promise of furnishing better proof to clinch the present thesis. However, the differentiation of those populations has not been satisfactorily established as yet, and the accumulated data are not of sufficient extent to enable me to use those data with assurance. While the examples cited are sufficient to prove the proposition in this preliminary paper, the subject evidently can not be expected to be exhausted in a single article.

#### THE ARBITRARY BOUNDARIES BETWEEN SPECIES, SUBSPECIES AND RACE.

The propriety and expediency of the arbitrary boundaries between the three main taxonomic units proposed in this paper may now be considered after having determined just how intergradation occurs in nature.

It may be suggested by a study of Table XVI that a more logical boundary to draw between the species and subspecies would be between two other pairs of population, namely, *Paralichthys lethostigma* and *P. albigutta*, and *Gobiosoma boscii* and *G. robustum*. That is, two populations are to be regarded as fully distinct species only when they differ in any single character in such a manner that there is no intergradation between them. However, this suggestion can be defended neither on theoretical nor on practical grounds.

First of all it may be stated that there is nothing of an inherently fundamental nature in such a boundary line. In a gradually continuous series such as we are dealing with, it is just as arbitrary as any other dividing line which may be proposed. Even when a gap exists between two species it may be possible to devise such a measure as will express the degree of the extent of the gap and the series denoting divergence continued in a gradual manner, although for our present purpose it is not deemed necessary to devise such a measure.

#### FOOTNOTES TO TABLE XVI.

<sup>8</sup> This column is added for the purpose of comparing the method here employed with the standard method, as discussed on page 279. However, this does not form an essential part of our method, and the column as well as the discussion may be left out of consideration by those readers who are not interested in making this comparison.

<sup>9</sup> The sampling of the pairs of populations of *S. ocellatus* and *H. hudsonius* is not altogether comparable as discussed on page 277. When the extreme populations of the latter species are compared the intergradation is 27%.

Second, it should be remembered that two diverging populations, especially when they reach such a high degree of divergence as to constitute species or subspecies, usually differ in several characters. Sometimes a high degree of divergence may be shown by two or more characters, although no single character may show a divergence of 100%. In such cases individual specimens may be referred with comparative ease to their proper species by at least one of these characters falling decidedly near the mode of its species. (This point is taken up more fully in my manuscript study of the genus *Paralichthys*). It is evident, therefore, that the boundary line under discussion can not be defended on theoretical grounds.

On practical grounds also such a boundary line will not prove satisfactory. If this boundary is adopted, possibly the majority or at least a large percentage of closely related species of fishes now universally recognized will have to be reduced to subspecific rank because of the general or at least frequent existence of intergrades. A case in point is the difference between *Gobionellus boleosoma* and *G. shufeldti* which forms one of the preceding illustrations. Probably no taxonomist who would compare and study authentic specimens of these two species would do otherwise but come to the conclusion that they represent fully distinct and independent species. In fact the differences between them are more numerous and saliently marked than in many other species which are now generally recognized. In spite of all this, their chief differentiating character intergrades in 8% of the individuals of *G. shufeldti*, or 7% as an average between the two.

It is evident, therefore, that a boundary line drawn so that two populations in which the average intergradation of the most divergent character is 7% or less are considered fully distinct, is not far fetched. The figure proposed herein, 10%, is not based on sufficient definite data, but is chosen chiefly for the simple reason that it represents a conveniently round number in our decimal system. Since such a boundary line is arbitrary anyway, the one proposed here tentatively is sufficient for the purpose of discussion. It is evident that the boundary line will be drawn the more advantageously in accordance with the facts of nature, the greater the number of cases which are studied in detail and correlated, and quite likely will change with increased knowledge. It may also be found advantageous to fix different boundaries in special cases or in certain groups in order to give in such cases an interpretation of the facts which will more closely approach nature.

The proposed boundary between the subspecies and the race also seems the most expedient as judged by the evidence considered.

In the arithmetical definition of species, subspecies and race given on page 260, it is to be noted that gaps are left in the continuity of the percentages at the boundary lines between the species and subspecies on the one hand and the subspecies and the race on the other. This is done on purpose. Also, the phrase "other things being equal" is used advisedly. As a matter of fact, other things usually are not equal. Populations, especially those that reach a sufficiently high degree of divergence to be regarded properly as species or subspecies, usually differ in many characters, the nature, number and variability of which vary widely with the particular populations, and all the characters have to be taken in consideration. Since any single character does not absolutely determine the taxonomic status of a population, it is evident that in appraising the sum total of values of the other characters in which two populations differ, there will be room for difference of opinion in cases where the difference between the two populations falls *near* any arbitrary lines which may be fixed. This is as it should be. The very nature of the subject matter excludes the possibility, at least for the present, of universal agreement in all cases. Consequently, the taxonomic status of border line populations will be determined to a large extent by a consideration of the other differentiating characters in addition to the one showing the greatest divergence. Leaving gaps between the proposed



limits of our taxonomic units thus allows leeway for the exercise of judgment in border line cases.

The necessity of exercising judgment in regard to populations falling near an arbitrarily fixed border line is shown by two pairs of populations cited above as illustrative examples, namely, the populations of *Sciaenops ocellatus*, and those of *Hippocampus hudsonius* (including all populations of the typical subspecies). Both pairs intergrade approximately by 30%. The intergradation of the latter pair is even a fraction greater in the samples examined. Nevertheless, the latter two populations are recognized as subspecies, and the former as races only for the following reasons: (1) Speciation in *Hippocampus* is rather unlike the usual. The species generally approach closely or even overlap (see Ginsburg 1937, p. 558 and *passim*). *Hippocampus* constitutes one of those groups in which different arbitrary lines between the categories will possibly have to be drawn in order to adequately represent the essential facts, as suggested on page 276. (2) The sampling of the two respective pairs of populations is not strictly comparable. Of *Sciaenops ocellatus* two extreme populations are compared, while of *Hippocampus hudsonius* intermediate populations are also included. Of the latter species, when the extremes are compared (see p. 268), the intergradation, 27%, falls within the arbitrarily fixed gap between the subspecies and the race as defined on page 260, and is less than in the extreme populations of *Sciaenops ocellatus*. (3) The populations of *Hippocampus hudsonius* diverge to a considerable extent in a number of other characters also, such as the number of dorsal rays, the number of pectoral rays, the relative length of the snout and the relative depth. (For a more detailed discussion of their differences see Ginsburg 1937, p. 557.) While the degree of intergradation in every character is considerable, an appraisal of the sum total of all the differences between the populations makes it evident that it is desirable to recognize them as subspecies rather than races. But for the populations of *Sciaenops ocellatus* no other well marked diverging characters are known at present.

The foregoing paragraph discusses some of the many factors involved which need to be considered in forming a final conclusion in regard to the status of a given pair of populations under study. A decision becomes especially difficult in cases where the samples available are manifestly inadequate, a frequent contingency in taxonomic practice. In such cases it would take an experienced, able and careful taxonomist, one who has a highly developed intuitive capacity, to form a decision which may stand the test of time and further, more adequate research. Even under the most favorable circumstances opinions regarding the rank of a given pair of populations may change as other, more divergent, characters are discovered. For instance, it is possible that some other characters may be discovered by which the populations of *Sciaenops ocellatus* may be shown to diverge to such a degree as to constitute subspecies.

The arbitrary lines suggested in this first attempt are admittedly tentative; but I believe that they approach closely to those which may be fixed after more extensive studies. Furthermore, any arbitrary line, no matter on how many concrete examples it may be based, will be from its very nature only generally indicative since all characters have to be considered in determining the taxonomic status of a pair of populations, as stated. Also, their proper use will always depend on the experience and ability of the taxonomist. Nevertheless, although the arbitrary lines here proposed are tentative, they are manifestly preferable to the rule of the thumb by which taxonomists now seem to decide regarding the category of particular pairs of populations. At least, they form a basis for immediate practice, as a general guide for taxonomists to determine whether any given pair of diverging populations are to be assigned specific, subspecific or racial rank. They also form a basis for discussion, improvement and refinement.

Irrespective of the question of the adequacy of the arbitrary lines here

TABLE XVII.  
Some commonly used statistics of the populations discussed above,<sup>10</sup> based on the data presented in Tables II-XV.

Population	M	R	$\sigma$	N	$E_N^{11}$	$M_1-M_2$	$E_D^{11}$	$\frac{M_1-M_2^{11}}{E_D}$
<i>Cynoscion regalis</i> , Chesapeake Bay	27.3750	5	.8856	40	.0944			
" " Florida coast	27.2727	5	.8833	110	.0568	.1023	.1102	0.9
<i>Cynoscion nebulosus</i> , Texas coast	25.4231	5	.7929	104	.0524			
" " Chesapeake Bay	25.2222	5	.8089	108	.0525	.2009	.0742	2.7
<i>Bairdiella chrysura</i> , Chesapeake Bay	21.2714	5	.8770	70	.0707			
" " Texas coast	20.8169	4	.7564	71	.0605	.4545	.0931	4.9
<i>Fundulus confluentus</i> , Florida coast	10.0000	3	.4000	25	.0540			
" " Norfolk, Va.	9.6034	2	.4892	58	.0433	.3966	.0692	5.7
<i>Hippocampus zosterae</i> , Key West, Fla.	9.8571	3	.4666	21	.0687			
" " Pensacola, Fla.	9.4615	2	.4985	13	.0933	.3956	.1159	3.4
<i>Leiostomus xanthurus</i> , Chesapeake Bay	30.7901	4	.8566	81	.0642			
" " Texas coast	30.0777	6	.8889	103	.0591	.712	.0873	8.2
<i>Sciaenops ocellatus</i> , Texas coast	24.6161	4	.7820	112	.0498			
" " Chesapeake Bay	23.7596	5	.7658	104	.0507	.8565	.0711	12.0
<i>Hippocampus hudsonius</i> <sup>12</sup>	36.8451	5	.9442	71	.0756			
" " punctulatus <sup>12</sup>	35.8462	5	.9484	26	.1255	.9989	.1465	6.8
<i>Cynoscion regalis</i> <sub>2</sub>	27.2579	5	.8595	190	.0421			
" " arenarius <sub>2</sub>	25.8739	5	.7510	119	.0464	1.3840	.0627	22.1
<i>Hippocampus zosterae</i>	12.0577	4	.5689	52	.0532			
" " regulus	10.9565	3	.3585	23	.0504	1.1012	.0733	15.0
<i>Gobionellus shufeldti</i>	12.9459	3	.3243	37	.0360			
" " boleosoma	12.0123	3	.2937	81	.0220	.9336	.0422	22.1
<i>Paralichthys lethostigma</i> <sup>13</sup>	68.2222	15	2.2235	153	.1212			
" " albigitia	58.7387	11	2.0565	111	.1317	9.4835	.1790	53.0
<i>Gobiosoma boscii</i>	1.7765	0.5	.1002	17	.0164			
" " robustum	1.3438	0.4	.1059	16	.0159	.4327	.0243	17.8
<i>Lepidogobius guaymasiac</i>	24.4528	5	.7286	106	.0477			
" " y-cauda	21.1250	3	.6398	40	.0682	3.3278	.0832	40.0
<i>Paralichthys dentatus</i>	16.1826	6	1.1079	115	.0697			
" " lethostigma	9.4863	4	.6541	146	.0365	6.6963	.0787	85.1



proposed, the fundamental thing to remember is that no matter where drawn, the lines must be arbitrary. This is proved by the gradual series here presented. It is either one or the other. Either the different categories have no existence in fact, and in that case our use of the terms "species," "subspecies," "race," etc., should be abandoned. Or, if the categories do exist in nature, they can be based only on relative degrees of divergence. The sum total of experience obtained as a result of careful population studies made up to now unmistakably shows that the latter interpretation represents the true state of affairs in nature.

#### COMPARISON BETWEEN THE SIMPLE METHOD EMPLOYED IN THIS PAPER AND THAT IN GENERAL USAGE.<sup>14</sup>

Attention has been called previously (p. 256) to the use of the standard method for comparing closely related populations as represented by the formula  $\frac{M_1 - M_2}{\sqrt{E_1^2 + E_2^2}}$ . This formula is not well adapted for our purpose, as may be shown by a consideration of the several factors which go to make up that expression.

First of all it may be stated that theoretically this expression in reality is not a measure of divergence. Rather, it is meant to be a test indicating, from a strictly mathematical point of view, the probable reliability of a difference between two sets of data, and consequently the probable value of any conclusions which may be drawn from such data. From a biological point of view, the usefulness of this test is limited in such a problem as we are confronted with. Since differences between populations exhibit all degrees of extensiveness, it follows as a consequence which can hardly be doubted that some average differences between natural populations exist, which are of such low magnitude as to be below the usually accepted mathematical "significance" obtained by the use of the above formula with samples which are ordinarily limited in practice. Such small differences must have a biological significance, although mathematically their significance appears doubtful. This test merely serves as a warning to proceed with caution in drawing conclusions in cases where the values are low, but it does not prove that such low values do not have any biological significance. However, while the above expression is strictly speaking not a measure of divergence, it may be used for that purpose. It is evident that, in general, the greater the divergence between two populations the greater is the numerical

<sup>14</sup> See also footnote to Table XVI, p. 275.

#### FOOTNOTES TO TABLE XVII.

<sup>10</sup> The symbols at the head of the columns stand for the following: M = arithmetical mean; R = actual range of the distribution on the X-axis;  $\sigma$  = standard deviation; N = number of specimens in composite sample;  $E_M$  = probable error of the mean;  $M_1 - M_2$  = difference between the means of the two populations compared;  $E_D$  = probable error of  $M_1 - M_2$ .

<sup>11</sup> Biological statisticians are now generally employing the standard error instead of the probable error. To reduce the figures given in this table to the standard error and the derivatives based on it, divide the probable error of the mean, and the probable error of the difference between the means by the modulus .6745, and multiply the figures in the last column, showing "significance," by the same number. The relative magnitudes of the comparative figures given in the last column will thus remain the same.

<sup>12</sup> The sampling of the populations of *H. hudsonius* is not altogether comparable with those of *S. ocellatus*, as discussed on page 277. The statistics for the extreme northern population of the former (see Table VIII, p. 268) are: M = 37.0556;  $\sigma$  = 1.0787;  $E_M$  = 0.1213; and as compared with the southern population, *punctulatus*,  $M_1 - M_2$  = 1.2094,  $E_D$  = .1745 and  $\frac{M_1 - M_2}{E_D}$  = 6.9, or nearly the same as when the total sample of *hudsonius* is compared with *punctulatus* (see discussion on p. 280).

<sup>13</sup> Omitting the one specimen at the extreme right of the frequency distribution (see Table XII, p. 271), the statistics for *lethostigma* are: M = 68.1645; R = 11;  $\sigma$  = 2.1134;  $E_M$  = 0.1156; and as compared with *albigutta*  $M_1 - M_2$  = 9.4258;  $E_D$  = 0.1752, and  $\frac{M_1 - M_2}{E_D}$  = 53.8.

value of this expression. Consequently, by the use of the above formula comparative figures are obtained which may indicate the relative degree of divergence of a pair of populations in a given series of pairs investigated. The question remains how useful is the standard method for our present practical purpose.

It will be noted that the above expression depends on: (1) the difference between the means which may be determined directly from the data by a simple arithmetical process of averaging, and (2) on the probable error which depends, in its turn, on a number of factors. The statistical formulae for the determination of the probable error are as follows:

$$\text{probable error of the mean} = .6745 \frac{\sigma}{\sqrt{N}}$$

$$\text{while, } \sigma \text{ (standard deviation)} = \sqrt{\frac{\sum f x^2}{N}}$$

The probable error then depends on the number of specimens in the composite sample and on the value of sigma. Now, the magnitude of sigma is determined primarily, (1) by the extent of the spread of the frequency distribution, the greater the spread the greater its value; and (2) by the form of the distribution; one having a sharply pronounced mode with the number of specimens diminishing rapidly at either end will show a comparatively smaller value for sigma, while a distribution the curve of which has a flattened form, or is skewed, will show a relatively greater value. (I am not considering very irregular distributions which may be due to faulty sampling, heterogeneity of the material or other causes.) It follows therefore that the value of the probable error depends chiefly on three factors, namely, (a) the number of specimens in the composite sample, (b) the spread of the distribution, and (c) the form of the distribution. Some of the factors involved are shown in Table XVII. The influence of the form of the distribution on the value of sigma is well shown by the two populations of *Fundulus confluentus*, for instance.

With these brief remarks we may now compare the method employed herein with the standard method. The final values obtained by these two methods are shown conveniently in parallel columns in Table XVI, page 274. Turning back to that Table it will be noted that of the 15 pairs of populations compared 10 occupy the same relative position by both methods, while 5 would occupy different positions if they were to be arranged in regular order by the standard method. A consideration of the latter cases throws considerable light on the relative merits of the two methods.

The first value out of place is that of *Hippocampus zosterae*, that obtained by the standard method being too low. The chief reason for the low value is shown in Table XVII. The composite samples are quite small, which results in a comparatively greater value for the probable errors. Although the spread of the distribution, and hence sigma, is small, its effect is not sufficient to counteract the influence of the small sample. On account of the relatively large probable error combined with the comparatively small difference between the means, the final expression obtained is relatively low.

The effect of the high probable error as a result of a small sample is also shown by the relatively low value obtained in comparing *H. punctulatus*, with *H. hudsonius*. Although in this case the sample of only one of the two populations compared is quite small and the difference between the means is higher, the effect of the small sample of the one population is sufficient to result in a low value.

The influence of the size of the sample on the final figure used for comparison is shown further by two different comparisons of the populations of *H. hudsonius*. The northernmost population of *hudsonius*, diverges to a greater extent than the populations from intermediate localities. from the



southernmost populations, *punctulatus*, (see Table VIII, p. 268). The two comparisons of these populations here made are as follows: (1) The intermediate populations are grouped with the northern one into the subspecies *hudsonius*, and the composite sample is compared with the southernmost populations, designated as the subspecies *punctulatus*, (see Table XVII, p. 278). (2) The northernmost population only of *hudsonius*, is compared with the southernmost ones, *punctulatus*, (see footnote to Table XVII). The "significant" figures obtained in these two comparisons are about the same, 6.8 and 6.9, respectively. The greater divergence of the populations from near the extremes of the geographic range of the species as a whole, is not indicated by these figures. The same two comparisons made by the method here employed are 30% and 27%, respectively, which does show the lesser intergradation, or greater divergence, of the populations from the extremes of the geographic range. The figures obtained by the use of the standard formula fail to show this greater divergence, evidently because the number of specimens in one of the composite samples used in the second comparison is considerably less than that in the first comparison.

On the other hand, the value for the comparison between *Cynoscion regalis*, and *C. arenarius*, is relatively high and for the same reason. In this case the samples are comparatively large, resulting in a low probable error, and this combined with the rather large difference between the means gives a relatively high figure as the final result. The magnitude of the figure obtained by the standard method in comparing a pair of related populations is thus greatly influenced by the number of specimens in the samples; but by far not to such an extent by the method employed.

The influence of the figure representing the probable error may also be shown by the following hypothetical examples. Let us suppose that of population A we study a sample  $n_1$  which is sufficiently representative for all practical biological purposes. Let us now take another sample  $n_2$  of the same population containing say ten times the number of specimens in the first sample. Biologically, as far as we may draw any conclusions from their study, the two samples are very nearly alike; but mathematically the probable error of the second sample will be smaller. Of course, this is perfectly logical. It simply shows that from a mathematical point of view the reliability of the sample increases as the number of specimens is increased. However, from a practical biological point of view let us see what will happen when population A is compared with another population. Let us suppose that we take a sufficiently representative sample  $m$  of a population B. If now we compare sample  $n_1$  with  $m$  we will get one figure; while by comparing  $n_2$  with  $m$  we will get a different and, quite likely, a widely divergent figure. Two separate comparisons of population A with B will thus yield two results.

In general, as  $n$  increases the numerical value of  $\frac{M_1 - M_2}{\sqrt{E_1^2 + E_2^2}}$  will increase. Consequently, the standard formula in the form in which it is generally employed is not suitable for the practical purpose of obtaining a series of comparative figures. On the other hand, by the method employed here the results will differ but little with the size of the samples, especially when such composite samples give fairly approximate representations of their populations.

Of even greater importance in comparing the two methods is the factor  $M_1 - M_2$ . It is obvious that pairs of populations the chief differentiating characters of which are not the same or in which the values of  $M_1 - M_2$  differ widely can not be fairly compared by any method employing this factor. A striking effect of the influence the factor  $M_1 - M_2$  exerts on the final value obtained by the standard method, is shown by the comparison between *P. lethostigma* and *P. albigutta*. The difference between the means in this case is comparatively high, resulting in a very high value for the final figure, although the probable error is also high because of the wide spread of the

distribution. In spite of the fact that this pair of populations shows a slight amount of intergradation, the index of their divergence obtained by the standard method is much greater than that of other pairs which do not intergrade at all. This example shows in a striking manner that the standard method is not well adapted for our purpose which requires the comparison of pairs of populations that differ by widely unlike characters.

The influence of the factor  $M_1-M_2$  is further shown by the comparison of the fifth pair of populations falling out of line, namely, that of *Gobiosoma bosci* and *G. robustum*. In this case, although the samples are small, nevertheless the probable error is relatively small, evidently because of the small range, according to the unit adopted. In spite of the small probable error, the final figure obtained is yet relatively small, evidently due to the small difference between the means.

It is evident that the standard formula is not well adapted for our purpose because the several factors involved do not result in fair comparative figures. It is preferable from the point of view of theoretical mathematics in determining probabilities; but for our purpose it is all too often not practically workable. One great drawback is that in practice we usually do not have samples of sufficient size that may be adequate according to mathematical usage. But irrespective of the size of the samples, the formula is not properly applicable because of the other factors involved, as discussed above. An application of the standard formula evidently is often bound to lead us astray. Although the method employed lacks the mathematical elegance of the standard method, in reality it gives a truer picture and interpretation of the facts of nature in connection with the problem under consideration. The relative degree of divergence of the pairs of populations, or their position in the series, with which this paper deals, is shown more nearly in keeping with the facts of nature or more accurately by our present method.

The method here employed also has the advantage of greater clarity. In using the standard formula biometricians seem to be chiefly concerned whether the resulting figure is "significant" or not; but once "significant" figures are obtained no particular stress seems to be laid generally on the relative value of figures of differing magnitude. For instance, let us say that we compare three pairs of populations and obtain the three "significant" figures of 5, 10 and 15, respectively. Now, definitely, just what is the meaning of these relative figures outside their implication of differing degrees of probability? Certainly, this is not clear to the average busy biologist. Of course, 5 is greater than 10, and 10 is greater than 15; but the differences between these figures do not convey any special meaning or idea in connection with our problem, since the biologist is not in the habit of thinking in such terms. Indeed, the relative magnitude of such figures hardly seem to have any definite meaning within rather wide limits even to the statisticians. Furthermore, such figures are not susceptible of conveying a very precise meaning with respect to divergence; because their value changes materially as the size of the sample is changed, and with other factors. Even their relative value in the series is likely to change with a change in these factors. On the other hand, by the method employed, if we compare three pairs of populations and find that the intergrades are 5, 10, and 15 per cent, respectively, of the total number of individuals in the composite samples, on the average, such figures immediately convey a definite and clear meaning to every biologist.

#### NOMENCLATURE OF TAXONOMIC UNITS BELOW FULL SPECIFIC RANK.

It has been shown that the boundary lines which may be drawn between the species and its subdivisions are arbitrary, and tentative limits have been proposed where to draw such lines. The nomenclature of the species and



its subdivisions may now be considered with profit, and a simpler method than the one now in use is here proposed.

According to present usage which is sanctioned by the international code of zoological nomenclature, subspecies are designated in the form of trinomials. The international code goes into the subject only as far as subspecies are concerned, and no units of lower rank are considered; but on account of the arbitrary nature of these categories there is no fundamental reason for stopping there, and some authors now are using quadrimomials, generally inserting the term "variety" between the third and fourth words of the full name. However, there is likewise no reason for stopping even there. One, conceivably, may even propose to use quinquinomials, sexinomials, etc., since in a gradual series such as we are dealing with where the boundary lines necessarily must be arbitrary, such boundaries may be increased.

It is evident that carried to its logical conclusion, the nomenclature of taxonomic units below specific rank would become clumsy and unwieldy, and assume a form very similar to the pre-Linnaean polynomial nomenclature; although it is true that the fundamental nature of the binomial system would be retained. It is evident, therefore, that there is room for improvement in our present method of naming taxonomic units below specific rank.

Another practical difficulty inherent in the present system is found in the relation of zoological considerations to nomenclature. It should be remembered that the Linnaean or binomial system of nomenclature serves two virtually independent purposes: (1) It supplies names to species and groups of higher or lower rank, such names being for the practical use of handles by which we may discuss these entities. (2) It also attempts to show relationship. In practice these two purposes cannot be made to work in entire accord. For the first purpose stability is a primary consideration, and it could be served most effectively by a set of arbitrary rules, such as the international code; but since the second purpose must also be considered, absolute stability is impossible, and part of the full names of organisms must change with increased knowledge, with our changing ideas of relationship, or with differences in the interpretation of relationship by individual biologists. Changes in nomenclature caused by zoological considerations are, or may be, chiefly of two kinds.

First, changes in the first word or the generic part of the name of a species are caused by the everlasting shifting about of species from one genus to another, or the frequent changing of the boundaries of genera by individual zoologists. Species are thus constantly shuffled with respect to their generic affiliations. Nomenclatorial instability of this kind is, of course, inherent in the system and is frequently unavoidable; although it would be well for zoologists to exercise restraint in their treatment of many cases of this kind by refraining from changing the constitution of genera on the slightest provocation.

Second, in genera in which the populations are now in an early and active state of diversification and ramification, questions may arise: (a) as to whether a given population is to be properly assigned specific or subspecific rank, and (b) if the latter, as to the proper species into which it is to be grouped. In such cases, any interpretation given of the relationship between closely related populations, on the basis of the available zoological evidence, is not the only possible one. The chief difficulty in the way of a single, consistent and acceptable interpretation in cases of this kind often lies in the uncertainty as to which one of the several populations is the more primitive one, and the consequent uncertainty as to the starting point of the argument. This is primarily due to our present very imperfect knowledge of the mechanism and methods of descent. While the available evidence may show to a high degree of probability that the several populations under consideration

should be assigned to taxonomic units of varying degree, yet the interpretation of their relationship on which such assignment must depend is of a speculative nature to a large extent. Examples of such genera are *Hippocampus* (see, for instance, page 549 of my review, 1937), and *Bathygobius* (a study of which I have now prepared in manuscript form). In such cases scrambling and unscrambling of the trinomial names of subspecies may well be expected to result from different interpretation of the data by individual zoologists.

In view of the possible resulting complexity of nomenclature as outlined above, the impossibility of being reasonably certain of relationship, in some cases, at the present time, and the necessarily arbitrary nature of limiting taxonomic units, the following method of naming species and their subdivisions is here proposed. All names are to be binomial. To indicate that a taxonomic unit is to be regarded as a full species the numeral 1 is inserted after the specific name of the binomial; a taxonomic unit of the next lower rank is to have the numeral 2 inserted in the same place; the next lower, the figure 3. Related populations of organisms of the rank of full species or lower are thus divided by arbitrary lines into categories and the categories designated by number, namely, a category of the first order or a full species, a category of the second order or a subspecies, a category of the third order or a race. In the case of a full species which is not subdivided the numeral may be left out in writing its binomial designation. By way of illustration, a taxonomic unit of the second category would be designated as:

$$A - us \quad a - us_2;$$

while a unit of the third category would bear the designation:

$$A - us \quad b - us_3.$$

The subspecies treated of in this paper are designated above according to the proposed method.

The proposed method is in consonance with the international code, except for the required use of trinomials for subspecies, which is not universally followed anyway. If anything it will tend to reenforce the system of binomial nomenclature which will thus become binomial in fact as well as in theory, and the necessity for using the clumsy trinomial and quadrinomial designations will be obviated. Another advantage is that this method does not imply a commitment as to the relationship of the populations named. It has already been pointed out that given a certain set of evidence relationship may be interpreted sometimes in more than one way. In such cases, if the nomenclature be used in the form here proposed it will be in accordance with the known facts and no more; the probable taxonomic rank of the particular unit may thus be indicated without the necessity of making a commitment in regard to relationship about which one may be uncertain.

An apparent advantage of this method of nomenclature is its flexibility. However, its very flexibility may turn out to be a disadvantage if the method is not used with caution. It may tend to put a premium on careless work. Without the necessity of using trinomials, quadrinomials, etc., it may result in the excessive multiplication of new names based on unimportant or irrelevant differences exhibited by a few specimens after a haphazard examination of such specimens. Nevertheless, the advantages of this method are so evident that they outweigh this possible disadvantage, and, in any case, there is no absolute insurance against careless or half-baked work. The undesirable contingency indicated may be obviated by a general agreement among systematists to refrain from formally naming categories of a rank lower than a subspecies, or at least the next lower or third category which would be equivalent to a quadrinomial as now used; otherwise the resulting great increase in new names will tend to make zoological nomenclature too burdensome.

## SUMMARY.

1. No absolute criterion exists by which to determine just what is a species. All proposed criteria hold only in part or in special cases. Morphology is the only practical and most generally applicable criterion, although it has only a relative value. The present study is based entirely on that criterion.

2. Intergradation in nature is universal. It is the rule rather than the exception. This is true of species as well as of subspecies or taxonomic categories of lower rank. (To a certain extent this is also true of categories higher than species, but this paper deals only with the species and its subdivisions.) Consequently the limitation of the species concept or that of any of its subdivisions must depend on the *degree* of intergradation.

3. The intergradation between, or the divergence of, natural populations is such that if some method be adopted for measuring intergradation, or divergence, and a sufficient number of pairs of closely related populations be compared, the figures expressing the measures and indicating the degree of intergradation, or divergence, will form a continuous series without any breaks. Consequently, it follows that any limitation given to our concept of species, subspecies, race, etc., necessarily must be arbitrary.

4. A definite measure which is determined by a simple arithmetical calculation is employed in the present study for the purpose of expressing intergradation, or divergence. This measure is based on the character showing the greatest divergence between the two populations.

5. The measure employed has the advantage of simplicity, clarity and ease of determination, and it gives a correct though approximate interpretation of the data.

6. Using this measure as a basis, definitions of the terms species, subspecies, and race are presented.

7. The necessity of proper sampling of the material from which the data are obtained, that form the basis of the measure, is indicated and discussed. The method of sampling the material used in the present study is stated.

8. A series of examples of pairs of related populations of fishes is presented, showing the application of the measure, proving the gradualness of intergradations, *inter se*, and showing that the necessarily arbitrary boundaries drawn in the definition of the species and its subdivisions, are more or less in accordance with the facts of speciation as they occur in nature.

9. A comparison is made between our method of measuring divergence and the standard method.

10. A method for the nomenclature of populations below specific rank is proposed.

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<sup>15</sup> Includes only those publications to which reference is made in the text.



## 14.

Eastern Pacific Expeditions  
of the New York Zoological Society, XIV.

Introduction, Itinerary, List of Stations, Nets and Dredges of the  
Eastern Pacific *Zaca* Expedition, 1937-1938.<sup>1</sup>

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(Text-figures 1 & 2).

[This is the fourteenth of a series of papers dealing with the collections made in the eastern Pacific by the expeditions of the New York Zoological Society. The first thirteen of the series appeared under the heading of "The Templeton Crocker Expedition." As it is necessary to simplify the titles of future reports, all publications dealing with the materials gathered in this region will appear from now on under the title of the "Eastern Pacific Expeditions of the New York Zoological Society." Under this name will appear the results of work of the *Noma* (1923), *Arcturus* (1925), *Antares* (1933), Templeton Crocker (1936) and the Eastern Pacific *Zaca* (1937-1938) Expeditions.]

## INTRODUCTION.

The Twenty-sixth Expedition of the Department of Tropical Research was made possible by Mr. Templeton Crocker's generous offer of the use of his yacht *Zaca* for the second time. Mr. Crocker accompanied the expedition together with his friend Mr. Maurice Willows. The scientific personnel was the same as on the first trip and consisted of four members of the Tropical Research Department, Dr. William Beebe, Director; Mr. John Tee-Van, General Associate; Miss Jocelyn Crane, Technical Associate; and Mr. George Swanson, Artist. Toshio Asaeda was, as before, photographer and preparateur, and together with Captain Alfred Pedersen and the entire crew were most efficient and helpful in every way.

The *Zaca* is a Diesel schooner, 118 feet over all, with a gross tonnage of 84. She is supplied with all of the usual apparatus for capturing fish and animals, such as seines, nets, submerged lights, etc.; in addition Mr. Crocker provided for these expeditions, a gasoline-engined winch and a 7,500-foot length of  $\frac{1}{4}$ -inch-diameter steel cable. With this apparatus we were able to trawl down to a maximum depth of 500 fathoms and to dredge on the bottom with deep-sea dredges. Two valuable features of the vessel were the bow pulpit and the boom-walk copied after those which I first used on the *Arcturus* in 1925.

<sup>1</sup> Contribution Number 560, Department of Tropical Research, New York Zoological Society.  
For corresponding List of Stations of the First *Zaca* Trip, see *Zoologica*, Vol. XXII, No. 2.

## ITINERARY.

The route of the expedition is shown on the two accompanying maps. We left San Diego on November 6, 1937, and disbanded at Balboa on April 5, 1938. The route is indicated by the successive numbers of the Stations.

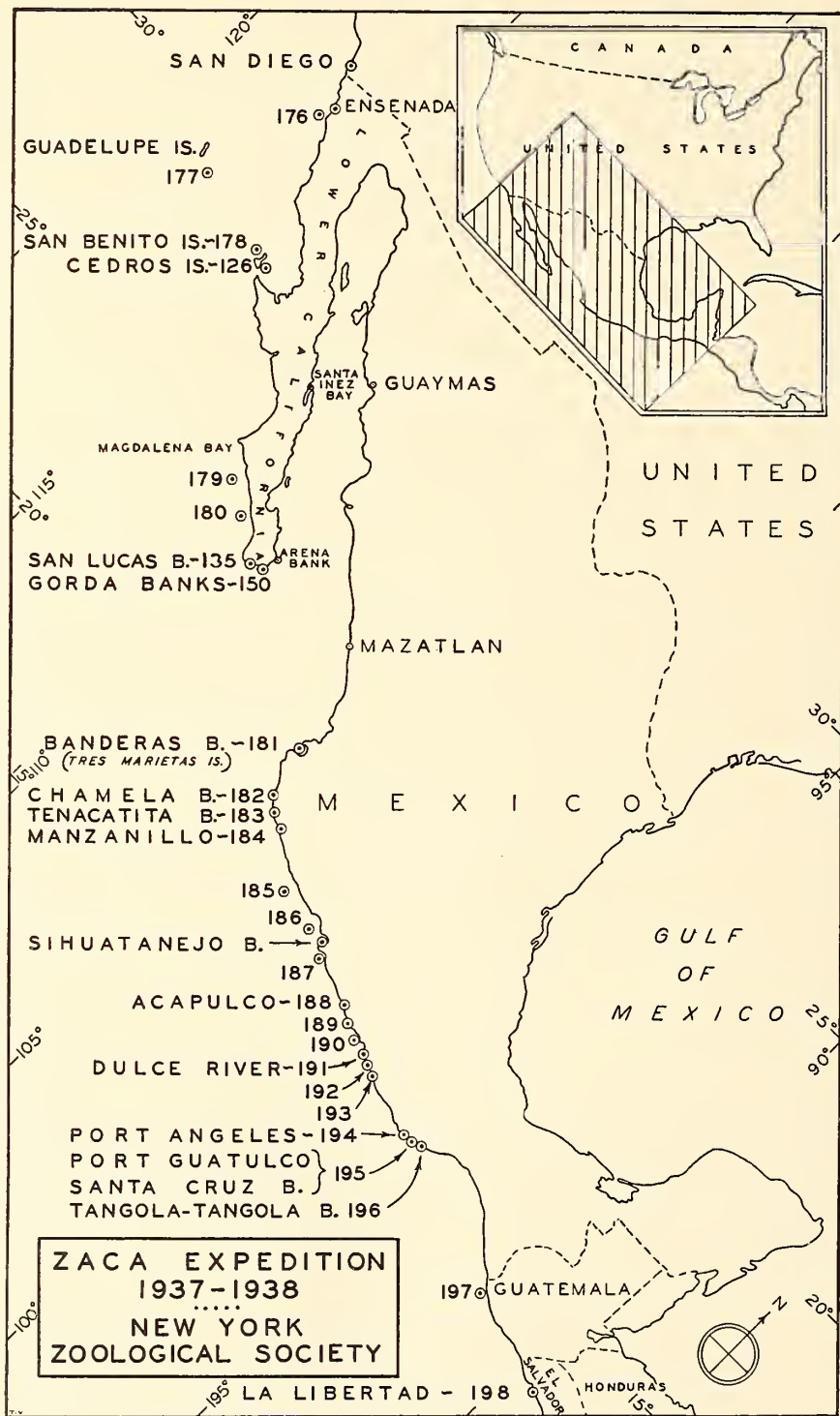
The dates and time spent at the various localities are as follows: San Diego, November 5; MEXICO: Ensenada, November 6; Guadalupe Island, November 8; San Benito Islands, November 9 and 10; Cedros Island, November 10; Cape San Lucas, November 13; Penas, Banderas Bay, November 15 and 16; Chamela Bay, November 17 to 20; Tenacatita Bay, November 20; Manzanillo, November 21 and 22; Sihuatanejo Bay, November 24; Acapulco, November 25 to 29; Port Angeles, December 1; Port Guatulco, December 2 to 7; Santa Cruz Bay, December 7 and 8; Tangola-Tangola, December 8 to 13; EL SALVADOR: La Libertad, December 16 to 19; La Union, December 20 and 21; Meanguera Island, December 21 and 22; Farrallone Islands, December 22; Conchaguita Island, December 22; La Union, December 22 and 23, and 26 and 27; NICARAGUA: Potosi River, December 23 to 25; Monypenny Point, December 25 and 26; Corinto, December 28 to January 7; San Juan del Sur, January 9 to 12; COSTA RICA: Port Parker, January 12 to 23;; Murcielago Bay, January 23; Potrero Grande Bay, January 23 and 24; Port Culebra, January 24 to 31; Cocos Bay, January 26, 29 and 31; Braxilito Bay, January 31 to February 1; Piedra Blanca Bay, February 1 to 6; Puntarenas, February 11 and 12; Cedro Island, February 12 and 13; Puntarenas, February 13 to 21; Cedro Island, February 21 and 22; Negritas Island, February 22; Jasper Island, February 22 to 25; Ballenas Bay, February 25 and 26; Puntarenas, February 28 to March 1; Uvita Bay, March 2 to 4; Golfito, Gulf of Dulce, March 5 to 9; Pavon Bay, March 9 and 10; PANAMA: Puerto Armuelles, March 11; Parida Island, March 11 to 13; Bahia Honda, March 13 to 19; Hermosa Bay, Coiba Island, March 19 and 20; Hannibal Bank, March 20; Balboa, C.Z., March 22 to 24; COLOMBIA: Gorgona Island, March 27 to April 2; PANAMA: Balboa, April 5.

## LIST OF STATIONS, NETS AND DREDGES.

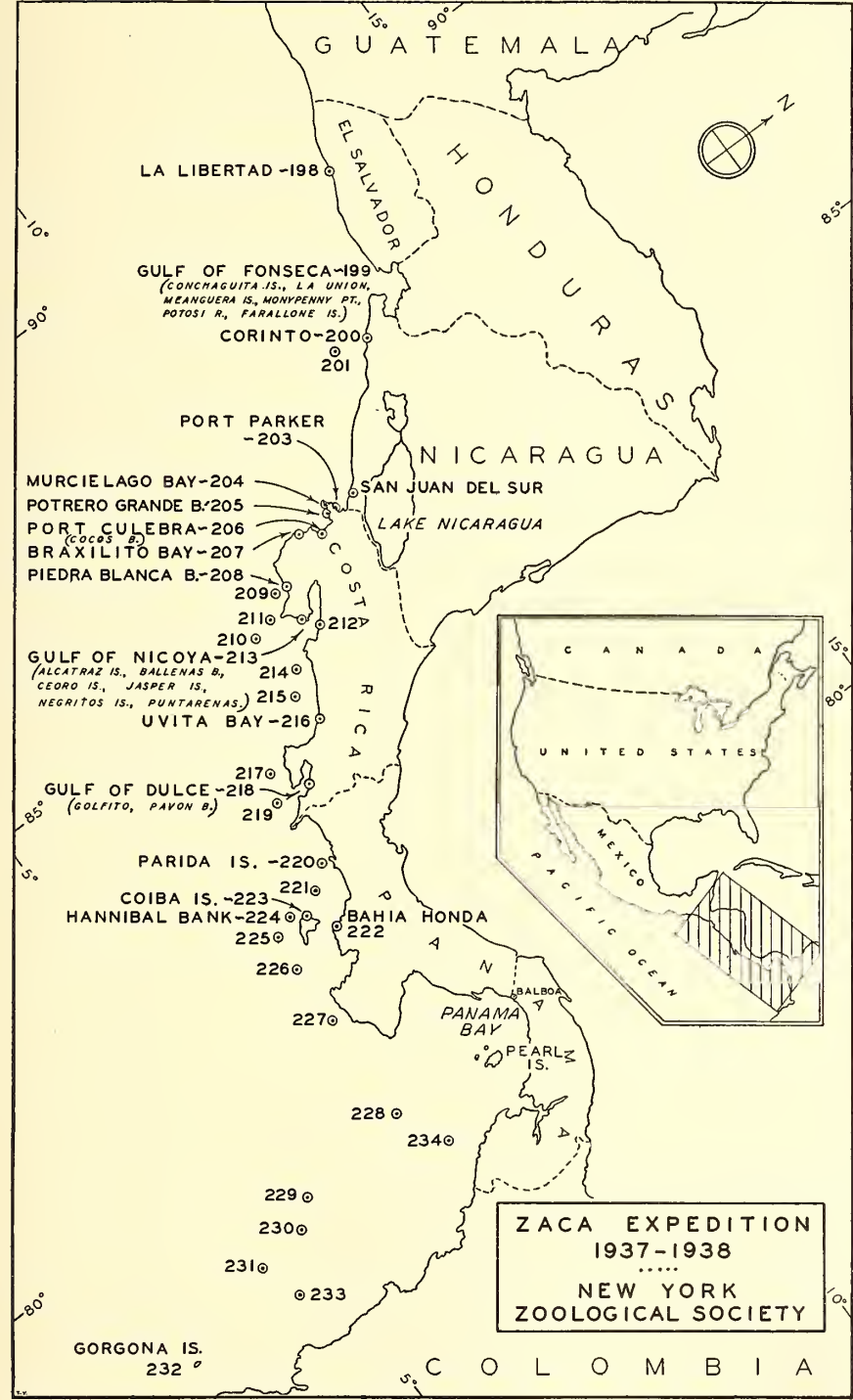
The data presented in the following tables are self-explanatory. Abbreviations are as follows: The Station numbers refer to the continuously numbered series of oceanographic stations of the Department of Tropical Research. In the second column the letter "D" refers to dredges, "T" to tow-nets and "L" to submarine night lights. Hence, 182, D-1 means the first dredge drawn at Station 182.

In the third column the dredges are separated into two- and four-foot ones, the measurement being across the mouth. Both sizes were of the Blake type, the bags being of two-inch and one-inch mesh respectively. The small dredges were drawn from launch or dory, the large ones being handled from the deck of the yacht, using the quarter-inch steel cable. The tow-nets of one-half and one metre diameter were of standard Michael Sars' type, with 2XX silk bolting cloth posteriorly and OXX bolting cloth anteriorly, the mouth of the net having a collar of shrimp netting. The lights indicated refer to night stations, where submerged electric lights were employed, and the captures made by the use of long-handled dip-nets.

