STUDIES ON THE POSTEMBRYONIC DEVELOPMENT OF THE FAIRY SHRIMP *STREPTOCEPHALUS SEALI* RYDER

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CONTENTS

I. Introduction

The subclass Branchiopoda is one of the most remarkable among freshwater crustaceans. They not only have an unusual morphology and life history, but exhibit some primitive and some advanced characters.

Claus (1873, 1886) described the morphology and a few developmental stages of *Branchipus stagnalis.* Spangenberg (1875) described the adult morphology of *Branchipus stagnalis* and development of the egg up to hatching. Packard (1883) gave a detailed description of the adult fairyshrimp, with brief notes on the developmental stages of several species of fairyshrimps; Sars (1896) worked mainly on the adult morphology of *Branchinecta paludosa* but described an incomplete series of larval stages. Shantz (1905) gave a brief description of the telson, cercopod, and the antenna of the male of *Branchinecta coloradensis.* Oehmichen (1921) provided a rather complete description of the external morphology of the head appendages of *Branchipus grubei,* but gave no information concerning their internal morphology. Heath (1924) gave a brief account of almost all the larval stages from nauplius to adult of *Artemia salina* and *Branchinecta occidentalis,* but with no description of the internal structures. Furthermore his studies were based mainly on random field collections. Cannon and Leak (1933) and Lowndes (1933) briefly discussed postembryonic development of the internal systems of *Chirocephalus diaphanus* and gave a good account of the external morphology of mouthparts and their use in feeding. Hsŭ (1933) worked mainly on the structure of adult *Chirocephalus nankinensis,* but also gave a brief morphological description of the larval stages. Linder (1941), besides giving a good account of the taxonomy of fairy shrimps discussed briefly a few morphological and developmental points. Dexter and Ferguson (1943) on *Eubranchipus serratus,* and Coopey (1950) on *Eubranchipus oregonus* published brief descriptions of morphology and life history. Preuss (1957) provided a fairly good description of the musculature of the thoracic appendages of *Chirocephalus grubei.* Nourisson (1958) published a brief description of the postembryonic development of the thoracic appendages of *Chirocephalus stagnalis.* Pai (1958) published a brief comparative description of the postembryonic development of three representatives of the subclass Branchiopoda.

II. Materials and Methods

Adult *Streptocephalus seali* were collected at Alton, Louisiana, on U.S. hwy. 11 about 4 miles north of Slidell. Most of the collections were made from two ditches located in the pine forest about 400 yards apart. The specimens were brought into the laboratory and 20 mature pairs were kept, one pair per dish in culture dishes having a diameter of four inches and containing pond water. They were fed with two drops of yeast suspension every other day. After three to four days eggs were laid at the bottom of the dishes. The eggs were removed and stored in small glass vials with a few drops of pond water for four to eight weeks. Hatching took place in distilled water; but, after hatching, pond water of the same volume as the distilled water was added to the dish.

The larval stages hatched in the laboratory were preserved at regular intervals in Zenker's fluid. Dissections were made in pure glycerine. Sections of the thoracic region and the abdomen were cut at 10 to 12 microns and stained with modified Van Geison's stain. The figures were made with the help of a camera lucida and drawn with black India ink.

III. Postembryonic Development

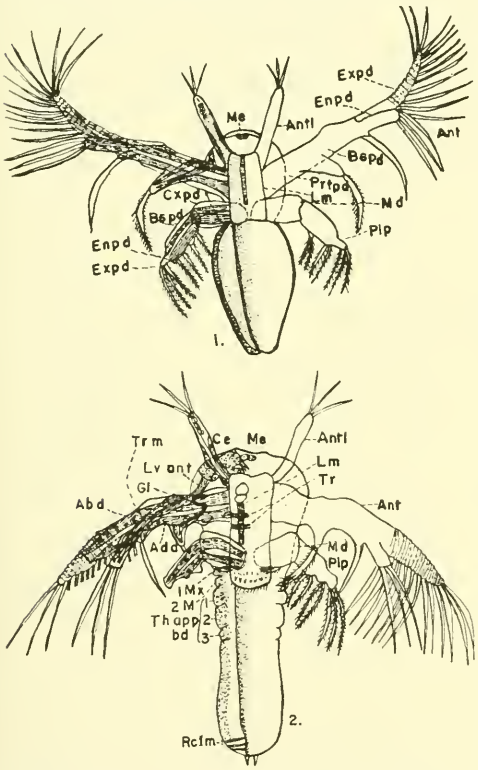
A. General Features

Heath (1924) described larval stages on the basis of the number of ecdyses. In the present study, after several attempts, the exact number of ecdyses could not be determined accurately. Following Weisz (1947) my descriptions of the various stages were based on the number of body segments with reference to the length of the body.

The egg and its hatching process.—The spherical egg varied from 0.20 to 0.31 mm in diameter (average 0.26 mm). They were yellowish-brown in color, with numerous ridges and furrows on the external surface.

During the hatching process, the nauplius of *Streptocephalus seali* made its way out of the egg shell in a way similar to that described by Myint (1956) for *Artemia salina.* A few hours before hatching the shell cracked and the nauplius, enclosed in two very thin transparent membranes, bulged

out. During emergence the posterior part of the nauplius showed jerky movements and the appendages moved vigorously over a limited range at regular intervals. Due to these movements the larva became free from the shell at the head end and released itself from the shell. The fully emerged larva was still enclosed within the inner membrane that was twisted and remained attached to the hind end of the outer membrane on one side and the inside of the shell on the other side. Due to twitching movements of the trunk and jerking of the appendages, the outer membrane broke open at the anterior end. This caused the inner membrane, with the nauplius enclosed, to move out and shifted the outer membrane posteriorly. The function of the two membranes may be as explained by Myint (1956). The out membrane (called emergence membrane) when burst helped move the larva for emergence, and gave a leverage point for the larva to pull out from the inner membrane. At the same time the larva was still inclosed within the inner membrane (called hatching membrane) which helped the larva to become free.



Figures 1-2. 1. Ventral view of nauplius; right side showing musculature; left side showing external features. 2. Ventral view of second larval stage; right side showing musculature; left side showing external features.

First larval stage or nauplius (fig. 1).—The free-swimming larvae hatched after 20 hours in the culture dish. Nineteen nauplii ranged from 0.24 to 0.46 mm (average 0.38 mm). The body was divided into two distinct regions, head and trunk. The head possessed three paired appendages: uniramous antennules, biramous antennae, and biramous mandibles. The head was larger than the trunk region and was covered dorsally with a round, plate-like structure, the dorsal (nuchal) organ. This covered the whole dorsal area of the head and continued posteriorly up to the bases of the antennae. The anterior part of the head bore a single pigmented median eye. At this time there was no indication of the paired compound eyes. On the ventral side and between the bases of the antennules and the antennae, a large labrum was directed from the head towards the trunk. It was elongated with a round distal margin and covered the mouthparts and a part of the postcephalic region.

The trunk (postcephalic part) was oval and elongated and had no segmentation or appendages. At its posterior end an anal invagination was noted. On either side of the anal opening there was one lobe consisting of the anlagen of the setae, but there was no external indication of the setae.

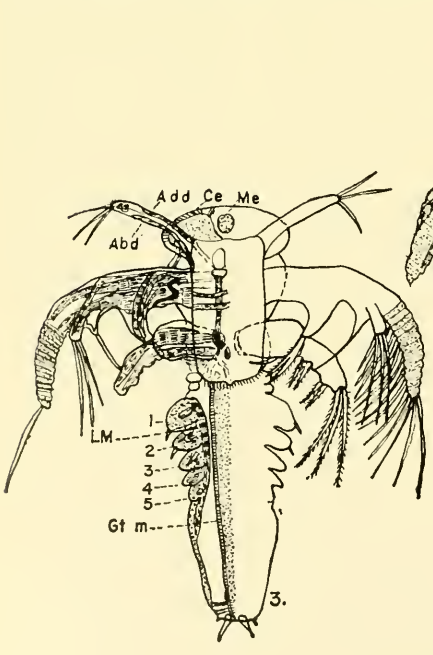
Second larval stage or metanauplius (fig. 2).—After the growth of the nauplius for 19 hours (or, after 39 hours from the time of immersion of the eggs) five segments were added posterior to the mandibular segment including two maxillary segments in the five added segments. Sixteen specimens ranged from 0.49 to 0.60 mm (average 0.55 mm) in length. The antennules and the antennae were more elongate than in the previous stage. The anlage of the paired compound eyes appeared on the anterolateral part of the head. The posteriorly directed labrum was reduced in length to the extent of just covering the mandibles, leaving the anlage of both maxillae uncovered. The first three thoracic segments were distinguishable. Heath (1924) in *Branchinecta occidentalis* observed eight thoracic segments in the second instar, but I observed only three segments with a minute seta on the

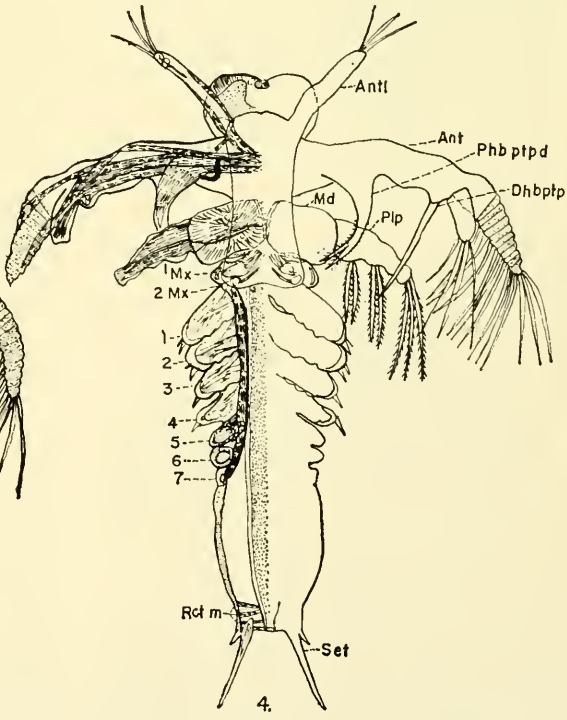
anterior end of each of the first two. The caudal setae developed one on either side of the anus.