Station No.	Net No.	Type of Net	Depth		Position		General Locality	Date 1937	Bottom	Duration	
			Fathoms	Metres	N. Lat.	W. Long.				Hrs.	Mins.
126	D-13	4' dredge	45	82	28° 12'	115° 07'	E. of Cedros Is., Mex.	Nov. 10	Mud, algae.	—	10
	D-14	4' dredge	45	82	28° 10'	115° 08'	"	10	"	—	10
	D-15	4' dredge	42	76	28° 09'	115° 08'	"	10	Mud.	—	10
	D-16	4' dredge	42	76	28° 07'	115° 08'	"	10	"	—	20
	D-17	4' dredge	40	73	28° 05'	115° 09'	"	10	"	—	10
	D-18	4' dredge	20	36	28° 01'	115° 10'	SE. of Cedros Is., Mex.	10	Rocks, algae.	—	10
	D-19	4' dredge	25	45	27° 59'	115° 09'	"	10	"	—	10
135	D-27	2' dredge	2-6	3.6-11	22° 53'	109° 54'	San Lucas Bay, Mex.	13	Sand.	—	20
150	D-27	4' dredge	60	108	23° 01'	109° 28'	Gorda Banks, Mex.	13	"	—	20
176	L-1	Light	—	—	31° 25'	116° 58'	23 m. S.W. of Banda Point, Mex.	7	—	1	10
177	L-1	Light	—	—	28° 42'	117° 50'	30 m. E.xS. of Guadalupe Is., Mex.	8	—	—	30
178	L-1	Light	—	—	28° 18'	115° 34'	San Benito Is., Mex.	9	—	2	00
179	T-1	½ Metre	0	0	24° 02'	111° 38'	18 m. SSE. of Pt. Tosca, Mex.	12	—	—	10
180	T-1	½ Metre	0	0	23° 31'	110° 54'	65 m. NW. of Cape Falso, Mex.	12	—	—	10
181	L-1	Light	—	—	20° 36' 30"	105° 16'	Banderas Bay, Mex.	15	—	2	0
182	D-1	4' dredge	8	14.5	19° 34' 30"	105° 08' 15"	Chamela Bay, Mex.	17	Sand, algae.	—	10
	D-2	4' dredge	12	22	19° 34'	105° 07' 30"	"	17	"	—	10
	D-3	4' dredge	15	27	19° 33' 45"	105° 07' 45"	"	17	"	—	10
	D-4	4' dredge	16	29	19° 33' 30"	105° 08' 15"	"	17	Sand, algae, cr. shell.	—	10
	L-1	Light	—	—	19° 34' 45"	105° 08' 30"	"	17	—	2	0
	L-2	Light	—	—	19° 34' 45"	105° 08' 30"	"	18	—	2	0
183	D-1	4' dredge	15	27	19° 17'	104° 51'	Tenacatita Bay, Mex.	21	Sand.	—	10
	D-2	4' dredge	30	54	19° 15' 30"	104° 51'	"	21	Muddysand.	—	15
	D-3	4' dredge	40	73	19° 14' 30"	104° 51' 30"	"	21	Sandy mud.	—	15
	D-4	4' dredge	40	73	19° 14' 30"	104° 52' 30"	"	21	Mud.	—	15
	L-1	Light	—	—	19° 18'	104° 51'	"	20	—	2	30
184	D-1	4' dredge	25	45	19° 03' 45"	104° 20' 45"	Manzanillo, Mex.	22	Sand.	—	10
	D-2	4' dredge	30	55	19° 04'	104° 22'	"	22	Grav'ly sand.	—	20
	L-1	Light	—	—	19° 03' 30"	104° 19' 45"	"	21	—	3	0
185	T-1	Metre	300	545	17° 45'	103° 05'	43 m. SE. of Pt. Telmo, Mex.	23	—	2	0
	T-2	Metre	400	730	17° 45'	103° 05'	"	23	—	2	0
	T-3	Metre	500	910	17° 45'	103° 05'	"	23	—	2	0
	T-4	½ Metre	0	0	17° 45'	103° 05'	"	23	—	0	30
186	L-1	Light	—	—	17° 38'	102° 00'	20 m. W. of Sihuatanejo, Mex.	23	—	2	30
187	L-1	Light	—	—	17° 17'	101° 16'	72 m. WNW. of Acapulco, Mex.	24	—	0	30
188	L-1	Light	—	—	16° 15' 30"	99° 55' 30"	Acapulco, Mex.	25	—	2	0
	L-2	Light	—	—	16° 15' 30"	99° 55' 30"	"	26	—	2	0
	L-3	Light	—	—	16° 15' 30"	99° 55' 30"	"	27	—	2	0
	L-4	Light	—	—	16° 15' 30"	99° 55' 30"	"	28	—	2	0
189	D-1	4' dredge	20	36	16° 40'	99° 43' 30"	17 m. SE.xE. of Acapulco, Mex.	29	Sandy mud, algae.	—	10
	D-2	4' dredge	20	36	16° 39' 30"	99° 42'	"	29	"	—	20
	D-3	4' dredge	13	23.5	16° 39'	99° 41'	"	29	Mud.	—	10
	D-4	4' dredge	28	51	16° 38' 30"	99° 40'	"	29	"	—	14
190	L-1	Light	—	—	16° 30'	99° 13'	45 m. ESE. of Acapulco, Mex.	29	—	1	0
191	D-1	2' dredge	8	14.5	16° 29'	98° 45'	Mouth of Dulce Riv., Mex.	30	—	0	10
192	D-1	4' dredge	26	47	16° 16' 30"	98° 37'	4 m. SSW. of Maldonado Pt., Mex.	30	Mud.	—	10







Station No.	Net No.	Type of Net	Depth		Position		General Locality	Date 1937	Bottom	Duration	
			Fathoms	Metres	N. Lat.	W. Long.				Hrs.	Mins.
192	D-2	4' dredge	33	60	16° 16'	98° 36'	4 m. SSW. of Maldonado Pt., Mex.	Nov. 30	Sand.	—	10
	D-3	4' dredge	38	69	16° 15'	98° 35' 30"	"	30	Mud.	—	10
193	L-1	Light	—	—	16° 05'	98° 17'	21 m. SE. of Maldonado Pt., Mex.	30	—	1	10
194	L-1	Light	—	—	15° 39' 15"	96° 30' 40"	Port Angeles, Mex.	Dec. 1	—	3	0
195	D-1	2' dredge	2.5	4.5	15° 44' 56"	96° 08' 03"	Port Guatulco, Mex.	4	Sand, algae.	—	3
	D-2	2' dredge	3	5.5	15° 44' 51"	96° 07' 51"	"	4	Sand.	—	4
	D-3	2' dredge	3.5	6.3	15° 44' 45"	96° 07' 53"	"	4	Sand, cr. shell	—	3
	D-4	2' dredge	4.5	8.2	15° 44' 40"	96° 07' 53"	"	4	Sand, algae, cr. shell.	—	3
	D-5	2' dredge	2	3.6	15° 44' 50"	96° 08' 09"	"	5	Sand, algae.	—	3
	D-6	2' dredge	3	5.4	15° 44' 45"	96° 08' 05"	"	5	Sand, algae, cr. shell.	—	3
	D-7	2' dredge	4.5	8.2	15° 44' 35"	96° 08'	"	5	Sand, algae, cr. shell.	—	3
	D-8	2' dredge	6	11	15° 44' 30"	96° 07' 56"	"	5	Sand, algae, cr. shell.	—	3
	D-9	2' dredge	7	12.6	15° 44' 28"	96° 07' 51"	"	5	Gr. sand, cr. shell.	—	5
	D-10	2' dredge	4	7.3	15° 44' 53"	96° 08' 03"	"	6	Gr. sand, cr. shell, dead coral.	—	3
	D-11	2' dredge	5	9.1	15° 44' 49"	96° 07' 59"	"	6	Gr. sand, cr. shell.	—	4
	D-12	2' dredge	6	11	15° 44' 42"	96° 07' 55"	"	6	Sand.	—	3
	D-13	2' dredge	8	14.6	15° 44' 33"	96° 07' 49"	"	6	"	—	3
	D-14	2' dredge	4	7.3	15° 44' 27"	96° 07' 57"	"	6	Coral.	—	5
	D-15	Diving	1.5	2.7	15° 44' 54"	96° 07' 57"	"	6	"	1	0
	D-16	2' dredge	10	18.2	15° 44' 35"	96° 07' 45"	"	7	Sand.	—	3
	D-17	2' dredge	6	11	15° 44' 39"	96° 07' 42"	"	7	"	—	5
	D-18	2' dredge	6	11	15° 44' 39"	96° 07' 49"	"	7	"	—	3
	D-19	4' dredge	17	31	15° 44' 22"	96° 07' 27"	"	7	Gr. mud, cr. shell.	—	5
	D-20	4' dredge	23	42	15° 44' 22"	96° 07' 08"	"	7	Mud.	—	10
	D-21	4' dredge	18	33	15° 44' 45"	96° 06' 55"	Santa Cruz Bay, Mex.	7	"	—	10
	L-1	Light	—	—	15° 44' 45"	96° 08'	Port Guatulco, Mex.	3	—	1	30
	L-2	Light	—	—	15° 44' 45"	96° 08'	"	4	—	2	0
	L-3	Light	—	—	15° 44' 45"	96° 08'	"	5	—	2	30
196	D-1	2' dredge	5	9	15° 45' 58"	96° 06'	Tangola-Tangola Bay, Mex.	9	Gr. sand.	0	3
	D-2	2' dredge	5.5	10	15° 45' 53"	96° 05' 57"	"	9	Sand.	0	3
	D-3	2' dredge	7	12.8	15° 45' 48"	96° 05' 54"	"	9	"	0	3
	D-4	2' dredge	8	14.5	15° 45' 44"	96° 05' 52"	"	9	"	0	3
	D-5	2' dredge	9	16.3	15° 45' 40"	96° 05' 50"	"	9	"	0	5
	D-6	2' dredge	7	12.8	15° 45' 34"	96° 06' 02"	"	9	Sand, cr. shell.	0	5
	D-7	2' dredge	6	11	15° 45' 34"	96° 06' 03"	"	9	Sand.	0	4
	D-8	2' dredge	9	16.3	15° 45' 37"	96° 05' 54"	"	9	"	0	5
	D-9	2' dredge	7.5	13.6	15° 45' 45"	96° 05' 59"	"	12	"	0	3
	D-10	2' dredge	5	9.1	15° 45' 51"	96° 06' 01"	"	12	"	0	3
	D-11	2' dredge	4.5	8.2	15° 45' 57"	96° 06' 02"	"	12	"	0	3
	D-12	2' dredge	4	7.3	15° 46' 02"	96° 05' 58"	"	12	"	0	5
	D-13	2' dredge	10	18	15° 45' 32"	96° 05' 52"	"	12	Gr. sand, cr. shell.	0	3
	D-14	2' dredge	5	9.1	15° 45' 34"	96° 06' 03"	"	12	Cr. shell.	0	5
	D-15	2' dredge	5	9.1	15° 45' 34"	96° 06' 03"	"	12	Cr. shell.	0	5

Station No.	Net No.	Type of Net	Depth		Position		General Locality	Date 1937	Bottom	Duration	
			Fathoms	Metres	N. Lat.	W. Long.				Hrs.	Mins.
196	D-16	4' dredge	16	29	15° 45' 22"	96° 05' 51"	Tangola-Tangola Bay, Mex.	Dec. 13	Mud.	0	5
	D-17	4' dredge	23	42	15° 45'	96° 05' 34"	"	13	"	0	3
	D-18	4' dredge	30	55	15° 44' 58"	96° 05' 13"	"	13	"	0	3
	D-19	4' dredge	30	55	15° 44'	96° 05'	"	13	"	0	3
	D-20	4' dredge	50	91	15° 43' 15"	95° 04' 15"	"	13	"	0	4
	L-1	Light	—	—	15° 45' 40"	96° 06' 05"	"	8	—	1	0
	L-2	Light	—	—	15° 45' 40"	96° 06' 05"	"	9	—	1	0
	L-3	Light	—	—	15° 45' 40"	96° 06' 05"	"	10	—	3	0
	L-4	Light	—	—	15° 45' 40"	96° 06' 05"	"	11	—	2	30
	L-5	Light	—	—	15° 45' 40"	96° 06' 05"	"	12	—	3	0
197	D-1	4' dredge	14	25	14° 16'	92° 03'	7 m. W. of Champerico, Guatemala.	15	Mud.	0	5
	D-2	4' dredge	14	25	14° 13'	92° 02'	"	15	"	0	5
198	D-1	4' dredge	13	24	13° 27' 20"	89° 19' 20"	La Libertad, El Salvador.	16	"	0	5
	D-2	4' dredge	14	25	13° 25' 50"	89° 19' 20"	"	16	"	0	5
	L-1	Light	—	—	13° 28' 11"	89° 19' 14"	"	16	—	1	30
	L-2	Light	—	—	13° 28' 11"	89° 19' 14"	"	18	—	2	00
199	D-1	4' dredge	16	29	13° 08'	87° 43'	Meanguera Is., Gulf of Fonseca, El Sal.	23	Sand, mud, cr. shell.	0	3
	D-2	4' dredge	5	9.1	13° 02' 30"	87° 29' 30"	Monypenny Pt., Gulf of Fonseca, Nicar.	24	Mud.	0	1
	D-3	4' dredge	6	11	13° 03'	87° 30'	"	24	"	0	2
	D-4	4' dredge	7	12.8	13° 03' 30"	87° 30' 20"	"	24	"	0	1
	D-5	4' dredge	7	12.8	13° 03' 30"	87° 30' 20"	"	24	"	0	1
	D-6	4' dredge	4	7.2	13° 02' 30"	87° 29' 30"	"	24	"	0	1
	D-7	4' dredge	6	11	13° 20' 07"	87° 49'	La Union, Gulf of Fonseca, El Salv.	27	Mud, mangrove leaves	0	1
	D-8	4' dredge	6	11	13° 19' 53"	87° 48' 43"	"	27	"	0	2
	D-9	4' dredge	5	9.1	13° 19' 45"	87° 48' 32"	"	27	"	0	2
	D-10	4' dredge	5	9.1	13° 19' 35"	87° 48' 19"	"	27	Mud.	0	3
	D-11	4' dredge	5	9.1	13° 19' 24"	87° 48' 00"	"	27	"	0	1½
	D-12	4' dredge	5	9.1	13° 19' 08"	87° 47' 30"	"	27	"	0	3
	D-13	4' dredge	6	11	13° 18' 50"	87° 47' 07"	"	27	"	0	1½
	D-14	4' dredge	5	9.1	13° 19' 40"	87° 48' 23"	"	27	"	0	1½
	D-15	4' dredge	6	11	13° 19' 52"	87° 48' 43"	"	27	"	0	1½
	D-16	4' dredge	6	11	13° 20' 03"	87° 48' 57"	"	27	"	0	1½
	D-17	2' dredge	4	7.2	13° 19' 54"	87° 49' 07"	"	27	Mud, mangrove leaves.	0	1½
	D-18	2' dredge	4	7.2	13° 19' 50"	87° 49'	"	27	"	0	1½
	D-19	2' dredge	3	5.4	13° 20' 03"	87° 49' 26"	"	27	"	0	1½
	D-20	2' dredge	3	5.4	13° 20' 03"	87° 49' 26"	"	27	"	0	1½
	D-21	2' dredge	3	5.4	13° 20' 03"	87° 49' 26"	"	27	"	0	1½
	D-22	2' dredge	3	5.4	13° 20' 03"	87° 49' 26"	"	27	"	0	1½
	D-23	2' dredge	3	5.4	13° 20' 03"	87° 49' 26"	"	27	"	0	1½
	D-24	2' dredge	6	11	13° 20' 03"	87° 49' 26"	"	27	"	0	1½
	D-25	2' dredge	6	11	13° 20' 03"	87° 49' 26"	"	27	"	0	2
	L-1	Light	—	—	13° 19' 59"	87° 49' 15"	"	20	—	3	0
	L-2	Light	—	—	13° 11'	87° 41' 15"	Meanguera Is., Gulf of Fonseca, El Salv.	21	—	2	0
	L-3	Light	—	—	13° 19' 59"	87° 49' 15"	La Union, Gulf of Fonseca, El Salv.	22	—	2	30
	L-4	Light	—	—	13° 02'	87° 29'	Monypenny Pt., Gulf of Fonseca, Nicar.	23	—	2	0
	L-5	Light	—	—	13° 02'	87° 29' 30"	"	24	—	2	40
200	D-1	2' dredge	6.5	11.8	12° 28' 25"	87° 10' 59"	Corinto, Nicaragua	29	Mangrove leaves.	0	1½

Station No.	Net No.	Type of Net	Depth		Position		General Locality	Date 1937	Bottom	Duration	
			Fathoms	Metres	N. Lat.	W. Long.				Hrs.	Mins.
200	D-2	2' dredge	5.3	9.7	12° 28' 27''	87° 10' 55''	Corinto, Nicaragua	Dec. 29	Mangrove leaves.	0	1½
	D-3	2' dredge	2	3.6	12° 28' 28''	87° 10' 51''	"	29	"	0	3
	D-4	2' dredge	½	.9	12° 28' 32''	87° 10' 42''	"	29	"	0	1½
	D-5	2' dredge	2	3.6	12° 28' 36''	87° 10' 48''	"	29	"	0	1½
	D-6	2' dredge	2.5	4.6	12° 28' 41''	87° 10' 42''	"	29	"	0	2
	D-7	2' dredge	2	3.6	12° 28' 45''	87° 10' 34''	"	29	"	0	2
	D-8	2' dredge	6.6	12	12° 28' 24''	87° 10' 58''	"	29	"	0	2
	D-9	2' dredge	6	11	12° 28' 27''	87° 11' 04''	"	29	"	0	2
								1938			
	D-10	2' dredge	7	12.8	12° 27' 46''	87° 11' 32''	"	Jan. 5	"	0	1½
	D-11	2' dredge	8	14.6	12° 27' 46''	87° 11' 32''	"	5	Sand.	0	1½
	D-12	2' dredge	3	5.4	12° 27' 20''	87° 11' 38''	"	5	Mangrove leaves.	0	1½
	D-13	2' dredge	3	5.4	12° 27' 14''	87° 11' 45''	"	5	"	0	3
	D-14	2' dredge	3	5.4	12° 27' 30''	87° 12' 06''	"	5	"	0	3
	D-15	2' dredge	1	1.8	12° 27' 32''	87° 12' 09''	"	5	"	0	5
	D-16	2' dredge	4-7	7-13	12° 27' 41''	87° 12' 08''	"	5	"	0	5
	D-17	2' dredge	7-10	13-18	12° 27' 46''	87° 12' 17''	"	5	Sand.	0	7
	D-18	2' dredge	5	9.1	12° 27' 38''	87° 12' 41''	"	5	Mangrove leaves.	0	5
	D-19	2' dredge	12-13	22-24	12° 28' 03''	87° 12' 39''	"	5	"	0	4
	D-20	2' dredge	1.5	2.7	12° 27' 19''	87° 11' 39''	"	7	"	0	3
	D-21	2' dredge	2	3.6	12° 27' 14''	87° 11' 38''	"	7	"	0	3
	D-22	2' dredge	1.5	2.7	12° 27' 07''	87° 11' 37''	"	7	"	0	5
	D-23	2' dredge	3	5.4	12° 27' 20''	87° 11' 35''	"	7	"	0	5
	D-24	2' dredge	6.5	11.8	12° 27' 15''	87° 11' 55''	"	7	"	0	5
	D-25	2' dredge	6.5-2.5	11.8-4.5	12° 27' 10''	87° 11' 57''	"	7	"	0	10
	D-26	2' dredge	2.5	4.5	12° 27' 24''	87° 11' 15''	"	7	"	0	3
	D-27	2' dredge	3	5.4	12° 28' 38''	87° 10' 42''	"	7	"	0	5
	D-28	2' dredge	3	5.4	12° 28' 31''	87° 10' 45''	"	7	"	0	5
	D-29	2' dredge	3	5.4	12° 28' 16''	87° 10' 49''	"	7	"	0	5
	D-30	2' dredge	3	5.4	12° 28' 27''	87° 10' 47''	"	7	"	0	6
								1937			
	L-1	Light	—	—	12° 28' 22''	87° 11' 05''	"	Dec. 28	—	2	15
	L-2	Light	—	—	12° 28' 22''	87° 11' 05''	"	29	—	1	30
	L-3	Light	—	—	12° 28' 22''	87° 11' 05''	"	30	—	1	0
								1938			
	L-1	Light	—	—	12° 09'	87° 24'	22 m. SW. of Corinto, Nicaragua.	Jan. 7	—	1	30
202	L-1	Light	—	—	11° 15' 12''	85° 52' 58''	S. Juan del Sur, Nicar.	9	—	1	30
203	D-1	4' dredge	15	27	10° 56' 05''	85° 49' 25''	Port Parker, Costa Rica.	20	Sandy mud, cr. shell.	0	4
	D-2	4' dredge	10	18.2	10° 55' 38''	85° 49' 21''	"	20	Shelly sand, algae.	0	5
	D-3	4' dredge	12	22	10° 55' 45''	85° 49' 05''	"	20	Shelly mud.	0	2
	D-4	2' dredge	7	12.8	10° 55' 06''	85° 48' 53''	"	22	Gravel, algae.	0	3
	D-5	2' dredge	3	5.4	10° 55' 10''	85° 49' 10''	"	22	Shells, dead coral.	0	2
	D-6	2' dredge	1	1.8	10° 55' 20''	85° 49' 18''	"	22	Rocks, gravel.	0	3
	D-7	2' dredge	9-5	16.4-9.1	10° 55' 43''	85° 49' 37''	"	22	Shells, algae.	0	5
	D-8	2' dredge	9	16.4	10° 55' 43''	85° 49' 46''	"	22	"	0	5
	D-9	2' dredge	1.5-4	2.7-7.2	10° 55' 51''	85° 49' 52''	"	22	Coral.	0	5
	D-10	2' dredge	6-2.5	10.9-4.5	10° 56' 15''	85° 48' 47''	"	22	Rocks.	0	3



Station No.	Net No.	Type of Net	Depth		Position		General Locality	Date 1938	Bottom	Duration	
			Fathoms	Metres	N. Lat.	W. Long.				Hrs.	Mins.
203	D-11	2' dredge	2-4	3.6-7.2	10° 56' 07"	85° 48' 52"	Port Parker, Costa Rica.	Jan. 22	Rocks.	0	3
	D-12	2' dredge	2	3.6	10° 55' 43"	85° 48' 44"	"	22	Gravel, algae, cr. shell.	0	2
	D-13	2' dredge	7-9	12.8-16.4	10° 55' 33"	85° 48' 30"	"	22	Shells, algae.	0	3
	D-14	2' dredge	4	7.3	10° 55' 29"	85° 48' 24"	"	22	"	0	5
	D-15	2' dredge	9-2	16.4-3.6	10° 55' 03"	85° 48' 25"	"	22	Mangrove leaves, cr. shell, algae.	0	3
	L-1	Light	—	—	10° 55' 22"	85° 48' 28"	"	12	—	3	0
	L-2	Light	—	—	10° 55' 22"	85° 48' 28"	"	14	—	1	30
	L-3	Light	—	—	10° 55' 51"	85° 48' 58"	"	16	—	1	30
	L-4	Light	—	—	10° 55' 51"	85° 48' 58"	"	17	—	1	45
	D-1	2' dredge	3	5.4	10° 52' 08"	85° 52' 30"	Murcielago Bay, Costa Rica.	23	Sand.	0	3
204	D-2	2' dredge	4	7.3	10° 52' 05"	85° 52' 27"	"	23	"	0	3
	D-3	2' dredge	2.5	4.5	10° 52' 01"	85° 52' 23"	"	23	"	0	5
	D-4	2' dredge	2	3.6	10° 51' 55"	85° 52' 19"	"	23	"	0	5
	L-1	Light	—	—	10° 50' 45"	85° 45' 30"	Potrero Grande Bay, Costa Rica.	23	—	2	30
206	D-1	4' dredge	14	25.5	10° 37' 03"	85° 41' 12"	Port Culebra, Costa Rica.	30	Sandy mud.	0	3
	D-2	4' dredge	14	25.5	10° 36' 47"	85° 41' 10"	"	30	"	0	4
	D-3	4' dredge	14	25.5	10° 36' 22"	85° 41' 08"	"	30	"	0	5
	L-1	Light	—	—	10° 37' 10"	85° 41' 18"	"	25	—	2	0
	L-2	Light	—	—	10° 37' 50"	85° 39'	"	28	—	1	45
	L-3	Light	—	—	10° 35' 45"	85° 40' 15"	"	29	—	1	45
	L-4	Light	—	—	10° 35' 45"	85° 40' 15"	"	30	—	2	15
207	L-1	Light	—	—	10° 25' 20"	85° 48' 45"	Braxilito Bay, Costa Rica.	31	—	2	40
208	D-1	2' dredge	6	11	9° 51' 57"	85° 29' 55"	Piedra Blanca Bay, Costa Rica.	Feb. 5	Rocks, sand, algae.	0	3
	D-2	2' dredge	5	9.1	9° 51' 54"	85° 29' 53"	"	5	"	0	3
	D-3	2' dredge	4	7.3	9° 51' 52"	85° 29' 46"	"	5	"	0	3
	D-4	2' dredge	6	10.9	9° 51' 49"	85° 29' 41"	"	5	"	0	3
	D-5	2' dredge	5	9.1	9° 51' 47"	85° 29' 34"	"	5	"	0	3
	D-6	2' dredge	3	5.4	9° 51' 48"	85° 29' 32"	"	5	"	0	5
	D-7	2' dredge	3	5.4	9° 52' 06"	85° 29' 49"	"	5	"	0	3
	D-8	2' dredge	3	5.4	9° 52' 06"	85° 30'	"	5	"	0	5
	D-9	2' dredge	3	5.4	9° 52' 05"	85° 30' 09"	"	5	"	0	5
	D-10	2' dredge	2	3.6	9° 51' 51"	85° 30' 20"	"	5	"	0	4
	L-1	Light	—	—	9° 51' 47"	85° 29' 56"	"	1	—	2	40
	L-2	Light	—	—	9° 51' 47"	85° 29' 56"	"	2	—	2	0
	L-3	Light	—	—	9° 51' 47"	85° 29' 56"	"	3	—	2	0
	L-1	Light	—	—	9° 45'	85° 26'	22 m. WNW. of Cape Blanco, Costa Rica	6	—	0	45
210	T-1	½ Metre	0	0	9° 41'	85° 24'	"	6	—	0	15
	L-1	Light	—	—	9° 15'	85° 09'	20 m. S. of Cape Blanco, Costa Rica.	7	—	2	0
	L-2	Light	—	—	9° 14'	85° 07'	"	8	—	2	30
	L-3	Light	—	—	9° 13'	85° 09'	"	26	—	3	0
	T-1	Metre	300	540	9° 12'	85° 05'	"	7	—	4	0
	T-2	Metre	400	730	9° 12'	85° 05'	"	7	—	4	0
	T-3	Metre	500	910	9° 12'	85° 05'	"	7	—	4	0
	T-4	½ Metre	2	3.6	9° 12'	85° 05'	"	7	—	0	30
	T-5	½ Metre	2	3.6	9° 12'	85° 05'	"	7	—	0	30

Station No.	Net No.	Type of Net	Depth		Position		General Locality	Date 1938	Bottom	Duration	
			Fathoms	Metres	N. Lat.	W. Long.				Hrs.	Mins.
210	T-6	Metre (3 nets)	500	910	9° 12'	85° 05'	20 m. S. of Cape Blanco, Costa Rica.	Feb. 7	—	2	53
	T-7	Metre (3 nets)	500	910	9° 09'	85° 04'	"	8	—	4	25
	T-8	Metre (3 nets)	500	910	9° 12'	85° 10'	"	27	—	3	26
	T-9	Metre	200	360	9° 11'	85° 08' 30"	"	27	—	3	32
	T-10	Metre (2 nets)	500	910	9° 11'	85° 08' 30"	"	27	—	3	32
	T-11	½ Metre	3	5.4	9° 11'	85° 08' 30"	"	27	—	1	0
211	L-1	Light	—	—	9° 29'	85° 08'	6 m. SW. of Cape Blanco, Costa Rica.	10	—	0	20
212	L-1	Light	—	—	9° 58' 15"	84° 59' 45"	Puntarenas, Costa Rica	11	—	8	0
213	D-1	2' dredge	8	14.6	9° 50' 52"	84° 53' 07"	Cedro Island, Gulf of Nicoya, Costa Rica	13	Mud.	0	3
	D-2	2' dredge	4	7.2	9° 50' 46"	84° 53' 05"	"	13	"	0	3
	D-3	2' dredge	4	7.2	9° 50' 41"	84° 53' 03"	"	13	"	0	1
	D-4	2' dredge	5	9.1	9° 50' 39"	84° 53' 07"	"	13	"	0	2
	D-5	2' dredge	4	7.2	9° 50' 37"	84° 53' 12"	"	13	"	0	2
	D-6	2' dredge	4	7.2	9° 50' 38"	84° 53' 14"	"	13	Mud, sand, cr. shell	0	2
	D-7	2' dredge	4	7.2	9° 50' 42"	84° 53' 17"	"	13	"	0	2
	D-8	2' dredge	4	7.2	9° 50' 45"	84° 53' 19"	"	13	"	0	3
	D-9	2' dredge	6	11	9° 50' 52"	84° 53' 23"	"	13	"	0	4
	D-10	2' dredge	10	18.2	9° 51' 01"	84° 53' 22"	"	13	Mud.	0	3
	D-11	4' dredge	35	63.7	9° 44' 52"	84° 51' 25"	Off Ballenas Bay, Gulf of Nicoya, Costa Rica	25	"	0	3
	D-12	4' dredge	35	63.7	9° 44' 24"	84° 51' 03"	"	25	"	0	5
	D-13	4' dredge	35	63.7	9° 43' 45"	84° 51' 08"	"	25	"	0	5
	D-14	4' dredge	35	63.7	9° 43'	84° 51' 17"	"	25	"	0	5
	D-15	4' dredge	40	73	9° 42' 10"	84° 51' 25"	"	25	"	0	5
	D-16	4' dredge	45	82	9° 41' 10"	84° 51' 45"	"	25	"	0	5
	D-17	4' dredge	35	63.7	9° 42'	84° 56'	"	25	"	0	5
	D-18	4' dredge	80	145	9° 29' 30"	85° 06' 40"	3 m. off Cape Blanco, Costa Rica.	26	"	0	10
	L-1	Light	—	—	9° 51' 30"	84° 52' 30"	Cedro Island, Gulf of Nicoya, Costa Rica	21	—	2	30
	L-2	Light	—	—	9° 47'	84° 53' 30"	Alcatraz Is., Gulf of Nicoya, Costa Rica	22	—	2	0
	L-3	Light	—	—	9° 46' 20"	84° 53' 05"	Jasper Is., Gulf of Nicoya, Costa Rica	23	—	2	30
	L-4	Light	—	—	9° 44' 25"	84° 59' 35"	Ballenas Bay, Gulf of Nicoya, Costa Rica	25	—	3	00
214	D-1	4' dredge	42	76.5	9° 19' 32"	84° 29' 30"	14 m. S.xE. of Judas Pt., Costa Rica	Mar. 1	Mud, shell.	0	5
	D-2	4' dredge	43	78	9° 18' 45"	84° 29' 15"	"	1	Mud.	0	10
	D-3	4' dredge	50	91	9° 18' 05"	84° 28' 25"	"	1	"	0	10
	D-4	4' dredge	61	112	9° 17' 40"	84° 27' 30"	"	1	Mud, rocks	0	10
215	L-1	Light	—	—	9° 03'	84° 06'	23 m. W. of Uvita Bay, Costa Rica.	1	—	1	30
216	L-1	Light	—	—	9° 08' 45"	83° 45' 25"	Uvita Bay, Costa Rica	2	—	4	0
	L-2	Light	—	—	9° 08' 45"	83° 45' 25"	"	3	—	2	0
217	L-1	Light	—	—	8° 19'	83° 36'	20 m. W. of Gulf of Dulce, Costa Rica	4	—	0	30

Station No.	Net No.	Type of Net	Depth		Position		General Locality	Date 1938	Bottom	Duration	
			Fathoms	Metres	N. Lat.	W. Long.				Hrs.	Mins.
218	D-1	4' dredge	100	183	8° 35' 30''	83° 15' 30''	Gulf of Dulce, Costa Rica.	Mar. 9	Mangrove leaves.	0	6
218	D-2	4' dredge	105	192	8° 35' 50''	83° 16' 40''	Gulf of Dulce, Costa Rica.	9	Mangrove leaves.	0	15
	D-3	4' dredge	80-60	145-109	8° 38' 10''	83° 16' 45''	"	9	"	0	10
	D-4	2' dredge	6	11	8° 38' 15''	83° 10' 25''	Golfito, Gulf of Dulce, Costa Rica	9	Mangrove leaves, mud, shells.	0	3
	D-5	2' dredge	6	11	8° 38' 15''	83° 10' 25''	"	9	"	0	3
	D-6	2' dredge	4	7.3	8° 38' 15''	83° 10' 25''	"	9	"	0	3
	D-7	2' dredge	6	11	8° 38' 15''	83° 10' 25''	"	9	"	0	3
	D-8	2' dredge	6	11	8° 38' 15''	83° 10' 25''	"	9	"	0	3
	L-1	Light	—	—	8° 38' 12''	83° 10' 45''	"	6	—	2	0
	L-2	Light	—	—	8° 38' 12''	83° 10' 45''	"	7	—	2	0
	L-3	Light	—	—	8° 26'	83° 08' 40''	Pavon Bay, Gulf of Dulce, Costa Rica	9	—	2	0
219	T-1	Metre (3 nets)	300	540	8° 08'	83° 17'	25 m. W.xN. of Pt. Burica, Costa Rica.	10	—	4	3
	T-2	Metre (3 nets)	500	910	8° 03'	83° 12'	"	10	—	2	0
220	L-1	Light	—	—	8° 07'	82° 22' 12''	Isla Parida, Gulf of Chiriqui, Panama.	11	—	4	0
	L-2	Light	—	—	8° 07' 52''	82° 18' 45''	"	12	—	2	30
221	D-1	4' dredge	35	64	7° 54' 45''	82° 04' 32''	Gulf of Chiriqui, Panama.	13	Sandy mud.	0	5
	D-2	4' dredge	35	64	7° 54' 15''	82° 04' 25''	"	13	"	0	5
	D-3	4' dredge	35	65	7° 53' 12''	82° 02' 45''	"	13	"	0	5
	D-4	4' dredge	38	69	7° 52' 45''	82° 02'	"	13	"	0	8
	D-5	4' dredge	40	73	7° 52' 30''	82° 01'	"	13	"	0	10
222	D-1	2' dredge	3	5.4	7° 45' 51''	81° 32' 21''	Bahia Honda, Pan.	18	Rocks, dead coral.	0	2
	D-2	2' dredge	4-8	7.2-14.5	7° 45' 46''	81° 32' 23''	"	18	"	0	3
	D-3	2' dredge	8	14.5	7° 45' 42''	81° 32' 24''	"	18	Dead coral.	0	3
	D-4	2' dredge	11	20	7° 45' 39''	81° 32' 21''	"	18	Dead coral, shells, gr. mud.	0	3
	D-5	2' dredge	11	20	7° 45' 35''	81° 32' 18''	"	18	Mud, shells, leaves.	0	10
	L-1	Light	—	—	7° 45' 15''	81° 32' 10''	"	13	—	2	15
223	L-1	Light	—	—	7° 32'	81° 52' 30''	Bahia Hermosa, Coiba Is., Panama.	19	—	3	30
224	D-1	4' dredge	40	73	7° 23' 30''	82° 03'	Hannibal Bank, Pan.	20	Rocks, dead coral.	0	4
	D-2	4' dredge	35	64	7° 23' 30''	82° 03'	"	20	Rocks, mud, dead coral.	0	10
	D-3	4' dredge	35	64	7° 23' 30''	82° 03'	"	20	Sand, shells, algae.	0	15
225	T-1	Metre (3 nets)	500	910	7° 08'	81° 57'	11 m. SW.xW. of Jicarón Is., Panama.	20	—	2	31
226	L-1	Light	—	—	7° 05'	81° 27'	22 m. ESE. of Jicarón Is., Panama.	20	—	0	30
227	T-1	Metre (3 nets)	500	910	7° 00'	80° 40'	20 m. SW. of Morro de Puercos, Panama.	21	—	3	41
228	T-1	Metre (3 nets)	500	910	7° 00'	79° 16'	52 m. SE.xE. of Cape Mala, Panama.	25	—	4	30
229	L-1	Light	—	—	6° 27'	79° 00'	83 m. SE. of Cape Mala, Panama.	25	—	0	35

Station No.	Net No.	Type of Net	Depth		Position		General Locality	Date 1938	Bottom	Duration	
			Fathoms	Metres	N. Lat.	W. Long.				Hrs.	Mins.
230	T-1	Metre (3 nets)	500	910	5° 10'	78° 42'	71 m. W.xS. of Cape Corrientes, Columbia.	Mar. 26	—	4	2
231	L-1	Light	—	—	4° 30'	78° 33'	85 m. SW. of Cape Corrientes, Columbia.	26	—	0	35
232	D-1	2' dredge	2-8	3.6-14.6	2° 57' 30''	78° 11'	Gorgona, Island, Columbia.	31	Sand.	0	30
	L-1	Light	—	—	2° 59'	78° 11'	"	27	—	2	30
	L-2	Light	—	—	2° 59'	78° 11'	"	28	—	4	0
	L-3	Light	—	—	2° 59'	78° 11'	"	29	—	3	30
	L-4	Light	—	—	2° 59'	78° 11'	"	30	—	4	0
	L-5	Light	—	—	2° 59'	78° 11'	"	31	—	4	0
233	T-1	Metre (3 nets)	500	910	4° 45'	78° 02'	55 m. SSW. of Cape Corrientes, Columbia.	Apr. 3	—	4	33
234	T-1	Metre (3 nets)	500	910	7° 24'	78° 35'	24 m. W.xS. of Pinas Pt., Panama.	4	—	4	27



## 15.

Eastern Pacific Expeditions  
of the New York Zoological Society, XV.  
Seven New Marine Fishes from Lower California.<sup>1</sup>

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&amp;

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(Plates I-III; Text-figures 1-5).

[This is the fifteenth of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. For data on dredges, localities, dates, etc., concerning the capture of specimens treated in this paper, refer to *Zoologica*, XXII, No. 2, pp. 33-46.]

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## MOBULIDAE.

***Mobula lucasana*, sp. nov.**

(Plate I, Figs. 1 &amp; 2; Plate II, Figs. 3 &amp; 4; Plate III, Fig. 5).

*Type*: Holotype ♀; No. 24,793, Department of Tropical Research, New York Zoological Society; San Lucas Bay, Lower California, Mexico; March 30, 1936; width across disk 1,035 mm. ( $40\frac{3}{4}$  inches); length from anterior part of disk to posterior margin of the pelvic fins, 584 mm. (23 inches). Type in the collections of the Department of Tropical Research, the head, posterior body and tail preserved, the latter damaged, only a length of 7 inches projecting beyond the outer margin of the pelvic fins.

<sup>1</sup> Contribution No. 561, Department of Tropical Research, New York Zoological Society.

*Description and Dimensions of Type:* Skin smooth, no trace of rugosities or spines anywhere. Width across disk 1,035 mm.; length from anterior margin of disk to posterior margin of the pelvic fin 584 mm. (anterior margin of the disk considered as being at the mid-line of the body, thus not including the cephalic projections); cephalic fins extending forward 80 mm. beyond the anterior margin of the disk, the distance between their tips approximately 150 mm., distance from upper margin of the cephalic fin to lower margin of the fin when the fin is unfurled, 58 mm. Eye lateral, 17 mm. in diameter, its anterior margin 88 mm. from the tip of the cephalic fin. Spiracle oblique, 31 mm. posterior to the eye. Mouth inferior, 128 mm. wide, very slightly concave when viewed from below, the margin of the upper lip 40 mm. from the anterior margin of the disk.

Teeth in each jaw in a narrow band, each band extending 70 percent. of the width of the mouth. Upper jaw with 80 transverse rows of teeth and 5 rows from back to front. Lower jaw with 97 teeth in a transverse series and with 4 or 5 rows from back to front. Teeth small, flattened, their surfaces slightly roughened, the posterior border with 2 to 5 dull, irregular points. A typical tooth in the center of the lower jaw measures 1.2 mm. in width and .5 to .6 mm. in depth.

Mouth to transverse line of first gill-openings 70 mm.; transverse distance between first gill-openings 133 mm.; transverse distance between last gill-openings 60 mm.; length of gill-slits of first four pairs of gill-openings 52 mm.; length of last gill-slit 37 mm.

Pelvic fins rather elongate, their tips extending 31 mm. beyond the posterior tip of the pectoral, the inner margin extending backward farther than the outer, the fin nearly uniform in width, averaging 38 mm.

Dorsal fin with its posterior one-fourth situated above the free portion of the tail, the base of the fin 57 mm., the height 46 mm.

Tail immediately beyond the dorsal fin flattened, the skin of its upper surface reticulated, the reticulations being in the form of minute, low, raised ridges of skin, the upper margins of which are roughened and occasionally slightly ciliate. Although the area mentioned above has this peculiar specialized skin there is no trace of a spine or of the beginnings of a spine. Tail beyond the expanded portion becoming attenuated near the tips of the pelvic fins, its diameter 50 mm. posterior to the tips of the pelvic fins being 3.5 to 4 mm.

*Color:* In life upper surfaces, including the area about the eye and the upper part of the cephalic fins, blackish-gray; lower surfaces whitish becoming bluish-gray toward the tips of the wings, this color darkest on the anterior portion of the fins. Leading edge of undersurfaces of pectoral fin dusky, the posterior edges similarly colored but the band of color narrower. An oval, dusky spot near the posterior margin of the lower side of the pectoral fin, slightly nearer the pelvic fins than the tip of the pectoral. Tip of the cephalic fin black.

The preserved type has the underside of the body, anterior to the mouth, and a narrow band along the lower jaw as well as the entire inner surface of the cephalic fin, brownish-black.

*Remarks:* Two species of *Mobula* are recorded from the eastern Pacific, *Mobula tarapacana* (Philippi) from the coast of Chile and *M. japonica*, recorded from Hawaii and known principally from the western Pacific.

*Mobula tarapacana* was described from a drawing of a dead specimen and there is considerable question as to the accuracy of the description and figure. The present species, *M. lucasana*, however, does not possess the peculiar long neck of the drawing of *tarapacana*.

In all of the available descriptions of *M. japonica* the bands of teeth are described as extending to, or nearly to, the angles of the jaws. The teeth of the present species by no means extend that far. In addition

*japanica* possesses a caudal spine and, even though the caudal of *lucasana* is damaged, there is sufficient to show that the spine is lacking. Jordan and Fowler's figure (*Proc. U. S. National Museum*, XXVI, p. 666, fig. 10) of a fetus of *japanica* shows quite clearly a spine on the tail close to the pelvic fins, a condition that is not true of *lucasana*. However, in the present species it is of interest that the skin of the upper portion of the base of the tail is modified, a condition that may or may not be significant in view of the absence of a spine. This modification is mentioned in the description of the species.

During the 1936 *Zaca* Expedition these fish were common at Cape San Lucas and San Lucas Bay and a number of individuals were seen somersaulting in the air and striking the water in descent with a sound audible for considerable distances. In January and February, 1938, numerous individuals, presumably of this species, were seen off Elena Point and Cape Velas, Costa Rica. Probably some of the west coast of Central America sight records of *Manta* can be assigned to the present new species.

The type of *lucasana* was captured on a baited hook.

#### MYRIDAE.

#### *Arenichthys*, gen. nov.

Body elongate; dorsal fin beginning close behind gill-opening; pectoral fins absent; anterior nostril in a tube; posterior nostril in a flap-like tube which is open on its inner posterior aspect, the tube as large and conspicuous externally as the anterior nostril; teeth as in the description of the species.

*Genotype*: *Arenichthys apterus* Beebe and Tee-Van.

#### *Arenichthys apterus*, sp. nov.

(Text-fig. 1a, 1b, 1c).

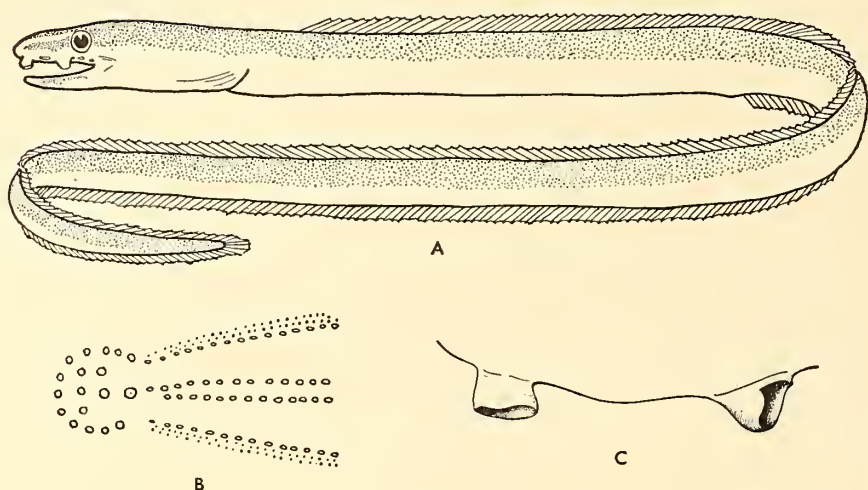
*Type*: Holotype, No. 25,361, Department of Tropical Research, New York Zoological Society; taken in dredge 136-D-16 in 45 fathoms, Arena Bank, Lower California (23°29'30" N., 109°25'30" W.), April 20, 1936; standard length 135 mm. Type in the collections of the Department of Tropical Research.

*Measurements of the type*: Length, standard, 135 mm.; depth 4.1 mm. (33); head 16.6 mm. (8.1); eye 1.6 mm. (10.2); snout 3.6 mm. (4.6); snout to gape 5.8 mm. (2.85); snout to dorsal fin 19 mm. (7.1); snout to anus 46 mm. (2.95); snout to anal fin 47.5 (2.84).

*Description*: Body elongate, worm-like, very slightly compressed, the depth 33 times in the length; head and trunk 2.95 in the length. Head 8.1 in the length, 1.76 in the trunk; gill opening oblique, at the level of the mid-sides. Gape extending backward slightly beyond the vertical of the posterior border of the orbit.

Maxillary teeth small, conical, in three rows, the teeth of the inner row considerably larger than the others; all are slightly depressible. Vomer anteriorly with a series of teeth about its border; progressing backward from these border teeth are three teeth set transversely on the median line followed by two teeth set on the median line; posterior to these are two lines of teeth on the shaft of the vomer, the two rows rather widely separated from each other, the teeth of the central portion of each row slightly heavier than those of the anterior and posterior portions. Lower jaw with a double row of small conical teeth becoming an irregular three rows anteriorly, the teeth of the inner row largest.





Text-figure 1.

- A.** *Arenichthys apterus*. **B.** *Arenichthys apterus*. Diagram of teeth of the upper jaw. **C.** *Arenichthys apterus*. View from inside of mouth of right side of upper lip, showing (left) the tubular anterior nostril, and (right) the posterior nostril.

Anterior nostril in a tube; posterior nostril in a flap-like tube which is open on its inner posterior aspect. Eye small, 10.2 in the head.

Dorsal fin beginning slightly less than an eye's diameter posterior to the vertical of the gill opening, confluent with the anal fin about the tip of the caudal. Pectoral fins absent.

*Color*: Brown above, white below, the boundary sharply demarcated, especially on the head. Here the brown of the interorbital space extends forward to the snout as a band the width of the interorbital space, leaving the upper lip and the side of the head white with the exception of a rather long, triangular, brown spot extending forward from the eye toward the snout. Lower jaw with a narrow brown band along the lip, most intense interiorly, and hidden by the upper jaw when the mouth is closed.

#### BOTHIDAE.

#### *Citharichthys gordae*, sp. nov.

(Text-fig. 2).

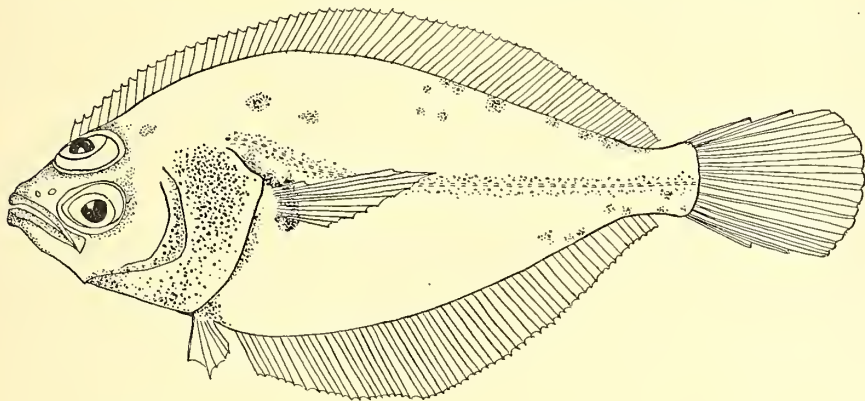
*Type*: Holotype, No. 25,785, Department of Tropical Research, New York Zoological Society; taken at Station 150, Dredge Haul 14; depth 60 fathoms, center of outer Gorda Bank, Lower California, April 23, 1936; standard length 97 mm. Type in the collections of the Department of Tropical Research.

*Dimensions of Type*: Total length 120 mm.; standard length 97 mm.; depth 40 mm. (2.4 in length); head 36 mm. (2.7 in length); eye 10.5 mm. (3.7 in head); interorbital space 1.3 mm. (8 in eye); maxillary 12 mm. (3 in head); pectoral length 22.5 mm. (1.6 in head).

*Counts of Type*: Dorsal fin 76; anal 57; pectoral 12; gill-rakers 19; lateral line scales 50; vertebrae 33.



*Description:* A medium-sized flounder (standard length up to 111 mm.), moderately deep (2.4 in length); eyes separated by a narrow, concave, scaled space which rises to a sharp ridge above lower eye; interorbital width similar in both sexes; dorsal beginning on blind side opposite front of eye; upper pelvic fin on ventral profile; head moderately compressed with the upper profile very slightly concave; anterior margin of the eyes are level or the lower slightly in advance; upper eye touching profile of head; maxillary not reaching middle of eye; teeth slightly enlarged anteriorly but not forming real canines; indications of an imperfect second row in the upper jaw; gill-rakers long and slender; scales relatively strongly ctenoid.



Text-figure 2.

*Citharichthys gordae*. Drawing by George Swanson.

*Color:* Immaculate below; brown above with various dark mottlings, sometimes reduced to several small spots, or increasing to larger blotches, the extreme is where the dark color has run together covering three-fourths of the upper surface. The fins are dusky, sometimes indistinctly mottled or spotted; opercular region and lateral line always dark.

In specimens of 50 mm. standard length or under, there is often a faint but distinct regular pattern. The body is pale with 6 to 8 broken cross bands, very distinct as mid-ray spots on the profile fins, and about as strong but of greater extent on the baseoste; these bands are very irregular on the body proper but in general follow the oblique muscle bands. The prepeduncular band is almost complete and the dark markings on the peduncle are reduced and concentrated to a pair of jet black dots in the profile.

*Variation:* Considering that 216 specimens of this new form were taken on Gorda Bank, measuring from 31 to 111 mm. in length, the extremes of variation shown were small. Depth in length 2.3 to 2.4 (average 2.3); head in length 2.68 to 2.7 (2.7); eye in head 3.4 to 4.15 (3.75); snout in head 5 to 6 (5.5); maxillary in head 2.78 to 3 (2.9); dorsal count 73 to 79 (76); anal count 57 to 62 (58.7); scales 48 to 50 (48.6); gill rakers 17 to 19 (18).

*General Relationships:* In general appearance and the more obvious external characters *C. gordae* approaches *C. fragilis*, a species which has been taken only in the upper half of the Gulf of California, from Guaymas northward. On the other hand the low vertebral count of *gordae* (34) removes it, according to Norman, from the subgenus *Orthopsetta* "species of the North Pacific," (with 37 to 40 vertebrae, including *sordidus*, *fragilis*,

*xanthostigma* and *stigmaeus*), and places it in the subgenus *Citharichthys* "species of the Atlantic and Tropical Pacific," (with 33 to 36 vertebrae), including the Pacific species *platophrys* and *gilberti*. In scale and gill-raker count and interorbital width it is indistinguishable from *fragilis*, while in dorsal and anal ray count it departs widely from this species and is within the range of both species of subgenus *Citharichthys*. In depth and pectoral length it is closest to *stigmaeus*. *C. gordae* differs from the two species *platophrys* and *gilberti*, in possessing smaller scales, a greater number of gill-rakers, a larger head, shorter maxillary and a much narrower interorbital. The distinctions between the two subgenera *Citharichthys* and *Orthopsetta* are very slight and may disappear on more intensive study.

*Local Distribution:* Two hundred and sixteen specimens of this new species were taken by us, 200 of which came up in ten dredge hauls at Station 150, on Gorda Banks. The single catch of these fish outside of the banks but in the same general locality was from Station 151 D-1, when 16 came up from a depth of 60 fathoms on April 24, half a mile south of Cape San Lucas and 20 miles south-west of Gorda Banks.

The ten catches on Gorda were made on April 21, 22 and 23, 1936. The extremes in vertical limits were 45 to 80 fathoms, in size 31 to 111 mm. and in abundance in hauls were 2 in D-6 and 50 in D-4. The ten hauls show a remarkable relation to sandy bottoms, none being on muddy or rocky areas.

The 16 flounders taken at Station 151 measure from 31 to 111 mm. in length, an average far and away smaller than those from Gorda, and this may have significance in the proximity of the locality to San Lucas Bay which proved, in the case of many other fish, to be a nursery for young stages.

#### SCORPAENIDAE.

#### *Scorpaenodes cortezi*, sp. nov.

(Text-fig. 3).

*Type:* Holotype, No. 24,889-A, Department of Tropical Research, New York Zoological Society. Taken at surface in weed, Station 138, 24° 55' N. Lat., 110° 20' W. Long., 10 miles east of San Jose Island, Gulf of California, April 8, 1936. Standard length 45.5 mm. Type in the collections of the Department of Tropical Research.

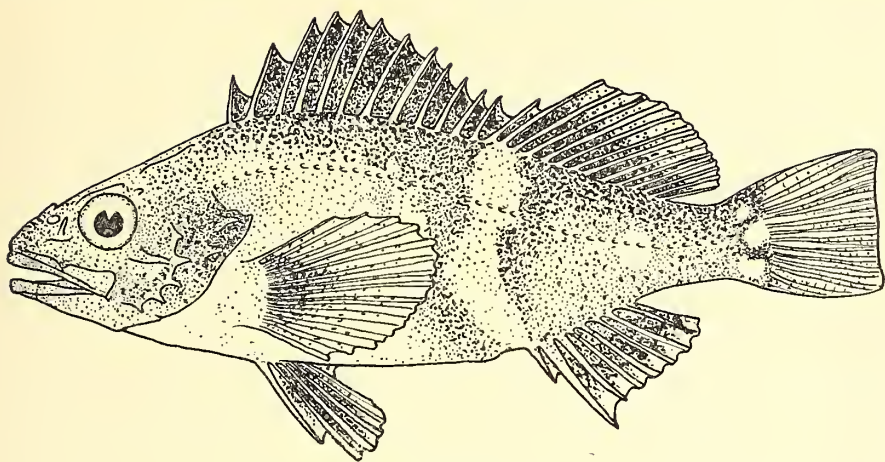
*Measurements and Counts of Type:* Length, total, 54 mm.; length, standard, 45.5 mm.; depth 16 mm.; width of body 8.8 mm.; head 15.8 mm.; eye 4.2 mm.; snout 5.3 mm.; maxillary 8.2 mm.; interorbital space, 3.2 mm.; snout to dorsal fin 16.1 mm.; snout to anal fin 31 mm.; dorsal fin XIII, 13; anal fin, III, 6; pectoral fin 18; pelvic fin I, 5; scales, approximately 63 rows; lateral line pores 41; gill-rakers 10 plus 20.

*Description:* Body considerably compressed, its width 5.2 in the length, depth 2.84; the dorsal outline evenly rounded.

Body, with the exception of snout, chin, maxillary, branchiostegal membranes and isthmus, covered with small, weakly ctenoid scales, approximately 63 rows from shoulder to caudal fin.

Lateral line continuous, prominent, following the dorsal outline and composed of 41 pores.

Head 2.86 in the length, about 1½ times as deep as wide. Spines of the head low, the following present: nasal, preocular, supraocular, postocular and parietal. Opercle posteriorly with two flat spines, the upper slightly longer than the lower, the lower heavier at its base. Preopercle with five rather prominent spines, the second and third slightly stronger than the others. Suborbital stay weak but evident without dissection.



Text-figure 3.

*Scorpaenodes cortezi*. Drawing by George Swanson.

Snout 3 in head. Eye small, 3.75 in the head. Nostrils small, slightly nearer eye than snout, the anterior with a slight raised rim.

Mouth terminal, the jaws equal. Maxillary 1.9 in the head, its posterior tip extending to the vertical of slightly beyond the posterior margin of the pupil. Upper and lower jaw with a band of small conical teeth, the band widening anteriorly. Vomer with small teeth on its head, none on the shaft. Palatine teeth apparently absent in the type specimen, but present as a band of minute teeth in a 39 mm. specimen that has been stained with alizarin and cleared in caustic potash.

Gill-rakers 10 plus 20 on the first arch; rakers slim, the longest about half an eye's diameter. No slit behind the fourth gill-arch.

Spines of the dorsal fin regularly increasing in length from the first to the fifth, the length of the latter being two in the head, the spines then decreasing in length, the last spine about half the height of the first ray. Soft dorsal fin anteriorly about as high as the highest spine, slightly lower posteriorly. First anal spine less than half the height of the second; second anal spine considerably stronger and heavier than the other two; tip of the second extending slightly beyond that of the third. Anal rays slightly longer than the second anal spine. Caudal fin truncate. Pectoral fin rounded posteriorly, all its rays simple, the tips of the rays expanded and flattened, the tips with heavy skin. Tips of the lower three to four rays free of membrane. Pelvic fins inserted posterior to the vertical of the pectoral fin base.

*Color*: A color sketch made from the living fish is as follows: Body dark reddish-brown with a yellowish tinge, paler below, the entire body covered with black punctulations and irregular greenish-yellow blotches, the latter especially marked posteriorly. Dorsal fin dark brown, the membranes of the spinous dorsal black, the soft dorsal irregularly blotched with lighter. Caudal fin yellowish-green, without pattern. Pectoral fin brownish, yellow toward the tip and dusky at the base. Pelvic fins black at base, yellow at tips and with scarlet along the anterior edge. Anal fin black at base, yellow on outer half and with a small scarlet patch at base of the first spine.

In preservative the body is dark brown with irregular, rather large, lighter blotches.



## AMMODYTIDAE.

***Ammodytes lucasanus*, sp. nov.**

*Type*: Holotype, No. 25,249-A, Department of Tropical Research, New York Zoological Society; from stomach of *Euthynnus alletterata* (Rafinesque), Cape San Lucas, Lower California, April 25, 1936; standard length 100 mm. Paratype: No. 25,541-A, from stomach of *Seriola colburni* Evermann and Marsh, Cape San Lucas, Lower California, May 6, 1936; standard length 103 mm. Types in the collections of the Department of Tropical Research.

Thirty-one other specimens (Nos. 25,249, 25,541 and 25,555), 50 to 106 mm. standard length, are also in the collections. They were taken from the stomachs of the following fish: *Euthynnus alletterata* (Rafinesque), *Seriola dorsalis* (Gill) and *Seriola colburni* Evermann and Marsh, and from a cormorant, *Phalacrocorax penicillata* (Brandt); all of these from Cape San Lucas, April 25, 1936 and May 6, 1936.

*Dimensions of Type*: Total length 114 mm.; standard length 100 mm.; depth 11.3 mm. (8.85 in length); width of body 8.6 mm. (2.72 in head); head 23.5 mm. (4.25 in length); eye 3.8 mm. (6.2 in head); interorbital space 2.6 mm. (9 in head); snout 6.6 mm. (3.55 in head); maxillary 7.7 mm. (3.04 in head); predorsal length 25 mm. (4 in length); preanal length 66 mm. (1.6 in head); pectoral fin length 10.2 mm. (2.3 in length); caudal peduncle depth 5.1 mm. (4.6 in length).

*Counts of Type*: Dorsal fin 47; anal fin 22; pectoral fin 15; 97 lateral folds; branchiostegal rays 7; gill-rakers 6 plus 23; vertebrae 56.

*Description*: Elongate, spindle-shaped, tapering toward head and caudal fin, the head quite sharp and pointed. Upper and lower profiles similar.

Body, with the exception of the head, covered with scales, the scales being cycloid but with traces of small points along the posterior edge, the whole suggesting a weakly ctenoid scale.<sup>2</sup> A series of 97 oblique folds along the sides, the upper margin of each fold being anterior to the lower. A fold of skin along the lower side of the belly ending near the beginning of the anal fin, this fold not noticeable in the preserved type but remarked upon in the field notes on fresh specimens.

Lateral line single, paralleling the back; anteriorly the lateral line partly surrounds the eye, having an angled branch descending to under the posterior lower edge of the eye, and an upper branch which runs obliquely forward ending posterior to the vertical of the eye; on the posterior head the lateral line follows closely the upper border of the opercular margin, then sharply ascends to the position of the line on the body; a short transverse branch of the lateral line on the nape, not meeting its fellow of the opposite side.

Head conical, 4.25 in the length, the lower jaw projecting considerably beyond the tip of the upper and with a heavy fleshy tab on its tip. Eye 6.2 in head. Nostrils subcircular, the anterior slightly larger, situated midway between the eye and the tip of the premaxillary, placed one before the other and widely spaced from each other. Mouth widely protractile, the jaws, vomer and palate toothless. Maxillary extending slightly beyond the vertical of the anterior border of the eye.

Opercular and preopercular borders smooth, the former ending posteriorly in a wide obtuse flap. Branchiostegal rays 7, the membranes free from each other, leaving a wide opening inferiorly.

Dorsal fin low, continuous, formed of rays only, originating slightly back of the pectoral origin. Caudal fin deeply forked. Anal fin low, con-

<sup>2</sup> This is also true of specimens of *Ammodytes personatus* from the San Juan Islands, Washington (Amer. Mus. Nat. Hist., 2712).



tinuous, formed of rays only, originating under the 29th dorsal ray. Pectoral fins small, pointed, situated below the median line of the body. Pelvic fins absent.

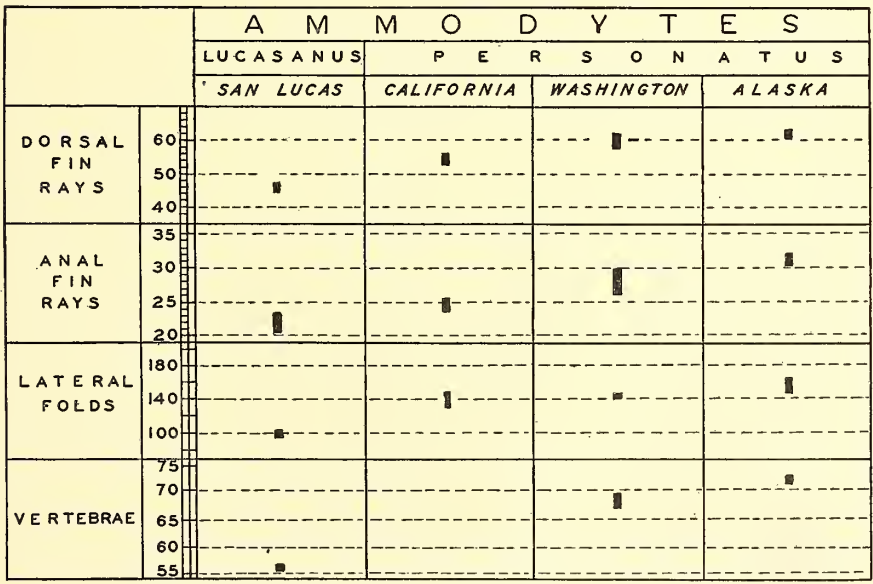
*Color:* Fresh specimens greenish above, silvery on sides with traces of bright golden yellow on the sides of the head and upper body. A series of rather widely placed black spots (8 in the holotype, 4 in the paratype) along the upper margin of the dorsal fin.

*Variation:* In a series of ten specimens examined, including the paratype, there is the following variation in proportions and counts: depth 7.8 to 9.45; head 4 to 4.25; eye 6.8 to 8; snout 3.5 to 3.8; dorsal fin count 45 to 46; anal fin count 20 to 23; lateral folds 97 to 100; gill-rakers 6 plus 22 to 23.

*Remarks:* During the last few years there has been a tendency to consider many of the northern forms of *Ammodytes* as being a single circumpolar species which sends representatives down the coasts of the continents to a greater or lesser degree, the distance depending upon the temperature of the water and other conditions.

As far as the Pacific is concerned, ichthyologists seem in agreement that all of the previously reported *Ammodytes* in that region are of one species. Thus the nominal form *alascanus* was merged during the latter part of the last century with *personatus*; Jordan in 1906 considered the Japanese form as the same species and in 1930 Soldatov and Lindberg utilized the name *personatus* for the northwestern Pacific fish. Finally Schultz in 1936 has related the Pacific form to the circumpolar species by using the name *Ammodytes tobianus personatus* (Girard) for the Pacific fish.

With this taxonomic history in mind the counts and measurements of two series of eastern Pacific *Ammodytes*, one series from Karluk Island, Alaska, and the second from Straits of Juan de Fuca, Washington, together with the records in the literature of California specimens, have been compared with those of our San Lucas material. The most pertinent counts are included in the following diagram; unfortunately we have not been able to procure California specimens, so that we have no vertebrae counts for this locality.



Examination of the table above demonstrates the apparent close relationship of *lucasanus* to the northern *Ammodytes*. In each of the characters shown there is a numerical diminution as one progresses southward, a condition similar to that found in other groups of fishes. In the case of the lateral folds, however, the fishes from California to Alaska are markedly closer to each other than they are to *lucasanus*; this similarity is shown to a lesser degree in the dorsal fin rays.

While it might be advisable to consider *lucasanus* as a southern representative of *personatus*, we think it better, for the present, to establish it as a separate form, principally for the following reasons:

1. A gap of 1,100 miles intervenes between the southernmost recorded locality of *personatus* (Monterey Bay, California) and the type locality of *lucasanus*. Specimens from this gap would help to establish the relationship between the two forms.

2. The San Lucas fish come from a sub-tropical faunal region, as opposed to the cold water habitat of *personatus*. San Lucas is about 420 miles south of Cedros Island where northern and southern faunas meet and cross.

3. With this faunal difference in mind it is possible that the lessened numerical characters may be constantly associated with the warm water habitation of *lucasanus* and that this species may have broken off completely from its northern parent form, leaving no intermediates.

#### EMBLEMARIIDAE.

#### *Emblemaria micropes*, sp. nov.

(Text-fig. 4).

*Type*: Holotype, ♂, No. 24,895, Department of Tropical Research, New York Zoological Society. Taken in loose weed floating along beach, Inez Point, Santa Inez Bay, Gulf of California, April 9, 1936. Standard length 33 mm. Type in the collections of the Department of Tropical Research.

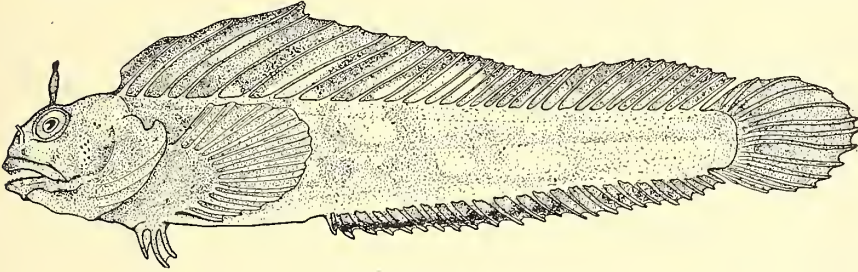
*Dimensions and Counts of Type*: Length, total, 37.6 mm.; length, standard, 33 mm.; depth 5.4 mm.; head 7.8 mm.; eye 1.4 mm.; snout 1.9 mm.; maxillary 3 mm.; interorbital space 1 mm.; snout to dorsal fin 5 mm.; snout to anal fin 15 mm.; height of dorsal fin 7 mm.; pectoral fin length 6.8 mm.; pelvic fin length 3.2 mm.; height of supraocular tentacle 2 mm.; dorsal fin, XIX, 12; anal fin, II, 21; pectoral fin 13; pelvic fin 3.

*Description*: Body elongate, considerably compressed posteriorly, the greatest width of body (across the swollen opercles) 6 in the length; depth 6.1.

Head 4.2 in the length; preopercular area and head considerably swollen. Upper profile of head a simple curve from nape to snout. A large flattened supraorbital tentacle, slightly longer than eye diameter. Preopercular margin not visible, hidden by the swollen sides of the head. Opercular margin smooth, the branchiostegal rays and membranes extending considerably beyond its margin, the tip of the outermost branchiostegal ray forming a slight forwardly-curved hook above; branchiostegal membranes broadly joined to each other but free from the isthmus.

Snout 4.1 in the head. Eye small, 5.6 in head, not entering the dorsal profile. Nostrils two on each side, the anterior with a small fleshy tentacle. Mouth small, the lips rather full; maxillary extending to posterior border of the eye. Teeth in the upper jaw strong, blunt and conical, the anterior ones strongest, in a single row, with a trace of asperities along the inner base of the anterior teeth resembling small teeth. Lower jaw with a similar series of teeth, the lateral anterior ones exceptionally strong and recurved. Vomerine teeth in a slightly curved row of four teeth. Palatine teeth similar in size and not quite continuous with the vomerine teeth.

Dorsal fin beginning on the nape, of 19 spines and 12 rays, the last ray connected by membrane with the caudal peduncle; a slight flap of membrane projecting forward from the edge of the 1st dorsal spine with the exception of the basal portion of the spine. Caudal fin rounded. Anal fin of 2 spines and 21 rays, similar to the dorsal but lower. Pectoral fins with lowermost five rays slightly thickened and with their tips free of membrane. Pelvic fins of three rays, short and thick, originating under the pectoral base.



Text-figure 4.

*Emblemaria micropes*. Drawing by George Swanson.

*Color*: The following notes were made upon the living fish. Head, supraocular tentacle, body and pectoral fins green, becoming more intense green on the caudal fin. Anterior three-quarters of the dorsal fin with alternate bands of green and bright red, each band including about two to three rays; posterior quarter of dorsal fin with faint pinkish patches distally in the webs. Anterior three-quarters of the anal fin green on its basal third, similar to that of the body, black on its median third and with the outer margin white; posterior quarter almost all green with only a hint of dusky and whitish.

*Remarks*: The five species of *Emblemaria* known from the eastern Pacific seem to be well differentiated from each other, not only by their coloration but by various combinations of other characters. In the following table the dorsal and anal fin counts and the head and pelvic fin proportions of the various species are gathered together.

Species.	Dorsal fin count.	Anal fin count.	Pelvic fin in length.	Head in length.
<i>nigra</i> , Panama	XXVII, 11	26-27	7.1-7.5	4.1-4.2
<i>nivipes</i> , Panama	XXIII-XXIV, 12-14	25	3.8	3.4-3.75
<i>hudsoni</i> , Peru	XXII-XXIII, 15-16	27	3.9	3.9
<i>oculocirrus</i> , Gulf of California	XXII, 13	25-26	4.9-5.75	3.75-4.1
<i>micropes</i> , Gulf of California	XIX, 12	23	10.3	4.2

This new species differs from the somewhat similar *Emblemaria oculocirrus* from the same region, in fin ray counts, smaller and differently shaped pelvic fins, low dorsal fin and in the supraocular tentacle. At first it was thought that the former was the opposite sex of the high-dorsalled *oculocirrus*, but careful dissection disclosed that all of the available specimens examined, four of *oculocirrus* and the type of *micropes*, were males. While perhaps of no importance, it is of interest that the specimen of



*micropes* was taken in weed along shore, while all three specimens of *oculocirrus* were washed out of empty augur shells taken on sandy shallows. For comparison with our materials of the genus we have examined the single specimen of *oculocirrus* taken by Dr. C. H. Townsend and recorded by Osburn and Nichols (*Bull. Amer. Mus. Nat. Hist.*, XXXV, (1916), p. 178).

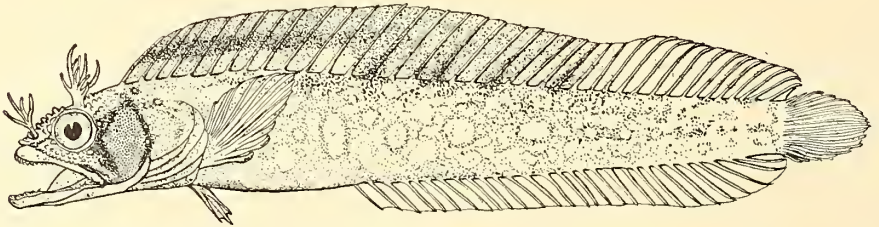
***Acanthemblemaria crockeri*, sp. nov.**

(Text-fig. 5).

*Type*: Holotype, No. 24,824, Department of Tropical Research, New York Zoological Society; taken with fulminating cap,  $3\frac{1}{2}$  fathoms deep, San Lucas Bay, Lower California, April 2, 1936; standard length 41 mm.; type in the collections of the Department of Tropical Research.

*Dimensions of Type*: Total length 46.2 mm.; standard length 41 mm.; depth 6.2 mm. (6.6 in length); head 10.2 mm. (4 in length); eye 2.1 mm. (4.85 in head); interorbital space 1.5 mm. (6.8 in head); snout 2.3 mm. (4.4 in head); maxillary 4.8 mm. (2.1 in head); predorsal length 6.5 mm. (6.3 in length); preanal length 18.2 mm. (2.2 in length); pectoral fin length 6.2 mm. (1.65 in head); pelvic fin length 3.4 mm. (3 in head); caudal peduncle depth 2.8 mm. (3.64 in head).

*Counts of Type*: Dorsal fin XXVI, 13; anal fin II, 27; pectoral fin 12; pelvic fin 3; caudal fin 19; branchiostegal rays 6.



Text-figure 5.

*Acanthemblemaria crockeri*. Drawing by Miss Eloise Southern.

*Description*: Body moderately elongate, the greatest depth at the base of the pelvic fins; the trunk compressed, especially posteriorly. The depth of the caudal peduncle 3.64 in the head length. Body scaleless. Anterior profile a simple curve from origin of dorsal fin to snout.

Head with short blunt spines anteriorly, those on the snout and at the anterior edge of the eye largest, the spines extending backward on the upper surface of the head slightly beyond the vertical of the posterior border of the orbit, the posterior margin of the spinous area forming a blunt angle at the mid-line of the body. Spines extending in a single palisade-like series about the orbit, except posteriorly where there is a slight elevated rim free of spines, and superiorly where there is a slight gap for the supraorbital tentacle; anterior orbital spines strongest. Interorbital space concave, its central portion free of spines. Supraorbital tentacle multifid, tree-like, with a number of major trunks and branches from which extend smaller ones, the height of one of the larger from its tip to the base of the tentacle, slightly greater than an eye diameter. Nasal tentacle of right side with a single-based bifid tentacle, that of the left side single-based but quadrifid distally, the tentacles about equal to an eye diameter in length. A group of pores extending slightly below and along posterior border of the eye; a series of 8 pores along the posterior border of the preopercle and on to the underside of the posterior portion of



the mandible; 3 pores, forming a triangle, at the nape immediately before the dorsal fin, and 4 pores on each side of the upper body above the preopercle and opercle. Branchiostegal membranes joined to each other but free from the isthmus, the rays extending upward beyond the opercular tip to form a small hook.

Dorsal fin beginning above the center of the preopercle, the tips of both rays and spines thickened; the fin connected by membrane to the caudal peduncle but not to the caudal fin. Anal fin originating under the 13th dorsal ray, similar to dorsal but its rays shorter and slightly heavier, the fin similarly joined to the caudal peduncle. Pectoral fin with tips of lower rays thickened. Pelvic fins originating before the pectoral, composed of 3 simple rays, the central ray longest, the inner ray shortest. Caudal fin rounded.

*Teeth*: Upper jaw with a single row of strong, conical, inwardly curved teeth, the teeth strongest anteriorly and much smaller along side of jaw; inside of this row anteriorly is a band of small conical teeth. Palatines with 2 rows of strong teeth. Vomer with about 5 strong teeth on each side.

Lower jaw expanded and flattened anteriorly, then constricted and expanded again posteriorly, the jaw, when viewed from above, shaped like an old-fashioned keyhole, or as suggested by Myers and Reid in their description of *Acanthemblemaria hancocki*, like the jaw of *Hippopotamus*. Lower jaw with a single series of flattened strong, conical teeth, paralleling which exteriorly, on the posterior half of the jaw, is a second row of somewhat similar teeth. Anteriorly behind the single strong series is a band of very small conical teeth.

*Color*: In life, general color of body brownish-tan, darker above; sides with small subcircular and oval spots of scarlet-red, these becoming dull brown superiorly. Head yellowish laterally and below, dull reddish-orange above and with a large oval patch of vinaceous-buff on the preopercle, this patch surrounded anteriorly, superiorly and posteriorly by a narrow blackish margin. Opercle with a small blackish patch near its posterior margin. Pectoral and pelvic fins with greenish-yellow rays. Vertical fins brownish-pink, the rays and spines pinkish. Caudal fin, rays of the dorsal fin and posterior rays of the anal with pinkish-red spots along the rays. Anterior portion of dorsal with a dull brown median band surmounted by a marginal orange band. Iris brownish-gold.

In preservative the scarlet and orange pigment has disappeared entirely and the specimen may be described as follows: General color pale buff, the entire body covered with minute brown chromatophores, the chromatophores on the sides and lower sides forming the borders of subcircular clear patches (These are the scarlet spots of the life coloration). Above, the chromatophores are more concentrated, forming irregularly-shaped patches which extend onto the base of the dorsal fin. Dorsal fin with brownish blotches, especially anteriorly where a spot of deep brown and black extends down the center of the fin. Anal fin with dark spots toward the outer margin, these especially marked anteriorly. Preopercle with a large ovoid brownish spot, heavily bordered anteriorly, superiorly and posteriorly with darker brown. Opercle mottled with brown.

*Remarks*: The genus *Acanthemblemaria* was previously represented in the eastern Pacific by the recently described *Acanthemblemaria hancocki* Myers and Reid 1936<sup>3</sup>, taken at Secas Island, Pacific coast of western Panama. The U. S. National Museum has kindly allowed us to have one of the paratypes of *hancocki* for examination. Comparison of the single specimen of *crockeri* with the original description of *hancocki* and the paratype of the latter has enabled us to draw up the following key to show the differences between the two species.

<sup>3</sup> Myers, G. S. and Reid, E. D., *University of Southern California Publications, The Hancock Pacific Expeditions*, Vol. 2, No. 2, pp. 7-9.

## KEY TO EASTERN PACIFIC SPECIES OF ACANTHEMBLEMARIA.

- A. Dorsal fin XXII to XXIII, 13 to 14; anal fin II, 24 to 25; spines of head relatively small and fine; supraorbital tentacle simple; head with a dark area like a large, hour-glass shaped saddle set transversely across the occiput and extending down on opercles to opposite lower rim of the eye; no oval, black-margined brown patch on the preopercle; body, in preservative, pale with conspicuous brown spots .. *hancocki*.
- AA. Dorsal fin XXVI, 13; anal fin II, 27; spines of head coarse and heavy; supraorbital tentacle complex and multifid; no hour-glass shaped dark figure on nape; an oval conspicuous, black-margined brownish spot on preopercle; body, in preservative, with pale spots surrounded with darker ..... *crockeri*.

## EXPLANATION OF THE PLATES.

## PLATE I.

- Fig. 1. *Mobula lucasana*. Dorsal view of freshly caught type specimen. Photograph by Toshio Asaeda.
- Fig. 2. *Mobula lucasana*. Ventral view of freshly caught type specimen. Photograph by Toshio Asaeda.

## PLATE II.

- Fig. 3. *Mobula lucasana*. Under anterior surface of body showing folded cephalic fins, mouth and teeth. The upper jaw teeth show as a dark band just below the margin of the upper jaw. Photograph by Toshio Asaeda.
- Fig. 4. *Mobula lucasana*. View of posterior end of animal from dorsal side, showing the dorsal and pelvic fins and the expanded base of the tail. Photograph by E. Osterndorff.

## PLATE III.

- Fig. 5. *Mobula lucasana*. Photograph of teeth of the lower jaw. Enlarged 33 times. Photograph by Mrs. Ruth Needham Nauss.



FIG. 1.



FIG. 2.

SEVEN NEW MARINE FISHES FROM LOWER CALIFORNIA.





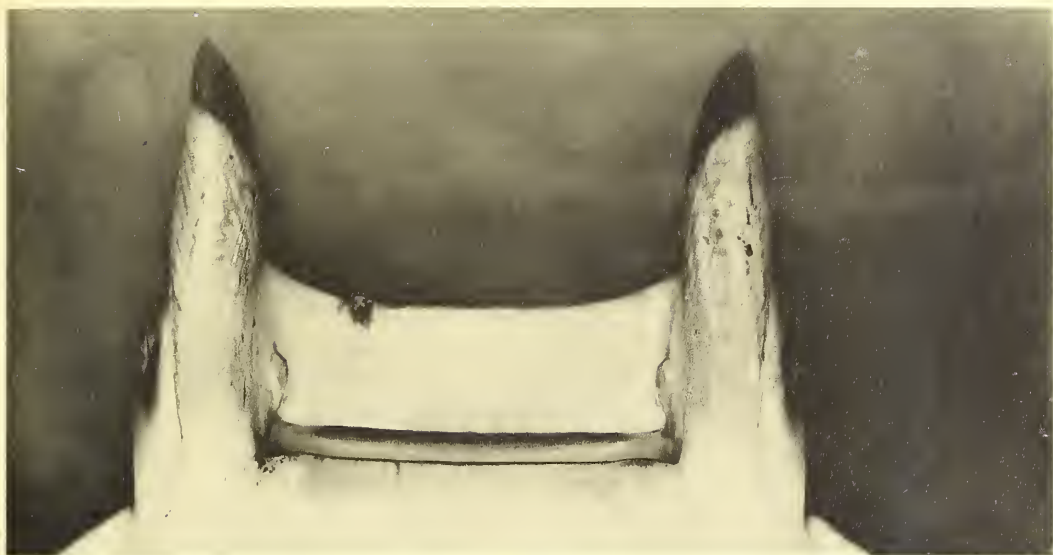


FIG. 3.



FIG. 4.

SEVEN NEW MARINE FISHES FROM LOWER CALIFORNIA.





FIG. 5.

SEVEN NEW MARINE FISHES FROM LOWER CALIFORNIA.





## 16.

Deep-sea Fishes of the Bermuda Oceanographic Expeditions.  
Family Anguillidae.<sup>1</sup>

A. VEDEL TÅNING

Copenhagen, Denmark.

(Text-figure 1).

Dr. William Beebe has kindly entrusted to me the collection of leptocephalus stages of the European and American eels made off Bermuda during the years 1929-1931. As rather few eel larvae have been collected in the deep water very close to Bermuda, it was of interest to me to see this material procured during 1,350 hauls off Nonsuch Island.<sup>2</sup> The specimens are preserved in alcohol and are accordingly probably shrunk about 2 mm. as compared with specimens preserved in formalin.

The collection is small, comprising only 46 specimens, of which 29 belong to the European eel and 17 to the American eel. The specimens were collected during the months of May through September, none being taken in April and none in October or November when relatively few hauls were made.

Moreover, rather few hauls were carried out in the water layers in which we should expect most of these larvae, that is, in subsurface water in depths between 25 and 200 fathoms. Only about 60 hauls were made in these upper layers from May through September, as against about 1,100 in deeper water layers.

The eel larvae are, according to Johannes Schmidt's experiences, most frequently taken during night hauls and of these comparatively very few were made during the Nonsuch investigations. In the collection only three specimens of *Anguilla anguilla* were caught during night hauls.

The facts mentioned explain why so few eel larvae have been caught, and we may moreover emphasize that the small net commonly used (1-metre net) is not the best implement for the capture of eel larvae of a length greater than about 40 mm., as these are rather rapid stages which easily escape the net. This is especially the case with larval stages of the American eel, of which some in the collection are approaching the metamorphosis-stage; during the latter period they become very strong and rapid in their movements.

In regard to literature on the subject, I refer the reader to Schmidt's various publications mentioned in the Bibliography.

In the accompanying Tables I give various particulars concerning the material, such as myomere counts. A few show the total number of 112 and 113 myomeres, and as an overlapping in numbers may occur in the two

<sup>1</sup> Contribution No. 562, Department of Tropical Research, New York Zoological Society. Contribution, Bermuda Biological Station for Research, Inc.

<sup>2</sup> For detailed data in regard to nets, locality, dates, etc., refer to *Zoologica*, Vol. XIII, Nos. 1, 2 and 3.

species, it could be assumed that the identification is not quite certain. Since, however, the pre- and postanal number of myomeres and the blood vessels furnish some help in the identification and since the size of the larvae and the season of capture give further help, I am rather certain that the few specimens showing the number of myomeres mentioned are referred to the proper species.

Tables I and II show the sizes during the different months.

TABLE I.

TABLE II.

<i>Anguilla anguilla</i>						<i>Anguilla rostrata</i>					
Length mm.	May	June	July	Aug.	Sept.		May	June	July	Aug.	Sept.
53										1	1
52										1	
51										1	2
50	1										1
49						I-group					
48		1								1	1
47			1							1	1
46		1								1	1
45		1		1						1	1
44					1	I-group					
43	2	1							1		
42											
41		1			1					1	
40											
39						I-group			1		
38											
37		1	1								
36			1	1							
35				3							
34				1	1	0-group					
33		1									
32		1									
31											
30			1								
29						0-group					
28			1								
27		2									
..											
18			1								
Total	3	10	7	6	3				2	6	9

The larval stages belonging to the European eel (*Anguilla anguilla*) are easily referred to the year's brood (O-group) and the previous year's brood (I-group); probably a few of a length of about 36-37 mm. in June and July and a single one of 41 mm. in September should actually be referred to respectively the I-group and the O-group, but this is of minor importance.

It is well known that during the movement of the larval stages a few may be behind the main stock moving toward Europe and remain as the

I-group for some time in the western Atlantic; the 13 specimens measuring between about 41 and 50 mm. taken from May to September belong to this slow-moving (and late spawned) part of the I-group.

On the other hand, the 16 smaller specimens, between 18 and 37 mm. long, taken from June to September, belong most probably to the faster-moving (and early spawned) part of the O-group which have already reached the vicinity of the Bermudas in June.

In considering now Table II, which shows the lengths of larval stages of the American eel (*Anguilla rostrata*) taken during the months mentioned, it is immediately obvious that these arrive in the Bermuda area later, in July and August, and are of larger size than those of the O-group of the European eel; this is quite in agreement with the fact that the breeding place of the American eel is situated more to the southwest than that of the other species, and that the spawning takes place earlier in the year.<sup>3</sup> According to Schmidt, metamorphosis takes place at a length of 60 to 65 mm. in the American eel. As is well known, the Bermuda fresh water eel is the American, not the European species. In regard to this, see William Beebe and John Tee-Van, "American Fresh-water Eels in Bermuda," *Bull. N. Y. Zool. Soc.*, Vol. XXXVII, 1934, pp. 181-183, and Johs. Schmidt, 1909, pp. 17-18.

The following table (Table III) gives a review of the actual number of larval stages taken in the different months and the number per 100 hauls. It is obvious that the European species is most common from June to August, and the American only during August and September. Actually, however, we know but very little concerning conditions during the months from October to April, and it would certainly be most interesting to get investigations also carried out during these months.

TABLE III.

	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Total
Total No. of hauls 1929-31.....	63	214	260	236	192	362	15	8	1,350
No. of <i>Anguilla anguilla</i> ....	0	3	10	7	6	3	0	0	29
No. per 100 hauls.....	..	1.4	3.8	2.9	3.1	0.8	..	..	2.2
No. of <i>Anguilla rostrata</i> .....	0	0	0	2	6	9	0	0	17
No. per 100 hauls.....	..	..	..	0.8	3.1	2.5	..	..	1.2

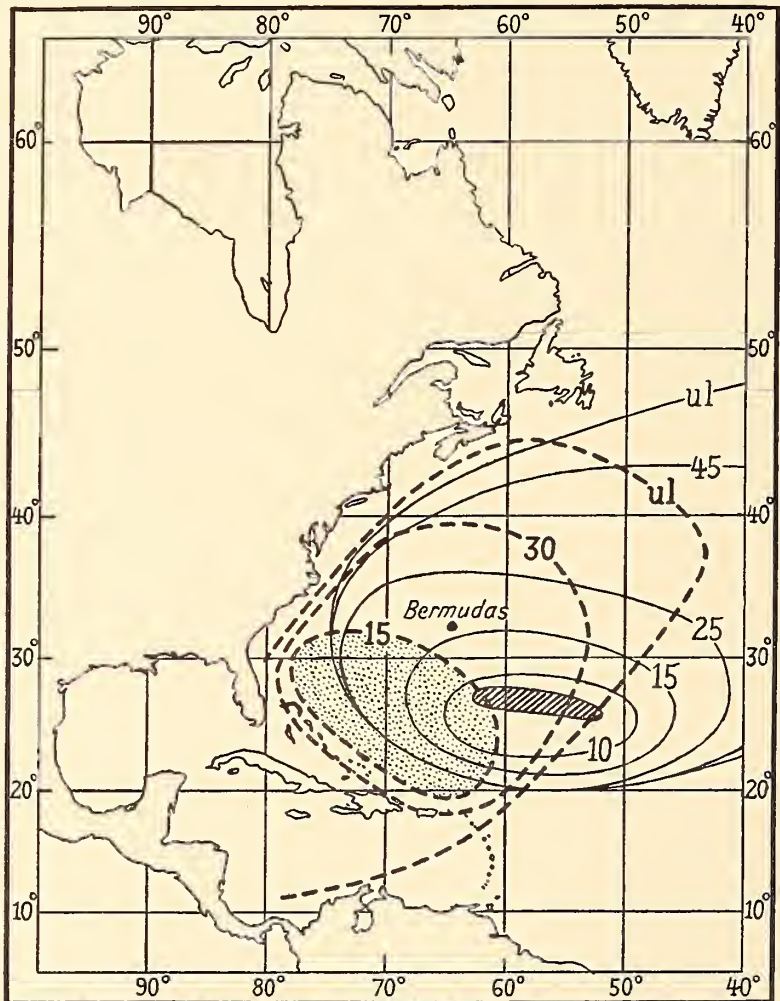
As in other areas of the Sargasso Sea the number of larval stages of *Anguilla anguilla* surpasses that of *A. rostrata*.

As to the relative frequencies in the different months and in different depths, the following table (Table IV) gives a clear review, showing that the larval stages of the European eel are by far the most common in the

<sup>3</sup> It is unlikely that the American eel spawns so close to Bermuda that eggs and young larvae could be met with there; at any rate post-larval stages smaller than 15 mm. have not yet been captured near Bermuda. Johannes Schmidt has previously (*The Danish "Dana" Expeditions 1920-22*, No. 1, p. 16, footnote, 1929) pointed out that the eggs without oil globule described by M. P. Fish (*Zoologica*, Vol. VIII, No. 5, p. 289 ff.) cannot be eggs of *Anguilla rostrata*. I have myself hatched eggs of the same or a very similar type and I am most inclined to refer the eggs in question to the Muraenoid species of which the larval stage is known as *Leptocephalus similis*. The information obtained by the 1,350 hauls made by Dr. Beebe off Bermuda supports the view that *Anguilla rostrata* propagates at a considerable distance from these islands.



subsurface waters off Bermuda from May through July, very few occurring in the deeper strata, where, however, the larval stages of the American eel are most commonly taken during August and September, owing probably also to the fact that the fishing during daytime in the lighter subsurface layers of the water is not able to catch the rapid stages of these larger sizes of American eel larvæ.



Text-figure 1.

Distribution in the western Atlantic of the different larval stages of the European and American eel. **Unbroken line** = European eel. **Broken line** = American eel. **Curves** show limits of occurrence: e.g., larvae less than 10 mm. have only been found inside the 10 mm. curve, etc. **ul**: curve showing limit of occurrence of unmetamorphosed larvae. **Striated area**: only place where the newly hatched larvae (5-7 mm. long) of the European eel have been recorded. American eel larvae less than 15 mm. have never been taken outside the **dotted area**; the actual spawning place inside the dotted area is, however, not yet known. (Redrawn from Schmidt, 1935).



TABLE IV.

Depth		Total No. of hauls		<i>A. anguilla</i>				<i>A. rostrata</i>			
Fathoms	Metres	May-July	Aug.-Sept.	May-July		Aug. Sept.		May-July		Aug.-Sept.	
				No.	No. per 100 hauls	No.	No. per 100 hauls	No.	No. per 100 hauls	No.	No. per 100 hauls
25-200	c.45-370	43	20	11	25.6	1	5.0	0	0.0	0	0.0
> 300	> c.550	606	506	9	1.5	8	1.6	2	0.3	15	3.0

Though the material to hand is very small it gives some valuable information as to the occurrence of the larval stages of the two species of fresh-water eels off Bermuda, and I wish to emphasize that the area is obviously very interesting for studies on the rate of growth and movement of the eel larvæ. Further studies would certainly give us much information which otherwise will be difficult to obtain. A glance at the small map (Text-fig. 1) will show immediately how excellent the position of Bermuda is for these studies.