Third larval stage (fig. 3).—Seven hours after the previous stage (or, 46 hours from the time of immersion of the eggs) eight specimens ranged from 0.67 to 0.83 mm (average 0.74 mm) in length. In the head region the paired compound eyes became more prominent and pigmented. The maxillae developed into conical structure, but both pairs were still devoid of setae. The first six thoracic segments with anlagen of the appendages appeared; five had one seta each on the distal end (future flabella). The abdominal segments were not yet differentiated. The caudal setae became longer and stouter. In other structures of this stage, no apparent change was observed.

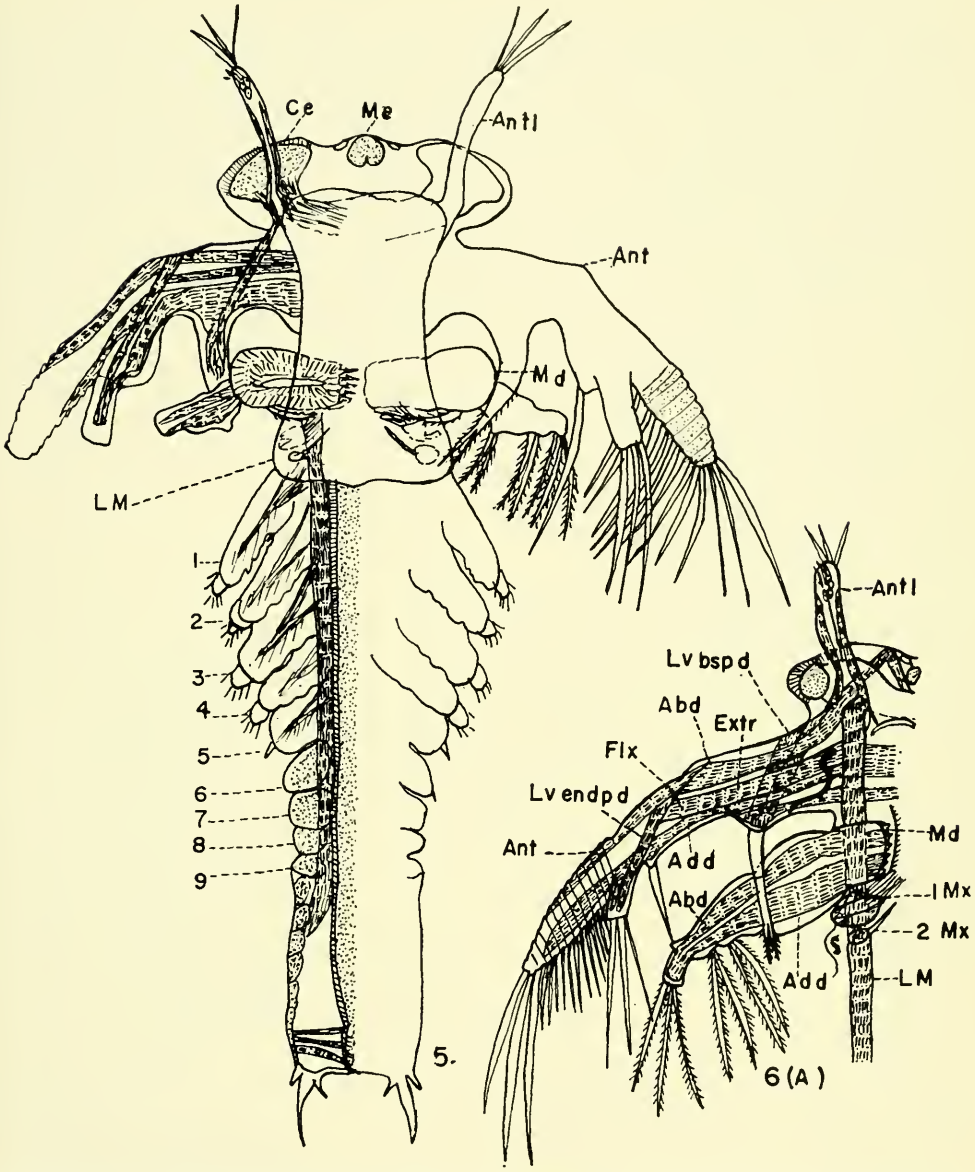
Fourth larval stage (fig. 4).—Nine specimens of the 56-hour stage, from the time of immersion of the eggs, ranged from 0.81 to 0.90 mm (average 0.86 mm) in length. In the head region the paired compound eyes showed rudimentary development of the eyestalks and became more pigmented. There was no apparent change in the first three head appendages. Both pairs of maxillae became more adult-like but were still without setae. The first seven thoracic segments were clearly differentiated. Six showed the development of appendages in a rudimentary stage with setae on the rudimentary flabella. The appendages also showed distinct endopodites and exopodites. Two caudal setae showed further development in length, and two additional setae were formed on either side of the cercopods.

Fifth larval stage (fig. 5).—Eight specimens of the 70-hour stage ranged from 1.00 to 1.20 mm (average 1.10 mm). The changes in the head region were slight except that the paired compound eyes became more prominent and more pigmented. The coxopodite of the mandibles became stouter, while the palps were slightly reduced. Both maxillae were developed into a spatulate form at the free extremities, but were still devoid of setae. The first five thoracic segments had well developed appendages; of these the anterior three had six endites. The development of the flabellum and other parts of the appendage will be discussed later. The remaining six thoracic segments were visi-





Figures 3-4. **3.** Ventral view of third larval stage. **4.** Ventral view of fourth larval stage.



Figures 5-6A. **5.** Ventral view of fifth larval stage. **6A.** Ventral view of right half of head region of sixth larval stage showing head appendages and their musculature.

ble but the last two (10th and 11th) were in a rudimentary stage. One more pair of caudal setae was added—making a total of three on each side.

Sixth larval stage (fig. 6: A, B).—Six specimens of the 91-hour stage ranged from 1.46 to 1.96 mm (average 1.78 mm). In the head region no change in the antennules or antennae was observed. The palp of the mandible was slightly reduced. First and second maxillae had attained their normal adult form but had few setae. In the thoracic region eleven segments were differentiated: The first nine segments had well developed appendages, and now the tenth and eleventh rudimentary appendages contained a seta on each rudimentary flabellum. Posterior to the eleventh thoracic segment the

first two abdominal segments were also differentiated; these were the anlagen of the external genitalia. Two more caudal setae (a total of four pairs) were added and setules were present on each seta. The rudiments of the cercopods also were formed as protuberances on either side of the anus.

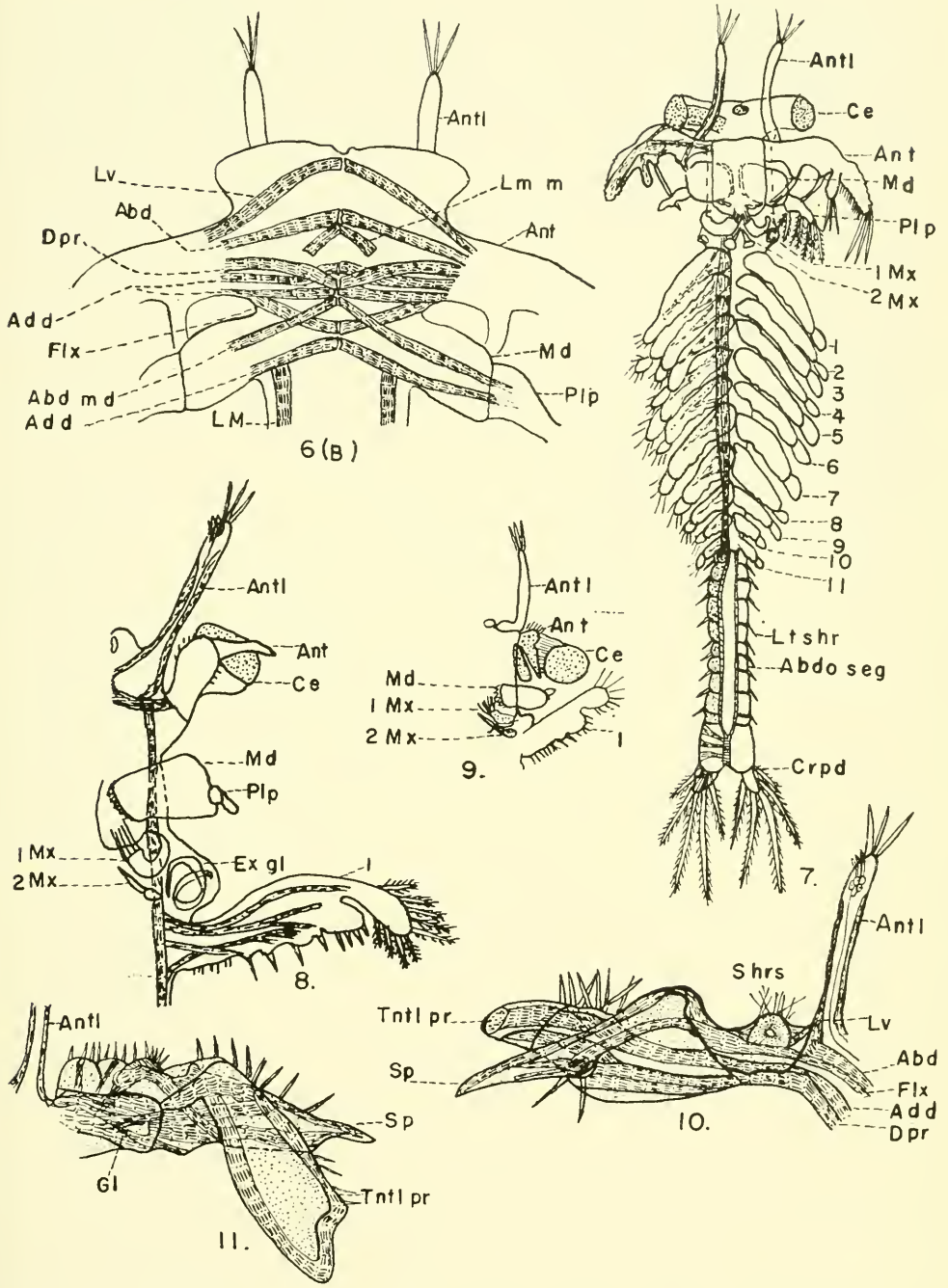
Seventh larval stage (fig. 7).—Six specimens of the 115-hour stage ranged from 2.26 to 2.34 mm (average 2.30 mm). In the head region the eyestalks were further elongated. The first ten thoracic appendages were fully developed, each bearing a flabellum. Seven more abdominal segments posterior to the first two abdominal (genital segments) segments were differentiated. Each genital and abdominal segment had a pair of sensory hairs attached on the posterolateral side near each segmental joint. Five well developed setae with setules were present on each developing cercopod.