I take this opportunity of thanking Miss Esther Hansen for valuable assistance.

#### STUDY MATERIAL.

The following list gives the catalogue number, net, depth in fathoms, date, length and myomere count of each *Anguilla leptcephalus* taken by the Bermuda Oceanographic Expeditions. All were caught in the cylinder of water off the Bermuda coast described in *Zoologica*, Vol. XVI, No. 1, p. 5.

#### *Anguilla anguilla.*

No. 9,858; Net 85; 200 fathoms; May 5, 1929; 50 mm.; 72+46 (118) myom.  
 No. 9,895; Net 90; 200 fathoms; May 11, 1929; 43 mm.; 70+45 (115) myom.  
 No. 9,895a; Net 90; 200 fathoms; May 11, 1929; 43 mm.; 68+48 (116) myom.  
 No. 11,046; Net 227; 800 fathoms; June 27, 1929; 32 mm.; 73+44 (117) myom.  
 No. 11,075; Net 229; 1,000 fathoms; June 27, 1929; 43.5 mm.; 71+42 (113) myom.  
 No. 11,184; Net 245; 800 fathoms; July 1, 1929; 30.5 mm.; 73+40 (113) myom.  
 No. 11,707; Net 313; 800 fathoms; July 22, 1929; 47.5 mm.; 73+43 (116) myom.  
 No. 11,772; Net 320; 1,000 fathoms; July 23, 1929; 37 mm.; 70+44 (114) myom.  
 No. 11,819; Net 326; 1,000 fathoms; July 24, 1929; 36.5 mm.; 71+45 (116) myom.  
 No. 15,625; Net 657; 700 fathoms; June 2, 1930; 27 mm.; 74+41 (115) myom.  
 No. 15,746; Net 683; 900 fathoms; June 7, 1930; 37.5 mm.; 71+44 (115) myom.  
 No. 17,789; Net 839; 700 fathoms; Sept. 3, 1930; 41 mm.; 70+44 (114) myom.  
 No. 18,351; Net 870; 100 fathoms; Sept. 11, 1930; 34.5 mm.; 68+44 (112) myom.  
 No. 18,386; Net 874; 500 fathoms; Sept. 11, 1930; 44 mm.; 69+46 (115) myom.  
 No. 20,985; Net 1035; 100 fathoms; June 25, 1931; 27.5 mm.; 70+43 (113) myom.  
 No. 20,985a; Net 1035; 100 fathoms; June 25, 1931; 33 mm.; 69+44 (113) myom.  
 No. 21,020; Net 1042; 100 fathoms; June 26, 1931; 45 mm.; 70+46 (116) myom.  
 No. 21,020a; Net 1042; 100 fathoms; June 26, 1931; 41 mm.; 70+45 (115) myom.  
 No. 21,043; Net 1047; 100 fathoms; June 27, 1931; 48 mm.; 71+45 (116) myom.  
 No. 21,043a; Net 1047; 100 fathoms; June 27, 1931; 46 mm.; 71+46 (117) myom.  
 No. 21,152; Net 1058; 300 fathoms; July 7, 1931; ca. 18 mm.; 66+47+ (113+) myom.  
 No. 21,342; Net 1080; 100 fathoms; July 14, 1931; 44.5 mm.; 71+46 (117) myom.

- No. 21,342a; Net 1080; 100 fathoms; July 14, 1931; 28 mm.; 73+ca. 43 (ca. 116) myom.  
 No. 21,858; Net 1129; 1,000 fathoms; Aug. 4, 1931; 34 mm.; 72+43 (115) myom.  
 No. 22,233; Net 1166; 900 fathoms; Aug. 11, 1931; 45.5 mm.; 72+46 (118) myom.  
 No. 22,409; Net 1184; 800 fathoms; Aug. 15, 1931; 35 mm.; 73+44 (117) myom.  
 No. 22,760; Net 1192; 1,000 fathoms; Aug. 17, 1931; 36 mm.; 72+44 (116) myom.  
 No. 22,934; Net 1244; 800 fathoms; Aug. 31, 1931; 35.5 mm.; 70+49 (119) myom.  
 No. 22,905; Net 1245; 1,000 fathoms; Aug. 31, 1931; 35 mm.; 73+43 (116) myom.

*Anguilla rostrata.*

- No. 11,650; Net 305; 600 fathoms; July 16, 1929; 43.5 mm.; 68+39 (107) myom.  
 No. 11,722; Net 314; 900 fathoms; July 22, 1929; 39.5 mm.; 67+39 (106) myom.  
 No. 12,877; Net 406; 800 fathoms; Sept. 2, 1929; 51 mm.; 69+39 (108) myom.  
 No. 13,125; Net 427; 900 fathoms; Sept. 5, 1929; 48 mm.; 68+40 (108) myom.  
 No. 13,193; Net 435; 1,000 fathoms; Sept. 6, 1929; 51.5 mm.; 71+38 (109) myom.  
 No. 13,343; Net 449; 1,000 fathoms; Sept. 9, 1929; 53 mm.; 71+39 (110) myom.  
 No. 17,759; Net 835; 500 fathoms; Sept. 3, 1930; 49.5 mm.; 70+38 (108) myom.  
 No. 18,029; Net 856; 800 fathoms; Sept. 6, 1930; 47.5 mm.; 69+39 (108) myom.  
 No. 18,098; Net 862; 800 fathoms; Sept. 8, 1930; 50 mm.; 69+40 (109) myom.  
 No. 18,549; Net 881; 600 fathoms; Sept. 12, 1930; 45 mm.; 69+38 (107) myom.  
 No. 18,496; Net 883; 700 fathoms; Sept. 13, 1930; 46.5 mm.; 68+38 (106) myom.  
 No. 22,305; Net 1169; 700 fathoms; Aug. 12, 1931; 51 mm.; 67+39 (106) myom.  
 No. 22,306; Net 1172; 1,000 fathoms; Aug. 12, 1931; 53 mm.; 70+39 (109) myom.  
 No. 22,667; Net 1209; 1,000 fathoms; Aug. 20, 1931; 41 mm.; 69+38 (107) myom.  
 No. 23,039; Net 1217; 600 fathoms; Aug. 24, 1931; 48 mm.; 70+39 (109) myom.  
 No. 23,040; Net 1240; 1,000 fathoms; Aug. 29, 1931; 45 mm.; 70+38 (108) myom.  
 No. 23,707; Net 1325; 500 fathoms; Sept. 19, 1931; 52 mm.; 70+39 (109) myom.

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## 17.

## The Phylogeny of the Characin Fishes.

WILLIAM K. GREGORY &amp; G. MILES CONRAD

*The American Museum of Natural History*

(Text-figures 1-37).

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## INTRODUCTION.

In the systematic history of the family Characidae, among the greatest contributors were Müller and Troschel (1844, +), Sagemehl (1884, +), Boulenger (1887, +), Eigenmann (1899, +), Rowntree (1903, 1906), and Regan (1911, +). In spite of all of these labors the broad evolutionary trends were so easily obscured by the details that it was only in 1917, with the publication by Eigenmann of the first part of his monograph on "The American Characidae," that the first attempt to outline the phylogenetic relationships of all of the South American subfamilies was made (Text-fig. 5). Unfortunately this outline from which we have made a phylogenetic diagram was never completely developed, for Dr. Eigenmann died before the completion of his memoir on the Tetragonopterinae and allied subfamilies.

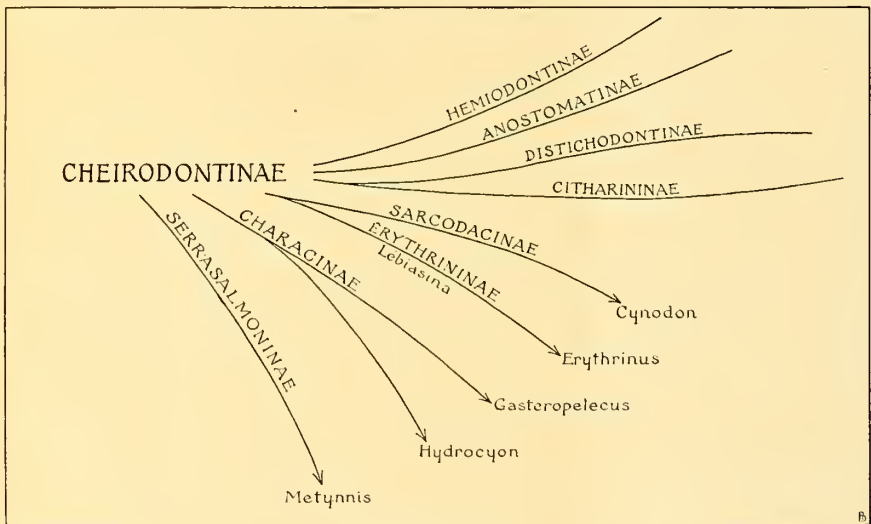
Rowntree (1903) examined the visceral anatomy of the characins and made several contributions of phylogenetic interest, including evidence against the idea of an amioid ancestry of the Erythrininae which had been suggested by Sagemehl. Much of the data concerning the visceral anatomy merely shows the differences in adaptation to an herbivorous diet on the one

DEC 30 1938

hand and a carnivorous diet on the other. Thus the differences and similarities noted in the stomach and intestine have little phylogenetic significance of subfamily rank, inasmuch as the herbivorous condition has apparently been developed independently several times within the family.

In 1911 Regan revised the classification of the Characinae and in so doing synthesized the groups of previous authors to a more workable system. However, in many respects the classification of Boulenger in the Cambridge Natural History is still useful.

Cockerell (1912, 1913) studied the scales of both the African and South American characins. His studies were very detailed and in some cases his results are confusing when compared with other data, but on the whole they served to clarify the phylogenetic relationships within certain groups.



Text-figure 1.

The phylogenetic relationships of the subfamilies of the Characidae.

The fossil records of this group are very meagre. From the Tertiary of Brazil and Peru three more or less doubtful genera are known: *Lignobrycon*<sup>1</sup> Eigenmann and Myers 1929, *Eobrycon*<sup>2</sup> Jordan 1907, *Characilepis* Cockerell 1920. These are apparently related to the Characinae. The teeth known as *Onchosaurus* Gervais 1852, which are found in the Upper Cretaceous of North America, Europe and Egypt, have been shown by Eastman (1917) to resemble the teeth of *Hydrocyon* and *Hoplias*. However, neither in general body form nor in tooth structure are any of these genera primitive and we must, therefore, with Eigenmann, fall back upon an analysis of the generalized conditions among living characins as the principal basis for a tentative reconstruction of phylogenetic history.

As a basis for our chart (Text-fig. 1) of the phylogenetic relationships of the family Characinae we have used first the monumental work, "The American Characidae," by C. H. Eigenmann, as well as many lesser papers by the same author. Nor have we neglected the important systematic and distributional studies of Regan, Boulenger and others. Our own material includes a series of skeletal and preserved specimens representing the vari-
































<sup>1</sup> Based on *Tetragonopterus ligniticus* Woodward, Catalogue of Fossil Fishes in the British Museum (Natural History), 1901, pt. 4, p. 298, pl. 17, figs. 2, 3.

<sup>2</sup> Based on *Tetragonopterus avus* Woodward, *ibid.*, p. 298, pl. 17, fig. 1.





# PICTORIAL CLASSIFICATION OF THE CHARACINS

CHEIRODONTINAE	SERRASALMONINAE	CHARACINAE	SARCODACINAE		ANOSTOMATINAE	DISTICHODONTINAE
<i>AMERICAN</i>  Cheirodon  Moenkhausia  Tetragonopterus	<i>AMERICAN</i>  Serrasalmo  Myletes  Stethaprion  Starksina  Metynnis	<i>AMERICAN</i>  Brycon  Diapoma  Corynopoma  Chalcinus  Gasteropelecus <i>AFRICAN</i>  Alestes  Hydrocyon	<p>-----</p> <i>AFRICAN</i>  Sarcodaces <i>AMERICAN</i>  Acestrorhynchus  Luciocharax  Cynodon		<i>AMERICAN</i>  Chilodus  Anostomus  Prochilodus  Curimatus	<i>AFRICAN</i>  Distichodus  Paraphago  Ichthyoborus  Phago
					CITHARININAE	
					<i>AFRICAN</i>  Citharinus	
					HEMIODONTINAE	
					<i>AMERICAN</i>  Poecilobrycon	
			ERYTHRININAE			
			<i>AMERICAN</i>  Erythrinus  Lebiasina			

Text-figure 2.  
A pictorial classification of the characin fishes.



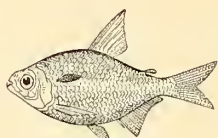
# PICTORIAL ACINS

## CHEIRODONTINAE

### AMERICAN



Cheirodon



Moenkhausia



Tetragonopterus

## SERRASALISTICHODONTINAE

### AMERICAN



Serranodon



Myxodon



Stethacanth



Stenacanth



Metacanth

### AFRICAN



Distichodus



Paraphago



Ichthyoborus



Phago



ous subfamilies; especially those brought back by Messrs. Lang and Chapin of the American Museum Congo Expedition of 1909-1915, and the Brazilian collections made by B. A. Krukoff in 1934 and 1935.
































As an aid to the construction of a tentative phylogenetic chart we have arranged a "Pictorial Classification of the Characins" (Text-fig. 2). This is based on a phylogenetic interpretation of the characters used in defining families, subfamilies, etc., by various authors. In view of the remarkable uniformity in basic morphology of all characins and of the existence of more or less annectant genera between the so-called families of earlier authors we have treated the entire series as a single family, Characinidae, coordinate in rank with the Gymnotidae, the latter being an extremely specialized and presumably early side branch.

To supplement the chart showing the inferred phylogenetic relationships of the general body forms we have added several other charts laid out on the same plan. First of these is a series of scales as figured by Cockerell (1912, 1913). Although Cockerell figured the circuli and radii of the scales, we have contented ourselves with the outlines (Text-fig. 3) which, by themselves, seem to present the several broad divergent trends within the family.

A series of diagrams of characin livers has been compiled from Rowntree's data. These drawings (Text-fig. 4) are quite schematic and are merely diagrams from verbal descriptions, but they afford an interesting contrast to the more or less stable characters relied on in the above charts. Whether the viscera, always in a more or less plastic state, have any really helpful significance in these studies is open to question except in certain cases, but it is noteworthy that in several places interrelationships are evident.




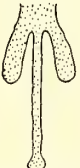










For convenience we insert at this point a summary of the subfamilies of the characins, as used in the present paper.

1. Cheirodontinae (Cheirodontinae and Tetragonopterinae of Eigenmann). Primitive, generalized characins; both maxilla and premaxilla bearing teeth; marginal teeth varying from pluricuspid to conical; mouth moderate to small. American: *Grundulus*, *Mizobrycon*, *Moenkhausia* (Text-figs. 2, 8), *Tetragonopterus* (Text-figs. 2, 7, 8), *Cheirodon* (Text-figs. 2, 6, 8), etc.
2. Serrasalmoninae (Stethaprioninae, Serrasalminae and Mylinae of Eigenmann). Extremely deep bodied; short, heavy jawed offshoots of *Tetragonopterus*. Nicely graded series of constantly increasing ratios of depth to length. Teeth grade from carnassial to molariform. American: *Stethaprion* (Text-fig. 2), *Mylesinus*, *Serrasalmo* (Text-fig. 2), *Mylosoma* (Text-figs. 7B, 8), *Metynnis* (Text-fig. 2), etc.
3. Characinae (Characinae (in part), Hydrocyoninae and Gasteropelecidae of Regan). The large central group of African and South American forms arising from the Cheirodontinae. Varying in body-form, but central type as in *Brycon*; hyporacoids usually forming prominent vertical laminae, but grading into forms with short median laminae and divergent coracoid fossae (*Cynopotamus*); lateral line decurved; no teeth on palatines. American: *Charax*, *Brycon* (Text-figs. 2, 9, 11, 12, 14, 16, 30), *Iguanodectes*, *Diapoma* (Text-fig. 2), *Corynopoma* (Text-fig. 2), *Chalcinus* (Text-figs. 2, 13, 14), *Gasteropelecus* (Text-figs. 2, 13, 14). African: *Alestes* (Text-figs. 2, 10, 15), *Hydrocyon* (Text-figs. 2, 11, 12, 17, 18, 19, 20, 21, 29).
4. Sarcodacinae (Sarcodacinae, Acestrorhamphinae, Cynodontinae and Xiphostomatidae of Regan). Predatory "pikes" derived from the Characinae. Jaws more or less elongate with caniniform teeth; a large prefrontal plus supraorbital bone; supraoccipital small, not elevated above flattened skull top; no interfrontal fontanelle. Ameri-

CHEIRODONTINAE	CHARACINAE	SARCODACINAE	ANOSTOMATINAE	DISTICHODONTINAE
AMERICAN	AMERICAN		AMERICAN	AFRICAN
 Cheirodon	 Charax		 Leporinus	 Eugnathichthys
 Hemigrammus	 Brycon		 Chilodus	 Distichodus
 Astyanax	 Creatochanes	AMERICAN	 Curimatus	
 Tetragonopterus	 Chalceus	Acestrorhynchus	 Prochilodus	
 Moenkhausia	 Chalcinus	AFRICAN	 Psectrogaster	
 Aphyocharax		Sarcodaces	 Anodus	
SERRASALMONINAE			CITHARININAE	
AMERICAN	AFRICAN		AFRICAN	
 Serrasalmo	 Alestes	ERYTHRININAE	 Citharinus	
	 Bryconaethiops	AMERICAN	 Citharidium	
	 Micralestes	 Hoplerythrinus	 Xenocharax	
	 Petersius	 Hoplias	HEMIODONTINAE	
	 Hydrocyon		AMERICAN	
			 Poecilobrycon	

Text-figure 3.

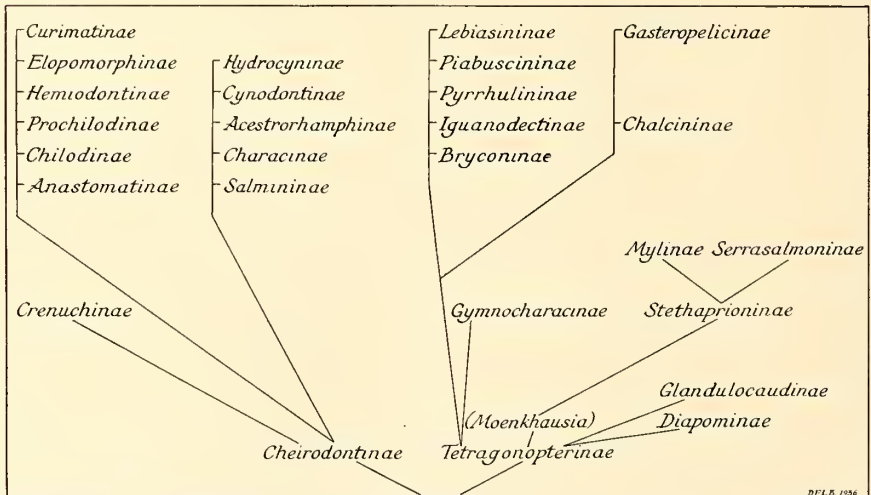
Chief variants in the form of characin scales. Based on data from Cockerell (1912, 1913).

CHEIRODONTINAE	SERRASALMONINAE	CHARACINAE	SARCODACINAE	ANOSTOMATINAE	DISTICHODONTINAE
AMERICAN 	AMERICAN 			AMERICAN 	AFRICAN 
Tetragonopterus argentatus	Serrasalmo			Leporinus	Distichodus
		AFRICAN 	AFRICAN 	Prochilodus	Eugnathichthys
Tetragonopterus fasciatus		Alestes nurse	Sarcodaces	Anostomus	Ichthyoborus
				Curimatus	Phago
		Alestes macrolepidotus			
				CITHARININAE	
		Alestes kotschyi		AFRICAN 	
			ERYTHRININAE	Citharinus	
		Bryconaeithiops	AMERICAN 	Xenocharax	
			Hoplias		
		Hydrocyon			
			Lebiasina		

Text-figure 4.

Chief variants in the form of the liver. Based on Rowntree's (1903) data.

- can: *Luciocharax* (Text-figs. 2, 23, 24), *Acestrorhynchus* (Text-fig. 2). African: *Sarcodaces* (Text-figs. 2, 23, 24).
5. Erythrininae (Erythrininae and Lebiasininae of Regan). *Amia*-like relatives of *Sarcodaces* with more or less broad, rounded heads. Opposite hypocoracoid fossae diverging sharply, median laminae short (*Lebiasina*) to absent; lateral line straight (lacking in *Lebiasina*). Teeth on palatines. American: *Erythrinus* (Text-figs. 2, 25, 26), *Hoplias* (Text-fig. 24), *Lebiasina* (Text-fig. 2).
  6. Hemiodontinae (Hemiodontidae of Regan). Small fusiform to slender offshoots of the Characinae with short anal fin, adipose typically reduced or absent; very small to small subterminal to terminal mouth; teeth uniserial, minute; "pterygoid movably articulated with quadrate, narrowed posteriorly ending in a small condyle" (Regan). American: *Hemiodus*, *Poecilobrycon* (Text-fig. 2), *Nannostomus*, *Parodon*.
  7. Anostomatinae (Anostomidae of Regan). Slender to deep-bodied herbivorous American characins. In scale and jaw characters paralleling some of the Citharininae and Hemiodontinae. "Pterygoid rather broad posteriorly, overlapping the quadrate" (Regan). *Anostomus* (Text-fig. 2), *Prochilodus* (Text-fig. 2), *Chilodus* (Text-fig. 2), *Curimatus* (Text-figs. 2, 28), *Leporinus* (Text-figs. 28, 29, 30, 31, 32).
  8. Citharininae (Citharininae, Hemistichodontinae and Xenocharacinae of Regan). An African group grading in scale characters from cycloid to ctenoid. Parallel in many characters to South American Anostomatinae. *Citharinus* (Text-fig. 2), *Xenocharax*.
  9. Distichodontinae (Distichodontinae and Ichthyoborinae of Regan). This African group seems to be related to the Citharininae, but is sharply separated in that the dentaries are movably articulated with the articulators. *Distichodus* (Text-figs. 2, 33), *Phago* (Text-figs. 2, 35), *Ichthyoborus* (Text-fig. 2), *Mesoborus* (Text-fig. 34), *Paraphago* (Text-fig. 2).



Text-figure 5.

The phylogeny of the South American characins, according to Eigenmann (1917, pp. 38, 39).



## PHYLOGENETIC REVIEW OF PRINCIPAL GROUPS.

## CHEIRODONTINAE.

Several authors, including one of us (Gregory, 1933), have considered the Erythrininae to be the most primitive existing subfamily of the Characinae, but further study indicates that this subfamily is relatively high in the phylogenetic series. After close study of Eigenmann (1916), we are indeed forced to the conclusion that the Erythrininae are less primitive than the Cheirodontinae.

Text-figure 6 represents the skeleton of *Cheirodon*. It closely resembles the generalized cheirodont which Eigenmann has pictured for us in words. It is a relatively deep-bodied type, with a long anal fin having its origin under the last dorsal ray and reaching almost to the origin of the caudal. The caudal is deeply forked. The mouth is terminal and relatively small. The teeth of the generalized type are in a single series, rather few in number and with lateral notches, occurring along the edge of the premaxilla, at the upper angle of the maxillary, and along the front and sides of the lower jaw.

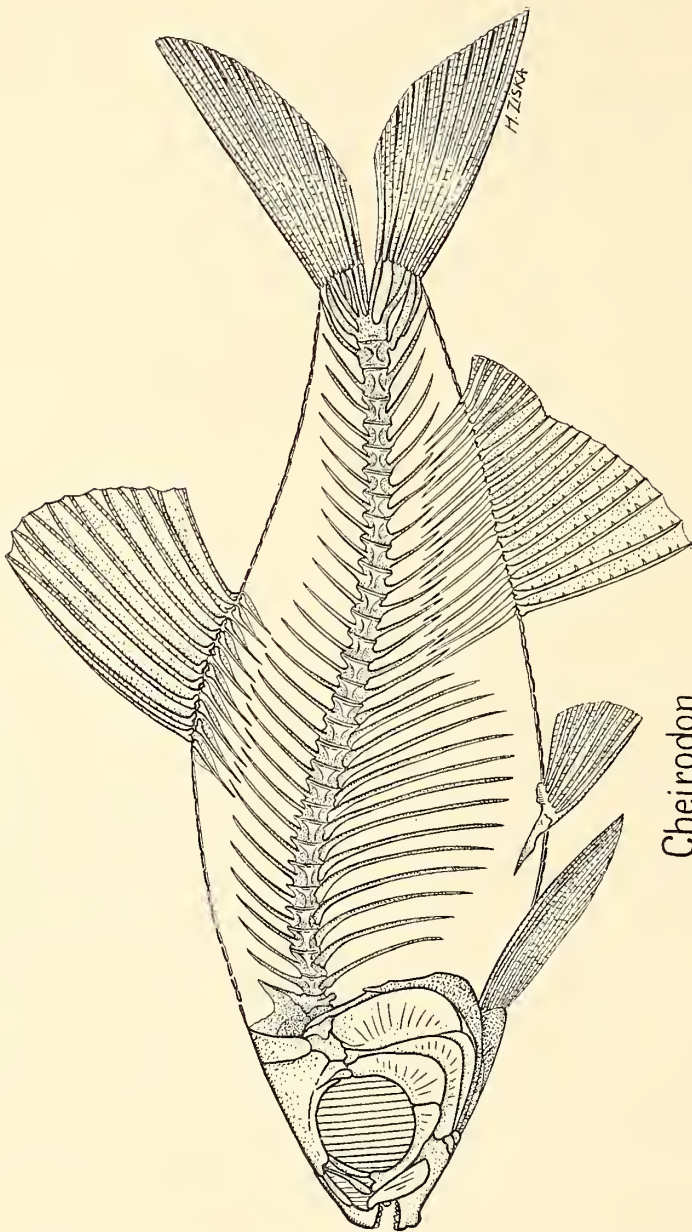
The Cheirodontinae, or some of them, also retain several other outstanding generalized characters from which those of almost any of the remaining subfamilies may have sprung. One of these is the extremely undifferentiated cycloid scales, almost elliptical in shape, from which the others have evidently developed. Another is the greatly variable tooth form, which, as noted by Eigenmann, ranges from the simple conical type of *Grundulus*, through the bicuspid teeth of *Macropsobrycon*, the tricuspid teeth of *Aphyocharax*, *Megalampodus*, *Parecbasis* to the octacuspids of *Cheirodon*. Thus, as far as teeth are concerned, this group is well prepared to account for all of the bizarre tooth-types encountered in the family, such as the caniniform teeth of *Hydrocyon*, the molariform teeth of the Mylinae, the incisor-like teeth of *Leporinus* and many others.

Eigenmann's generalized cheirodont exhibits the well developed chain of suborbital bones which are constantly cropping out in various genera of the Characinae and which apparently first led Sagemehl to the belief that *Erythrinus* had amioid affinities (since wholly disproved by several authors). An adipose fin is present in the generalized type of the Cheirodontinae as well as in most other Characinae. However, the cheirodont genera *Grundulus* and *Spintherobolus* lack one, this indicating that the possession of an adipose is in an unstable condition in even the more primitive characins. Some of the Cheirodontinae also have the median fronto-parietal fontanelle which is so frequent in other subfamilies.

Arising from the Cheirodontinae (*sensu strictu*), then, are the several diverging subfamilies. The Tetragonopterinae of Eigenmann are very near to the primitive stock of the characins and may have been derived from the Cheirodontinae or from a common stem. In either event Eigenmann points out the significant similarity of the heavy teeth and cheek armor in *Mixobrycon* (Cheirodontinae) and that of *Hyphessobrycon* (Tetragonopterinae). A glance at *Moenkhausia* (Text-fig. 2), a tetragonopterine, will show the general similarity of its body form to that of *Cheirodon pulcher*. *Tetragonopterus* proper (Text-fig. 2) is a greatly deepened form which through some species such as *T. argenteus* has given rise ultimately to the extremely deep-bodied and strangely modified Serrasalmoninae.

## SERRASALMONINAE.

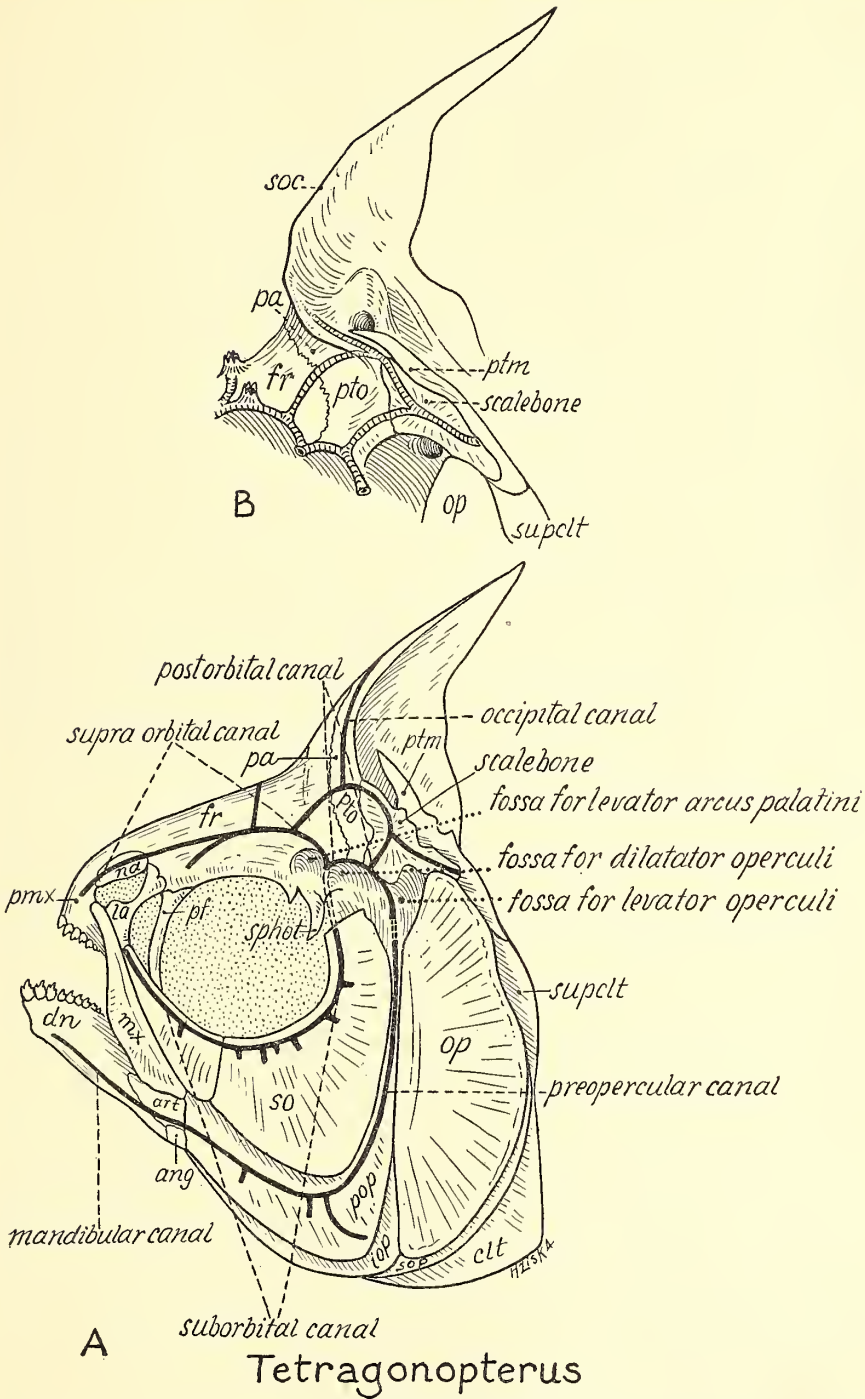
We have seen above that *Tetragonopterus argenteus*, which we refer to the Cheirodontinae, approaches very closely to the body form of the Stethaprioninae and differs from the latter chiefly in the lack of a "pre-dorsal spine" insofar as external gross characters are concerned. Both Cockerell



Cheirodon

Text-figure 6.  
Skeleton of *Cheirodon* ( $\times 4$ ).

(1913) and Eigenmann and Myers (1929) noted the relationship between *Stethaprion* and another cheirodont, *Moenkhausia*, but Eigenmann (1907) states, "the members of the Stethaprioninae mark the direct road from the genus *Tetragonopterus* in its narrowest sense to the Mylinae and Serrasalmoninae. In the deep *T. argenteus* the post-ventral region is trenchant, the pre-ventral region flat. In *Stichonodon* both pre-ventral and post-ventral regions are trenchant. In *Stethaprion*, *Brachyhalcinus*, and *Fowlerina* the post-ventral region is incipiently serrate and there is a pre-dorsal spine.



Text-figure 7.

A, skull of *Tetragonopterus*, showing lateral line canals and principal muscle fossae. B, *Mylosoma*, detail of occipital region, showing canals.



In *Mylesinus* of the Mylinae the abdomen is serrate behind the ventrals and in the rest of the Mylinae and Serrasalmoninae the ventral edge is serrate both in front and behind the ventrals." This series is supported again by Eigenmann and Myers in 1929. On the entire chart of body forms (Text-fig. 2) there is no series so convincing as this one, especially in the constantly increasing ratio of depth to length until finally, in *Metynnis*, the depth almost equals the length. There is a transition from the sharp, shearing, carnassial-like teeth of *Serrasalmo* to the more blunt, molariform teeth of *Myletes*, while the jaws in both remain short and blocky. In liver form (Text-fig. 4) *Serrasalmo* appears to be very generalized.

The skulls of the Cheirodontinae and the Serrasalmoninae are often quite small and paper thin so that in order to facilitate the identification of the bones a detailed study of the sensory canals was made. Text-figure 7, an outline picture of the skull of the typical genus, *Tetragonopterus*, shows the position and names of the canals and the diagnostic muscle fossae.

The lateral line passes from the body into the posttemporal bone and from there it continues into the "scalebone." In the scalebone it forks into two branches, one leading toward the postorbital canal, the other, the occipital canal, passing dorsally through the parietal bone. Just above the scalebone the occipital canal is met by a branch from the supraorbital canal. At the most ventral point of the surface of the pterotic the preopercular canal arises. This preopercular canal runs directly into the mandible. Starting at the origin of the preopercular canal and bordering the fossa of the dilatator operculi is the postorbital canal which continues forward to the junction of the suborbital canal with the main trunk. The suborbital canal joins the main canal at the "peninsula" which marks the separation of the fossa for the levator arcus palatini from that of the dilatator operculi. From this junction forward the sensory canal is known as the supraorbital canal and gives off several branches as it passes through the frontal bone. This canal passes through the nasal bone and, in *Tetragonopterus* at least, seems to continue into the premaxilla.

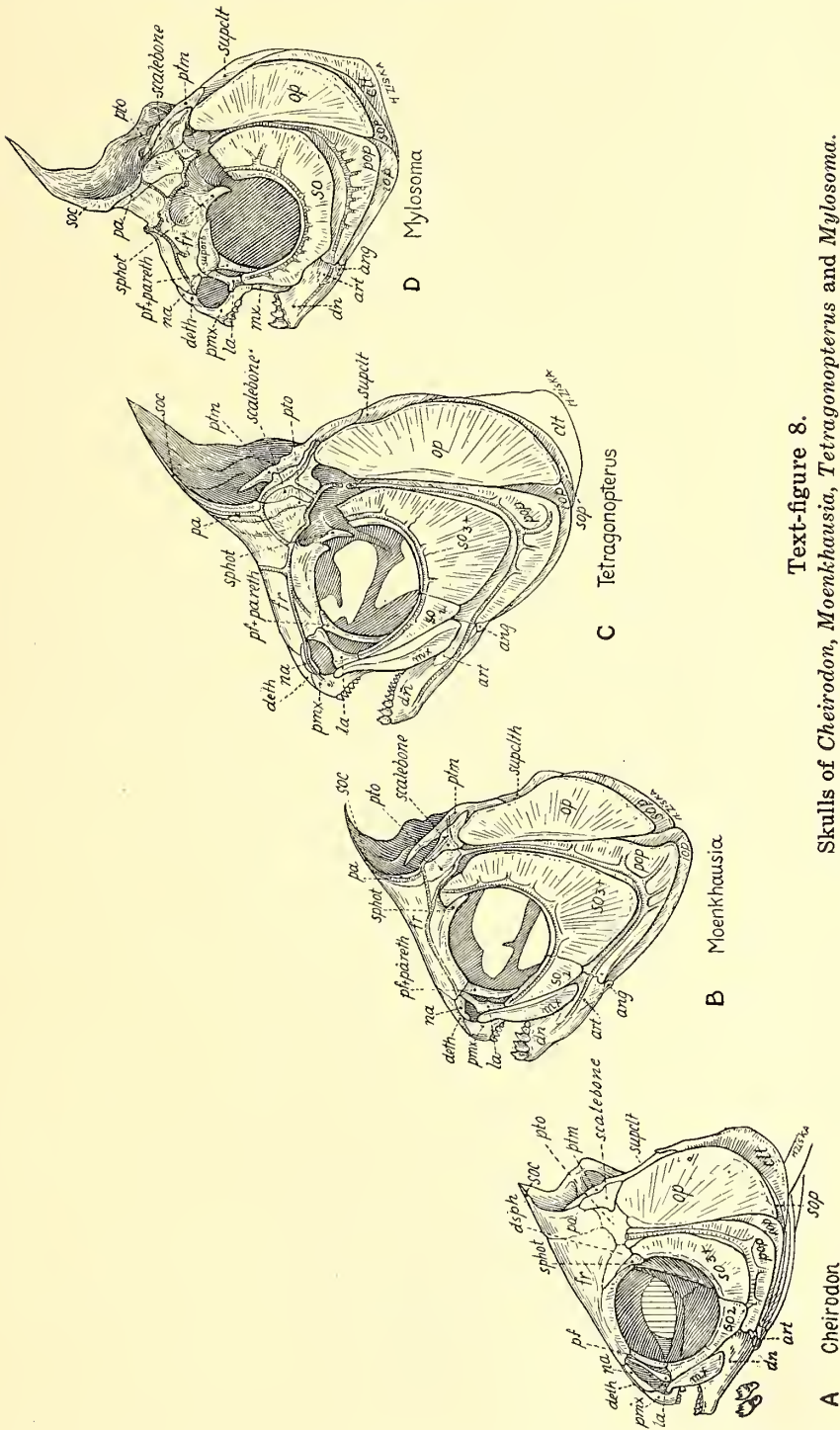
The nicely graded series of body forms which has been noted in the cheirodont-serrasalmonine branch is reflected in the skull structures. *Cheirodon* (Text-fig. 8A) has the skull of a more or less fusiform habitus. The dorsal curvature of the skull is slight and convex and there are sizable parietals, which might imply a lack of the forward curling of the occiput that is seen as we proceed up the scale. The dermosphenotic is present in this primitive form. The jaws are relatively compact and strong and are not elongate.

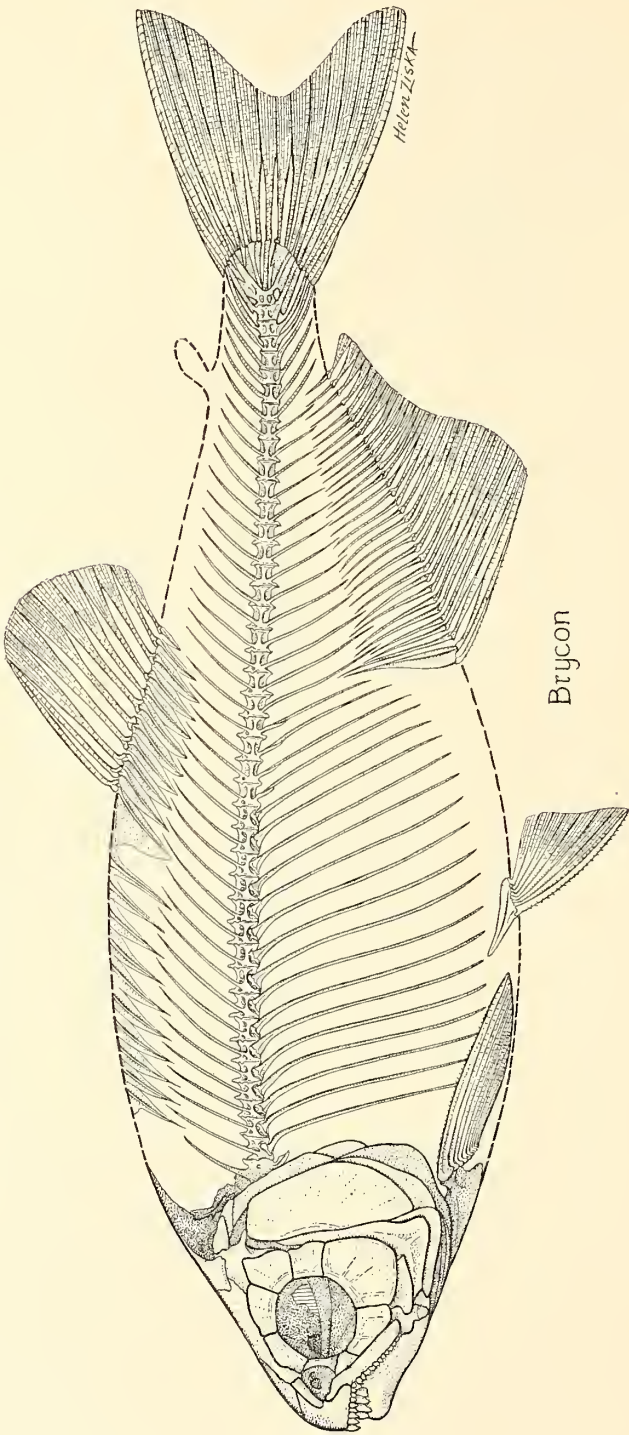
*Moenkhausia* (Text-fig. 8B) reflects the slightly deeper body and the supraoccipital crest is a bit more steep than in *Cheirodon*. Indeed the entire skull shows a dorso-ventral emphasis. The dermosphenotic disappears in *Moenkhausia* and is lost in those latter specimens of this series which we have examined. The parietal and pterotics have been reduced.

The skull of *Tetragonopterus* (Text-fig. 8C) resembles very closely that of *Moenkhausia*. As might be inferred from the progressively increasing body-depth, the supraoccipital bone is so upturned that the frontal is quite concave in side view. The suture between the frontals and the parietals and pterotics is in the form of two acute angled, overlapping bevels. Thus the surface extent of the parietals is a great deal less than the cranial. This suggests a mechanical shoving forward of the temporal region. The postorbital portion of the circumorbital chain has been dissected away so as to show the various muscle fossae as well as the postorbital process of the sphenotic bone.

As a representative of the Serrasalmoninae, *Mylosoma* (Text-fig. 8D) serves admirably. Here is the ultimate in the deep-bodied forms in some of which the depth almost equals the length. It is no wonder, therefore, that the fronto-parieto-supraoccipital contour in side view is so concavo-

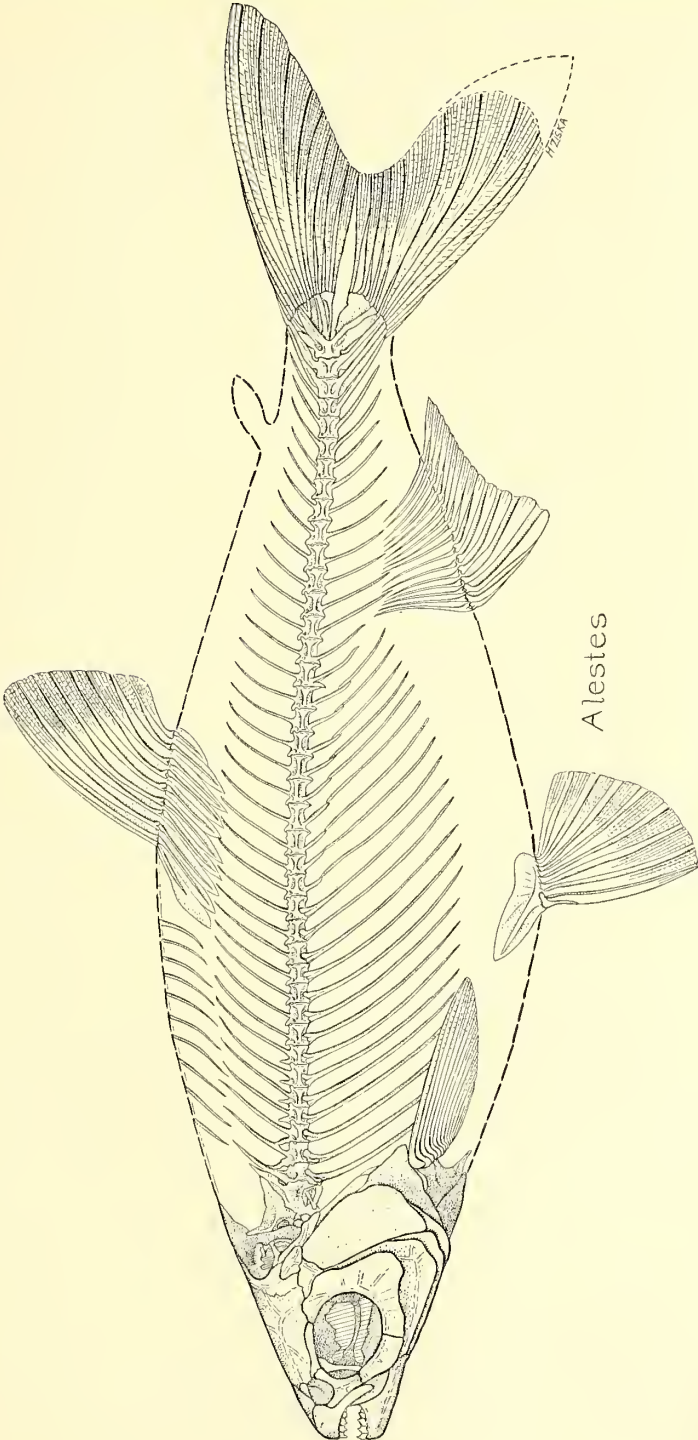






*Brycon*

Text-figure 9.  
Skeleton of *Brycon*.

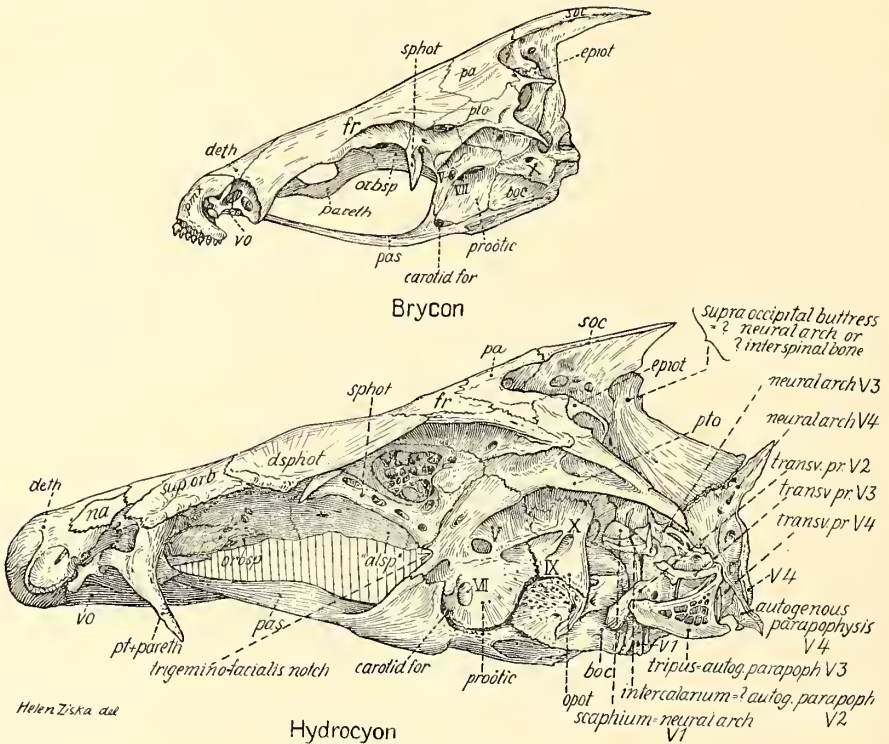


Text-figure 10.  
Skeleton of *Alestes*.



convex as to form a feeble S. In *Tetragonopterus* a perpendicular line passing through the posterior tip of the supraoccipital would also pass close to the rear margin of the operculum, while in *Mylosoma* such a line would pass through the center of the postorbital portion of the circumorbital chain. For the first time in this series a new bone appears, the supra-orbital. The sensory canal system retains the basic plan of Text-fig. 7A, but in response to the necessity of the openings passing through the thick layer of fatty tissue (which cushions the concave part of the skull) there have been developed several bony "craters" which carry the canals to the surface. The word, crater, is really descriptive of them for they look much like a volcanic crater—an eruption of the bone. As another innovation the occipital canal passes behind the crest, which is usually placed at the posterior edge of the parietal. However, in *Mylosoma* this crest has moved forward on the parietal, while the canal presumably maintains its primitive position (see inset, Text-fig. 7B).

The most salient feature of this phylogenetic branch is the constant anterior movement of the occipital region while the rest of the skull remains stationary. The loss of the dermosphenotic and the appearance of the supraorbital are observed. The fontanelles are left intact throughout the group.



Text-figure 11.

Neurocrania of the African *Hydrocyon* and the South American *Brycon*. The first four vertebrae with their attendant Weberian apparatus are included with the skull of *Hydrocyon*. Although the Weberian ossicles and anterior vertebrae have not been added to the skull of *Brycon*, a close similarity in basic plan of the neurocrania is noted in these two members of the Characinae.

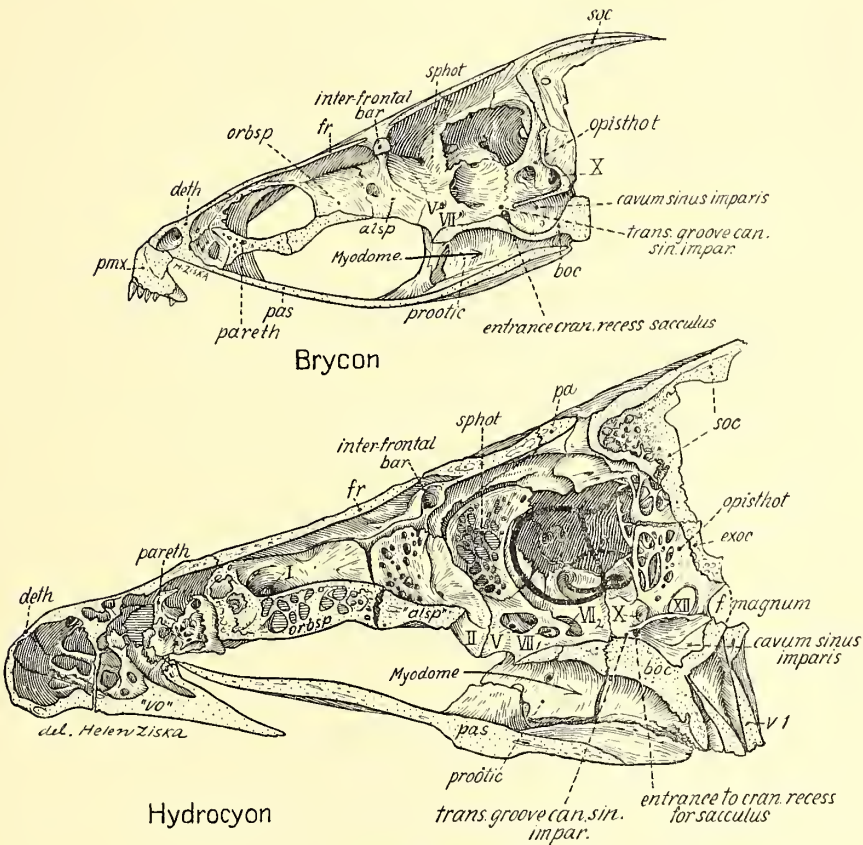


CHARACINAE.

This group is the most extensive of the family, abounding as it does in both South American and African forms which range from the primitive African genus, *Alestes*, to the South American fresh-water flying fish, *Gasteropelecus*. Although the interrelationships of the group are obscure and are in the sense used by Eigenmann (1917) probably polyphyletic, there is little doubt that they are all traceable to the completely primitive Cheirodontinae. The Characinae include on our chart (Text-fig. 2) as representatives of the group, the following genera:

(A) American

*Brycon*  
*Diapoma*  
*Corynopoma*  
*Chalcinus*  
*Gasteropelecus*



Text-figure 12.

Neurocrania of *Hydrocyon* and *Brycon*, longitudinal sections. These sections show even more strikingly the basic similarity of the African and South American genera of Characinae. The heavy black lines in *Hydrocyon* indicate the position of the semicircular canals.

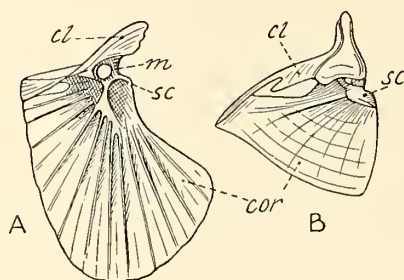


Fig. 13

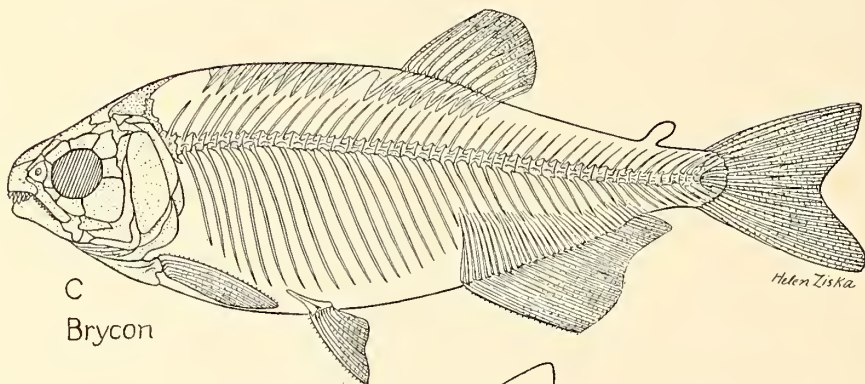
C  
BryconB  
ChalcinusA  
Gasteropelecus

Fig 14

Text-figure 13 (upper).

Cleithrum and primary pectoral arch (except radials) of A. *Gasteropelecus* *pectorosus* and B. *Chalcinus* *trachypomus*. After Regan, 1911.

Text-figure 14 (lower).

Skeletons of *Gasteropelecus*, *Chalcinus* and *Brycon*.

## (B) African

*Alestes*  
*Hydrocyon*

This group may be split into several series, all of which seem to be ultimately derivable from cheirodont beginnings. The African members are closely related to their South American allies in the fundamental pattern of skull structure (Text-figs. 11, 12) as well as in many curious details of body form, scalation, etc.

According to Eigenmann the Glandulocaudinae, here represented by *Diapoma* and *Corynopoma* (Text-fig. 2), are linked quite definitely to the Cheirodontinae by *Paragoniates*, with its general shape and backward position of the dorsal fin, and by *Compsura* and *Odontostilbe*, with the peculiar caudal scalation of the males.

*Brycon* (Text-figs. 2, 9) seems to be the central type of the group and from it, according to Eigenmann (1917), arose one line leading to *Iguanodectes* and *Pyrhulina*. Eigenmann and Myers (1929) describe the subfamily Iguanodectinae as "slender, elongate, moderately compressed, smelt-like fishes of small size . . ." Cockerell (1913) remarks that the iguanodectine scales are not far from the condition noted in *Cheirodon*. *Pyrhulina* is apparently near to the point at which the hemiodontines branched from the cheirodont stem.

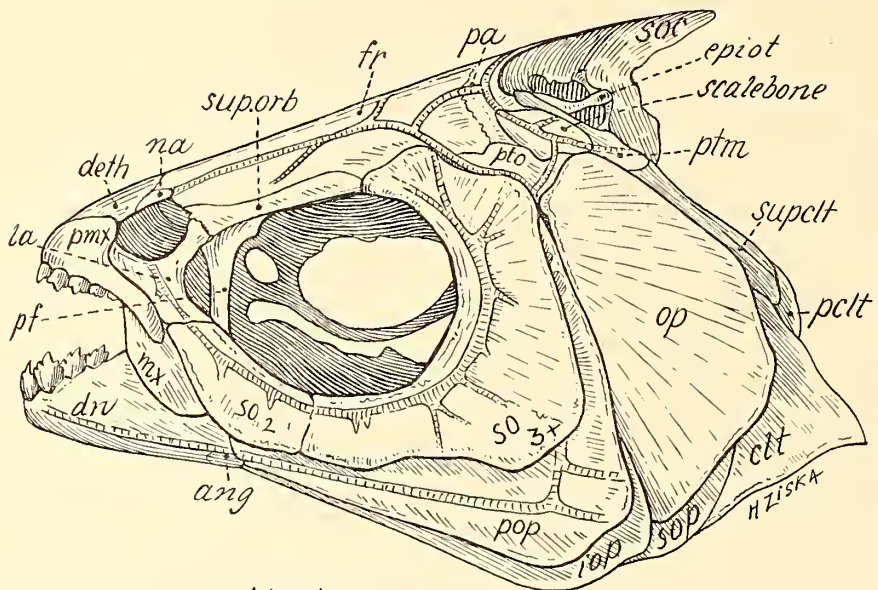
*Chalcinus* (Text-fig. 2), in its deepened coracoids and large pectoral fins, seems to afford a favorable point of departure for *Gasteropelecus* (Text-fig. 2). Regan (1911, p. 20) rejected this connection and stressed the structural relationships with *Tetragonopterus*. But the latter differs widely from *Chalcinus* (Text-fig. 14B) in the low position of the pectorals, general form of body and mouth, and undoubtedly points rather to *Serrasalmo*. After comparing the skeletons of *Chalcinus* and *Tetragonopterus* with the skeleton of *Gasteropelecus* (Text-fig. 14A), we incline to the opinion that *Chalcinus* is much the nearer to the structural ancestor of *Gasteropelecus*.

*Alestes* (Text-figs. 2, 10), a relatively primitive predator, is typical of several African members of the Characinae, such as *Bryconaethiops*, *Micralestes*, and *Petersius*, which vary from fusiform to fairly deep-bodied shapes. The teeth vary from very small pluricuspid to large compressed shearing types; some even have molar-like teeth on the inner row of the upper jaw.

That the African genus *Alestes* is surely close to the American *Brycon* is undoubted. The general shape of the skulls (Text-figs. 15, 16) is very much alike. They both possess the supraorbital, but whereas *Brycon* retains the dermosphenotic, it is noteworthy that in *Alestes* the frontal is excluded from the orbit by a prolongation of the suborbitals. However, in *Alestes* the dermosphenotic may be so completely fused with the suborbitals as to be indistinguishable from them. At any event, the postorbital portion of the circumorbital chain serves the purpose of protecting the muscle fossae noted in Text-fig. 8, as does the dermosphenotic when present. In both genera the lacrymal is present (not shown in Text-fig. 14) and well separated from the prethmoid, as in primitive characins.

*Hydrocyon* (Text-figs. 17, 18) is an extreme predaceous, pike-like offshoot of this African stock. Regan (1911) separates it as a distinct subfamily from the rest of his Characidae largely on the basis of the movable premaxillae, but this character is developed independently in other groups of characins (e.g., Anostomatinae, Hemiodontinae, Citharininae and Distichodontinae) and should not outweigh the many marks of close kinship with other African Characinae. If we are to grade taxonomic rank according to intensity of specialization then the complex symphyseal hinge-joint of *Hydrocyon* (Text-figs. 19, 20, 21) should entitle it to the grade perhaps of a superfamily. However, other characins (Text-fig. 22) and even its own





## Alestes

Text-figure 15.  
Skull of *Alestes*.

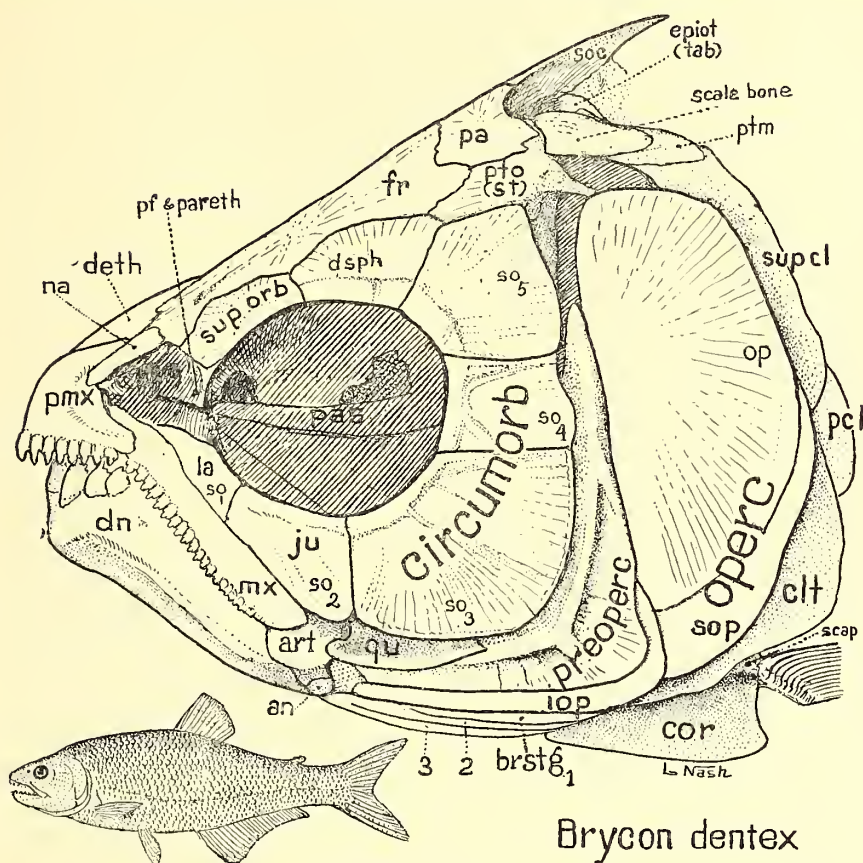
young clearly point the way toward the complex hinge-joint of *Hydrocyon*.

The complex symphysial hinge-joint of *Hydrocyon* and other characins is described in more detail by Gregory and Conrad (1936) as follows:

"Thus the story of the development of the complex hinge-joint in *Hydrocyon lineatus* starts at a stage when the 'hinge' is nothing more than an interdigitating articulation with but three knuckles to each dentary [Text-fig. 21, I.]. The dorsal border of the dentary then produces another knuckle, *C*, on the right and *b* on the left. The ventral border of the left dentary gives rise to *f* [Text-fig. 21, II.]. The next stage [Text-fig. 21, III.] sees the first advance toward the adult interlocked hinge for, as pointed out above, the knuckles begin to curl from the posterior to the anterior borders of the dentary, leaving an opening or fenestra at the pivotal point. By inserting here an hypothetical phase in which this forward curling is wholly finished and the knuckles are interdigitated, it can be seen that by the coalescence of the knuckles arising from the same dentary the condition in IV. [Text-fig. 21] would occur. Now all the elements are present [Text-fig. 20, V.; Text-fig. 21, IV.] and the left hinge-stop is completely formed, while the right one is in process of coalescence. Finally, in VI. [Text-fig. 20] the hinge-joint reaches its completely formed complex condition, which will with later growth be pulled out and distorted both vertically and horizontally, while at the same time retaining its mechanical efficiency.

"A glance at [Text-fig. 22] shows that the most common condition of the hinge in Characins is that seen in *Moenkhausia* (*Tetragonopterinae* Eigenmann), *Piaractus* (*Mylinae* Eigenmann), and *Alestes* (*Characinae* Regan). In all of these the knuckles are arranged in planes radiating posteriorly from the anterior border of the dentary. Our detailed studies on the family suggest that *Hydrocyon* has evidently arisen from an *Alestes*-like ancestor, and a comparison between the *Alestes* hinge in [Text-fig. 22] and that of *Hydrocyon* in [Text-fig. 21] (II.) shows that the latter passes





Brycon dentex

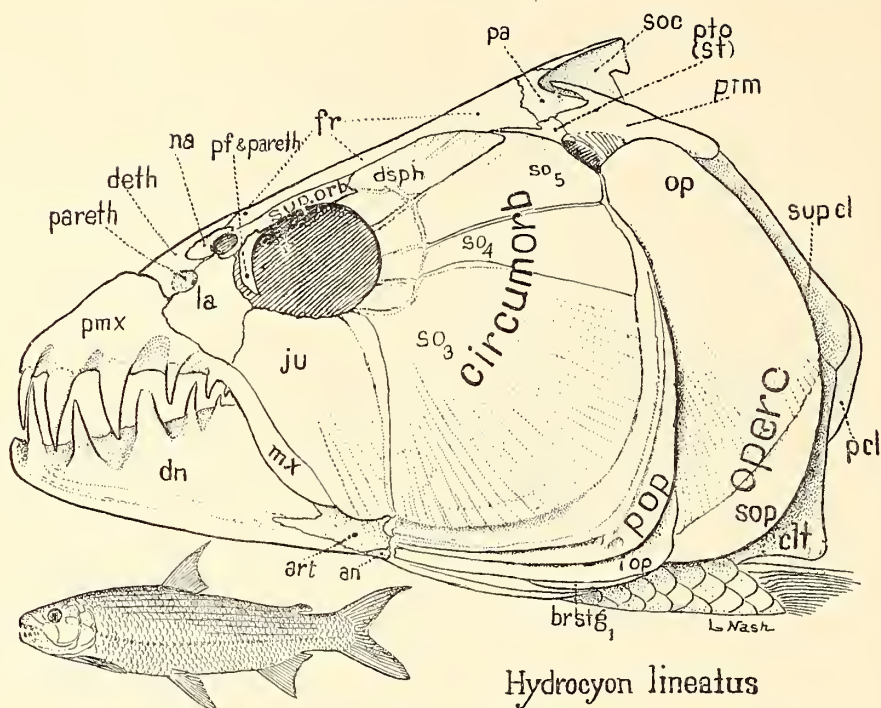
Text-figure 16.

Skull of *Brycon*. After Gregory, 1933, fig. 70.

through an *Alestes* stage in development. Returning to [Text-fig. 22] we notice that the primitive hinge condition is upset in *Erythrinus* and *Hoplias* which have moved the 'area of radiation' posteriorly, so that the knuckles radiate both anteriorly and posteriorly. The condition in *Erythrinus* may possibly be that of *Hydrocyon* in [Text-fig. 21] (IV.) just before any of the knuckles have coalesced.

"In conclusion, the complex hinge-joint in the symphysis mandibulae of *Hydrocyon lineatus* Bleeker develops its most complex features, the so-called hinge-stops described above, after the post-larval and infantile stages have been completed.

"The hinge is formed from interdigitating processes analogous to the knuckles of a mechanical hinge. These knuckles represent subdivisions of the subalveolar ridge of the dentary bone. They are typical polyisomeres in the sense defined by one of us (Gregory, 1934). They grow inward toward the mid-plane like fingers, decussate across the mid-plane, and curl around and join themselves into the hinge-stops on either side of the mid-plane. Here they behave like typical anisomeres, which arise by the differential growth and fusion of polyisomeres.



Hydrocyon lineatus

Text-figure 17.

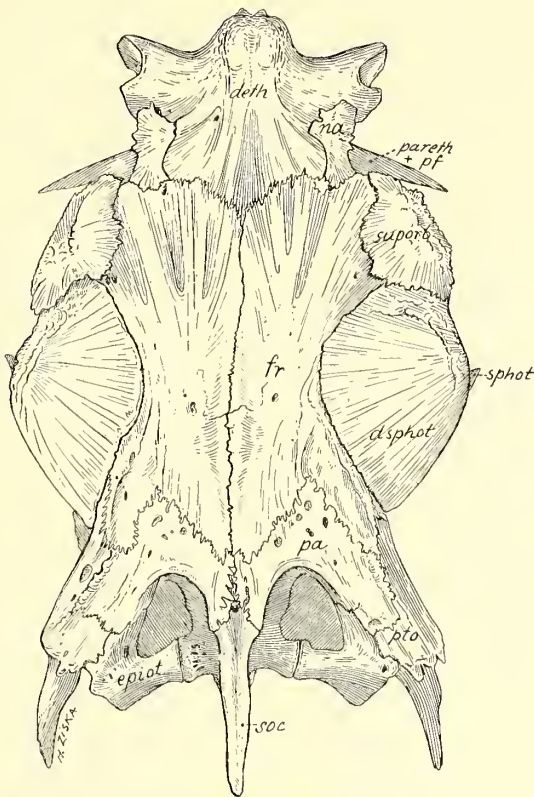
Skull of *Hydrocyon*. After Gregory, 1933, fig. 69.

"The earlier structural stages of the condition in *Hydrocyon* are found in *Alestes* and other primitive Characins and in an arrested stage in the subfamily *Erythrininae*."

## SARCODACINAE.

*Acestrorhyncus*, with its comparatively long jaws and with its premaxillaries fixed and firmly attached to the mesethmoid, has apparently given rise to the elongate, pike-like Xiphostomatidae of Regan (represented on our chart (Text-fig. 2) by *Acestrorhyncus* and *Luciocharax*).

The similarity of the skulls of *Sarcodaces* (Text-figs. 23, 24), an African form, and *Luciocharax*, a South American, is amazing. Text-figure 23 shows the dorsal views of these skulls. It is seen that the dorsal fontanelle is completely closed over in both and that a triangle is formed by the dermosphenotics, frontals and pterotics. This wedge-like arrangement of the cranial elements is highly suggestive of relationship, coupled as it is with a well developed prefrontal plus supraorbital which is so rare among the other characins examined. The scale bone is not figured in *Luciocharax*. There is no supraopercular bone in *Luciocharax*, but this is a derm bone which might easily be lost. As seen in side view (Text-fig. 24) the two skulls are likewise comparable, with their plate-like lacrymals which are so different from those of the more primitive characins. The prefrontals lie dorsal to the lacrymals instead of behind them as in more generalized forms. The suborbital bones of both are very similar in cut, the bones marked so2 being strikingly alike. There is a persistence of the dermosphen-



Hydrocyon

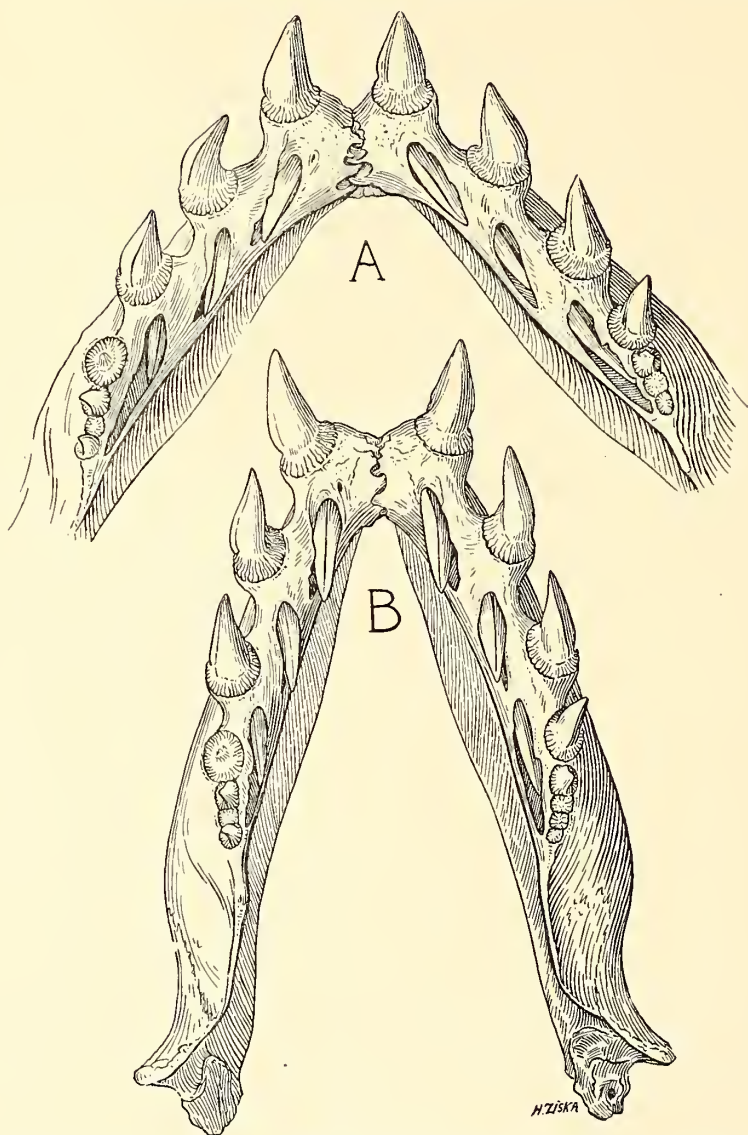
Text-figure 18.

Skull of *Hydrocyon*, dorsal view.

otics of the primitive characin. The cut of the operculum is quite similar in both. The premaxilla and dentary of *Luciocharax* have been elongated and the maxilla is somewhat reduced. That the increased number of teeth in *Luciocharax* is secondary is highly probable.

The similarity of these two is so great that it seems warranted to refer *Sarcodaces* to the Sarcodacinae (which includes *Luciocharax* and others) as here understood (page 321). The connection of *Sarcodaces* with *Alestes* and allied genera seems much more remote than with *Luciocharax*. In *Sarcodaces* the lacrymal and prefrontal overlap, as they do in *Luciocharax*, whereas in *Alestes* which has the typical characin lacrymal placement, they are well separated from the parethmoid-prefrontal complex. A supraorbital is present in *Sarcodaces* and *Luciocharax* and is also present in *Alestes*. *Alestes* lacks the dermosphenotic that is present in the others. The general heavily armored character and the telescoped occipital region common to *Sarcodaces* and *Luciocharax* is lacking in *Alestes* and the Characinae generally. The large, well developed circumorbitals of *Sarcodaces* are noted in *Hydrocyon*, but the lacrymal and parethmoid are well separated in the latter. *Hydrocyon* has a well developed supraorbital but at the same time retains the dermosphenotics of the primitive *Cheirodon*. The supraopercular found in some few characins, such as *Sarcodaces*, is lacking in *Hydrocyon*. The





Text-figure 19.

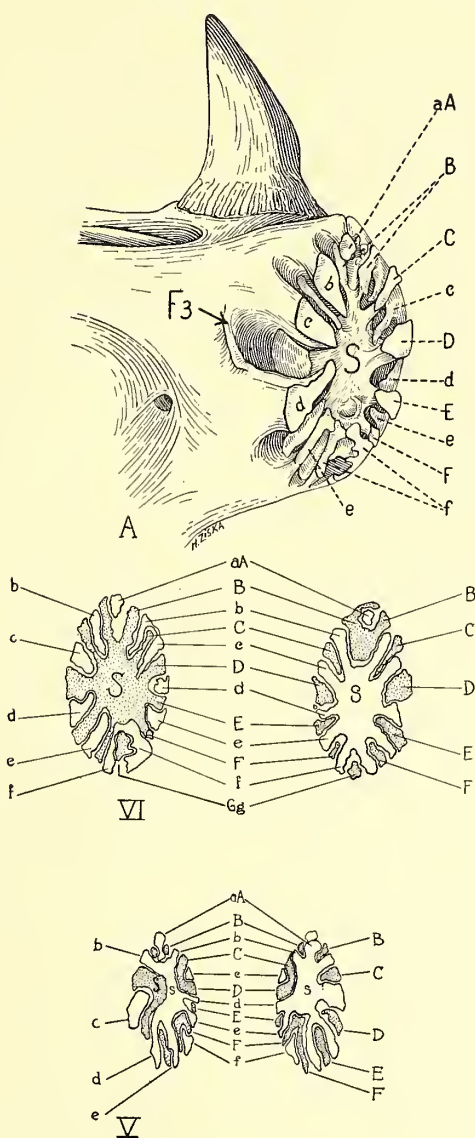
Lower jaw of *Hydrocyon lineatus*, showing the dentaries spread to greatest extent in A and closed as tightly as possible in B. After Gregory and Conrad, 1936, fig. 1.

supraoccipital is produced sufficiently far back to include *Hydrocyon* among the more central Characinae.

*Luciocharax*, while it retains most of the osteological characters of the Characidae of Regan, has developed a somewhat movable upper jaw and the maxillaries have become firmly united with the premaxillaries.

The scales of the Acestrorhamphinae (our Sarcodacinae) according to Cockerell (1913) are like those of the Serrasalmoninae. However, this prob-

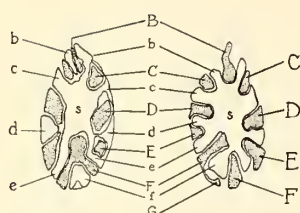




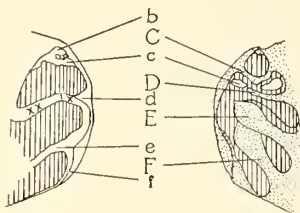
Text-figure 20.

A, distal portion of left half of mandible of adult *Hydrocyon*, oblique mesial view of S turned slightly. VI, median sagittal section of same specimen. V, section of a much smaller specimen, measuring 23 cm. (Stippled portion represents right dentary; unstippled, left.) After Gregory and Conrad, 1936, fig. 6.

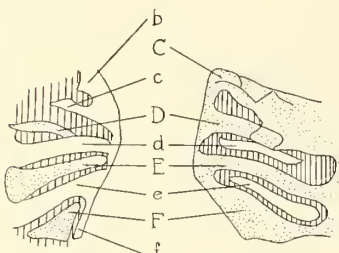
ably indicates only a community of origin for the two groups have developed into as many diverging types. While the Serrasalmoninae have become increasingly deep-bodied as noted above, the sarcodacines have been pulled out antero-posteriorly to form, in *Luciocharax*, an astonishingly pike-like fish. Thus the Sarcodacinae like the Serrasalmoninae may be traced back to the Cheirodontinae.



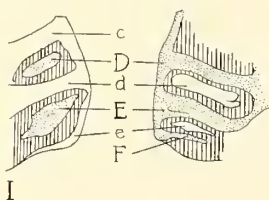
IV



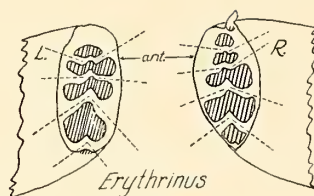
III



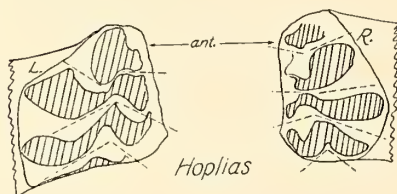
II



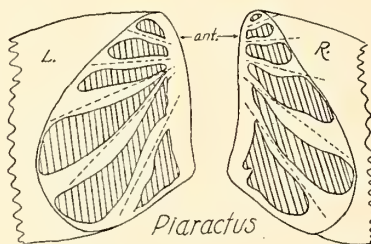
I



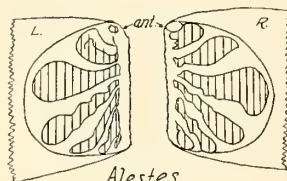
Erythrinus



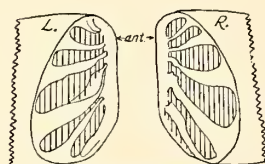
Hoplias



Piaraactus



Alestes



Moenkhausia

## Text-figure 21 (left).

Median sagittal sections of symphysis in *Hydrocyon lineatus*. IV, a specimen about 21 cm. long; III, a fish about 5.5 cm. in length; II, a specimen 5 cm. long; and I, about 2.5 cm. long. After Gregory and Conrad, 1936, fig. 7.

## Text-figure 22 (right).

Diagrams of disarticulated symphyseal hinges in various characins; mesial views. The hatched portion represents the cavities and the light, the knuckles. The dotted lines are merely an aid in noting the directions of the knuckles. L, left dentary; R, right dentary; ant., anterior border of the dentary. After Gregory and Conrad, 1936, fig. 5.

## ERYTHRININAE.

As noted above the primitive appearance of the Erythrininae is apparently only secondary. In a study of the visceral anatomy of the characins Rowntree (1903) notices the striking resemblance between the Erythrininae and *Sarcodaces*, "not only in cranial characters, as shown by Sagemehl, but also in certain visceral characters, notably in the opening of the ductus pneumaticus far to the left on the alimentary canal, in the character of the ovaries, and in the features of the air-bladder." This asymmetric position of the ductus pneumaticus is, according to Rowntree, a specialized condition inasmuch as a symmetric or mid-dorsal position of the duct is the primitive one. That Rowntree and Sagemehl noted several points common to the Erythrininae and *Sarcodaces* is an interesting observation for, of all the skulls studied, the only ones forming possible links between the Erythrininae and the remainder of the Characinidae are those of *Sarcodaces* and related genera.

Rowntree further notes that *Macrodon* (*Hoplias*), alone among the Characinidae, possesses but two of the usual three liver lobes. Insofar as scales are concerned Cockerell (1913) shows that the Erythrininae combine characters of the characins and cyprinids.

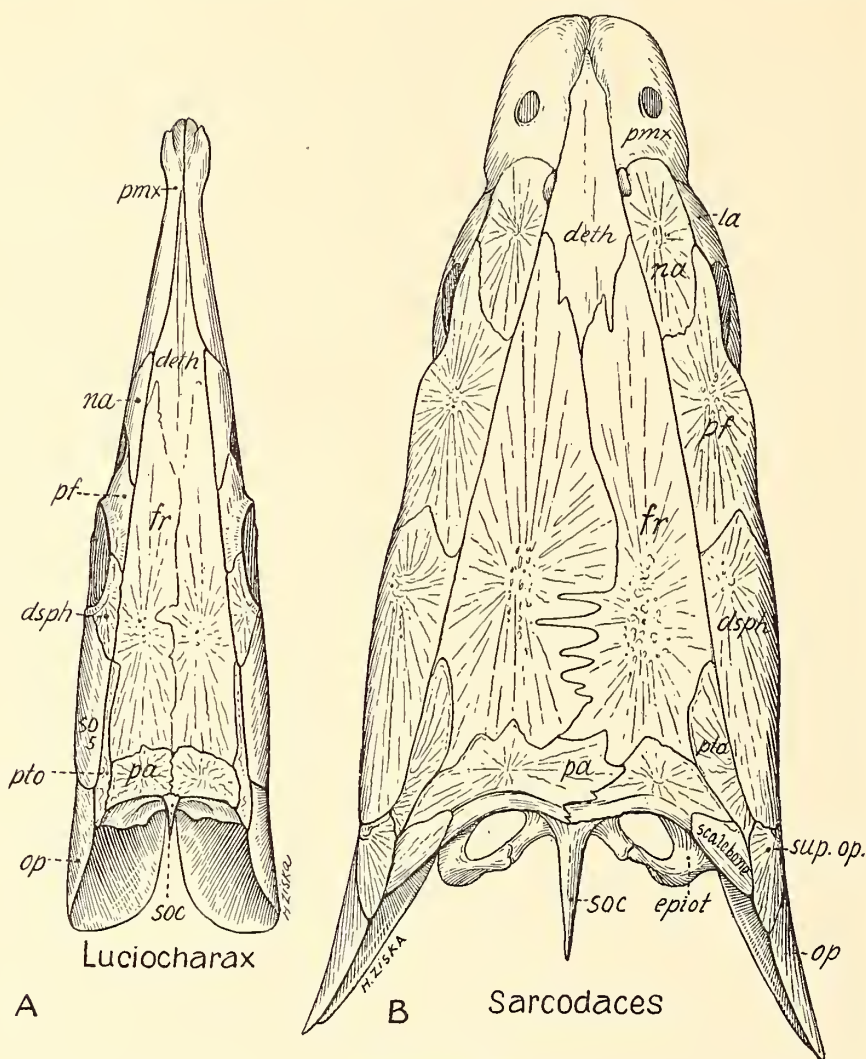
Studies on the symphyseal hinge-joints in characins seemed to indicate at first that the condition noted in *Erythrinus* (Text-fig. 22) was a precursor of that found in *Hydrocyon*. Upon further consideration (see above, page 337), however, it is more probable that the *Erythrinus* condition of the symphyseal hinge-joint is merely that of *Hydrocyon* in an arrested stage.

In any event it becomes evident that the Erythrininae are well along in the evolutionary series, but in spite of their amazing similarity to the cyprinids in the scales it is doubtful that they are near to the stem leading from the primitive Ostariophysi to that group. The well developed upper and lower jaws are armed with conical, canine-like teeth much as in *Sarcodaces* (Text-fig. 24). The condition of their jaws and teeth and the lack of an adipose fin are early noted in the cheirodont *Grundulus*, and the *Erythrinus* body-form has been developed time and again within the family Characinidae.

The heavily armored, tightly built skull of the Erythrininae (Text-figs. 24B, 25, 26) closely resembles those of the Sarcodacinae. *Hoplias* (Erythrininae) (Text-fig. 24B), with its elongate dermosphenotic and separate supraoperculum, seems to form a connecting link between *Sarcodaces* and *Erythrinus*. The lacrymal and the pre-fronto-parethmoid articulate in this subfamily and are not separated from each other as they are in more primitive characins. However, the Erythrininae resemble the primitive subfamilies in not having the frontal excluded from the orbit, whereas in *Sarcodaces* and *Luciocharax* the enlarged prefrontal plus supraorbital do exclude the frontal from the orbital margin. Both *Erythrinus* and *Sarcodaces* have large nasals. The interfrontal sutures and the sutures between the parietals are very similar in the two, but *Erythrinus* lacks the characteristic triangular dorsal view in *Sarcodaces*. The fontanelles are entirely covered over in both genera. The dentition of *Hoplias* is quite like that of *Sarcodaces*. The cut of the lower border of the operculum in the Erythrininae and *Sarcodaces* is peculiar, but this is approached also in *Curimatus* (Anostomatinae).

*Lebiasina* and *Piabucina* (Text-fig. 26), referred by Regan to his Characidae (*sensu strictu*), show a close approximation to *Erythrinus* not only in the body-form but even in the skull. The fronto-parietal fontanelle is completely closed over; the operculum is very similar; the lacrymal-parethmoid relationship is as in the Erythrininae; and there is a sizable dermosphenotic. The only specimen available does not seem to have a supraopercular. The dorsal aspect affords a favorable comparison with *Erythrinus*. The coracoids of *Lebiasina*, according to Regan, have the median





Text-figure 23.

Skulls of *Luciocharax* and *Sarcodaces*, dorsal views.

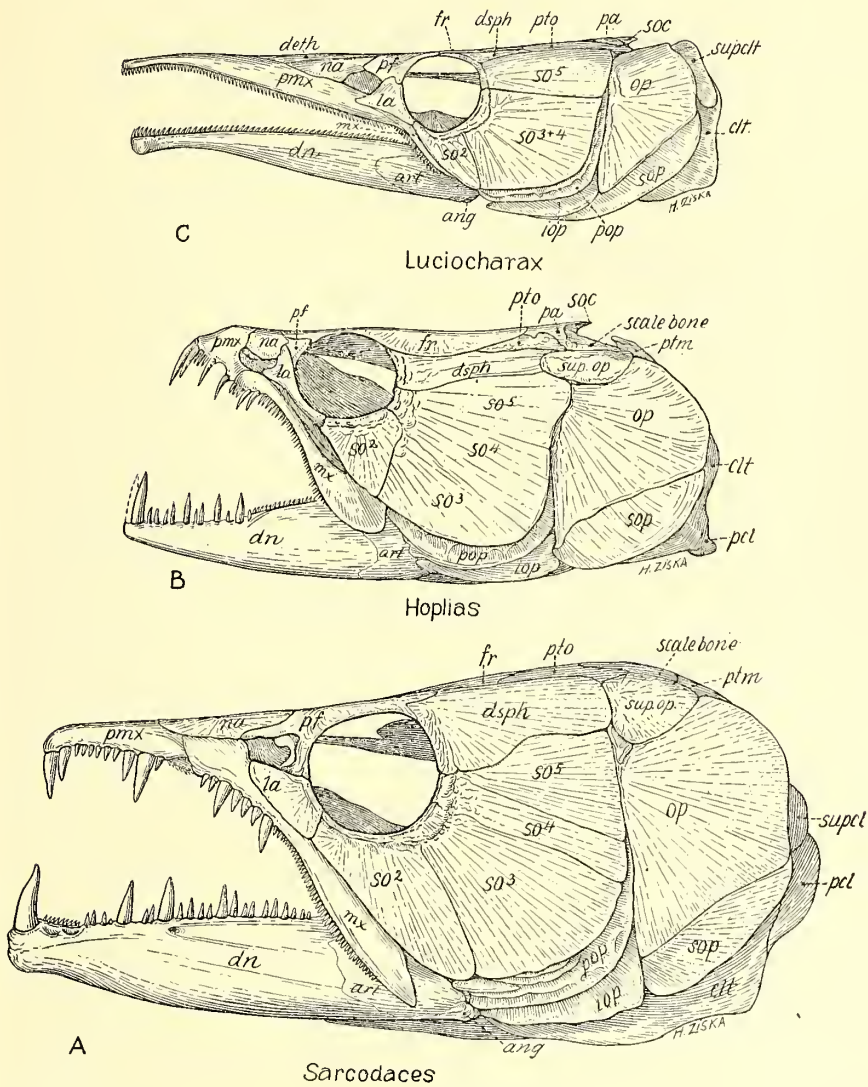
ventral laminae present but short whereas in the Erythrininae generally these are absent.

Thus the Erythrininae may easily have been derived either from a cheirodont near to the *Alestes-Hydrocyon* stem or from the immediate ancestors of the Sarcodacinae.

#### HEMIODONTINAE.

Regan (1911) points out that with the exception of certain diagnostic skull characters, the osteological characters of the Hemiodontinae are "essentially similar to the Characidae." As noted above (p. 321) his "Characidae" has been redefined in part as the Characinae. Cockerell (1913) notes that

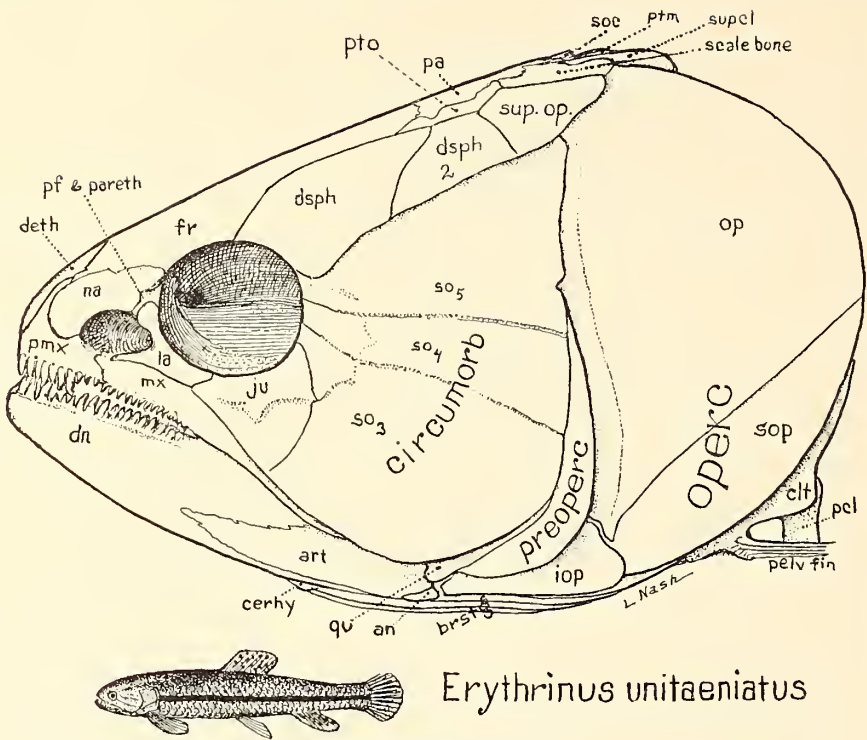




Text-figure 24.