Eighth larval stage (figs. 20, 30, 32, 36, 43, 54).—Six specimens of the 132-hour stage ranged from 2.65 to 3.00 mm (average length of males: 2.67 mm; females: 2.87 mm). In the head region the eyestalks were well differentiated. The palp of the mandible was further reduced. All evelen thoracic appendages were well developed and had flabella. The first eight thoracic appendages were differentiated, each with six endites. The twelfth and thirteenth trunk segments showed the development of two lobe-like protuberances which later gave rise to the external genitalia. For the first time the sexes could be distinguished by the structure of the antennae. In the male antenna the setae on the exopodite and on the first antennal segment were degenerated or reduced. The endopodite of the male antenna was completely degenerated. At the distal end of the basal joint of the male antenna, a tentacle-like process protruded. But in the female antenna the reduced endopodite was retained and the setae on the exopodite persisted. One pair of minute sensory hairs near each genital and segmental joint (posterolaterally) distinguished nine abdominal segments. Eight setae with setules were observed on each developing cercopod.

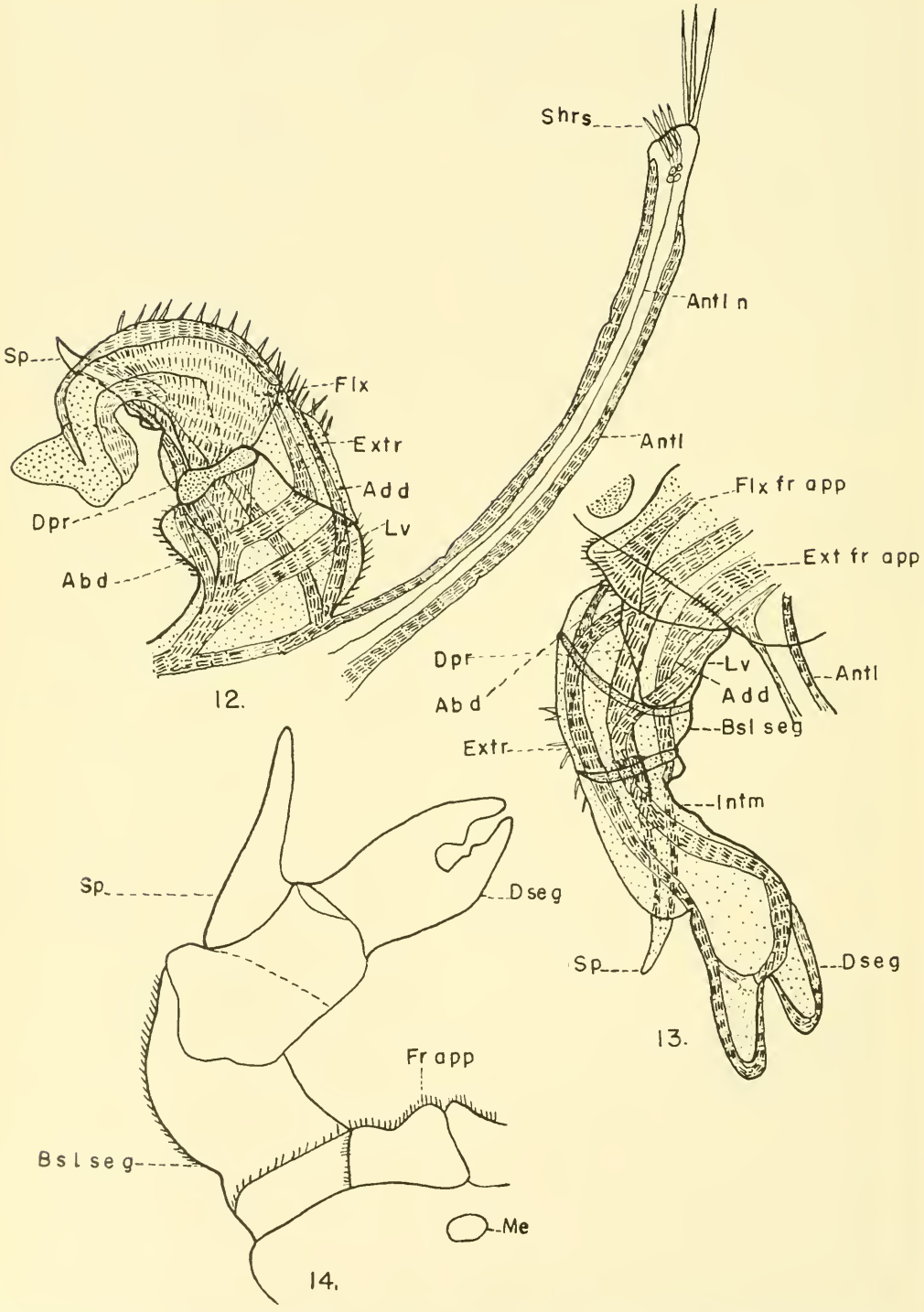
Ninth larval stage (figs. 8, 21, 22, 33, 49, 55) —Seven specimens of the 160-hour stage ranged from 3.35 to 4.00 mm (average length of males: 3.49 mm; females: 3.91 mm). In the head region the female antenna still retained setae, but they were shorter and stouter, with a vestigial endopodite. In the male antenna the tentacle-like process became elongated, and the antennae moved slightly toward the anterior side of the head. All the thoracic appendages now had six endites, and the exites were each differentiated into a praeepipodite, epipodite and flabellum. In the female the two genital segments were fused and grown out laterally to form the rudiment of the egg pouch (fig. 49). In the male the anlagen of the male gentialia consisted of two small tube-like protuberances projecting on the ventral side of the two fused genital segments. The seven abdominal segments were now differentiated with a pair of lateral sensory hairs persisting near each segmental joint. Eight setae with setules were observed on each further elongated cercopod.

Tenth larval stage (figs. 10, 23, 45, 46, 56).—Six specimens of the 178-hour stage ranged from 4.23 to 4.68 mm (average length of males: 4.23; females: 4.68 mm). in the head region the antennae of the male and female were further moved to the anterofrontal part of the head. The male antennae showed further growth of the tentacle-like process, and the length of the hook (the remnant of the exopodite) remained the same as in the previous stage. On the female antenna all setae were degenerated, and the basal segment was flattened including the greatly reduced exopodite on its distal margin. In both sexes the mandibular palps and the sensory spines on the ventral side of the coxopodite of the mandibles were degenerated with their setae. The thoracic appendages were now completely developed. The male genitalia were further elongated and extended up to the whole length of the 14th body segment. The egg pouch in the female also was elongated. The abdominal segments also showed growth in length. The cercopods were further elongated and had twenty setae with setules on each.

Eleventh larval stage (figs. 11, 24, 34, 46, 50, 57).—Five specimens of the 210-hour stage ranged from 4.72 to 5.27 mm (average length of males: 4.72; females: 5.25 mm) The antenna of the male was elongated and the tentacle-like process was further developed. In the female antenna the exopodite showed further degeneration and the protopodite (or, basal segment) was broader with sensory hairs developed on its anterior mar-



Figures 6B-11. **6B.** Dorsal view of head of sixth larval stage showing attachments of antennae and mandibular muscles (diagrammatic). **7.** Ventral view of seventh larval stage showing external and internal structures. **8.** Ventral view of head region of male ninth larval stage. **9.** Ventral view of tenth larval stage. **10.** Ventral view of antennule and antenna of male tenth larval stage showing musculature and external morphology. **11.** Ventral view of male antenna of eleventh larval stage.



Figures 12-14. **12.** Anterior view of male antennule and antenna of twelfth larval stage. **13.** Anterior view of male antenna and frontal appendage of thirteenth larval stage. **14.** Anterior view of male antenna and frontal appendage of fourteenth larval stage.

gin. The genitalia in both the sexes were more differentiated. The cercopods were further elongated and there were twenty-six setae with setules on each of them.

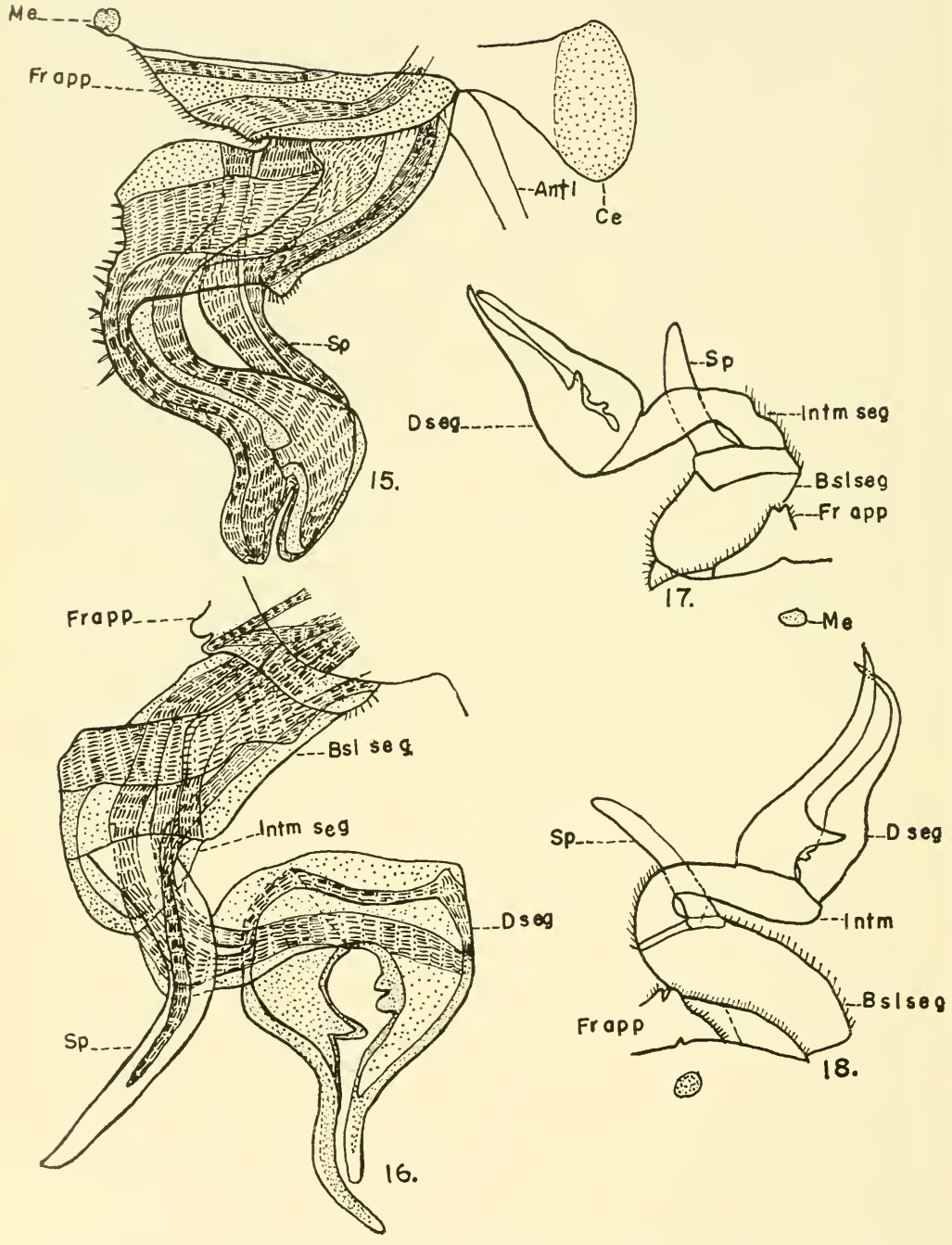
Twelfth larval stage (figs. 12, 25, 51).—Five specimens of the 245-hour stage ranged from 5.40 to 6.17 mm (average length of males: 5.80 mm; females: 6.17 mm). The antennules showed increase in length. The male antennae were further differentiated; a third segment originated from the second segment which had been the tentacle-like process of the earlier stages. This was the anlage of the terminal hand of the adult fairy shrimp. The three antennal segments were distinct in this stage. From the lateral side of the first antennal segment a protuberance developed; this was the anlage of the frontal appendage of the adult. The antennae of the female showed further expansion of the protopodites and the reduction of the exopodites to spine-like projections arising from the anterior apices; also, the anterior margins showed the numerous sensory hairs. The palps and the spines of the mandibles were completely degenerated. The number of setae with setules on the maxillae was adult-like. The compound eyes with their eyestalks were completely developed. The excretory gland was completely differentiated and was enclosed in the body on either side and located between the second maxilla and the first thoracic appendage. The thoracic appendages increased serially in length from first to fifth and then decreased from sixth to eleventh. The eleventh appendage was the smallest and nearly equal to the first. The genitalia of both sexes showed little development from the previous stage except for further elongation of the body and distinction of the internal structures. Lateral sensory hairs of the abdominal segments had degenerated. Each cercopod had fifty setae with setules.

Thirteenth larval stage (figs. 13, 61).—Five specimens of the 300-hour stage ranged from 6.50 to 7.60 mm (average for males: 6.50; females: 7.60 mm). Antennae of males and females now had completely moved to the anterior portion of the head. The male antennae were longer and the segments were more distinct. The distal end of the terminal segment was developed into a bifurcated claw-like structure, which was the anlage of the chitinous hooks of adult fairy shrimp. The lateral proturberances on the basal segment of the male antennae had moved between the antennae to form the future median frontal appendage. The female antennae showed no change from the previous stage. The genitalia were further differentiated into adult-like form. The cercopods were further elongated and had sixty setae with setules on each.

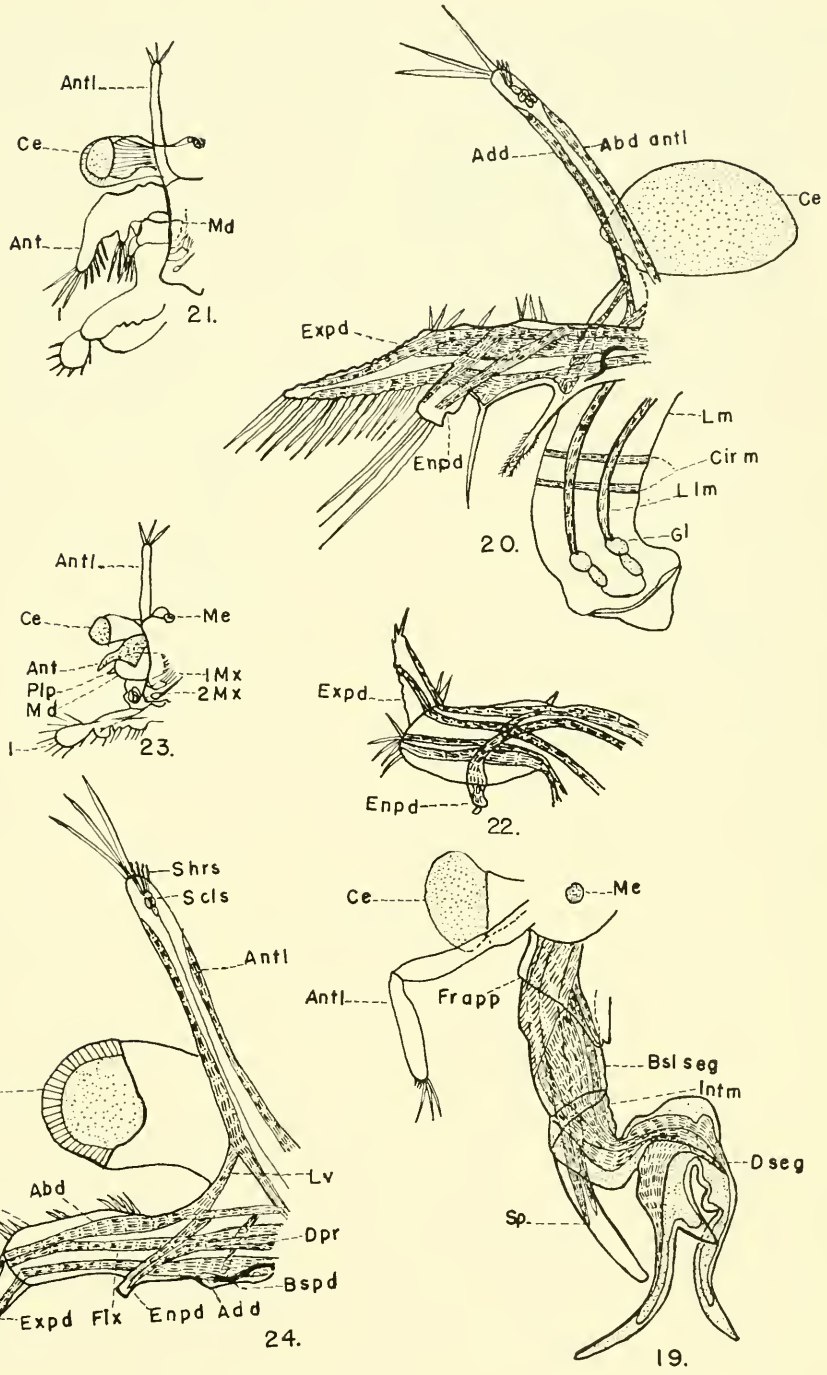
Fourteenth larval stage (figs. 14, 28, 52, 58).—Five specimens of the 336-hour stage ranged from 7.65 to 8.75 mm (average for males: 7.70; females: 8.42 mm). The hand (third segment) of the male antenna differentiated on its inner edges into chitinous projections on the left hook and two blunt protuberances on the right hook. The lobes on the basal segment of the male antennae moved into a median position and fused basally. The male genitalia showed little modification from the previous stage, but the egg pouch of the female was more elongated and the upper and lower lips of the egg pouch were now clearly distinct. Each cercopod had seventy setae with setules.