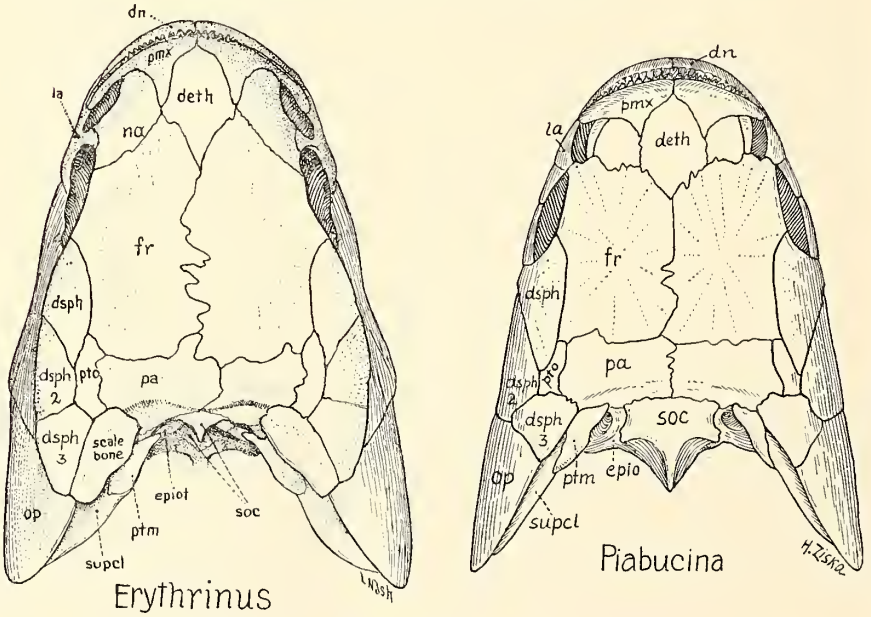
Skulls of *Sarcodaces*, *Hoplias* and *Luciocharax*, lateral views.

the scales of the "Pyrrhulinae," which we refer to the Characinae, are very similar to those of *Nannostomus* of the subfamily Hemiodontinae. On the other hand Cockerell states that the scales of *Hemiodus*, *Anisistia* (Hemiodontinae), and *Anostomus* (Anostomatinae) are of the curimatine type (*Curimatus* being referred by us to the Anostomatinae), while the scales of *Poecilobrycon* (Hemiodontinae) and *Nannostomus* (Hemiodontinae) are like those of *Leporinus* (Anostomatinae), indicating for the hemiodontines a position close to the anostomatine series. However, because of the slight affinities of *Pyrrhulina* and other members of the Characinae to the Hemiodontinae we consider the subfamily Hemiodontinae as a side



Text-figure 25.

Skull of *Erythrinus*, lateral view. After Gregory, 1933, fig. 67.

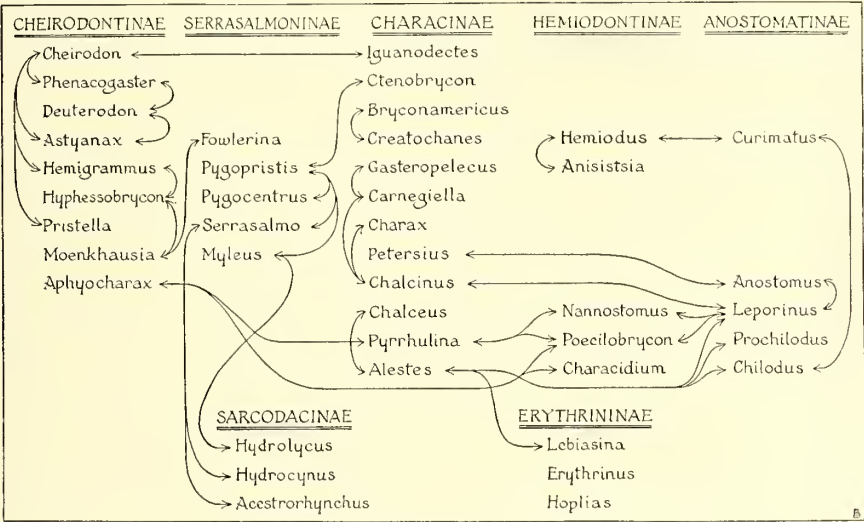


Text-figure 26.

Skulls of *Erythrinus* (after Gregory, 1933, fig. 68) and *Piabucina*, dorsal views.

shoot of the *Cheirodon-Curimatus* line. *Parodon* (Hemiodontinae) with its rather short body seems to be a primitive forerunner of the elongate, fusi-form *Poecilobrycon* (Text-fig. 2). The Hemiodontinae and Prochilodinae of Regan both have a single headed hyomandibular in contrast to the double headed condition seen in the remainder of the family.

The subfamily resemblances between the scales of various genera as observed by Cockerell (1913) may, according to our classification, be tabulated as in Text-fig. 27.



Text-figure 27.

Resemblances between the scales of various genera of characins as noted by Cockerell, 1913.

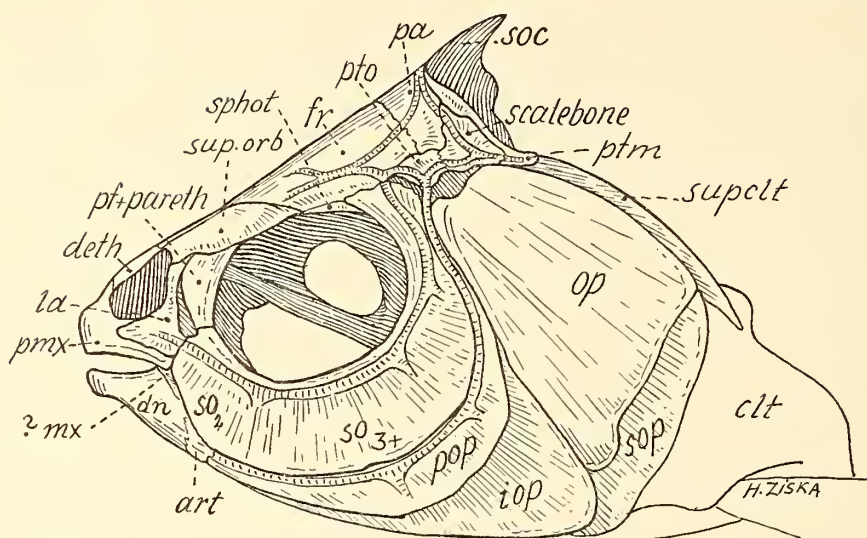
# ANOSTOMATINAE.

The Anostomatinae, a rather compact group, are represented in the "Pictorial Classification" (Text-fig. 2) by *Anostomus*, *Prochilodus*, *Chilodus* and *Curimatus*. The series starts with *Anostomus*, which possesses a small, non-protractile mouth and has the rami of the lower jaw short and stout. *Leporinus* is very close to *Anostomus*; it is said by Cockerell (1913) to have curimatoid shaped scales with a very definite alestoid relationship. *Chilodus* also has scales of curimatoid shape with evidence of a part of the alestiform pattern. Cockerell goes so far as to state the belief that this group supplies the link between *Distichodus* and *Alestes* because their scales undoubtedly illustrate the beginning of the development which culminates in the specialized ctenoid scales of the African *Xenocharax*. In *Prochilodus* we have at least a real development of the ctenoid scale, combined with an alestoid radial pattern. It is apparent from scale studies that *Prochilodus* leads us toward a separate offshoot of the curimatoids, possibly to the African distichodonts, but certainly near and parallel to them.

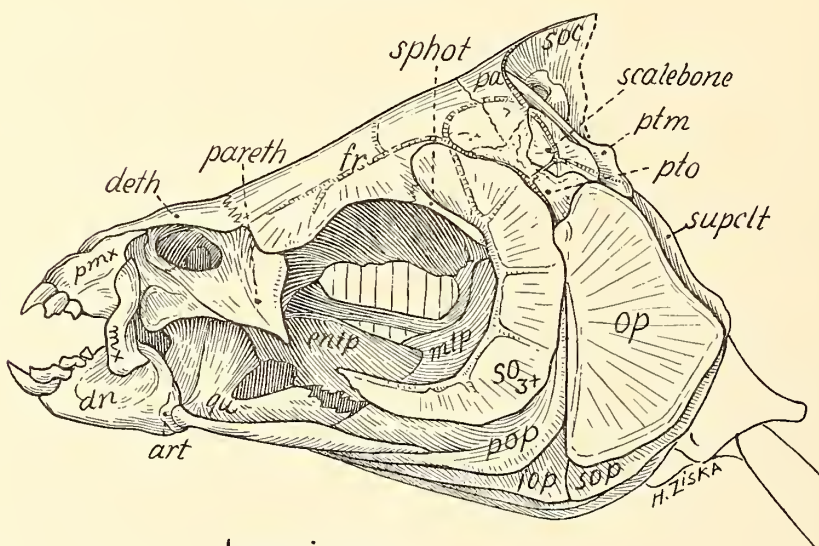
The curimatoids proper are represented in our "Pictorial Classification" by *Curimatus*. This toothless form constitutes the "end-genus" of this line of divergence from the Cheirodontinae.

As a whole the subfamily Anostomatinae is highly specialized and far from its original ancestor, a generalized cheirodont. These conclusions con-





### Curimatus



### Leporinus

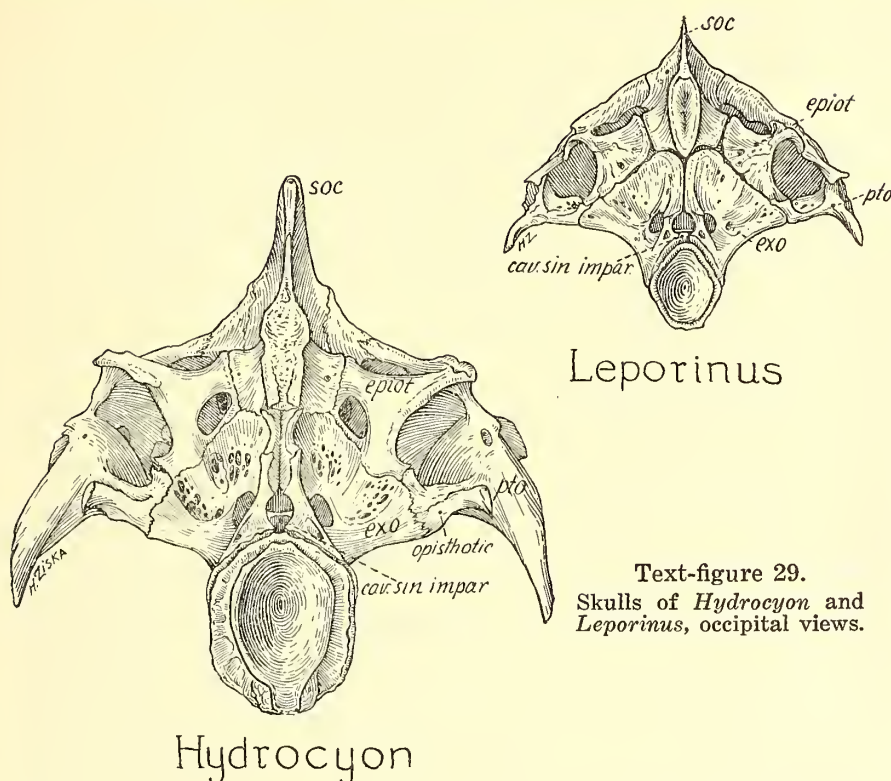
#### Text-figure 28.

Skulls of *Leporinus* and *Curimatus*.

cerning the relationships of this group, based largely upon scale structure, are in accord with Eigenmann's systematic studies (1917).

The skulls of this group that we have been able to study are *Curimatus* and *Leporinus* (Text-fig. 28). A supraorbital bone is present in *Curimatus* and *Prochilodus* but is absent in *Leporinus*. The fontanelle in both *Curimatus* and *Leporinus* completely separates the frontals from the occiput





Text-figure 29.  
Skulls of *Hydrocyon* and  
*Leporinus*, occipital views.

to the dermethmoid; the lacrymal and parmethmoid are well separated; the supraoccipital is produced posteriorly; the maxilla is greatly reduced, the small nibbling jaws retain strong teeth in *Leporinus* but are edentulous in *Curimatus* and some others. The lower border of the operculum in *Curimatus* is truncate postero-inferiorly as in *Sarcodaces*. The opercular region of the skull extends postero-ventrally in *Curimatus* but to a much lesser degree in *Leporinus*.

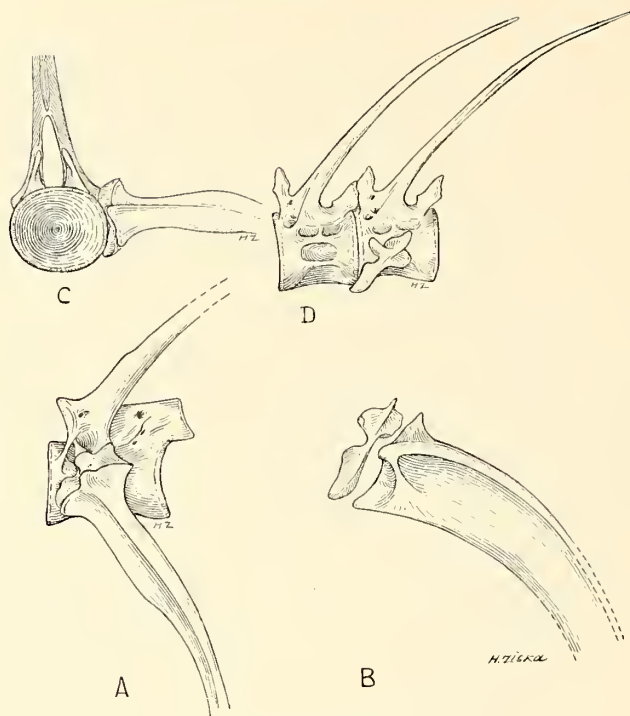
Text-figure 29 shows the great similarity between the occipital regions of the skulls of the African characine, *Hydrocyon*, and the South American anostomatine, *Leporinus*.

The implied relationship on the chart (Text-fig. 1) between the Anostomatinae and the Citharininae is strengthened by the skulls. It may be, however, that these resemblances are merely due to parallelism for both subfamilies reflect their cheirodont ancestry.

The ribs of *Leporinus* and other genera, along with those of the remainder of the Characinidae, are articulated to the centrum by auto-genous parapophyses. Text-figures 30, 31 give front and side views of vertebrae in the abdominal and caudal regions. Text-figure 32 shows the arrangement of the hypurals in *Leporinus*.

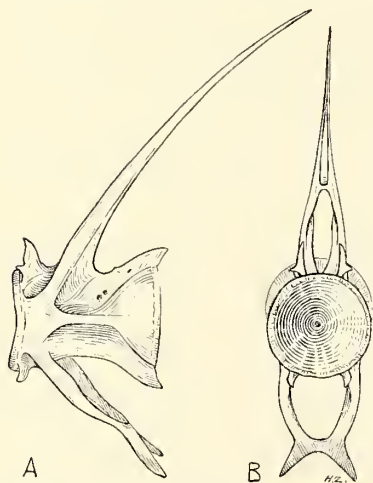
#### CITHARININAE.

Regan (1911) refers the African *Citharinus* (Text-figs. 2, 3) and its ally *Citharidium* (Text-fig. 3), along with many other African genera, to



Text-figure 30.

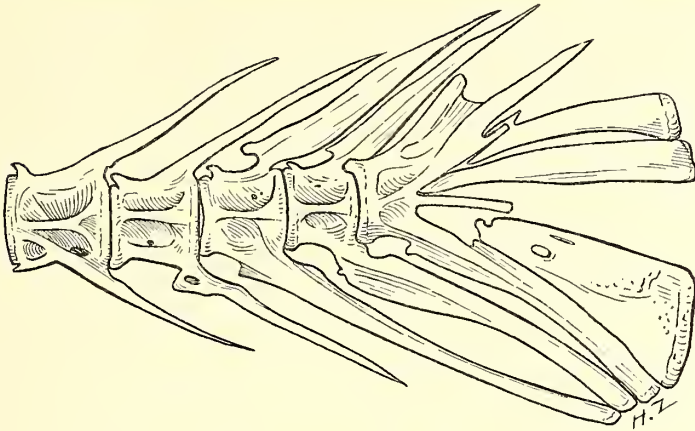
A, C, side and front views of abdominal vertebra of *Leporinus*, showing rib and autogenous parapophysis. B, autogenous parapophysis and rib of *Brycon*; D, with autogenous parapophysis attached to centrum in *Brycon*.



Text-figure 31.

A, lateral view and B, front view of caudal vertebra in *Leporinus*.

the family Citharinidae. We, however, prefer to segregate *Citharinus* and *Citharidium* and their near allies, *Nannaethiops*, *Neolebias*, *Xenocharax* (Text-fig. 3), *Hemistichodus*, in a more primitive subfamily, Citharininae,



Text-figure 32.  
Arrangement of hypurals in *Leporinus*.

characterized by the absence of the high specializations of the mouth parts seen in the Distichodontinae, as here understood.

Boulenger in the Cambridge Natural History, places both *Prochilodus* (Text-figs. 2, 3), a definitely ctenoid South American anostomatine, and *Curimatus* (Text-figs. 2, 3) in the Citharininae; nor was this classification wholly unwarranted, for his conclusions are supported by other anatomical features, i.e., both have movable upper jaws, premaxillaries articulating on the mesethmoid, maxillaries articulated with or adherent to the premaxillaries, palate toothless, lateral line straight, etc.

Cockerell (1912) separates the scales of the African subfamily Citharininae into the *Citharidium* type and the *Citharinus* type, the former with ctenoid and the latter with cycloid scales. It is evident that *Citharinus* with the more primitive cycloid scale is the forerunner of the ctenoid *Citharidium*.

The skull of *Citharinus* compares rather well with that of the Anostomatinae, especially *Prochilodus* or *Curimatus* (Text-fig. 28). The similarity and extent of the fontanelle and the presence of supraorbital are noteworthy. The jaws, too, are quite similar in both subfamilies.

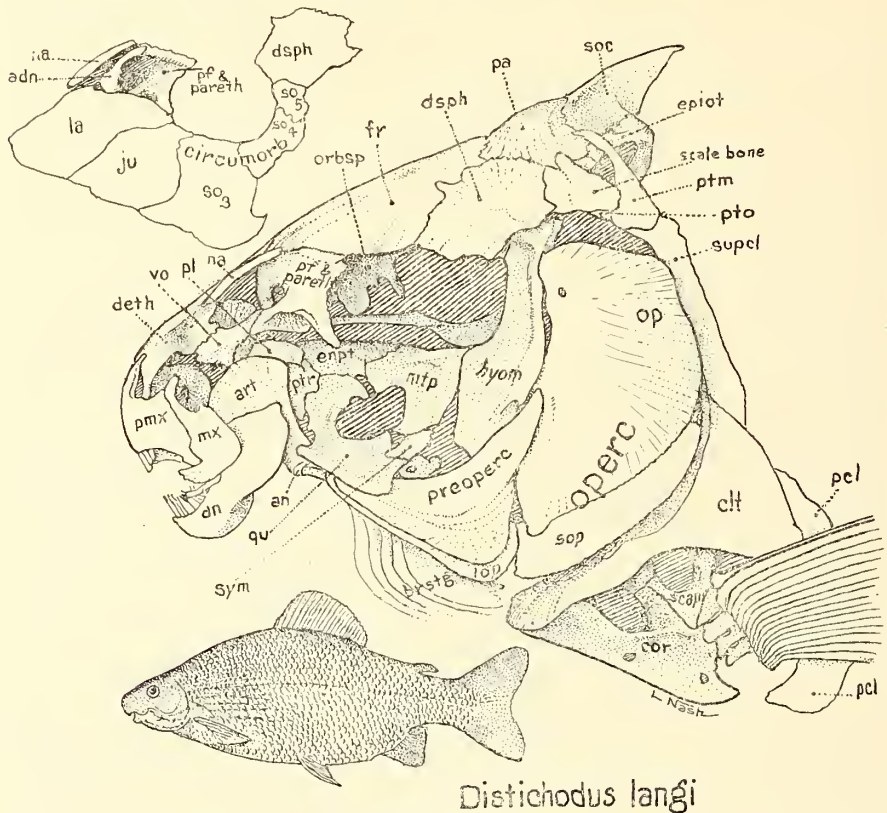
In further support of an early connection between the Anostomatinae and the Citharininae, Rowntree (1903) writes of an accessory branchial organ arising as a blind sac from the upper margin of the last gill cleft; this character seems to be peculiar to the herbivorous forms, *Hemiodus* (Hemiodontinae), *Prochilodus*, *Caenotropus*, *Curimatus* (Anostomatinae), and *Citharinus*, *Xenocharax* (Citharininae). Sagemehl identified this structure as an organ arising from the rudimentary fifth branchial arch. "If this conclusion," says Rowntree, "be correct the presence of the organ in the herbivorous Characinids, and in these only, becomes of great interest, in view of the fact that traces of a fifth gill have not been found in any living ganoid, but only in fishes of yet lower organization—certain Selachians and Dipnoids."

Apparently, however, both Sagemehl and Rowntree failed to realize that selachians and dipnoans have no connection with teleosts and that the so-called fifth branchial arch has no definite claim to be homologized with those of selachians and dipnoans, but is more probably a secondary response to the presence of an accessory branchial organ.

Rowntree then proceeds to draw these conclusions, "(1) that the herbivorous Characinids which possess it (the accessory branchial organ) form a natural group; and (2) that this division of the family cannot be derived from either the Erythrinoids or the other carnivorous Characinids, but is at least as ancient as either of these groups." His first conclusion, at least, seems safe and serves as more positive evidence in showing the inter-relationship of the anostomine-citharinine group.

#### DISTICHODONTINAE.

Regan's subfamilies, Distichodontinae and Ichthyoborinae, are closely linked by the possession of more or less massive dentaries, firmly united at the symphysis and *movably articulated with the articulars*.



Text-figure 33.

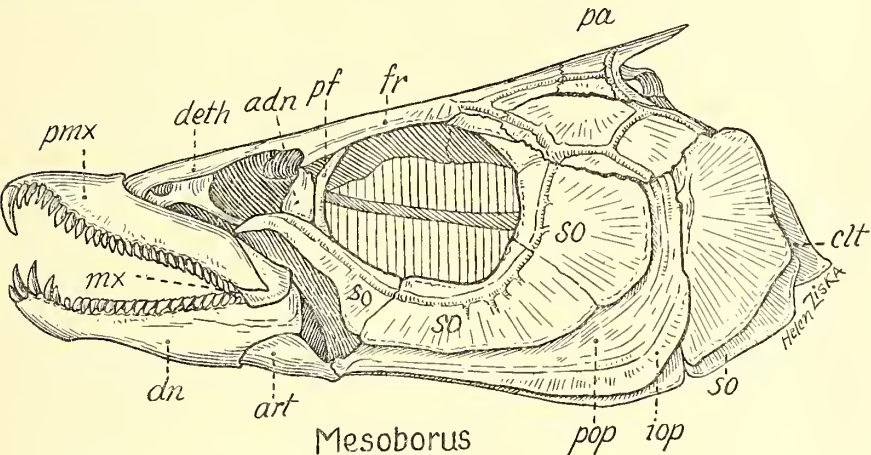
Skull of *Distichodus*. After Gregory, 1933, fig. 71.

That these African forms were derived from the ctenoid African Citharininae seems more likely than that they came from the ctenoid South American anostomatines. Apparently drift toward the herbivorous distichodonts took place in or near the stem of the Anostomatinae and Citharininae (Text-fig. 1).

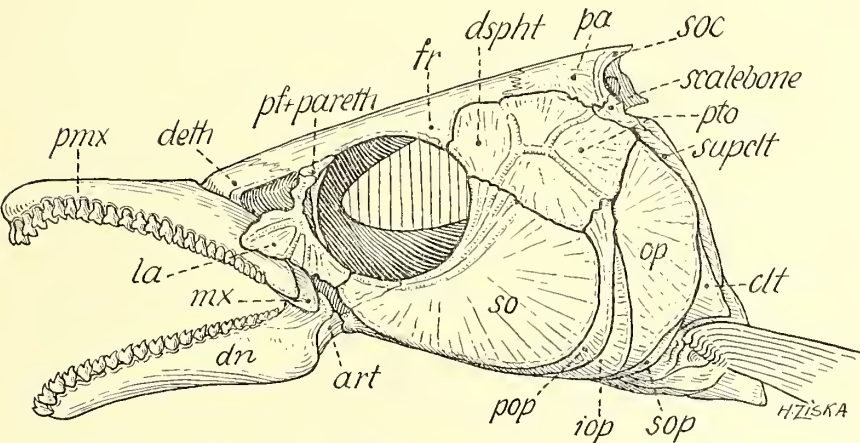
*Distichodus* (Text-fig. 33) is apparently more primitive than *Mesoborus* (Text-fig. 34), *Ichthyoborus*, or *Phago* (Text-fig. 35). The lengthening of



body and jaws in *Ichthyoborus* and the development of unicuspid teeth are probably secondary conditions as contrasted with the primitive short jawed, deep bodied *Distichodus*. With regard to the scales Cockerell (1912) notes that there is nothing to distinguish the scales of *Ichthyoborus* from those of *Distichodus*.



Text-figure 34.  
Skull of *Mesoborus*.



Phago  
Text-figure 35.  
Skull of *Phago*.

GYMNOTIDAE.

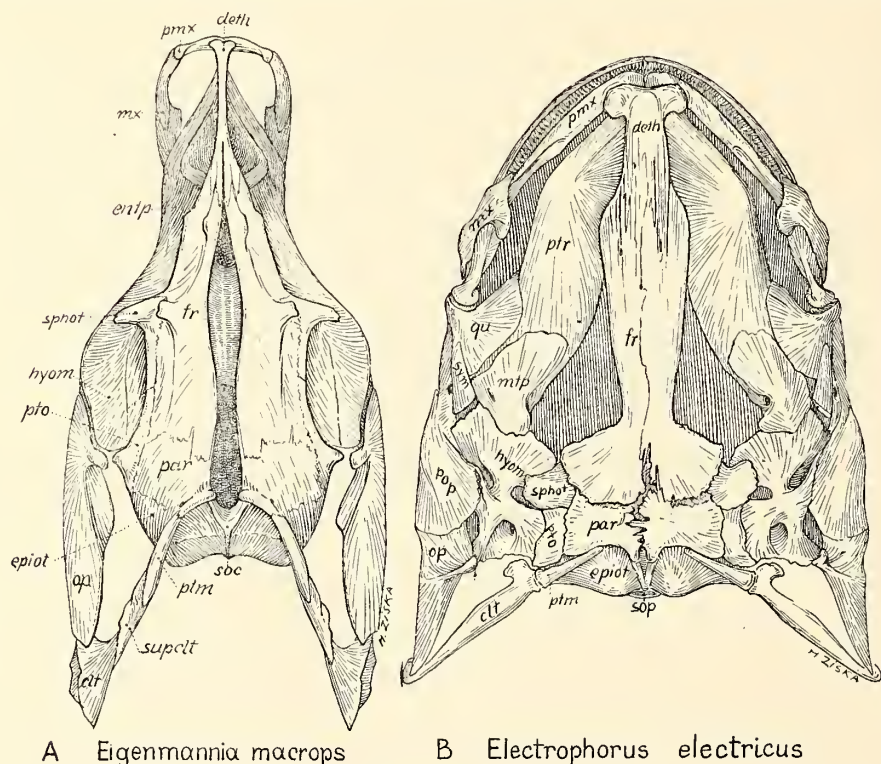
To judge from the cranial osteology the gymnotids have probably been derived from some primitive member of the Characinae. The chief habitus specializations are:

- (1) Marked forward inclination of the entire suspensorium, primitively correlated with a small projecting mouth;
- (2) Varied reduction or emphasis of premaxilla and maxilla;
- (3) Reduction and loss of true pterygoid correlated with enlargement of entopterygoid (mesopterygoid) and symplectic;
- (4) Loss of parethmoid (prefrontal) and varied reduction of mesethmoid;
- (5) Loss of suborbital series including lacrymal;
- (6) Reduction or loss of postorbital process (dermosphenotic);
- (7) Varied emphasis or reduction and loss of interfrontal fontanelle.

Regan has noted that the pectoral girdle of *Rhamphichthys* is much less specialized than that of the typical "Sternarchids." This genus has a greatly elongated, decurved snout with a very small mouth and thus parallels some of the long-snouted mormyrids.

A possible explanation of the peculiar specializations of the gymnotid skull as above noted may be as follows:

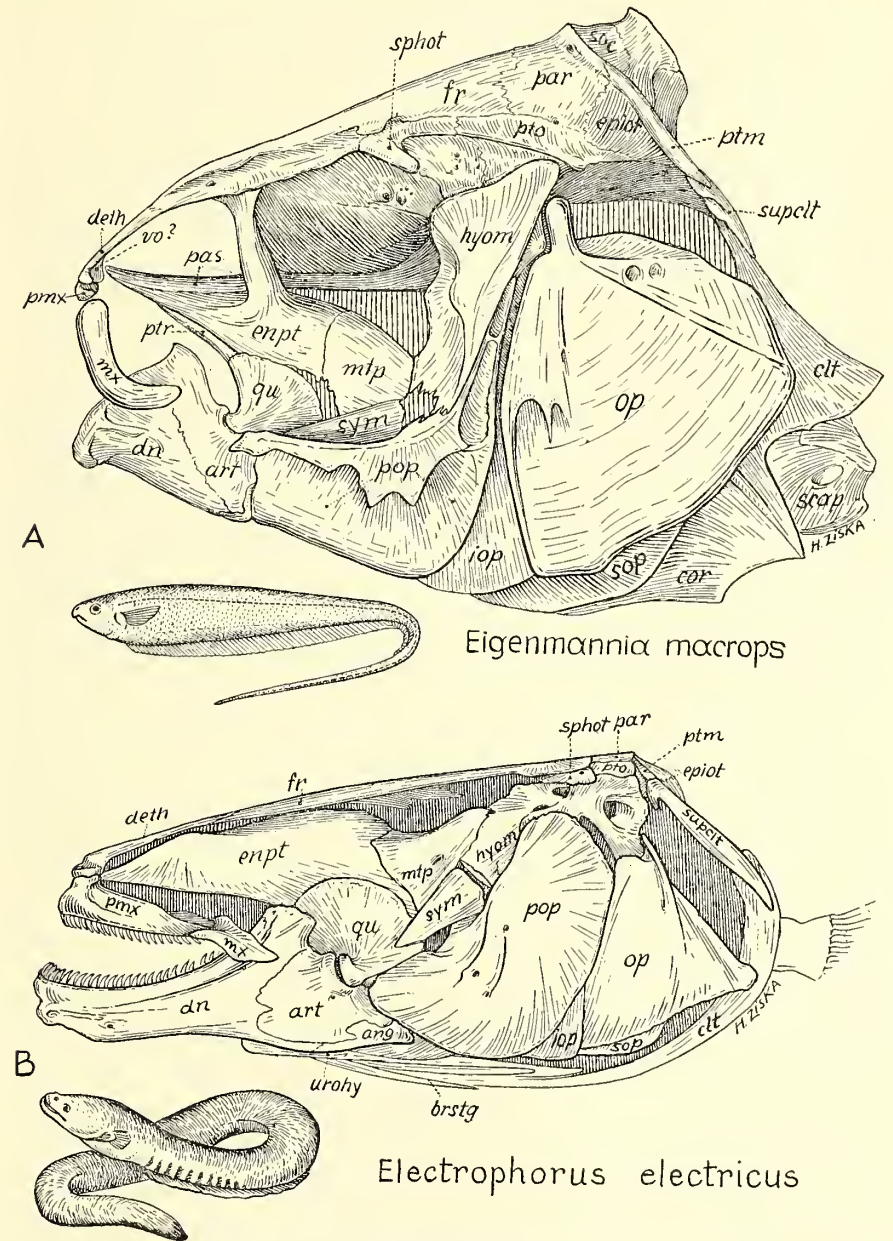
All primitive gymnotids being lost, the genus *Rhamphichthys*, even with its "mental vent," may be near the structural starting point for the remaining genera. We have only to suppose that with the extreme elongation of the snout the maxilla lost its normal connection with the reduced



Text-figure 36.

Skulls of *Eigenmannia* and *Electrophorus*, dorsal views. After Gregory, 1933, fig. 72.

palatine, retaining only its contact with the premaxilla, the latter resting only upon the prolonged mesethmoid. As the palatine disappeared the true pterygoid became reduced and the entopterygoid enlarged. Meanwhile the entire suspensorium was swinging far forward as the mouth became



Text-figure 37.  
Skulls of *Eigenmannia* and *Electrophorus*, lateral views. After Gregory, 1933, fig. 73.



smaller and smaller at the end of the lengthening edentulous snout. In the line leading to *Sternarchus* and *Eigenmannia* (Text-figs. 36, 37) a reverse movement then set in involving the secondary shortening of the snout and the secondary widening of the mouth which even acquired secondary teeth. The end-stage is *Electrophorus* (Text-figs. 36, 37) in which the mesethmoid is secondarily enlarged and strengthened and the median frontal fontanelle is completely closed to support the upward thrusts of the stout upper and lower jaws. Meanwhile the maxilla, having long since lost its primitive contact with the palatine, remains as a vestigial tab on the distal end of the secondarily enlarged premaxilla.

To those who hold to current interpretations of "Irreversibility of Evolution" such an explanation can only appear fantastic. But if we once grasp the idea of secular rise and recession of specializations the above steps will be seen to be supported by strong morphological evidence as well as by closely analogous series among the long-snouted mormyrids *Gymnarchus* and their secondarily short-snouted relatives, such as *Petrocephalus* (Gregory, 1933, Figs. 62B, 64).

#### THE CHARACINS AND THE SUPPOSED SOUTH AMERICAN-AFRICAN BRIDGE.

The unique distribution of the Characidae in Africa and South America alone has long engaged the attention of ichthyologists. Africa and South America each serve as subsidiary centers for adaptive radiation of the group, the Cheirodontinae, Serrasalmoninae, Erythrininae, Anostomatinae and Hemiodontinae being characteristic of South America while the Citharininae and Distichodontinae are confined to Africa. The Characinae and Sarcodacinae, however, as here understood, have representatives in both continents and the resemblances between certain African and South American forms are so striking (Text-figs. 9, 10, 11, 12, 22, 23, 24, 29) as to leave a strong impression of close relationship.

Accordingly, the preceding study leads us to the following tentative conclusions:

- (1) that the African and South American characins are closely related;
- (2) that so far as known characins are wholly absent from ancient freshwater deposits of North America;
- (3) that there is much evidence analyzed by C. W. Andrews, Schuchert and others for the reality of a narrow isthmian land or archipelago connecting Brazil with West Africa even in possibly late Tertiary times.

Dr. Bequaert, however, in the light of his wide knowledge of the faunae and floras of South America and Africa, tells us that neither the botanists nor the entomologists would favor the assumption of an extreme or prolonged contact between the two continents in Tertiary times on account of the large number of endemic families on either side of the Atlantic.

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#### ABBREVIATIONS USED IN THE ILLUSTRATIONS.

“adn”—adnasal  
 “alsp”—alisphenoid  
 ang—angular  
 art—articular  
 boc—basioccipital  
 brstg—branchiostegal  
 cerhy—ceratohyal  
 cl, clt—cleithrum  
 cor—hypocoracoid  
 cran—cranial  
 Deth—dermethmoid  
 dn—dentary  
 dsph, dsphot—dermosphenotic  
 entp—entopterygoid  
 epiot—epiotic

exo—exoccipital  
 f, for—foramen  
 fr—frontal  
 hyo—hyomandibular  
 iop—interopercular  
 ju—jugal  
 la—lacrymal  
 m—mesocoracoid  
 mtp—metapterygoid  
 mx—maxilla  
 na—nasal  
 op, operc—opercular  
 opisthot, opot—opisthotic  
 orbsp—orbitosphenoid  
 pa—parietal

pareth—parethmoid  
pas—parasphenoid  
pelt, pcl—postcleithrum  
pf—prefrontal  
pl—palatine  
pmx—premaxilla  
pop, preoperc—preopercular  
ptm—posttemporal  
pto—pterotic  
ptr—pterygoid  
qu—quadrate  
sc, scap—hypercoracoid (scapula)

so—suborbital  
soc—supraoccipital  
sop—subopercular  
sphot—sphenotic  
supcl, supclt—supracleithrum  
sup. op.—supraopercular  
sup. orb—supraorbital  
sym—symplectic  
tab—tabular  
v—vertebra  
vo—vomer



## 18.

Eastern Pacific Expeditions of the  
New York Zoological Society. XVI.

Holothurians from the Western Coasts of Lower California and  
Central America, and from the Galápagos Islands.<sup>1</sup>

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(Text-figures 1-15).

[This is the *Sixteenth* of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Eastern Pacific *Zaca* (1937-1938) and the *Arcturus* Oceanographic (1925) Expeditions. For data on localities, dates, dredges, etc., of these expeditions, refer to *Zoologica*, Vol. VIII, No. 1, pp. 1-45 (*Arcturus*) and *Zoologica*, Vol. XXIII, No. 14, pp. 287-298 (Eastern Pacific *Zaca*).]

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<sup>1</sup> Contribution No. 564, Department of Tropical Research, New York Zoological Society.

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## INTRODUCTION.

The holothurians brought back by the Eastern Pacific *Zaca* Expedition of 1937-1938 are of even greater interest than those secured in 1936.<sup>2</sup> Twenty different species were collected and only five are identical with those brought back in 1936 (two of these were then described as new). Of the remaining fifteen species four are new, while three are reported for the first time since the types were described. Only eight may be designated as common and even here the material in hand has in two cases given very valuable additional information and helped to straighten out some moot questions.

A few shore species from the Galápagos Islands (secured by the *Arcturus* Oceanographic Expedition in 1925) have been included, thereby bringing the total number of species discussed up to twenty-three. Some of the species in the *Arcturus* collection were also taken by the *Zaca*.

I beg Dr. William Beebe to accept my sincere thanks for the opportunity of studying this interesting collection.

## ORDER ASPIDOCHIROTA.

## Family Stichopodidae.

Genus *Parastichopus* H. L. Clark, 1922.*Parastichopus californicus* (Stimpson).

For diagnosis, synonyms, etc., see Deichmann, 1937, p. 163.

*Local Range*: Two large specimens from Cedros Island, 40 fathoms, (Station 126 D-17).

*Parastichopus parvimensis* (H. L. Clark).

*Stichopus parvimensis* H. L. Clark, 1913, p. 234; 1922, p. 70, pl. 1, figs. 13-14; G. H. Parker, 1921, p. 205.

*Parastichopus parvimensis*, Deichmann, 1937, p. 163 (*passim*).

*Diagnosis*: Resembles *P. californicus* but is normally dark brown with black tips to the papillae. Spicules minute tables (disk up to 0.05 mm.) and small buttons (length 0.08 mm.). Shallow water form.

*Type*: U.S.N.M.

*Type Locality*: Cedros Island, west coast of Lower California, 3.5 feet.

*General Distribution*: From San Pedro to Cedros Island, in shallow water.

<sup>2</sup> See Deichmann, 1937.

*Local Range*: One much contracted specimen from Cedros Island, 20 fathoms, (Station 126 D-18).

*Remarks*: The specimen agrees in every respect with various individuals from Corona del Mar, California.

Genus ***Stichopus*** Brandt, 1835.

***Stichopus fuscus*** Ludwig.

For diagnosis, synonyms, etc., see Deichmann, 1937, p. 163.

*Local Range*: Two large, well expanded specimens from Hood Island, Galápagos, 15 feet depth (*Arcturus* Oceanographic Expedition).

*Remarks*: The first record of this characteristic form from the Galápagos. Previously it had been reported from Ecuador (Ludwig).

Family Holothuriidae.

Genus ***Labidodemas*** Selenka, 1867.

*Labidodemas* Selenka, 1867, p. 309; Sluiter, 1901, p. 21; Fisher, 1907, p. 674.

*Diagnosis*: Medium sized forms with 20 small tentacles, terminally placed; anus subterminal. Feet few, arranged in three double rows ventrally and in two single to double rows on the dorsal side; either all the feet are cylindrical or the dorsal ones are more papilliform. Skin thin, soft. Inner anatomy as in a typical *Holothuria*. Spicules form a more or less scattered layer of tables with spire of various degrees of development; besides also a few plates or buttons with large holes; C-shaped spicules said to be present in some cases. In one species the spicules seem to be completely reduced. Shallow water.

*Type Species*: *Labidodemas semperianum* Selenka.

*Remarks*: Three or four species were hitherto described, ranging from the East Indies to Hawaii; [the latter locality represents supposedly the type locality for *L. semperianum*, but the label in the M.C.Z. says Society Islands.] According to Sluiter (1901, p. 21) three of the species are identical (see Fisher, 1907, p. 675), while the fourth species lacks spicules.

The species described below differs so markedly from the other species known that it cannot be considered a variety of any of these.

***Labidodemas americanum*** sp. nov.

*Diagnosis*: Ventral feet cylindrical, in double rows; dorsal feet papilliform, in two scattered rows. Spicules delicate tables with four central holes and a circle of marginal holes. Spire low, mostly incomplete or reduced to four knobs. Ventral feet with large end plate and plates with four to five holes, possibly reduced tables. Dorsal papillae with no end plate but the same kind of plates as the ventral feet. Skin soft, golden brown in color to greenish, appendages mostly dark brown.

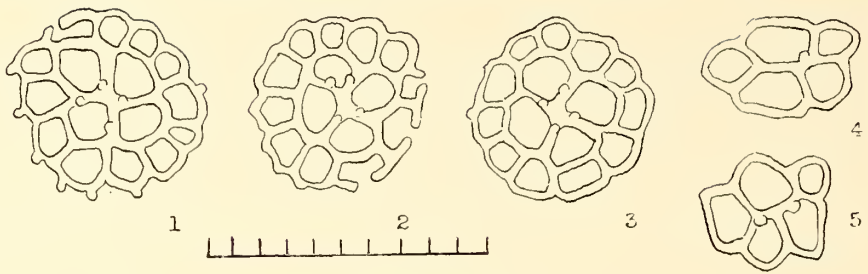
*Type*: M.C.Z.

*Type Locality*: Jasper Island, Costa Rica.

*General Distribution*: Probably widespread in the Panamic region.

*Local Range*: Two contracted specimens from Jasper Island, Gulf of Nicoya, Costa Rica.

*Remarks*: The material has been compared with the type material of *L. semperianum* from Hawaii, (or Society Islands) in the M.C.Z. The latter



Text-figure 1.

*Labidodemus americanum* sp. nov. 1-3, Tables with reduced spire from skin. 4-5, Buttons in wall of feet, probably derived from tables. Scale 1/100 mm.

species has much stouter spicules with long spines on the top of the spire, so it is out of question that the present species is identical with Selenka's species as one would be inclined to expect.

The specimens are small (5-6 cm. long) and not well suited for anatomical studies. The radials are large squarish while the interradials are low; both are thin and delicate in structure. The Polian vesicle is small and ventrally placed; the single stone canal is embedded in the dorsal mesentery, its flattened head projecting free to the right. The intestine is partly torn and filled with coarse coral debris. No traces of gonads are present in the types.

#### Genus *Holothuria* Linnaeus.

#### *Holothuria arenicola* Semper.

*Holothuria arenicola* Semper, 1868, p. 81, pl. 20, pl. 30, fig. 13, pl. 35, fig. 4; Théel, 1886a, p. 7; Fisher, 1907, p. 662; Deichmann, 1930, p. 66, pl. 4, figs. 1-9; 1937, p. 165 (*passim*); Panning, 1935, IV, p. 88, text-figure 73.

*Holothuria maculata* Ludwig, 1887, p. 2.

*Nec Holothuria maculata* Ludwig, 1894, p. 1 (= *H. inhabilis* Selenka; see Deichmann, 1937, p. 165).

**Diagnosis:** Slender tapering form (up to 20 cm. long); mouth almost terminal with 20 small tentacles; anus terminal. Feet cylindrical, in scattered bands almost equally numerous ventrally and dorsally and only very slightly smaller on the dorsum. Calcareous ring low; ring canal unusually far behind the calcareous ring (1-2 cm.); normally one small stone canal attached to the mesentery; one or two Polian vesicles. Cuvierian organs present but seem normally to be small; gonads numerous tubes in a tuft behind the vascular ring.

Spicule tables with 4-8 marginal holes and a low four-pillared spire with 8-12 spines on top. Buttons smooth, regular, usually with 6 holes often decreasing in size with advancing age; few buttons present in young individuals. Feet with end plate and straight supporting rods with perforated ends and often holes along the middle sometimes developed as regular large buttons with numerous holes.

Color mottled gray, with either two rows of dark spots on the dorsum or irregularly spotted.

**Type:** Possibly in Germany.

**Type Locality:** Bohol, Philippines.

**General Distribution:** Almost circumtropical. Common in the West Indies and Hawaii, in shallow water often buried in sand.



*Local Range:* Two small specimens from Tangola-Tangola Bay, Mexico, in coral (Station 196 D-15); one small specimen from Ballena Bay, Costa Rica (Zaca 1938); one from Gardner Bay, Hood Island, Galápagos (*Arcturus*, 1925).