Fifteenth larval stage (figs. 15, 47).—Six specimens of the 385-hour stage ranged from 9.00 to 10.30 mm (average for males: 9.00 mm; females: 10.10 mm). The antennae of the male had become coiled and there was further elongation of the third segment and more differentiation of the hand. The frontal appendage became more inclined toward the median position. The antennae of the female showed no apparent change. The genitalia in both sexes differentiated into adult-like structures. The number of setae with setules increased to eighty on each cercopod.

Sixteenth larval stage (figs. 16, 26, 53).—Five specimens of the 475-hour stage ranged from 10.50 to 12.50 mm (average for males: 10:50; females: 11.75 mm). The antennae of the male showed further coiling of the third segment; the hook originated from the first (or, basal) segment, and also was longer than in the previous stage. The hand of the third antennal segment of the male had developed chitinous hook-like claspers and had assumed the adult form except for the protuberances on its inner side. The frontal lobes of both antennae were fused except at the anterior tip, which had the form of the adult frontal appendage. The male genitalia had developed the basal lobe, a chitinous spur with four minute setae on its ventral side, and the membranous eversible part of the penes had had developed minute spines



Figures 15-18. **15.** Anterior view of male antenna and frontal appendage of fifteenth larval stage. **16.** Anterior view of male antenna and frontal appendage of sixteenth larval stage. **17.** Anterior view of male antenna and frontal appendage of seventeenth larval stage. **18.** Anterior view of male antenna and frontal appendage of eighteenth larval stage.



Figures 19-24. **19.** Anterior view of male antenna and other structures of fully grown fairy shrimp. **20.** Lateral view of antennule, antenna, and labrum of female eighth larval stage. **21.** Ventral view of head region of female larval stage. **22.** Ventral view of female antenna in ninth larval stage. **23.** Ventral view of female head region of tenth larval stage. **24.** Ventral view of antennule and antenna of female in eleventh larval stage.

on the inner side as in the adult. The egg pouch of the female also assumed the adult shape. There was no increase in the number of setae on the cercopods.

Seventeenth larval stage (figs. 17, 27).—Five specimens of the 576-hour stage ranged from 13.00 to 14.79 mm (average for males: 13.60 mm; females: 14.70 mm). The antenna of the male showed some minor changes from the previous stage: the second segment was narrower, the distal part of the third segment had increased in length, and the chitinous projections on both hooks of the hand were further differentiated. No apparent change in the female antennae was noticed. The genitalia of both sexes also showed no change. The number of setae with setules on the cercopods remained the same in both sexes.

Eighteenth stage (figs. 18, 59).—Twelve specimens of the 696-hour stage ranged from 14.85 to 20.00 mm (average for males: 16.00 mm; females: 17.50 mm). The fairy shrimp now had acquired all the adult features except that the third segment of the male antenna showed further elognation and coiling of the hooks of the hand. The egg pouch of the female contained matured eggs though no copulation had been observed. On the female, setae with setules increased to eighty-six on each cercopod, but on the male the number was reduced to seventy-five on each cercopod. Spines had developed at the bases of some degenerated setae on the male cercopods.

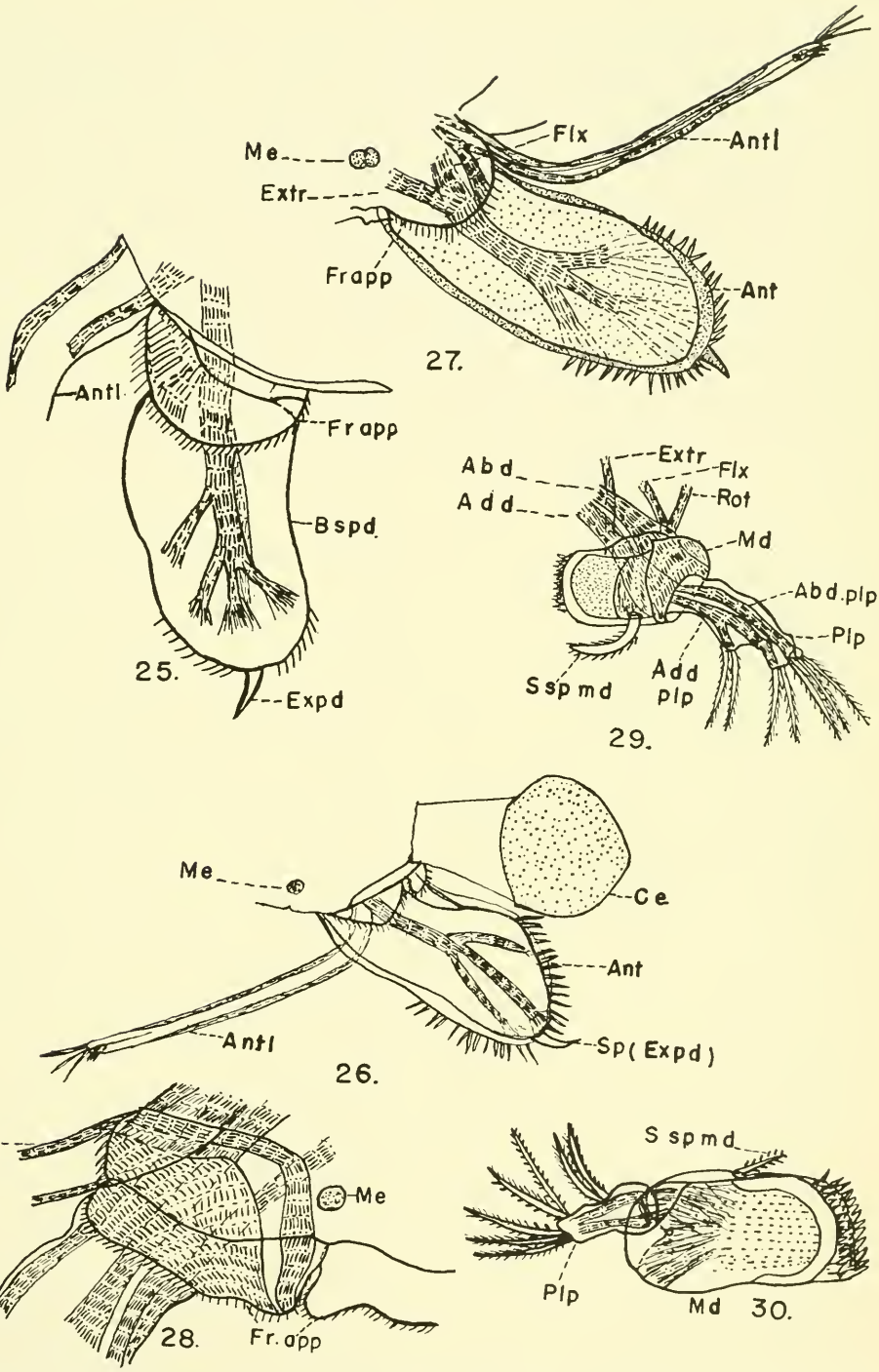
Fully grown fairy shrimp (figs. 19, 31, 37(9), 60, 62).—Ten specimens of more than the 30-day stage had increased in body length, but showed little difference from the structures of the eighteenth stage. The third segment of the male antennae showed further elongation of the claspers of the hand. The chitinous projection on the median hook of the hand was well developed; also the two tooth-like structures had formed on the inner side of the lateral hook of the hand. The frontal appendage was completely fused except at the distal end which had a bifid tip. The cercopods of the male now consisted of fifty-two setae with setules and eighteen spines on each cercopod. This indicated the reduction in the number of the setae and spines from seventy-five to seventy from the eighteenth stage. The cercopods were now completely fused with a single telson which was fused with the preceding abdominal segment. In the cercopods of the female there was no development of the spines on the distal end of the cercopods, but the setae retained the bristle-like structure that was present in the earlier larval stages.

B. Head Appendages and Their Musculature

Antennules (figs. 1-8, 10, 12, 19, 20, 24).—In the nauplius stage, the antennules were short finger-like rods, projecting anteriorly from the anterolateral head region. The length at the time of hatching was 0.09 mm. They were uniramous, non-segmented, and their distal ends each had three setae and five minute sensory setae, which were connected with the nerve fibers. In the second larval stage the antennules had increased to 0.12 mm in length. In the third stage the rudiments of the nerve fibers and two muscle fibers extended into the cavity of the antennules. In later stages there was not much change in structure, except for an increase in length and more differentiation of the nerve and muscle fibers. In the eight stage the length reached 0.32 mm. In the seventeenth stage the length of the antennules was 1.67 mm in females, and 1.31 mm in males. In the adult stage the length in the female was 2.18 mm and in the male was 1.84 mm.

The musculature of the antennules consisted of two muscle fibers, which originated from the head and ran along the inner walls of the antennules. These muscles are used for lowering and raising the antennules; they may be called depressors (Dpr) and levators (Lv) of the antennules.

Antennae (figs. 1-7; *male,* figs. 9-19; *females,* figs. 8, 20-27).—In the first larval stage the antennae were biramous and had a length of 0.23 mm. The antennae were swimming appendages and were attached ventrolaterally on the head. Each antenna consisted of a protopodite, endopodite, and exopodite as found in a typical crustacean birmaous appendage. The protopodite was composed of basipodite and coxopodite (Oehmichen, 1921). The coxopodite had a process on the posterior side which was terminated into a single seta with setules, but in later stages this seta was bifurcated at the distal end. The basipodite also was a single process with a long seta having setules. At the distal



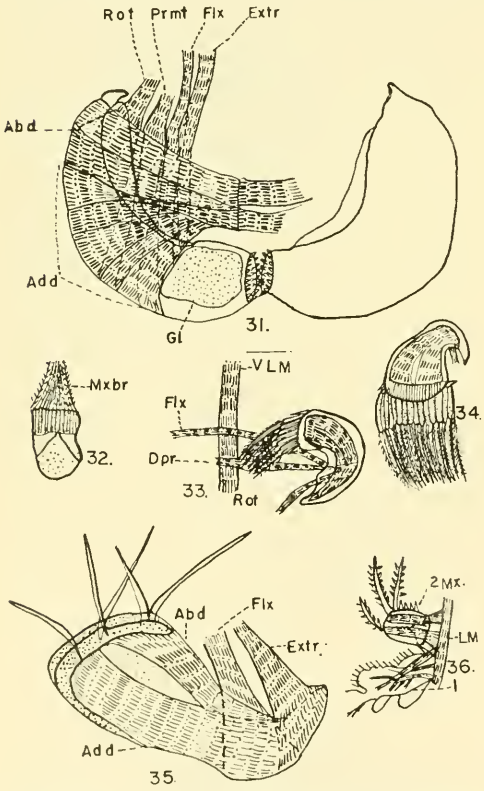
Figures 25-30. **25.** Anterior view of female antennule and antenna of twelfth larval stage. **26.** Anterior view of female antennule and antenna of sixteenth larval stage. **27.** Anterior view of female antennule and antenna of seventeenth larval stage. **28.** Anterior view of male frontal appendage of fourteenth larval stage. **29.** Ventroposterior view of mandible with musculature of sixth larval stage. **30.** Right mandible of eighth larval stage.

end of the basipodite there was an endopodite with one short and three long setae bearing setules on its distal end. The basipodite also had an exopodite with thirteen setae and setules on its posterior side. At the base of the antenna the anlagen of the antennal gland was present. In later stages (up to 7th stage) the antennae in both sexes increased in length and moved slightly to the anterolateral side of the head. After the seventh stage the antennae had slow rate of growth in length and began to show male and female characteristics. The differentiation became apparent in the eighth larval stage when the length was 2.69 mm. In the female the endopodiate and the exopodite were reduced successively in the later stages, while the protopodite expanded and became sac-like. In the adult stage of the female the endopodite completely degenerated and the setae on the protopodite and the exopodite were lost. In the twelfth larval stage the exopodite appeared as a spine-like structure at the distal end of the expanded protopodite. Numerous sensory hairs also were developed on the distal margin of the protopodite. The basal part of the protopodite had a reduced lobe which could be compared to the well developed frontal appendage of the male antennae. The basal lobe of the female antenna had sensory hairs around its margin and served as a sensory organ. The female antenna in the eighth stage showed an indication of migration anteriorly from the sides of the head; migration was completed in the twelfth stage.

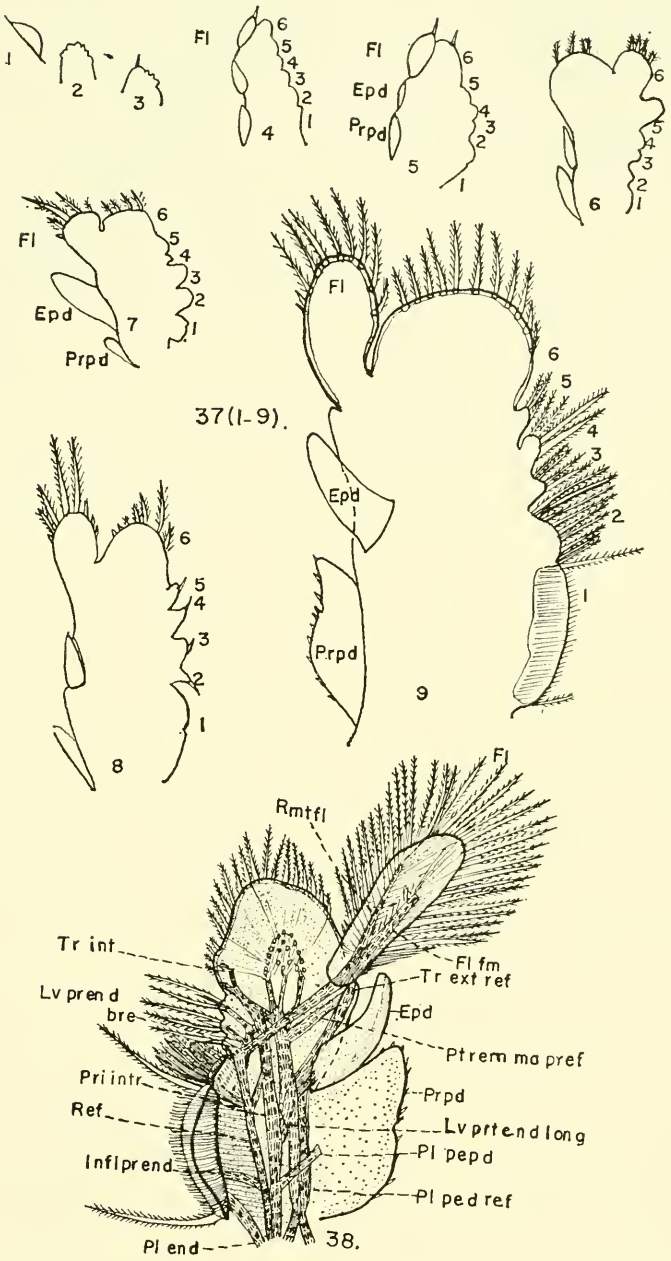
In the male, antennae, development of the complicated clasping organs was completed progressively starting with the seventh stage, even though the male fairy shrimp was sexually mature at the 16th stage, development of the antennae continued through four or five later stages.

Modification of the male antenna started in the advanced seventh larval stage. At the anteroventral region of the protopodite a fold-like protuberance developed, and at the same time the two segments of the protopodite fused. The exopodite with its setae and the endopodite started to reduce in the eighth stage, and were completely degenerated in the ninth stage. At the same time the male antennae started to move towards the anteromedian side of the head. The fold-like protuberance increased in length and developed into two triangular plates at the ends of the antennae (fig. 13, D *seg*) as seen in the thirteenth stage. From the fourteenth stage to the adult, the third antennal segment was developed from the curved second segment and its distal end acquired the hand-like structure. The hand included one chitinous projection on the inner side of the median hook and two blunt chitinous, tooth-like projections on the inner side of the lateral hook (fig. 19). The antenna of the first stage was 0.23 mm long; and in the adult was 4.39 mm. Thus in the female the antennae reduced in size proportionately in subsequent stages, while in the male the antennae showed increase in length proportionately from the eighth stage to the adult.

Internally the muscle cells were differ-



Figures 31-36. **31.** Mandibles of adult with musculature of right mandible. **32.** Ventroposterior view of first maxilla of eighth larval stage. **33.** Ventral view of first maxilla with musculature of ninth larval stage. **34.** Dorsal view of first maxilla, with some muscles, of ninth larval stage. **35.** Ventroposterior view of second maxilla with musculature of sixth larval stage. **36.** Ventral view of second maxilla with musculature of eighth larval stage.



Figures 37-38. **37.** Development of thoracic appendage: 1. anlage of thoracic appendage; 2. second stage of developing appendage; 3. third stage; 4. fourth stage; 5. fifth stage; 6. sixth stage; 7. seventh stage; 8. eighth stage; 9. ninth stage (completely developed). **38.** Ventroposterior view of third thoracic appendage with musculature of the adult.

entiated into muscle fibers in the sixth stage, and attained their elaborate form. A dorsal set of the muscles composed of five pairs of indivdual strands originated in the dorsal organ (fig. 6(B), *Lv, Abd, Dpr, Add, Flx*). Three additional pairs of muscles originated ventromedially beneath the anterior portion of the intestine and also just posterior to the esophageal connection (fig. 6(B), *Lm m, Abd md, Add*). These muscles were so arranged that they formed a continuous horizontal, contractile band, running between the antennae and the mandibles. Both dorsal and ventral muscles were inserted along the inner side of the antennal wall. According to the function of each muscle strand the following terminology is suggested; the anterior muscle strand whch raises the antennae is called levator of the antennae (*Lv*). It originates from the anterior portion of the dorsal (nuchal organ) and insertes on the inner anterior surface of the antennal wall. The second strand which moves the antennae away from the body is called abductor of the antennae (*Abd*). The third muscle strand which moves the antennae back is called depressor of the antennae (*Dpr*). Adjacent to the depressor muscle, two muscles originate anteroventrally and posteroventrally, and are inserted in the exopodite region of the antenna. These pull the antennae toward the body and are called adductors of the antennae (*Add*). Another muscle band, which originates ventrally, adjacent to the mandibular tendon, and is inserted at the posterior part of the exopodite flexes the antennae towards the body; these are called the flexors of the antennae (*Flx*).