*Remarks:* This widespread species was recorded from the Galápagos by Théel, 1886a, and from Panama by Ludwig in 1887<sup>3</sup>. Later Ludwig mistook *H. inhabilis* from off Cocos Island, 66 fathoms, for this common species. It has been reported by most collectors working in the Panamic waters.

### ***Holothuria impatiens* (Forskål).**

*Fistularia impatiens* Forskål, 1775, p. 121, pl. 39, fig. B.

*Holothuria impatiens* Théel, 1886a, p. 7; Fisher, 1907, p. 667; Panning 1935, IV, p. 86, text-fig. 72 (complete list of references); Deichmann, 1930, p. 64, pl. 3, figs. 17-18.

*Diagnosis:* Medium sized form (10-15 cm. long), slender, often distinctly bottle-shaped with long narrow "neck." Tentacles 20, small, mouth and anus both terminal. Feet cylindrical, slightly more papilliform on the dorsal side, scattered over the entire body without any apparent order, often placed distinctly on warts. Calcareous ring low; stone canal free; Polian vesicles usually 2-4; Cuvierian organs unusually thick tubes; gonads placed in anterior part of body.

Spicules regular tables with 8 large marginal holes; spire with one or two cross beams and numerous short spines on the top. Buttons smooth oval with 6 large holes. Feet with end plate, often reduced in the dorsal appendages and numerous slightly curved supporting rods, heavy, with few holes in the ends and on each side of the middle, occasionally developed as complete buttons. Color mottled, gray, skin decidedly sandy to the touch.

*Type:* Lost.

*Type Locality:* Red Sea.

*General Distribution:* Almost circumtropical. Common in the West Indies and in Hawaii; shallow water to few fathoms depth.

*Local Range:* Five small individuals from Situatanejo, Mexico; 6 from Station 195 D-15; two fragments from Galápagos (*Arcturus* 1925).

*Remarks:* This common species was reported from the Galápagos in 1886, by Théel; from Lower California in 1913 by H. L. Clark.

### ***Holothuria inhabilis* Selenka.**

For diagnosis, etc., see Deichmann, 1937, p. 164.

*Local Distribution:* Three large specimens from Corinto, Nicaragua, 2 and 1 fathoms (Station 200 D-5 and D-15).

*Remarks:* The specimens agree with those previously reported from Lower California, Cocos Island and Clarion Island. The depth is exceptionally low but very likely the larger individuals migrate shorewards as is known to be the case in other species.

### ***Holothuria inornata* Semper.**

*Holothuria inornata* Semper, 1868, p. 252, pl. 40, fig. 1; Panning, 1934, II, p. 33, text-fig. 28 (reproduction of Semper's figure).

*Diagnosis:* Large form (20 cm. or more) with thick skin; 20 large tentacles; mouth ventrally directed; anus terminal; ventral feet numerous,

<sup>3</sup> Deichmann (1937) erroneously writes "1875" instead of "1887."

cylindrical, forming a crowded sole; dorsal appendages mostly papillae, many arranged on more or less distinct warts. Inner anatomy not remarkable except for a cluster of 5-6 free stone canals; Cuvieran organs present.

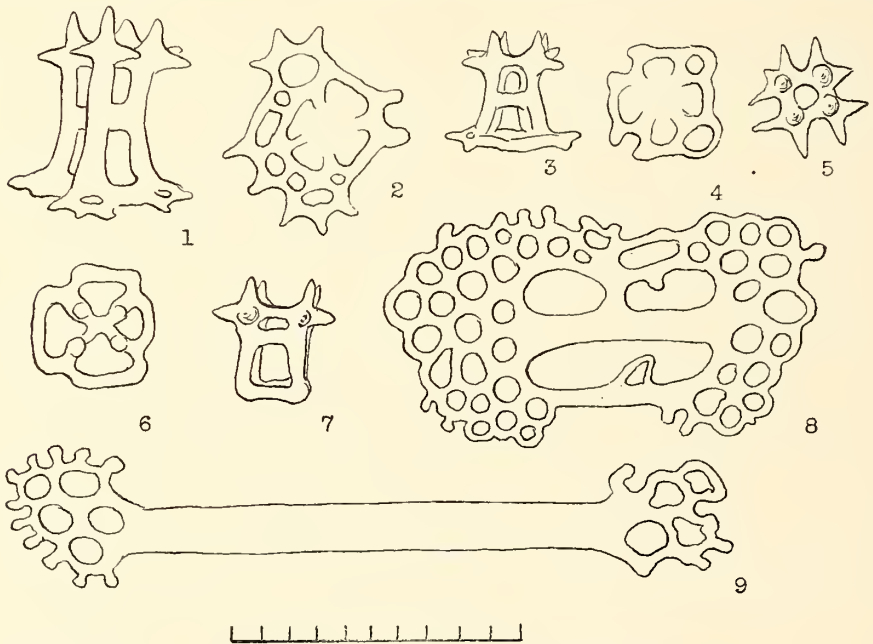
Spicules a thinly scattered layer of tables; dorsally they are large with mostly complete disk consisting of four central holes and four marginal ones and with about 12 marginal spines; ventrally most of the tables are smaller with disk completely reduced; spire with four pillars, usually one cross beam and ending in four upright and 8 vertical spines. Feet with end plate and no supporting rods or plates except a number of perforated plates close to the end plate; dorsal appendages with a vestigial end plate and numerous supporting rods, straight or curved, smooth with perforated ends. Color almost black with a reddish tinge.

*Type*: Hamburg.

*Type Locality*: Mazatlan, Mexico.

*General Range*: Probably the entire Panamic region. Shallow water.

*Local Range*: Two small specimens from Ballena Bay, Costa Rica, shore; one small from Corinto, Nicaragua; two large from Galápagos (*Arcturus*, 1925).



Text-figure 2.

*Holothuria inornata* Semper. 1-5, Tables of various development from skin and dorsal appendages. 6-7, Typically reduced tables from ventral appendages. 8, Supporting plate from near end plate in ventral appendages. 9, Straight supporting rod from dorsal appendage. Scale 1/100 mm.

*Remarks*: The species has not been reported since the original type specimens were secured. The general exterior of the animal is slightly suggestive of *H. grisea* Selenka from the West Indies, and the coasts of Brazil and West Africa, but it is much larger and more darkly colored and has numerous stone canals.

Although it is not impossible that *H. atra* occurs in the Galápagos

Islands and Clipperton Island (see Panning, chart, p. 29) it is very likely that the two records actually refer to this species.

### *Holothuria languens* Selenka.

*Holothuria languens* Selenka, 1867, p. 335, pl. 19, figs. 80-81; H. L. Clark, 1920, p. 149; Panning, 1934, II, p. 45, text-fig. 37.

*Holothuria imitans* Théel, 1886a, p. 7.

**Diagnosis:** Slender form (rarely more than 10 cm. long); tentacles small, mouth and anus terminal; feet ventrally cylindrical, dorsally papilliform, in indistinct longitudinal rows, scattered. Inner anatomy not remarkable. Cuvieran organs apparently lacking.

Spicules a crowded layer of tables with reduced disk, except in very young individuals (3 cm. long) where it is circular with smooth edge; spire tall with normally one cross beam and ending in a Maltese cross of 8 flat spines; in the juvenile tables the spire is more tapering, often with two cross beams and insignificant teeth. Feet with end plate and curved supporting rods, either smooth with perforated ends or with lateral projections which ultimately may become united so they form a series of holes along the sides. Dorsal papillae lack end plate but are filled with curved supporting rods with spinous or perforated ends.

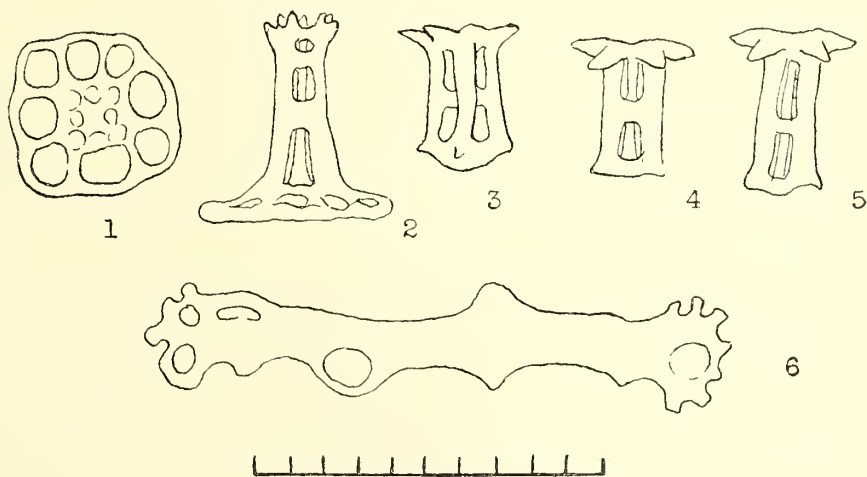
Color mottled reddish-brown, lighter below; tentacles yellow. Skin slightly sandy to the touch.

**Type:** In Germany; paratype in M.C.Z.

**Type Locality:** Panama.

**General Distribution:** Probably the entire Panamic region, including Galápagos. Shallow water.

**Local Range:** One specimen from Santa Cruz Bay, Mexico, 4 and 15 fathoms (Station 195 D-14 and D-15); one from Jasper Island, Gulf of Nicoya, Costa Rica (Station 213 L-3); two from Galápagos (*Arcturus*, 1925).



Text-figure 3.

*Holothuria languens* Selenka. 1-2, Juvenile table, disk and lateral view, from small specimen from the Galápagos Islands. 3-5, Normal reduced tables, lateral view from adult specimens. 6, Straight supporting rod from dorsal appendage. Scale 1/100 mm.



*Remarks:* The species differs from the common West Indian form, *H. surinamensis* Ludwig, in its smaller size, its total lack of large flat rods scattered in the skin, and in the flat undivided spines on the top of the spire.<sup>4</sup> It differs from the Indo-Pacific form, *H. imitans* Ludwig from the Navigator Islands, in the more delicate tables with smooth margin to the disk, which is preserved only in very young individuals, while *H. imitans* apparently retains the disk on most of its tables.

*H. languens* was described from Panama, and as far as known it is restricted to that region. Semper referred (1868, p. 87) an incomplete specimen from British Guiana to *H. languens*, as it seemed to resemble Selenka's species. Undoubtedly he was dealing with Ludwig's *H. surinamensis*, described a few years later from Dutch Guiana (Surinam)—a species which never has been reported from outside of the West Indies. Sluiter's record (1910, p. 331) of *H. languens*, from St. Thomas, W. I., also undoubtedly refers to *H. surinamensis*.<sup>5</sup>

Ludwig withdrew, but as I consider incorrectly, *H. surinamensis*, making it a synonym of *H. imitans* which he, in the same paper (1887), reported from Panama and Galápagos. He did not mention Selenka's species at all, being probably misled by Selenka's very untypical figure. It is not clear whether he refers to his original material from the Navigator Islands or to his Panamic-Galápagos material when he speaks of the presence of tables with spinous margin. As far as the present material shows, the disk is smooth in *H. languens*. H. L. Clark (1920, p. 148) describes an *H. imitans* from somewhere in the Pacific Ocean—*Albatross* cruise, locality label lacking—and emphasizes the spinous disk and the tapering spire with 12-20 teeth, different from *H. languens* which he records from the Gulf of Panama.

### ***Holothuria lubrica* Selenka.**

*Holothuria lubrica* Selenka, 1867, p. 329, pl. 18, fig. 59; Panning, 1934, p. 45, text-fig. 38 (copied from Lampert, 1896, fig. 2).

*Holothuria kapiolaniae* Bell, 1887, p. 533; Fisher, 1907, p. 653.

For diagnosis, etc., see Deichmann, 1937, p. 165.

*Local Range:* Four specimens from Ballena Bay, Costa Rica, shore; 1 from Corinto, Nicaragua, shore.

*Remarks:* The typical form seems to be restricted to Panamic waters and possibly Hawaii (*H. kapiolaniae* Bell). The records from the Malay Archipelago, given by Sluiter (1901, p. 8), need re-investigation. Sluiter gives no measurements of the spicules and it is possible that he was dealing with the other species with similar but shorter spicules before him, viz., *H. parva* Lampert, type locality east coast of Africa, or possibly *H. moebii* Ludwig.

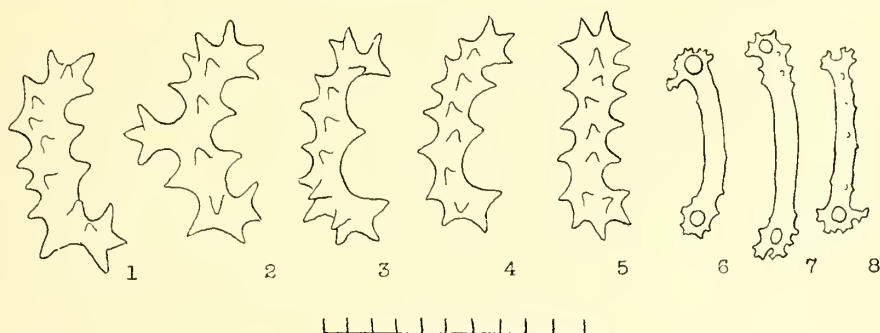
Théel's record of *H. lubrica* from St. Bartholomew, W. I., has unfortunately been repeated uncritically by various writers. Actually Théel says about his West Indian material: "either *lubrica* or the foregoing species," (= *H. glaberrima*), and the description is decidedly of *H. glaberrima*.

Ludwig maintains (1898, p. 434) that he has found spicules of the *glaberrima* type in specimens from Mazatlan, Mexico, but he has not

<sup>4</sup> Deichmann (1926, pl. 1, fig. 1) selected the most reduced table she could find in *H. surinamensis*, as well as the most complete type. Unfortunately this figure was selected by Panning (1934, 11, text-fig. 34) instead of the more typical tables figured in 1930, pl. 3, figs. 12-15, 19. Normally *H. surinamensis* has heavy double spines on the top of the spire.

<sup>5</sup> The records of *H. imitans* from Bermuda are due to Panning who refers Clark's material of *H. surinamensis* (1898, p. 412, and 1899, p. 118) to Ludwig's Indo-Pacific species. His reasons are that Clark states that flat bars apparently are lacking in the Bermuda specimens (but may have been overlooked) and that he sometimes has found spines on the edge of the tables in specimens from Bermuda as well as from Jamaica, adding that these tables may have more spines (18-20) on the top of the spire. Presumably this is merely an untypical variation, and *H. imitans* must be removed from the list of West Indian species until a careful comparison has been made.





Text-figure 4.

*Holothuria lubrica* Selenka. 1-5, Typical spinous rods from integument.

*Holothuria glaberrima* Selenka. 6-8, Typical rods from integument. Scale 1/100 mm.

compared them with spicules of the true *glaberrima*. Although the spicules vary somewhat in development and are of approximately the same size, I have always found that they cannot be confused. Moreover, the two species are rather different in exterior. *H. glaberrima* is dark brown and robust, while *H. lubrica* is smaller and grayish in color, often with yellow feet and two rows of dark spots on the dorsum.

***Holothuria marenzelleri* Ludwig var. *théeli* var. nov.**

*Holothuria marenzelleri* var. ? Théel, 1886a, p. 7.

*Holothuria marenzelleri* Ludwig, 1887, p. 2, pl. 2, fig. 12; Panning, 1934, II, p. 47, fig. 41 (copy of Ludwig's figure).

**Diagnosis:** Large robust form (up to 20 cm. long) with 20 large bushy tentacles; ventral side covered by numerous cylindrical feet; dorsal side with numerous small papillae. Single free stone canal.

Spicules in young individuals short spectacle-shaped rods, often developed as asymmetrical or symmetrical plates; surface smooth; margin scalloped. In larger individuals the spicules change into larger rods with more or less rough surface and numerous holes in the ends and along the margins. Color dark brown.

**Type:** M. C. Z. cat. no. 665. Ludwig's types of the typical form from the Nicobars are probably in Germany.

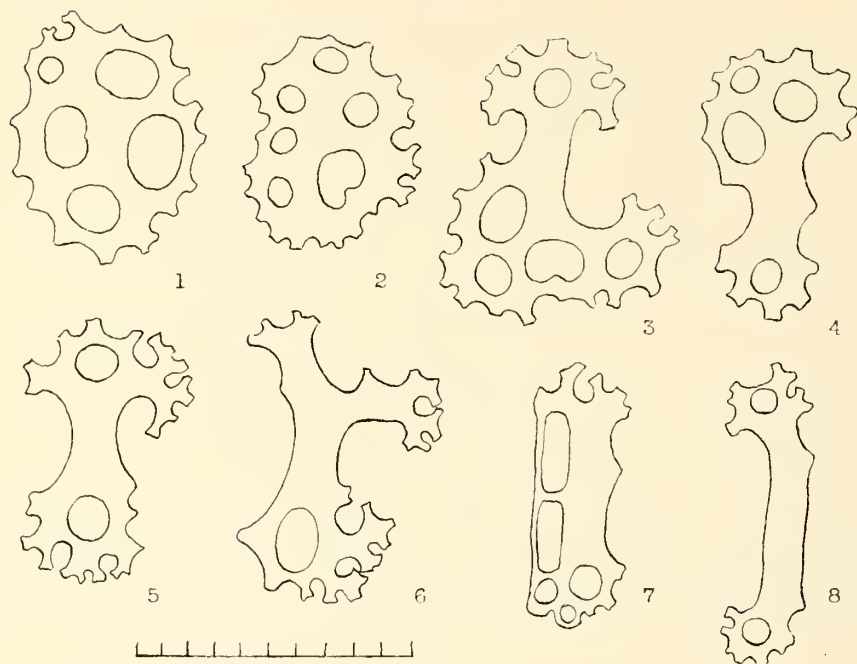
**Type Locality:** Galápagos Islands.

**General Distribution:** According to Panning (chart, p. 44) taken only in the Galápagos Islands.

**Local Range:** Nine specimens ranging from small to large, from Tower Island and Hood Island, Galápagos (*Arcturus*).

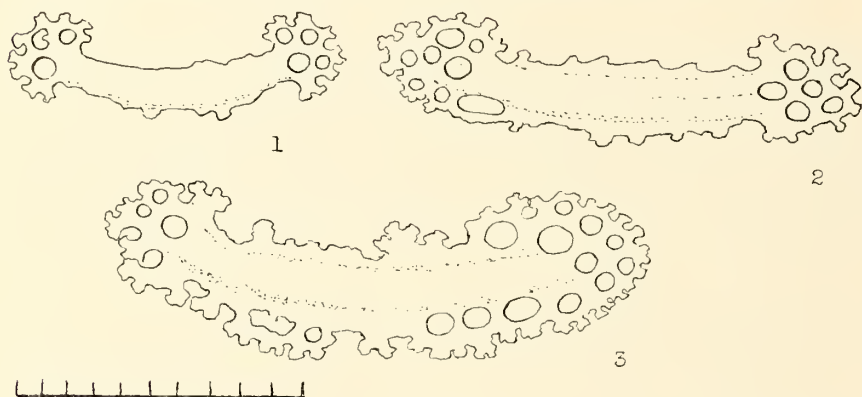
**Remarks:** Ludwig gives no figures of the spicules in his species from the Nicobars and his description may equally well refer to *H. erinaceus* Semper—a widespread form in the East Indies. Théel was the first to express his doubt whether the Galápagos specimens were identical with the typical *H. marenzelleri*.

Only examination of the types of *H. marenzelleri*, or of specimens from Nankauri, Nicobars, can decide whether two species are concealed under one name or not. Apparently there are no records of *H. marenzelleri* occurring between the Galápagos Islands and the Malay Archipelago.



Text-figure 5.

*Holothuria marenzelleri* Ludwig var. *théli* var. nov. 1-8, Typical smooth plates and rods from young individuals from Galápagos. Scale 1/100 mm.



Text-figure 6.

*Holothuria marenzelleri* Ludwig var. *théli* var. nov. 1-3, Typical rods with numerous holes and rough surface from large individuals from same locality as the small individuals figured above. Scale 1/100 mm.

It is with great hesitation that the large individuals with rather different spicules are referred to *H. marenzelleri* var. *théli*. But it is quite possible that the small smooth spicules are completely reduced and the spicules in the older individuals become large and rough.

***Holothuria gyrifer* (Selenka).**

*Stichopus gyrifer* Selenka, 1867, p. 319.

*Holothuria monacaria*, Fisher, 1907, p. 659; H. L. Clark, 1923, p. 163; 1938, pl. 16, fig. 7 (colored figure); Panning, 1934, III, p. 69, text-fig. (complete list of references).

*Holothuria* ? *patagonica* R. Perrier, 1904, p. 13.

*Stichopus* (*Holothuria* ?) *patagonicus* R. Perrier, 1905, pp. 11-17, pl. 1, figs. 1-3.

*Nec Psolus monacarius* Lesson, 1830, p. 225, pl. 76.

**Diagnosis:** Slender form, of medium length (10-5 cm.), slightly bottle-shaped, with pronounced "neck" when normally expanded. Tentacles 20, cylindrical feet small; mouth and anus terminal. Feet few, in indistinct rows; ventrally cylindrical feet, dorsally papillae. Inner anatomy rather similar to that of *H. impatiens*.

Spicules a crowded layer of tables and buttons. Tables with round disk with a complete circle of marginal holes, edge smooth, spire moderately high with four pillars and mostly one cross beam and few teeth on the top. Buttons smooth with six large holes. Ventral feet with large end plate but no special supporting rods, except for a few reticulated plates next to the end plate or the typical buttons may be slightly larger. Dorsal appendages with no end plate and besides the typical buttons a number of long curved rods with short transverse projections which often unite so they form a row of lateral holes on each side.

Color bright brown, ventrally paler; appendages white, base surrounded by a circular white area.

**Types:** M. C. Z. and Göttingen, Germany.

**Type Locality:** Hawaii.

**General Distribution:** Indo-West Pacific to Hawaii, and Gulf of California (Clark, 1923). A specimen without spicules, tentatively described as a new species, reported from Chile by R. Perrier, 1904.

**Local Range:** Two large specimens from Jasper Island, Gulf of Nicoya, Costa Rica, shore.

**Remarks:** It has been deemed advisable to change the name *monacaria* Lesson to *gyrifer* Selenka, since it is absolutely certain that the species usually called *monacaria* has nothing to do with the species which Lesson described and figured from Tahiti, while the type of *gyrifer* has been examined. It is a mystery how the present species with few appendages has been confused with Lesson's species which has numerous conical appendages on the dorsal side while the ventrum is covered by numerous cylindrical feet. What Lesson's species actually is cannot be said offhand—possibly it is a well known form and the name *monacaria* may be placed among the synonyms.

*H. gyrifer* is a most strikingly colored species (see Clark's colored figure, 1938) and it can hardly be confused with any other form. It resembles *H. impatiens* in general shape but it is more brightly colored and the skin is less rough to the touch. The spicules resemble those found in *H. arenicola*, but differ in the presence of a complete circle of holes in the margin of the disk, and the holes are often rectangular, while in *H. arenicola* the holes are more circular and frequently the marginal holes are reduced to four. Also the buttons in *gyrifer* are large while in *arenicola* they tend to become very small.

*Stichopus patagonicus* R. Perrier, from Sta. Cruz, Patagonia, is unquestionably this species. The single individual measured 5.3 cm. (strongly contracted) and the spicules were dissolved and the calcareous ring slightly corroded. Possibly it was wrongly labelled, as it is most unlikely that this tropical form should occur so far south.

***Holothuria pardalis* Selenka.**

*Holothuria pardalis* Selenka, 1867, p. 336, pl. 19; fig. 85; Fisher, 1907, p. 664, pl. 69, figs. 1, 1a-g; Panning, 1935, V, p. 3, text-fig. 106.

**Diagnosis:** Small to medium-sized form (10-12 cm.) slender, with 20 small tentacles; mouth and anus terminal; feet cylindrical, in indistinct bands, not crowded, rarely retracted into warts.

Spicules tables with reduced or low spire and small disks often composed of four holes, margin spinous. Buttons with 6-8 holes, often incomplete and frequently twisted. Feet with end plate, slightly smaller in the dorsal appendages and supported by curved supporting rods with perforated ends.

Color mottled gray, extremely variable, reminiscent of *H. arenicola* Semper.

**Type:** M. C. Z. and Göttingen, Germany.

**Type Locality:** Hawaii.

**General Distribution:** Indo-West Pacific and Galápagos Islands.

**Local Range:** Three specimens from Darwin Bay, Galápagos Islands (*Arcturus*).

**Remarks:** The specimens were kept in formalin but the spicules are well preserved and agree with those figured by Fisher.

**ORDER DENDROCHIROTA.****Family Cucumariidae.****Genus *Cucumaria* Blainville, 1834.**

For definition and diagnostic characters, see Deichmann, 1938, p. 103.

***Cucumaria californica* Semper.**

*Cucumaria californica* Semper, 1868, p. 235, pl. 39, fig. 16, pl. 40, fig. 10; Théel, 1886a, p. 9.

Nec *Cucumaria californica*, Edwards, 1910, p. 601. (= *Cucumaria fallax* Ludwig).

**Diagnosis:** Medium sized forms (about 10 cm.) with ten bushy tentacles of equal size. Skin soft, smooth; feet large, soft, completely retractile, arranged in five bands, not scattered in the interambulacra. Calcareous ring simple, single stone canal and one or two Polian vesicles.

Spicules four-holed buttons or longer oblong plates with holes mostly in two rows; surface knobbed or smooth. Feet with no end plate or a vestige and a few three-armed supporting rods. Tentacles with few plates or rods or no spicules at all. In older individuals the spicules may be almost completely lacking.

Color varying from almost black to slate-colored or almost white with dark tentacles and anterior end which always seems to be blackish.

**Type:** Possibly in Germany.

**Type Locality:** Mazatlan, Mexico.

**General Distribution:** Probably widespread in the Panamic region.

**Local Range:** Eighteen specimens from Situatanejo Bay, Mexico, shore.

**Remarks:** A well marked species which can hardly be confused with any other species described from the Panamic region.

The name *C. californica* Semper has by a curious error been applied to



a large *frondosa*-like form, *C. fallax* Ludwig, which is common in the Bering Sea. A large individual of the latter species, from the *Albatross* cruises, received in one way or another the label Galápagos. Edwards, who identified the material, assumed that the label was correct and that this species was identical with Semper's *C. californica*. He referred several of the specimens from the Bering Sea to Semper's species while other, mostly smaller, individuals from the same area, were correctly named *C. fallax* Ludwig.

### Genus *Pentamera* Ayres, 1852.

*Pentamera* Ayres, 1852, p. 207; Deichmann, 1938, p. 105.

*Diagnosis*: Small to medium sized forms (rarely more than 10 cm.); ventral tentacles small; feet long, non retractile, arranged in five bands but never scattered in the interambulacra. Calcareous ring with long posterior prolongations on the radials. Spicules two-pillared tables, or reduced derivatives of these or developed as acorn-like bodies. Feet with large end plate and numerous supporting tables usually with well developed spire, in some cases completely reduced. Tentacles with rods or plates, in some forms no spicules, at least in older individuals. Spicules usually numerous, but in some species scarce and reduced with advancing age.

*Type Species*: *Pentamera pulcherrima* Ayres.

*Remarks*: The diagnosis is here modified to include also *Pentamera chierchia* (Ludwig) and *P. zacae* sp. nov., the former with few and mostly reduced spicules, the latter with peculiar acorn-shaped bodies, as it seems unwise for the present to segregate these two forms which otherwise conform well with the typical members of the genus.

The type species seems to represent the only form in the tropical western Atlantic, while *P. calcigera* (Stimpson) is a typical form in the northern waters, of both Atlantic and Pacific, and a series of seven related species are known from the west coast of North America (see Deichmann, 1938).

From the Panamic region (and Chile) four species are known.

#### KEY TO THE SPECIES OF *Pentamera* KNOWN FROM THE PANAMIC REGION AND CHILE.

1. Spicules in skin acorn-shaped bodies, possibly derived from tables. Feet with large end plate and numerous curved supporting tables with well developed spire composed of two rods with flattened top with blunt lobes or teeth. Color white.....*Pentamera zacae* sp. nov.
1. Spicules in skin two pillared tables or derivatives of these with spire reduced .....2.
2. Spicules scarce; disk with normally four holes and spinous edge; spire low with few teeth or reduced to two knobs. Feet with large end plate and a varying number of spectacle-shaped rods with or without two knobs representing the spire. Color dark brown or black  
*Pentamera chierchia* (Ludwig).
2. Spicules numerous with well developed spire, disk with smooth edge. Feet with large end plate and well developed supporting tables with curved disk and tall or even excessively tall spire.....3.
3. Supporting tables in feet often excessively tall. Tables small with tuft of slender spines on top.....*Pentamera beebei* sp. nov.
3. Supporting tables in feet not excessively tall. Tables large with fairly stout short spines on top.....*Pentamera chiloensis* Ludwig, 1887.  
(*Syn. Cucumaria tabulata* Perrier, 1904). *Type Locality*: Chiloe Island, Patagonia.

***Pentamera beebei* sp. nov.**

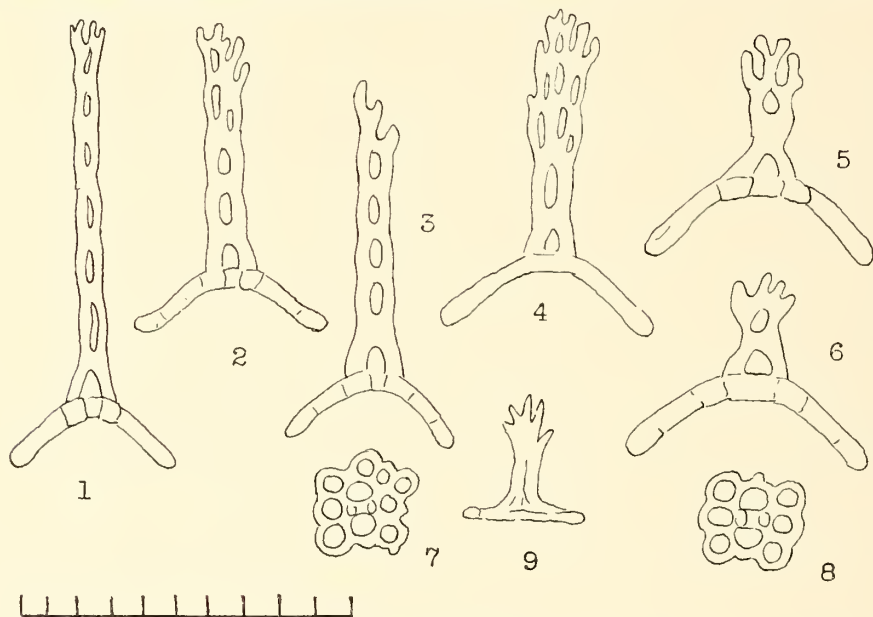
**Diagnosis:** Small form (few cm. long), externally and internally typical of the genus. Spicules minute tables with mostly four larger holes and four marginal ones; spire two pillared, ending in a tuft of slender spines. Feet with large end plate and curved supporting tables with from 2-7 cross beams in the spire which ends in a few flattened lobes or teeth. Color white.

**Type:** M. C. Z.

**Type Locality:** Ballena Bay, Gulf of Nicoya, Costa Rica, 40 fathoms.

**General Distribution:** Known from the type locality. Costa Rica.

**Local Range:** One small specimen from Ballena Bay, Gulf of Nicoya, Costa Rica, 40 fathoms (Station 213 D-15).



Text-figure 7.

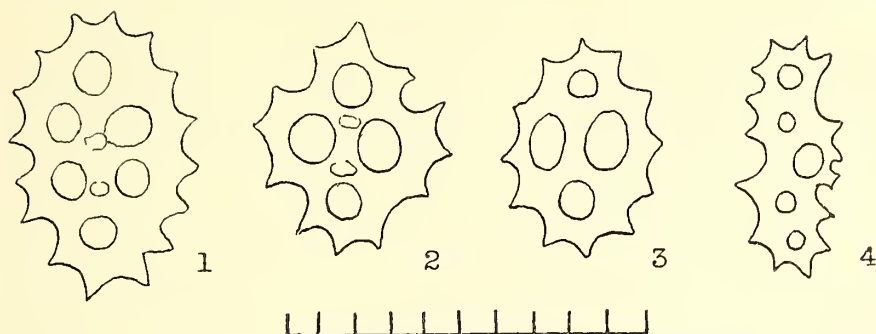
*Pentamera beebei* sp. nov. 1-6, Supporting tables of various degree of development. 7-9, Tables from integument. Scale 1/100 mm.

**Remarks:** Superficially the species resembles others of the smaller pentamerids, but the peculiar spicules set it apart from any other species known. The very tall spires may possibly disappear completely but the excessively small tables will be sufficient to distinguish it from other related forms.

***Pentamera chierchia* (Ludwig).**

*Cucumaria chierchia* Ludwig, 1887, p. 13, pl. 1, fig. 5.

**Diagnosis:** Small form (3-6 cm.), soft skinned with numerous cylindrical feet in five bands; ventral tentacles small. Calcareous ring with long posterior prolongations. Spicules present in varying number but not crowded. Tables with mostly four central holes and dentate margin; spire low, two-pillared, often completely lacking; feet with large end plate and few short spectacle-shaped rods, rarely with a trace of a spire. Tentacles with curved perforated plates and rods. Color dark brown, almost black.



Text-figure 8.

*Pentamera chierchia* (Ludwig). 1-3, Tables with reduced disk from integument. 4, Supporting rod from appendage. Scale 1/100 mm.

*Type*: Possibly in Germany.

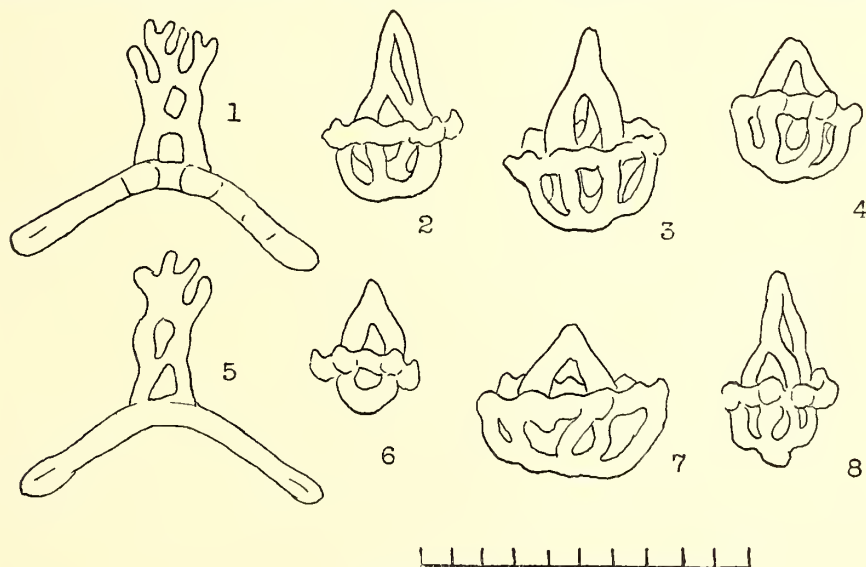
*Type Locality*: Coast of an island in the Gulf of Panama (shore; one single specimen secured).

*General Distribution*: Probably widespread in the Panamic region, in shallow water.

*Local Range*: Five from Situatanejo Bay, Mexico, shore; one from Jasper Island, Gulf of Nicoya, Costa Rica, shore; one from Port Parker, Costa Rica, 1.5-4 fathoms (Station 203 D-9).

***Pentamera zacae* sp. nov.**

*Diagnosis*: Small form (few cm. long) with body strongly curved, tapering toward both ends. Feet cylindrical, nonretractile, in five bands,



Text-figure 9.

*Pentamera zacae* sp. nov. 1 & 5, Supporting tables from appendages. 2-4 & 6-8, Acorn-shaped spicules from integument. Scale 1/100 mm.

most numerous on the ventrum, more sparingly on the dorsum and toward the oral and anal ends. Spicules form a crowded layer of peculiar small bodies resembling acorns, with a tapering spire, mostly composed of two rods and basal cup-shaped part. Feet with large end plate and numerous supporting tables with curved disk with four holes and a small hole in each end; spire with two pillars ending in few flattened lobes or blunt teeth. Color dirty white.

*Type*: M. C. Z.

*Type Locality*: Tangola-Tangola Bay, Mexico, 23 fathoms.

*General Distribution*: Known only from the type locality.

*Local Range*: Tangola-Tangola Bay, Mexico, 23 fathoms (Station 196 D-17).

*Remarks*: The tentacles and calcareous ring are lacking, but nevertheless it can hardly be doubted that the species belongs in the genus *Pentamera*.

### Genus *Thyone* Oken, 1815.

*Remarks*: The genus is extremely heterogenous and needs a revision, but the time is hardly yet ripe for undertaking the task. The type species is *Thyone fusus* (O. F. Müller), a well known form from the northeastern Atlantic with a closely related representative in the West Indies. The two species listed below undoubtedly deserve separate genera.

#### *Thyone bentii* Deichmann var. *zacae* var. nov.

*Thyone bentii* Deichmann, 1937, p. 170, text-figs. 2, 1-11 (*partim*).

*Diagnosis*: Like the typical form, from Puget Sound, but the disk of the tables seems to become more quickly reduced and large heavy rods are totally lacking in the tentacles whereas rosettes are numerous.

*Type*: M. C. Z.

*Type Locality*: East of Cedros Island, Lower California; 40 fathoms.

*General Distribution*: The variety is apparently restricted to the waters of southern California and as far south as Cedros Island. The typical form is known from Puget Sound and may be expected as far south as Point Conception, California.

*Local Range*: East of Cedros Island, Lower California; 40 fathoms (Station 126 D-17).

*Remarks*: The specimen in hand measures about 3 cm. and has its tentacle crown and calcareous ring. It resembles otherwise the larger individual which had lost these organs, from the same locality (*Zaca* 1936), except that the feet have just barely begun to spread out into the interambulacra. No gonads were developed in this small individual.

#### *Thyone gibber* (Selenka).

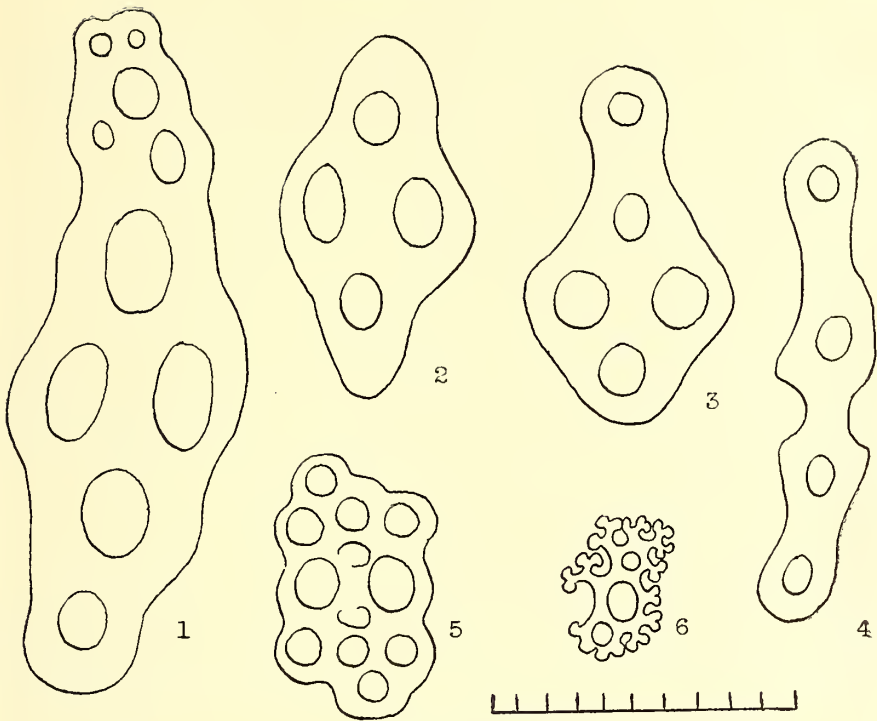
*Stolus gibber* Selenka, 1867, p. 356.

*Thyone gibber* Deichmann, 1921, p. 205, text-fig. 4; 1936, p. 64 (*passim*).

*Thyone similis* Ludwig, 1887, p. 23, pl. 2, fig. 7; Deichmann, 1936, p. 64 (*passim*).

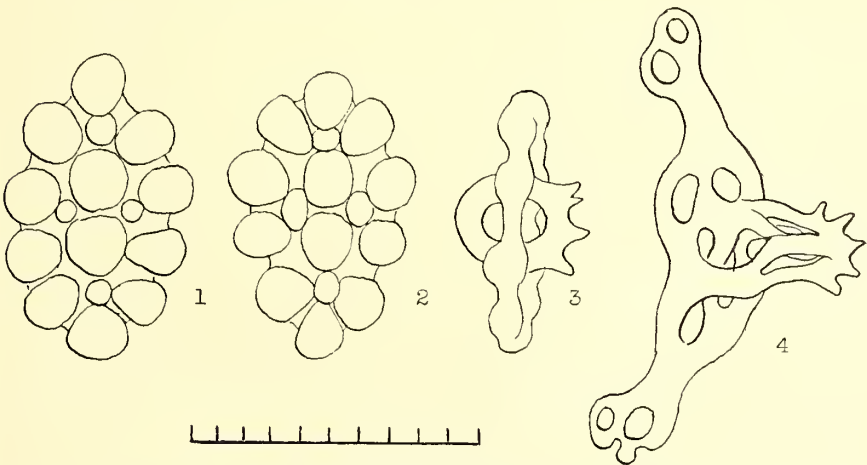
*Diagnosis*: Medium sized form (5-10 cm.), robust, with thick skin packed with spicules and numerous feet covering the entire surface of the body; tentacles large, bushy, the two ventral smaller. Calcareous ring with long posterior prolongations on the radials. Spicules regular four-holed knobbed buttons, often with the central knobs united into a handle which





Text-figure 10.

*Thyone bentii* Deichmann var. *zacae* var. nov. 1-3, Tables with spire completely reduced. 4, Supporting rod with no trace of spire. 5, Table from introvert. 6, Rosette from tentacles. Scale 1/100 mm.



Text-figure 11.

*Thyone gibber* (Selenka). 1-2, Knobbed buttons from integument. 3, Knobbed button with spinous handle, from external layer of buttons. 4, Supporting tale from appendages. Scale 1/100 mm.

on the external side of the surface spicules may carry spines. Feet with large end plate and large supporting tables with a low spire composed of several twisted rods. Introvert with two-pillared tables and disk perforated by numerous holes, almost lace-like, forming transition to rosettes. Tentacles with heavy rods or oblong plates and numerous rosettes. Color black or purplish-brown or white with tentacles and anterior part more or less black.

*Type*: M. C. Z.

*Type Locality*: Panama.

*General Distribution*: Widespread in the Panamic region, in shallow water.

*Local Range*: Four from Situatanejo Bay, Mexico, shore, (Station 186 L-1); one from Jasper Island, Gulf of Nicoya, Costa Rica.

*Remarks*: From the Panamic region only one other species is known with similar spicules, viz., *T. panamensis* Ludwig (1887, p. 22). The latter seems to lack the spines on the handles of the buttons and has no heavy rods in the tentacles. From Californian waters a smaller species, *Thyone rubra* H. L. Clark, is known. It has knobbed buttons but the entire surface of the external side of the superficial buttons is covered by a reticulum and the supporting tables have mostly large reticulated spires.

### Family Phyllophoridae.

*Diagnosis*: Dendrochirotes with 12-30 tentacles, either definitely arranged in an external circle with 10 large tentacles and an inner with 5 or 10 much smaller ones, or the two circles more or less confluent and the size and number of the tentacles variable. Feet either restricted to the ambulacra or scattered over the entire surface. They are mostly cylindrical; in some forms the dorsal appendages are conical, more papilliform. Calcareous ring simple or with posterior prolongations. Third mesentery attached in left interambulacrum.

*Remarks*: The family is at present in a state of upheaval, as are the other Dendrochirotes and it is therefore necessary briefly to summarize the history to understand the viewpoint adopted here. In this connection there are no grounds for discussing the genera in which the feet are restricted to the ambulacra as these forms are not known from the Panamic region. (For these species, see Ohshima, 1912, and Engel, 1933). Moreover they seem to form well defined genera which have given little cause for trouble.

Two genera, viz., *Thyonidium* Düben & Koren, 1844, and *Phyllophorus* Grube, 1840, have for a long time constantly been confused and most authors have in despair chosen to unite all the species in the oldest genus *Phyllophorus*. The reason for this state of affairs has been that the tentacles in the common northern species, *T. pellucidum* Düben & Koren, have either been counted as 15 or 20—never any number between these (except occasionally 16 which has been considered an abnormality). The species showed therefore apparently almost as wide a variation as in *Phyllophorus* in which the number ranged from 12 to 20, so there seemed no valid grounds for separating the two genera on account of the tentacles. The differences in the type of calcareous ring seems to have been completely ignored.

Recent studies of Heding (1936, pp. 19-26) have revealed that the five inner pairs of small tentacles in *T. pellucidum* are merely five tentacles which usually are so deeply cleft that they simulate five pairs, and were described and figured as such by Düben & Koren (1844, p. 217, pl. 11, fig. 57), and also that the full number is reached very quickly in this species (Heding, p. 22). The same has been found by the writer to be true of *T. commune* Forbes where specimens 1 cm. long exhibit the full number of tentacles (in this species five small inner pairs of tentacles). In *Phyllophorus*, on the other hand, the tentacle number remains low for a long

period. Sars describes (1857, p. 137) how specimens of *P. urna* which measure 3-4 cm. in length have only 17 tentacles, (12 external of unequal size and 5 small inner ones), and gradually more are added. The same irregularity in the appearance of the last tentacles is also noticed by Engel, 1933, so it seems to be a characteristic feature of the genus *Phyllophorus*.