The musculature of the adult male antenna showed little difference from that of the early larval stage as described above. The transverse muscle (*tr m*) of the endopodite after the degeneration of the endopodite became attached to the spur of the antenna of the adult which was located at the distal end of the protopodite.

The musculature in the female antenna of the adult degenerated. Instead of the five muscle strands as in the sixth larval stage, there were now only two muscle bundles arranged as two overlapping bands of the muscles in a dorsoventral position. Minute muscle fibers that originated from these bundles were inserted into the anterior margin of the protopodite and spine-like exopodite. This stage of the musculature and the antenna was reached in the twelfth stage of the female. This stage was almost adult-like except that the antenna was shorter than in the adult.

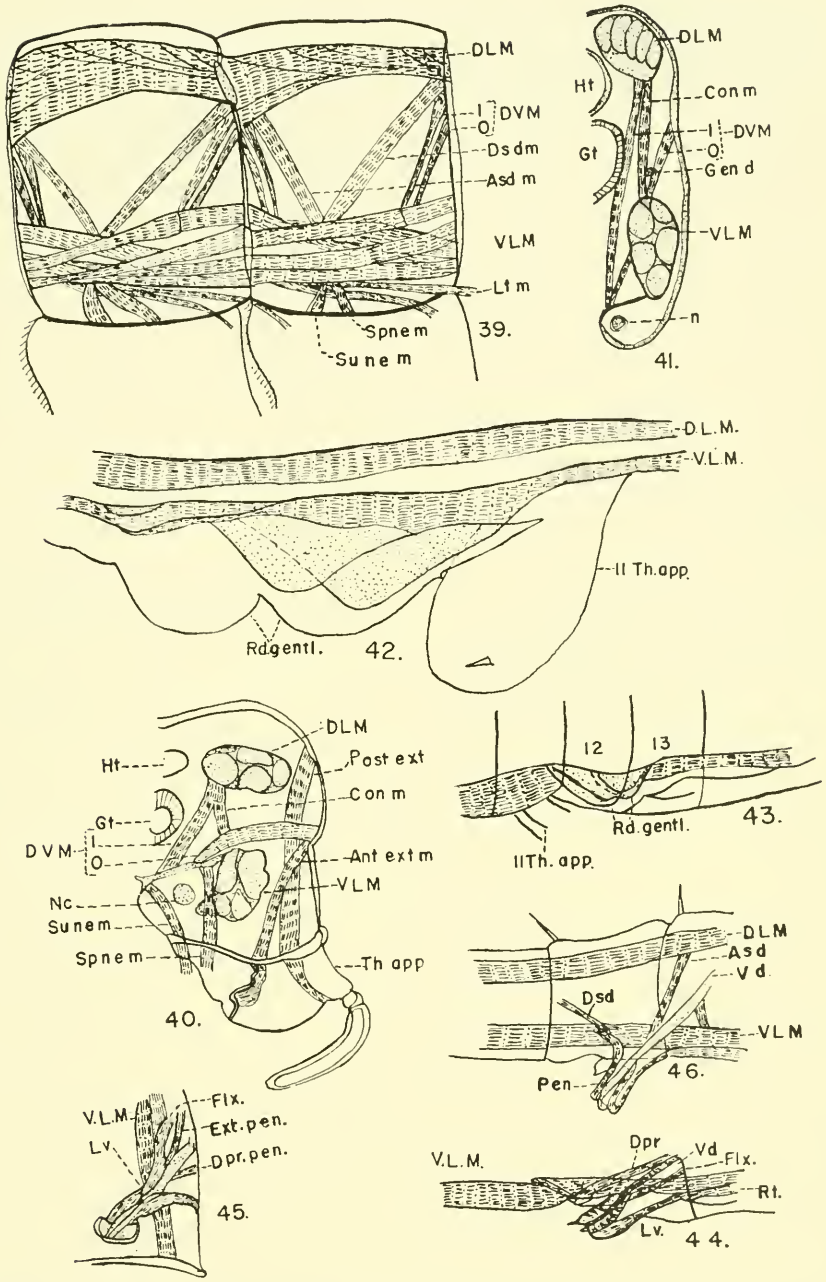
Frontal appendage (figs. 11-19, 28).— The development of the frontal appendage was worked out by Claus (1886) on *Streptocephalus torticornis,* Health (1924) on *Branchinecta occidentalis,* and by Hsŭ (1933) on *Chirocephalus nankinensis.* In *Streptocephalus seali* development of the frontal appendage started from the eleventh stage when the larva was 4.70 mm long. In that stage a small outgrowth developed from the dorsolateral side of the basal joint of the male antenna, which had sensory hairs around its margin (fig. 11). In subsequent larval stages this outgrowth of the male antenna moved into the anteromedian position at the base of the antenna and then migrated from the antenna to the head. In the fourteenth stage the two lobe-like structures of the antennae came closer and ultimately coalesced at their bases forming a common anterior union of the head and antennae. In the adult stage the fusion was almost complete except at the tip which remained bifid indicating the fusion of two basal lobes of the antennae. A similar type of frontal appendage development was observed by Claus (1886), and Linder (1941) in other species of the genus *Streptocephalus.*

The musculature included flexor muscles (*Flx*) of the two basal lobes of the antennae, coalesced to form a single strand, which was inserted in the anterior end of the dorsal or nuchal organ and functioned to raise as well as bend the frontal appendage of the adult. The extensor muscle (*Extr*) remained separate inside the frontal appendage. They originated from the anterolateral side of the dorsal or nuchal organ and functioned to straighten the frontal appendage (fig. 28).

In the female similar outgrowths at the base of the antennae were observed. Each developed into a lobe at the base of the antenna, but the two were separated from each other and each had sensory hairs around the margin.

The musculature was not as well developed in the adult female as in the male; two minute muscle strands originated from the head and inserted in each basal lobe of the antennae.

Mandible (figs. 1-9, 21, 23, 29-31).—The mandibles in the first larval stage were swim-



Figures 39-46. **39.** Lateral view of thoracic region of adult showing musculature. **40.** Transverse section of thoracic region of adult showing musculature. **41.** Transverse section of abdominal region of adult. **42.** Lateral view of anlage of genital apparatus of seventh larval stage. **43.** Lateral view of male genitalia of eighth larval stage. **44.** Lateral view of male genitalia of tenth larval stage. **45.** Anterior view of the same (*i.e.*, fig. 44). **46.** Lateral view of male genitalia of eleventh larval stage.

ming appendages. They were articulated on the dorsal plate of the mandibular segment which was quite distinct between the head plate and nuchal plate. They were biramous and consisted (Oehmichen, 1921) of a protopodite having a chitinous coxopodite and the basipodite. The coxopodite consisted of a rudimentary jaw and a sensory spine with setules located at the lateral side of the coxopodite and at the base of the palp. The basal segment of the palp (the basipodite) had two backwardly directed setae with setules. On the distal end of the basipodite there were two small processes, the exopodite and the endopodite. The exopodite had two setae with setules, while the endopodite had three setae with setules. In the later larval satges the development of the mandible involved degeneration of the palp and the sensory spine. Each chitinous jaw was differentiated on the distal edge of the coxopodite during the development of the later stages. The degeneration of the mandibular palp and the sensory spine was completed in the twelfth stage in both sexes, when the male was 5.80 mm long and the female was 6.17 mm. After the twelfth stage the mandibles attained adult form.

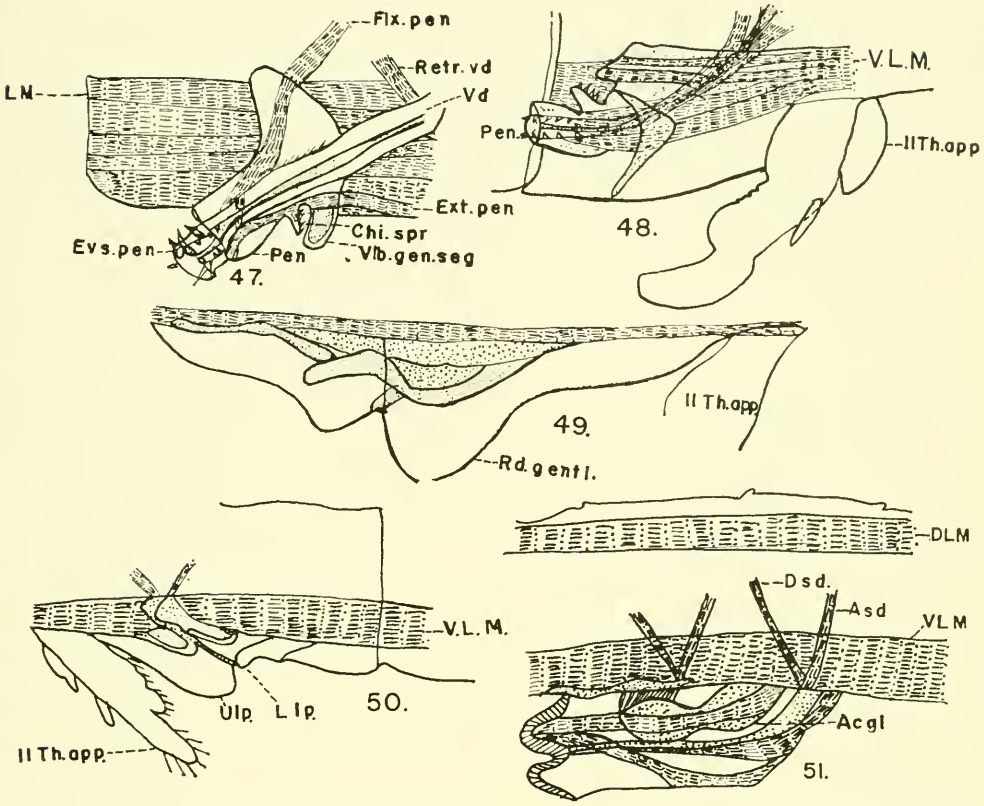
The development of the musculature involved formation of the transverse and horizontal muscle bands laid down in the first larval stage; these were fully differentiated in the third stage. These muscles were attached to the lateral wall of the coxopodite, converged to a point in the median plane, and were ventral to the intestine (fig. 6B). Two longitudinal muscles (*L M*) originated at the posterior tendinous points of the dorsal or nuchal organ, and were inserted in the distal part of the protopodite and the mandibular palp respectively. The muscles of the mandibular palp degenerated in later stages.