In the following an attempt is made to draw the line between the genera belonging to the Phyllophoridae with feet scattered in the interambulacra. Three new genera are proposed, one to take in *Phyllophorus granulatus* Grube, one to accommodate the *Thyonidium*-like forms known from the tropical areas, and one to include the forms which have 20 tentacles in two well defined circles, as *Thyonidium*, but a calcareous ring with long posterior prolongations, as *Phyllophorus*. Furthermore Selenka's old genus *Pattalus* is re-established.

#### KEY TO THE GENERA OF PHYLLOPHORIDAE WITH INTERAMBULACRAL FEET.

1. Tentacles arranged in an external circle of five pairs of large tentacles and an inner circle of much smaller tentacles, five deeply divided or five pairs .....2.
1. Tentacles arranged in two indistinct circles, of unequal size although those in the inner circle are small, as are also some of those in the outer circle. Number of tentacles varying from 12-20, frequently 16.....4.
2. Calcareous ring tall, tubular with long deeply divided posterior prolongations and long narrow interradians.....*Neothyonidium* gen. nov.  
Type Species: *N. hawaiiense* (Fisher), 1907.
2. Calcareous ring low, with long anterior teeth but no distinct posterior tails, at most low protuberances.....3.
3. Spicules four-pillared tables which rapidly disappear with age; tentacles with perforated rods or plates, but no rosettes. Arctic and boreal forms.....*Thyonidium* Düben & Koren, 1844.  
Type Species: *T. pellucidum* Düben & Koren, 1844.
3. Spicules four pillared tables with spire often reduced to knobs or spines. Spicules sometimes reduced with advancing age. Tentacles with rosettes. Tropical forms.....*Euthyonidium* gen. nov.  
Type Species: *E. seguroensis* (Deichmann), 1930.
4. Calcareous ring low, simple. Spicules apparently plates, which are quickly reduced: Large forms, 20 cm.....*Pattalus* Selenka, 1867.  
Type Species: *P. mollis* Selenka, 1867.
4. Calcareous ring tall, with posterior prolongations.....5.
5. Feet tubular, spicules tables with two to four pillars in spire and apparently not reduced with advancing age.....*Phyllophorus* Grube, 1840.  
Type Species: *P. urna* Grube, 1840.
5. Feet partly conical, papilliform on the dorsal side.  
*Euphyllophorus* gen. nov.  
Type Species: *E. granulatus* Grube, 1840.

<sup>6</sup> Heding's proposal (1936, p. 23) to transfer *T. commune* (Forbes) to *Phyllophorus* cannot possibly be accepted. Aside from the difference in the number of inner tentacles (which may be a variable character in *T. pellucidum*), the two species differ very slightly from each other in general features, early appearance of the full number of tentacles, etc. It is a regrettable slip when Heding also states (p. 23) that the genus *Thyonidium* "usually" has many spicules, in contrast to "*Phyllophorus*" in which they disappear. Both *T. pellucidum* and *T. commune* lose their spicules very rapidly—hence the difficulty in distinguishing between the two forms (see among others Mortensen, 1927, pp. 411 and 413). But in no case is it known that the spicules disappear completely in any member of *Phyllophorus*. Sars says that the tables often are scarce in the adult individuals of *P. urna* (1857, p. 138); Théel, 1886, p. 150, mentions the presence of end plate and supporting rods in the largest individuals while tables are practically lacking. Usually careful examination of fragments of the integument reveals the presence of some tables. More important, however, is the entirely different type of calcareous ring which is characteristic of the members of the genus *Phyllophorus*.



**Euthyonidium** gen. nov.

**Diagnosis:** Medium sized forms (10 cm. long) with fairly robust feet scattered over the entire body, rarely with trace of being arranged in bands. Tentacles five large pairs in an external circle and five small pairs in an inner circle, often contracted so they are difficult to observe. Calcareous ring simple or with insignificant posterior protuberances. Spicules tables or derivatives of tables with spire reduced, often scarce in older individuals. Feet with large end plate and a few supporting rods. Tentacles with delicate rods and rosettes.

**Type Species:** *Euthyonidium seguroensis* (Deichmann).

**Remarks:** The genus represents the tropical counterpart of the northern genus, *Thyonidium* Dübén & Koren, 1844. Two species are known from the West Indies, viz., the type species and *E. occidentalis* (Ludwig). Re-examination of Selenka's *Thyone ovulum* from Acapulco, Mexico, showed a complete circle of five pairs of small inner tentacles, while a microscopical examination of the skin revealed the presence of a few tables with reduced spire—of exactly the same shape as those found in an *Euthyonidium* brought home by the *Zaca*.

**Euthyonidium ovulum** (Selenka).

*Stolus ovulum* Selenka, 1867, p. 365, pl. 20, fig. 117.

*Thyone ovulum*, Deichmann, 1936, p. 64.

**Diagnosis:** Agrees in exterior with diagnosis given for the genus. Calcareous ring with radials posteriorly deeply incised, and with long anterior tooth; interradials heart-shaped with posterior margin slightly incised. Numerous free stone canals and Polian vesicles. Spicules a scattered layer of tables with cross-shaped disk with spinous or branching edge and spire in most cases reduced to 1-4 spines. Feet with large end plate and apparently few supporting rods; tentacles with few rosettes and delicate rods. Spicules more or less completely reduced with advancing age and except for the large end plate, easily overlooked. Color reddish-brown.

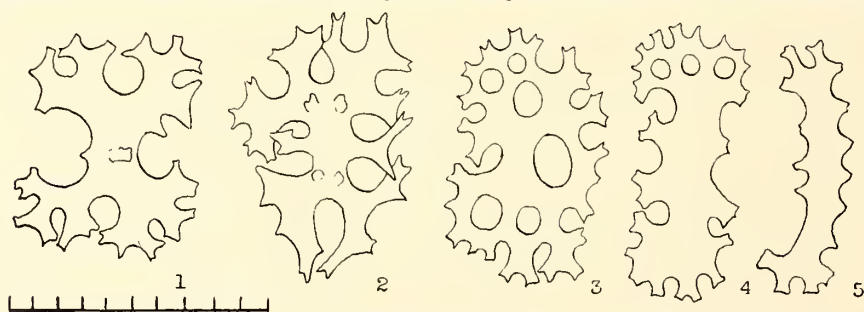
**Type:** M.C.Z.

**Type Locality:** Acapulco, Mexico.

**General Distribution:** Probably widespread in the Panamic region.

**Local Range:** One specimen from Port Parker, Costa Rica, 1.5-4 fathoms (Station 203 D-9).

**Remarks:** The *Zaca* specimen, which decidedly is a polychirote form, showed so remarkable a similarity with *Thyone ovulum* that a re-examina-



Text-figure 12.

*Euthyonidium ovulum* (Selenka). 1-3, Plates with reduced spire from integument. 4-5, Supporting rods from appendages. (From Selenka's type, M. C. Z.) Scale 1/100 mm.



tion of Selenka's material was undertaken and the presence of five pairs of small tentacles demonstrated as well as the presence of a few tables with reduced disks of the same type as those found in the *Zaca* specimen. "*Thyone ovulum*" must therefore be transferred to *Euthyonidium*. The *Zaca* material represents the first record since the types were described.

### Genus *Phyllophorus* Grube, 1840.

**Diagnosis:** Medium sized forms (rarely more than 10 cm. long) with robust cylindrical feet distributed over the entire surface and with 12-20 tentacles of different size in two indistinct circles; the last tentacles appear at intervals after the animal has reached a considerable size. Calcareous ring with distinct long posterior prolongations on the radials; interradials shorter or longer and often overlapping the radials. Spicules delicate tables; feet with end plate and sometimes a few oblong, curved supporting tables; tentacles with few delicate rods and rosettes. Spicules apparently preserved throughout the animal's entire life.

**Type Species:** *Phyllophorus urna* Grube.

**Remarks:** Defined this way the genus comprises the Mediterranean *P. urna* Grube and five of the seven species known from the tropical western Atlantic, some species from the Indo-Pacific (see Engel, 1933) and two species from the Panamic region, including the species described below. From the west coast of North America no Phyllophoridae are known (except *Thyonidium commune* Forbes; unpublished record, material in U.S.N.M.) nor has any been reported so far from the coast of Chile (except *Pattalus*). Two Phyllophoridae were described in 1907 from Hawaii by Fisher.

Not included is *P. granulatus* Grube from the Mediterranean which seems to differ in so many respects (papillae on the dorsal side and reticulated plates, etc. [see Koehler, 1927, p. 199]), that it unquestionably deserves its own genus for which the name *Euphyllophorus* is proposed.

#### KEY TO THE SPECIES OF *Phyllophorus* KNOWN FROM THE PANAMIC REGION.

1. Spicules tables with oval disk with smooth edge and 8-12 small marginal holes; spire with four pillars and ending in wreath of 8-12 spines. Feet with end plate and supporting tables with an enormous four-pillared spire ending in a long conical tooth which perforates the skin.

*Phyllophorus aculeatus* Ludwig.

(Panama, shallow water. Only the type specimen known, U.S.N.M.; Ludwig, 1894, p. 128, pl. 13, figs. 6-11).

1. Spicules tables with oval disk with four large and four smaller marginal holes, the latter more or less wedge shaped. Spire with two pillars and ending in four tufts of few spines. Feet with large end plate and few supporting tables with oval curved disk and low two-pillared spire ending mostly in two diverging spines.....*Phyllophorus zaca* sp. nov

### *Phyllophorus zaca* sp. nov.

**Diagnosis:** Medium sized form with 15 (probably up to 20) tentacles of unequal size, in confluent circles. Feet stout, distributed over the entire body, not crowded. Calcareous ring with well developed posterior prolongations on the radials; anteriorly the radials have a long rectangular tooth with a constriction at its base; interradials with broad base and short anterior tooth, and overlapping the radials. Spicules delicate tables with oval disk with four large and four smaller marginal holes, often wedge shaped, spire with two pillars, ending in four tufts of few spines. Feet with large end plate and with few oblong supporting tables with mostly oval disk

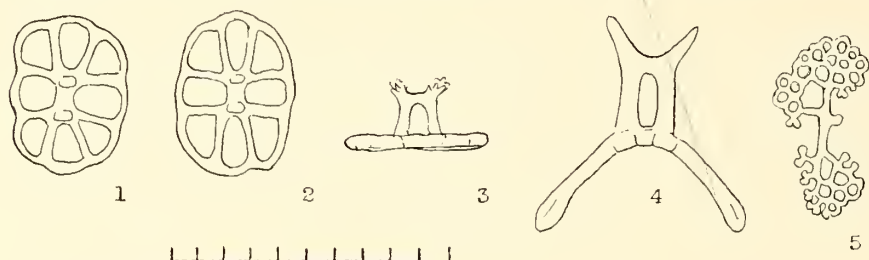
with numerous holes and a two-pillared spire ending mostly in two diverging horns or teeth. Tentacles with few delicate rods and rosettes. Color reddish.

*Type*: M.C.Z.

*Type Locality*: Tangola-Tangola Bay, Mexico, 10 fathoms.

*General Distribution*: Known only from the type locality.

*Local Range*: One contorted specimen from Tangola-Tangola Bay, Mexico, 10 fathoms (Station 196 D-13).



Text-figure 13.

*Phyllophorus zacae* sp. nov. 1-3, Tables from integument. 4, Supporting table from appendages. 5, Rosette from tentacles. Scale 1/100 mm.

*Remarks*: The species is closely related to *Phyllophorus destichadus* Deichmann (1930, p. 146, pl. 18, fig. 3) from the West Indies. It differs in the presence of supporting tables in the feet and in minor details of the calcareous ring and the spicules.

From Hawaii Fisher (1907, p. 712, pl. 79, figs. 2, 2a-c) has described a species with similar spicules but with the tentacles arranged in two distinct circles and of pronouncedly different size and with a very different calcareous ring—with long narrow interradians. For that species the genus *Neothyonidium* has been proposed.

#### Family Psolidae.

#### Genus *Thyonepsolus* H. L. Clark, 1901.

#### *Thyonepsolus beebei* Deichmann.

For diagnosis, etc., see Deichmann, 1937, p. 172, text-fig. 3.

*Local Range*: Two specimens from Situatanejo Bay, Mexico, shore; one from Jasper Island, Gulf of Nicoya, Costa Rica, shore.

*Remarks*: The specimens are larger and more robust than the single type specimen secured in 1936 from Arena Bank, Gulf of California. The present records indicate that the species occurs widespread in the Panamic region, as was to be expected.

#### ORDER MOLPADONIA.

#### Family Caudinidae.

#### Genus *Paracaudina* Heding, 1931.

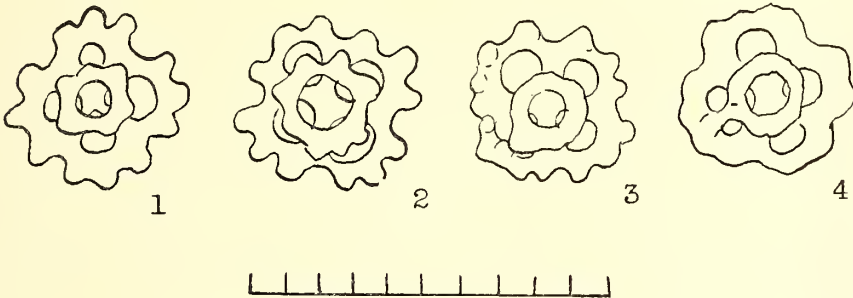
*Caudina* Auctores.

*Pseudocaudina* Heding, 1931, p. 283.

*Paracaudina* Heding, 1931, p. 455; Clark, 1935, p. 267.

**Diagnosis:** Caudinids of medium size or large (up to 20 cm.) with 15 tentacles with two pairs of digits but no unpaired terminal digit. Calcareous ring with short undivided posterior prolongation on the radials. Third loop of intestine supported by powerful pseudomesenteries attached to the lateral body walls while the normal ventral mesentery is reduced or lacking. Spicules small cross-cups or four-holed plates with spinous to lobate margin, with age degenerating into irregular deformed plates. No phosphatic bodies present but older individuals may have certain spicules surrounded by a reddish substance. Color white. Shallow water forms.

**Type Species:** *Paracaudina chilensis* (J. Müller).



Text-figure 14.

*Paracaudina chilensis* (J. Müller). 1-4, Cross-cups from *Zaca* specimen, from 35 fathoms depth.

**Remarks:** The number of species belonging to this genus has been the subject of much discussion. Clark (1935) holds that there are two Australian species with fairly simple spicules while the type species can be divided into a number of varieties which differ merely in the development of the spicules. One argument against uniting the widespread forms under one name has been the discontinued distribution of the species. It was first in 1938 that some specimens were taken between Chile, the type locality, and California, viz., off Guatemala and Mexico, (Deichmann, 1938, p. 23, text-figure) and the zoögeographic gap thereby closed. The *Zaca* expedition has furthermore secured two specimens from off Costa Rica, an indication that *P. chilensis* is by no means uncommon in the Panamic region.

***Paracaudina chilensis* (J. Müller).**

*Molpadia chilensis*, J. Müller, 1850, p. 139; 1854, pl. 4, fig. 14, pl. 9, fig. 1.

*Caudina chilensis*, H. L. Clark, 1908, p. 175.

*Paracaudina chilensis*, H. L. Clark, 1935, pp. 267-284. (discussion of the species problem). Deichmann, 1938, p. 23, text-fig.

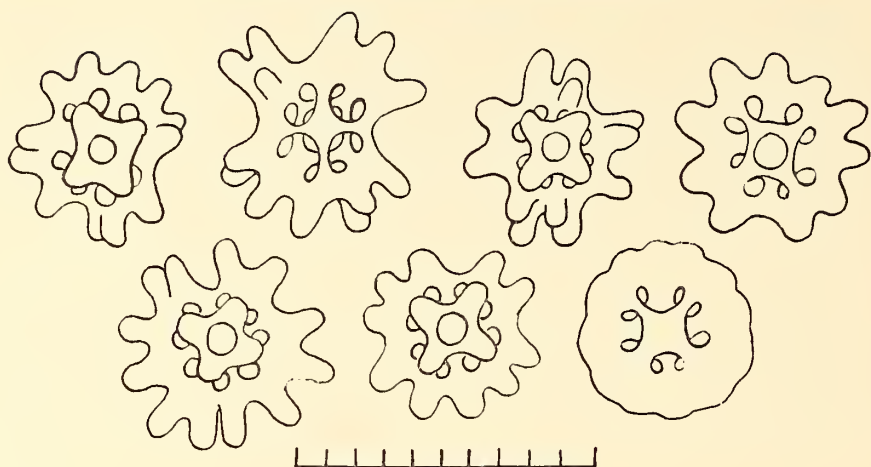
**Diagnosis:** As for the genus. Spicules numerous cross-cups with marginal projections, shorter or longer, often as rounded lobes; reduced to simple plates in older individuals.

**Type:** Museum of Berlin.

**Type Locality:** Coast of Chile.

**General Distribution:** From the Strait of Magellan, along the west coast of South, Central and North America to Japan, Coasts of China and North Australia—varieties chiefly with long marginal projections on the cross-cups; from New Zealand and West Indies—varieties chiefly with





Text-figure 15.

*Paracaudina chilensis* (J. Müller). Spicules from specimens from off Guatemala, 10 fathoms (upper row) and from off Mexico, 7 fathoms (lower row). Reproduced from Deichmann, 1938.

reduced marginal projections (this type may also occur in numbers in specimens from the west coast of Central America). Shallow water to about 40 fathoms.

*Local Range*: Two specimens, 4 and 5 cm., from Ballena Bay, Gulf of Nicoya, Costa Rica, 35 and 40 fathoms (Station 213 D-12 and D-15).

*Remarks*: The spicules selected at random from the *Zaca* material shows the extreme variability of the calcareous spicules in this species when contrasted with the figures of spicules from the specimens from Guatemala and Mexico, from respectively 10 and 7 fathoms depth.<sup>7</sup> Possibly the greater depth from which the *Zaca* material came may account for the variation of the spicules.

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<sup>7</sup> Record of depth omitted in the original report (Deichmann, 1938).



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## 19.

A Note on Eggs and Young of *Leioheterodon madagascariensis*  
(Duméril & Bibron).

ROGER CONANT

*Zoological Society of Philadelphia*

(Plate I).

The life histories of the great majority of reptiles are so poorly known that even the most fragmentary observations may be of value. Certainly herpetology, which has made extraordinary gains in the past few decades, is still far behind other fields, especially ornithology, when the lack of details on the sizes of eggs and young, etc., is considered. While I have no particular interest in the fauna of Madagascar, and scarcely know its literature, I publish this brief note in the belief that it may help to bridge the gap in our knowledge of an interesting snake. Monsieur F. Angel, of the Paris Museum, the principal worker on the Malagasy herpetofauna, in response to an inquiry, writes under date of November 13, 1937, "Je ne connais pas de travaux particuliers traitant de reproduction des *Leioheterodon*."

A large female *Leioheterodon madagascariensis* arrived at the Philadelphia Zoological Garden on May 11, 1937, in an exchange shipment from the London Zoological Gardens. On the morning of July 18, 1937, it was discovered coiled about 13 eggs which it had laid during the night. It did not move while photographs were being taken, and only slightly shifted its position when it and the eggs, which were laid on the cage floor, were covered with damp peat moss. However, it left them and lay in the rear of the cage during the afternoon, but returned to its former position in the evening. The next morning it moved away from the eggs again and, possibly as a result of being accidentally disturbed, did not approach them for many hours. They were removed, therefore, to an aquarium and buried in a mixture of slightly damp, rotten wood and peat. In this mixture they were kept, at ordinary room temperatures, until they hatched.

The eggs were adherent to one another and grouped in a single cluster. The shells were white, parchment-like and yielded slightly to the pressure of one's fingers. Small, hard nodules, slightly raised above the surrounding surfaces of the eggs, were scattered over them.

Owing to their positions in the cluster it was impossible to measure all of the eggs. The lengths, in five of them, varied from 46.1 to 50.0 and averaged 47.8 mm.; the widths, in seven, varied from 29.9 to 34.1 and averaged 32.3 mm. Their weight, as a unit, was 376.1 grams, or an average of 28.9 grams for each egg. The female was 1,483 mm. in length and weighed 926.6 grams. (All weights and measurements recorded July 20, 1937).

The first indications of hatching were observed early during the afternoon of October 16, 1937, when it was noticed that the shell of one of the

eggs had a small slit in it. Protruding from this opening was the snout of a young snake, surrounded by a mass of bubbles resembling spittle. Two hours later snouts were found protruding from two other eggs; five heads were out early in the morning of October 17 and a total of seven were visible the evening of October 18. At this time, however, none of the young snakes had yet left their shells. They seemed very wary, and even when their heads were entirely out they withdrew them inside their shells when an observer approached. Even passing one's hand over the aquarium or turning on a photo-flood lamp caused them all to retreat back into the eggs. Masses of bubbles, such as the one described above, were seen around or near each head. Some of the eggs had two or more slits in them.

The cluster of eggs and the hatching medium were examined in detail the afternoon of October 19. Two young had escaped from the shells and buried themselves in the peat. Another was out by early evening and by the next afternoon a total of six had emerged. All were very lively, sought to burrow in the peat when they were handled and one expanded its neck in a manner very similar to that employed by *Heterodon contortrix* when alarmed. All of them strongly resembled the female in coloration and pattern except that their lighter markings were more vivid.

The last of the 13 little snakes left its shell shortly after noon, October 22, and the entire brood was weighed and measured soon afterward. The figures obtained are as follows:

Snake	Weight	Length
1.	18.2 grams	324 millimeters
2.	19.1 "	335 "
3.	18.3 "	336 "
4.	20.3 "	343 "
5.	19.0 "	337 "
6.	18.7 "	339 "
7.	16.2 "	314 "
8.	18.2 "	343 "
9.	19.4 "	348 "
10.	18.1 "	337 "
11.	19.5 "	338 "
12.	19.8 "	342 "
13.	18.0 "	334 "
Average	18.68 "	336 "

With a single exception the eyes of all of the little snakes were over-cast, indicative of an approaching moult. In the snake with clear eyes, and one of the others, egg teeth were still in place; all the rest had lost them. This was the only time during the entire hatching period that any egg teeth were observed, although the snouts protruding from all the top-most eggs were examined several times with a lens. The two young in which egg teeth were seen must have come from eggs lower in the cluster and must have been among the last to hatch. One specimen shed its skin on October 27, two on October 28, seven on October 29, two on October 30 and one on October 31.

Attempts to feed the small snakes were almost 100% unsuccessful. They consistently refused to eat the small frogs, baby mice, earthworms, insects, etc., which were put in their cage, except as indicated in the following notes: One snake seized a frog by the head but let go and lost

all interest when the frog kicked its legs. Specimens refused the legs of freshly killed frogs. Two started to swallow them when they were forced into their mouths but rejected them almost immediately thereafter. One snake chased a young mouse and caught it by the tail. It attempted to constrict it, but instead coiled around its own body. The mouse was removed, killed, returned to the cage and wiggled by the fingers. The snake constricted it and started to swallow it tail first but gave up the job before the mid-point of the body was reached. One little snake pursued a small, green frog, *Rana clamitans*, seized it, but let it go at once. Another snake caught it and swallowed it.

In contrast to the lack of interest in food displayed by the young snakes, the adult female has thrived in captivity and has accepted several kinds of animals as food. She has eaten *Rana clamitans*, *Rana pipiens*, *Rana catesbeiana*, white mice, rats and baby chicks. Small prey she seizes and swallows as it struggles; larger animals are constricted.

The several specimens of *Leioheterodon* were noticeably similar to *Heterodon* in several respects. The keeled and turned up rostral, the robust body and the habit of flattening the neck (noticed in the female and several young of the group) are all suggestive of the hog-nosed snakes. In no case, however, did the specimens of *Leioheterodon* keep their necks in the flattened position for any length of time, as is such a common habit with *Heterodon*. They returned to their normal positions almost at once. This may have been due to captivity, however, for in *Heterodon* captive specimens usually fail to perform after one or two demonstrations.

I wish to express my indebtedness to Mr. Arthur Loveridge, Dr. Howard K. Gloyd and Dr. E. R. Dunn for helpful suggestions during the preparation of this manuscript.

#### SUMMARY.

1. Thirteen eggs, averaging  $47.8 \times 32.3$  mm. in length and width, and 28.9 grams in weight, were laid by a specimen of *Leioheterodon madagascariensis* in the Philadelphia Zoological Garden, July 18, 1937.

2. The eggs started hatching 90 days later and the last of the brood left its shell 96 days after the eggs were laid. The young snakes averaged 336 millimeters in length and 18.68 grams in weight.

3. The young snakes showed little interest in food although one ate a frog and one started to eat a mouse. The female ate frogs, rats, mice and chicks.

## EXPLANATION OF THE PLATE.

## PLATE I.

- Fig. 1. Female *Leioheterodon madagascariensis* coiled around her clutch of thirteen eggs a few hours after they were laid.
- Fig. 2. Eggs of *L. madagascariensis* hatching. The snouts of two of the baby snakes may be seen protruding from the shells. A third is visible beneath the slit in the shell of the right-hand egg. Photographs by Mark Mooney, Jr.





FIG. 1.



FIG. 2.

A NOTE ON EGGS AND YOUNG OF *LEIOHETERODON MADAGASCARIENSIS*  
(DUMÉRIL & BIBRON)



## 20.

## An Unusual Aberrantly Colored Pleuronectid.

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*New York Aquarium.*

(Plate I).

Abnormal coloration in the Heterosomata has been under study by Gudger and Firth for some time and in their records they have included an analysis of the earlier literature. See Gudger (1934 and 1935) and Gudger and Firth (1935, 1936a, b, c, and 1937). The case here recorded (A.M.N.H. 14142) differs from any described by them in certain interesting respects.

This specimen, a nearly ripe female, *Pseudopleuronectes americanus* (Walbaum), measures 195 mm. in standard length and 244 mm. in total length. It was caught by Mr. William Stratton near Bayside, Long Island, on November 8, 1938, and sent to the New York Aquarium through the courtesy of Mr. Fred Fletcher.

The abnormality in coloration amounts to a complete absence of pigmentation on the upper side of the body. The vertical fins, however, are normally pigmented, although in the state of preservation received (iced) seemed to represent a pale phase, a feature not uncommon to iced fish in a fairly soft condition. The pectoral fin of the upper side is pigmented, as are both the pelvics, while the pectoral of the lower side is without pigment as is normal in this species. All the pigmented fins are encroached upon with varying pigmentless areas at their bases.

The head is also without pigment on the upper side, except for the protruding parts of the eyes and a small triangle between and ahead of them, which, however, does not reach the lips. The eyes themselves are normally pigmented. This fish, then, represents a reversal of the more usually reported abnormal color differential in which the dark pigment of the upper side appears on the normally white lower surface. There is here a pretty problem in the dynamics of coloration involving the inverse of those dark on the normally white lower side.

There is no evidence of a hooked dorsal or other morphological anomaly sometimes associated with atypical coloration in these fishes. There is, however, a very evident traumatic peculiarity. As though it were not enough alone for this specimen to grow to maturity, it clearly survived and healed perfectly what appears to have been a bite out of the middle of its back. Such healed injuries are common enough in fishes generally, there usually being one or more such specimens present in the collections of the New York Aquarium. These arrive along with other fishes and are generally not placed on exhibition for obvious reasons. This particular case is, however, of unusual interest since it raises the question of the protective value of flounder coloration. Specimens of this species, along with flounders generally, are extremely inconspicuous as they lie on the sea floor. Not



only do they blend well with the bottom colors, but actually go through extensive color and pattern changes in which the tone and texture of their surroundings are very closely approximated. See, for example, Sumner (1911) and Mast (1916). In addition to, or in spite of this, they further hide themselves, when the nature of the bottom permits, by causing a flurry in the sand or mud in which they then sink so that only their eyes protrude. Such being the case, it might be inferred that since the present individual was white on the top side, it became an easy mark. To offset this conspicuousness it may be imagined that it buried itself deeper than others so that most of the time only its *pigmented* eyes protruded. However, as a matter of fact, the greatest hazard to these flat fish occurs when they are swimming, for even the normally colored ones can then be easily seen, and, indeed, even when buried they are frequently caused to swim by larger fishes rooting in the bottom, presumably to dislodge them.

This sketch of flounder life and hazards is given merely as a background against which to point out that in spite of the normal hazards of all flatfish, this one without the alleged protection of changeable coloration and the fact that something did bite a chunk out of it, nevertheless grew to adulthood. It will be noted that this is all that is necessary for survival. This fish may have spawned last winter, or at least could have this winter if it had not suffered the fate of so many Long Island flounders—one not in the least associated with *any* of its individual peculiarities.

Lest it be thought that perhaps its injury was in some way connected with a decoloration of the upper surface, it may be pointed out that the writer, as already indicated, is more than usually familiar with injuries of this sort because of circumstances, and that in no case known to him is there any instance where abnormal pigmentation followed even vastly greater injuries. See, for example, figures of other similar injuries in Breder (1925 and 1934). It may be noted in Plate 1, along with the other items discussed, that the pigmentation of the fin adjacent to the wound is normal and in the pigmentless areas scales have covered the area of the wound.

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1936b. A reversed, almost wholly ambicolorate summer flounder, *Paralichthys dentatus*. *Amer. Mus. Novitates* (896): 1-5.

1936c. Ambicoloration, partial and complete in the southern flounder, *Paralichthys lethostigma*. *Amer. Mus. Novitates* (897): 1-7.

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## EXPLANATION OF THE PLATE.

*Abnormal Pseudopleuronectes americanus.*

Fig. 1. Eyed or upper side.

Fig. 2. Blind or under side.

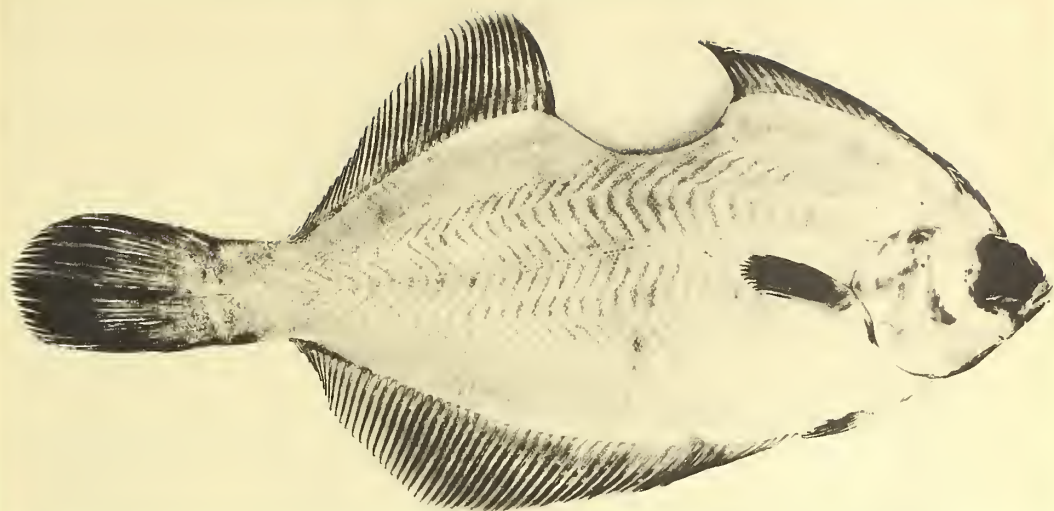


FIG. 1.

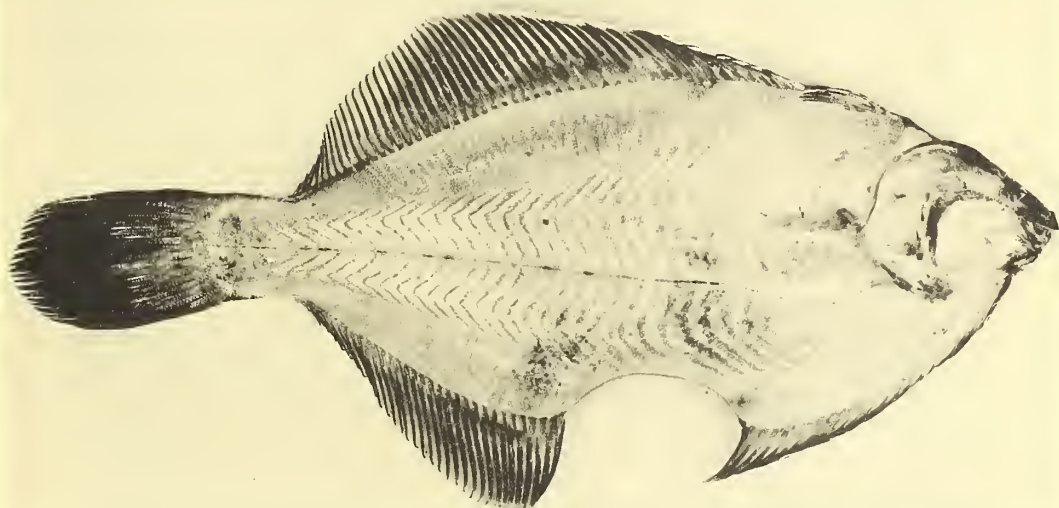


FIG. 2.

AN UNUSUAL ABERRANTLY COLORED PLEURONECTID.





## 21.

A Diagnostic Test for the Recognition of Tuberculosis  
in Primates; a Preliminary Report.

CHARLES R. SCHROEDER

*Veterinarian, New York Zoological Park.*

(Plates I &amp; II).

A practical and simple test which might be applied to captive Primates for the early recognition of tuberculous infection is urgently needed (Schroeder, 1938). Tuberculosis was recognized as a disease to be coped with in the late 1890's in many zoological gardens. Recently the wholesale use of the Rhesus Macaque (*Macaca mulatta*) by laboratories has further shown the immediate need for a test applicable to large groups of newly imported monkeys. Penrose, White, Brown and Pearson, of the Penrose Laboratory of the Philadelphia Zoological Society, adapted to monkeys the test used in dairy cattle by the Bureau of Animal Industry (Fox, 1923). The test was used successfully at the Philadelphia Zoological Garden by these early workers. Their successful results were continued in the hands of White and Fox (White & Fox, 1909). Alterations and improvements in the test were made which depended upon a thermal response to an injection of K.O.T. The interesting discovery by early workers, indicating that Primates have a wider diurnal temperature variation than most other animals, made it imperative to record pre-injection temperatures so that an increase subsequent to the injection of tuberculin could be properly evaluated against the pre-injection graph (Simpson & Galbraith, 1906).

The Bureau of Animal Industry early recognized the necessity of altering its test, which was dependant on a regular systemic temperature rise following the subcutaneous administration of tuberculin. It was necessary to simplify it and make unnecessary the detailed taking and recording of temperatures on which depended the accuracy of the test. They adopted the intradermal test, at first in conjunction with the ophthalmic installation of tuberculin, later with a dual intradermal test (caudal fold and vaginal labia), and finally with a single caudal fold intradermal injection which has given best results because of its simplicity. The subcutaneous test is still admittedly accurate.

European investigators have done some work but nothing on a sufficiently large scale to be conclusive. The complete bibliography of Primate tuberculosis prepared by Dr. Margaret A. Kennard of Yale University School of Medicine gives no clew to a satisfactory test, in Europe or elsewhere, for laboratory animals.

A modification of the Bureau of Animal Industry's intradermal test in cattle has been evolved in the New York Zoological Park for use in monkeys.<sup>1</sup>

<sup>1</sup> The author wishes to acknowledge the assistance given by Dr. N. D. C. Lewis and Dr. S. E. Barrera of the New York State Psychiatric Institute for permitting the routine testing of incoming Rhesus monkeys; Dr. Herbert Fox of the Penrose Laboratory of the Philadelphia Zoological Society, Dr. Jacob Traum of the University of California, Dr. A. R. Dochez and Dr. F. S. Cheever of the Presbyterian Hospital, College of Physicians and Surgeons, Dr. Margaret A. Kennard of the Yale University School of Medicine and Dr. Clarence Carpenter of Columbia University for their timely aid and cooperation; and Dr. Florence B. Seibert, who prepared and donated the tuberculin used.

## SITE OF INJECTION.

A simple site for injection, easily available in all Primates and readily seen, was to be selected. For intradermal testing, the skin on the back proved most satisfactory, but required shaving and would necessitate handling the monkey to read the test (monkeys usually face an observer and the shaved area could not easily be seen without handling). The belly and thighs, by repeated trials, would not permit easy intradermal administration. The tuberculin usually broke through to the subcutaneous tissues and rapidly spread. The eyelid was a location easily seen, which could be readily approached, and has remained our choice of site for the injection.

## THE TUBERCULIN.

It seemed important to select a tuberculin which could be prepared in great concentration, so that when the injection was made the greatest dose of sensitizing agent per cell could be given (Sabin & Joyner, 1938). It is a well-known fact that monkeys do not react allergically to proteins as well as humans or domestic animals (Kopeloff & Kopeloff, 1938). In addition, a tuberculin was required which would be standard wherever used, and one which would not lose potency. We selected Purified Protein Derivative as prepared by Dr. Florence Seibert of the Henry Phipps Institute of the University of Pennsylvania because it best met these requirements<sup>2</sup> (Seibert, 1934).<sup>3</sup> It was necessary to use a tuberculin for the first test which would have sufficient concentration to bring down all reactors, regardless of severity of reaction. The final tuberculin used, which proved to be quite harmless to all non-tuberculous Primates, was a 1% solution of P.P.D. (0.1 cc. = 1 mgm. P.P.D.).<sup>4</sup> (Human type of organism is usually demonstrated).

## THE TEST.

The animal to be tested is restrained by placing its arms behind it, legs extended. It is placed on its back, head extending over the edge of a bench or table, arms pulled down over the edge of the table at a right angle to the long axis of the body. The operator approaches from behind and grasps the head in the left hand. A 1 cc. tuberculin syringe and  $\frac{3}{8}$ -inch 27-gauge needle is used. The syringe is held in the right hand, the needle inserted (bevel up) just under the skin in the upper lid of the right eye close to the margin. One-tenth cc. of the tuberculin is injected. This quantity will leave a lentil-size raised area. The operation is simple and not hazardous for attendant, operator or monkey. The specimen is placed in a cage and observed, without further restraint, after 16 hours. A reaction will usually begin to make its appearance at this time in a tuberculous monkey, and persist for 72 hours, depending upon the severity of the reaction. Primates too large for usual manual restraint can be anesthetized with Nembutal (29 mgm. per kilo, intraperitoneally).

## INTERPRETATION OF THE TEST.

A positive reaction consists of edema of the lid with redness and, on rare occasions, a small area of necrosis. The extent of the reaction is immaterial. All reacting monkeys should either be destroyed or used for short-

<sup>2</sup> In a personal communication from Dr. Florence B. Seibert the following data on the stability of P.P.D. were offered: "We have found that a 1% P.P.D. solution kept in the incubator at 37.5° for one month loses no potency. Furthermore, a 1% P.P.D. solution kept in the icebox for nearly 5 years has lost very little potency."

<sup>3</sup> Some laboratories are using O.T. (Human) 0.1 cc. = 1.0 mgm. tuberculin (= 0.2% P.P.D.).

<sup>4</sup> No systemic reaction was demonstrated in non-tuberculous Orang-utans, Chimpanzees, Gorillas, Gibbons, Baboons, the Macaques, Mangabeys, the more delicate Douracoulis and the related New World monkeys.

time experiments. Those monkeys having active, advanced clinical disease will often succumb to this test dose of 1 mgm. P.P.D. In early or terminal infections the monkey may not react. In terminal infection, the tuberculin will either kill the specimen or bring about a profound systemic reaction, in which event it should be destroyed. Retesting after two months is important to detect infection in those specimens which did not have sufficiently advanced disease at the time of the first test to produce a reaction.

#### DISCUSSION.

The test as presented leaves much room for further experimentation. It has proved to be quite satisfactory, however, and is being used routinely in some laboratories and zoological gardens. Recently the author, with one assistant, tested 15 Rhesus monkeys in a laboratory in 35 minutes. This period of time included catching the monkeys, injecting the tuberculin, and returning the animals to their cages. The following day the readings were made simply by observing the monkeys in their cages. The value of such a test can be determined only by extensive trial to accumulate experience, statistics on a large scale, so that correlation of tuberculin tests and autopsies can be made.

Probably 90% of Primate tuberculosis is acquired between time of capture and delivery to the final user of the specimens (Schroeder, 1937). Testing at origin, before shipment, will eliminate the ultimate planting of tuberculosis in all monkeys shipped in the same crate with a tuberculous specimen. When laboratories and zoological gardens demand tuberculosis-free monkeys from commercial distributors, tuberculosis in Primates will no longer be a problem.

#### CONCLUSIONS.

1. Monkeys will react locally to concentrated tuberculins.
2. The site of injection is the subcutaneous tissue at the margin of the upper eyelid.
3. The allergin used is 1/10 cc. of a 1% solution of Purified Protein Derivative tuberculin (0.1 cc. = 1 mgm. P.P.D.).
4. Reactors show swelling and redness of the lid, visually evident without removing the specimens from their cages, in 16 hours, and persisting for 72 hours.

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## EXPLANATION OF THE PLATES.

### PLATE I.

- Fig. 1. Manner of restraining monkeys weighing up to 10 kilos, for injection of tuberculin. Larger specimens should be anesthetized. When the operator touches the eyelid with the needle the monkey usually closes his eyes, which facilitates the proper administration of the tuberculin.
- Fig. 2. The 27-gauge needle, attached to a 1 cc. Luer end tuberculin syringe, is inserted bevel up in the lid near its lower margin, and 0.1 cc. is administered.

### PLATE II.

- Fig. 1. An average reaction consists of edema with or without apparent redness. The edema prevents the specimen from completely uncovering the pupil. Such a reaction can be recognized without restraining the specimen for close observation. Some reactions are more intense, with pronounced redness involving adjacent structures and edema which may close the eye.

Photographs by Hans Gehrung, N. Y. State Psychiatric Institute.





FIG. 1.



FIG. 2.

A DIAGNOSTIC TEST FOR THE RECOGNITION OF TUBERCULOSIS IN PRIMATES;  
A PRELIMINARY REPORT.





FIG. 1.

A DIAGNOSTIC TEST FOR THE RECOGNITION OF TUBERCULOSIS IN PRIMATES;  
A PRELIMINARY REPORT.





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*Names in bold face indicate new genera, species or varieties; numbers in bold face indicate illustrations.*

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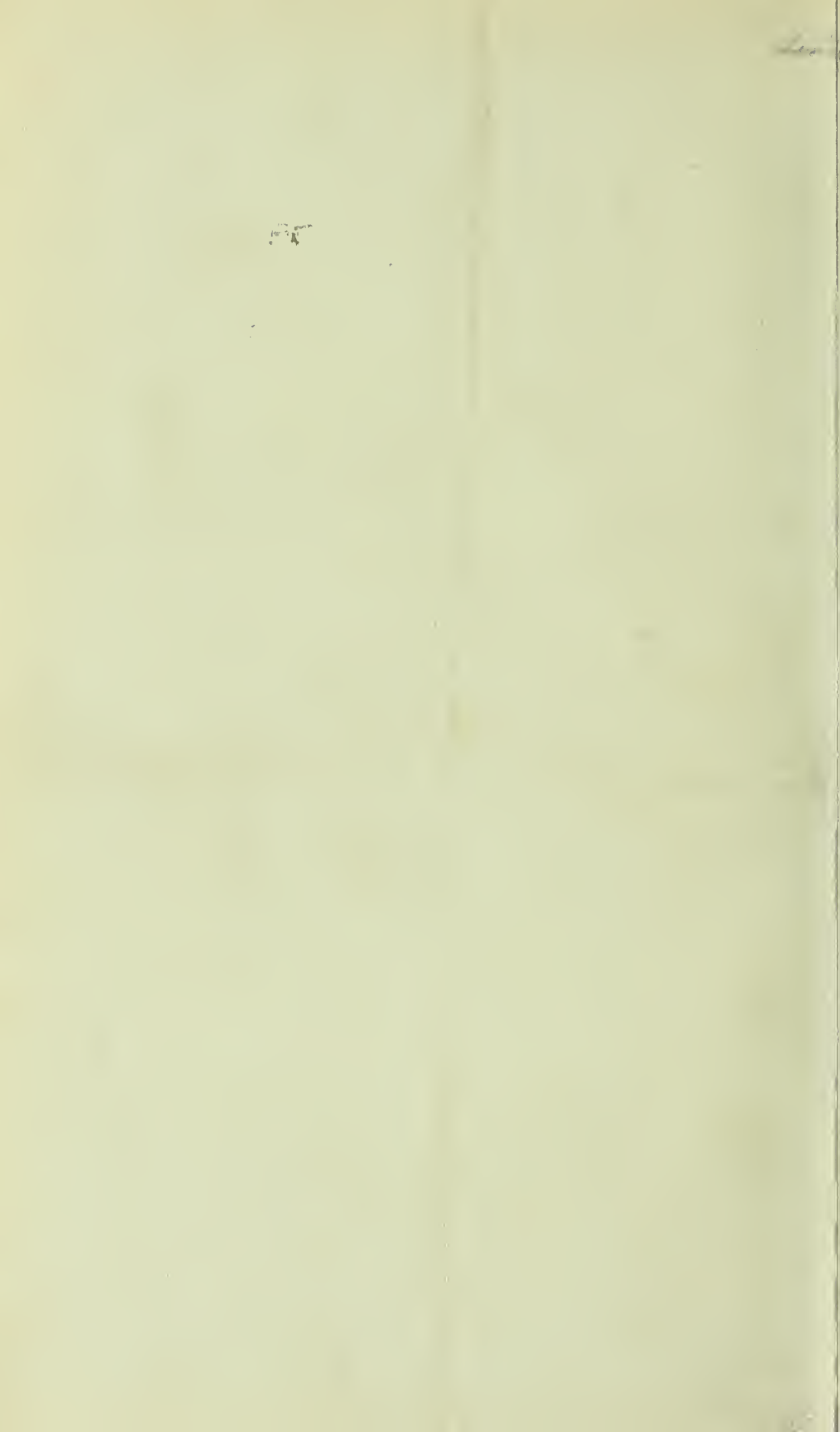
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