The terminology of the mandibular muscles given by Snodgrass (1950) is partially followed for the mandibular muscles of *S. seali* (fig. 31). The ventral muscle of the mandible consisted of two well developed strands called *adductor* (*Add*) and abductor (*Abd*) respectively, which functioned to close or open the jaws. In the median part of the nuchal organ two pairs of suspensory ligamentous muscles originated. They were inserted in the tendinous part of the ventral muscles; flexor (*Flx*) and extensor (*Extr*), to pull the jaw inward and to straighten it. There were also two longitudinal muscle strands called anterior dorsal remotor (*Rot*) and posterior dorsal promotor (*Prmt*) muscles respectively. Their contractions, apart from moving the palp in the early larval stages, pulled the mandibles outward and slightly forward, a movement opposite to that produced by the transverse ventral muscles.

Maxillae (first and second), (figs. 2-6, 32-36).—In the first larval stage the anlage of both pairs of maxillae consisted of layers of cells on either side and surrounded by the ventral ectodermal cells of the head. In the second stage the bud of the first maxilla was developed and resembled a short sac-like outgrowth. In the following stages the first maxilla enlarged and assumed a stubby finger-like shape. In the first four stages the first maxilla appeared as an elevation without setae at the distal end. In the seventh stage, when the larva was 2.15 mm long, the first maxilla consisted of two segments; one proximal, the protopodite, and one distal, the exopodite. The latter became the maxilla proper of the adult. The distal segment of the first maxilla terminated in nine setae with interlocking setules. In subsequent stages there was an increase in the number of the setae. In the eleventh stage the first maxilla was adult-like. Finally in the adult stage the number of the setae had increased to thirty-one.

The second maxilla appeared as an elevation without setae in the second larval stage. The second maxillae were located at the base of the first pair of developing thoracic appendages. The anlage of the second maxilla developed subsequently into a very short, minute round appendage, located on either side and posteromedial to the first pair of maxillae.

The musculature of the maxillae differentiated in the fifth larval stage. At this stage the fibers of some of the muscles at their points of attachment had lost the striations characteristic of muscle tissue; thus, they were considered as non-contractile and tendinous in function. The muscles of the first maxilla consisted of a ventral transverse bundle which originated on the nuchal organ and formed a connection between the maxillae. Three dorsal longitudinal muscles (*DLM*) were also present: one originated from the median mandibular tendon bridge; the other two originated from the lateral



Figures 47-51. **47.** Lateral view of male genitalia of fifteenth larval stage. **48.** Lateral view of male genitalia of fully grown fairy shrimp. **49.** Lateral view of female genitalia of ninth larval stage. **50.** Lateral view of female genitalia eleventh larval stage. **51.** Lateral view of female genitalia of twelfth larval stage.

side of the mandibular and antennal tendon bridges. These three muscle bands called flexor (*Flx*), retractor (*Retr*) and rotator (*Rot*), respectively, were used for moving and rotating the first maxilla in upward and downward directions. These movements were used for filtering food with the setae before it reached the mandibles for chewing.

In the second maxilla the muscles developed in a way similar to that of the first maxilla, but the muscles were not well developed and apparently nonfunctional. The chief function of the second maxillae seemed to be sensory due to the presence of five minute setae in the sixth larval stage; these were reduced to three in the eighth stage. In the adult the second maxilla became membranous with a basal lobe and two long, thick setae with setules. No movement was observed, which explained the reduction of the musculature and indicated the sensory function.

Labrum (figs 1-5, 9, 20-23).—In the nauplius stage a labrum on the ventromedian side of the head was directed backward and covered the mouth region. It was elongate with a round distal margin and extended to the trunk region. In the sixth stage the labrum was reduced in size and reached only to the mandibles. In subsequent stages the labrum showed no external changes and retained the same structure to the adult form. Functionally the labrum represented the most anterior portion of the food grooves leading to the mouth; the posterior part was formed by the first endites of the thoracic appendages. The most distinct components of the labral cavity were numerous storage cells, which were fully developed by the third larval stage.

A muscle strand on each side attached to

the wall of the labrum (fig. 20, *L lm*) was differentiated in the second larval stage. These longitudinal muscles ran laterally to the intestine and originated from the anteriormost tendon of the nuchal organ. Contraction of these muscles raised the labrum towards the ventral head surface. Two transverse or circular muscles (fig. 2, *Tr*) also differentiated in the third larval stage; they were used for the transverse contraction of the labrum.

C. Median and Compound Eyes

The anlage of the median eye was present in the first larval stage (fig. 1, *Me*); at that time it was pigmented and light sensitive. In later stages the median eye increased steadily in size and pigmentation (figs. 2-10).

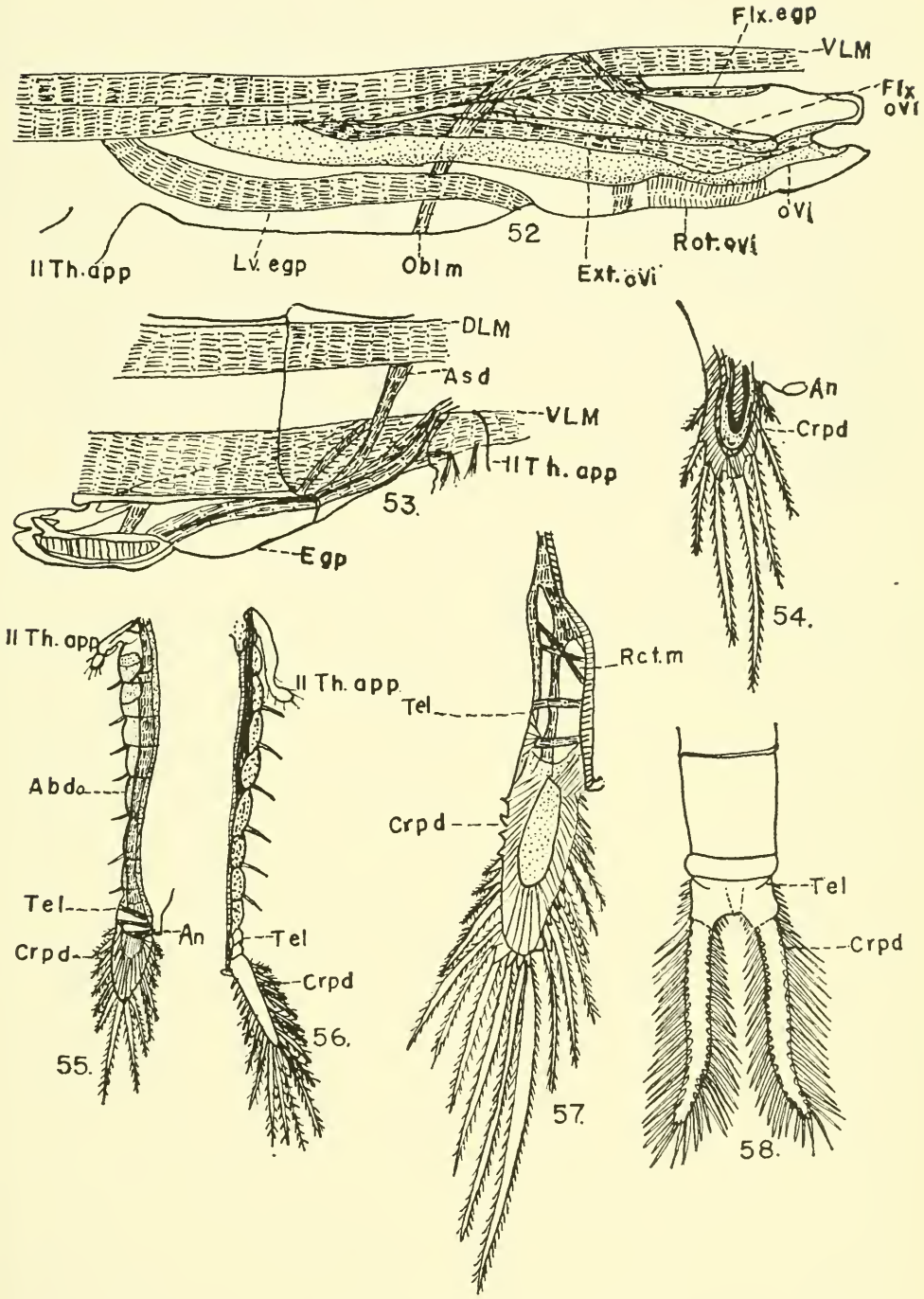
In the first larval stage there was no indication of paired eyes. In the second stage rudiments of compound eyes occurred as slight lateral ectodermal proliferations just behind the bases of the antennules. In the fourth stage the ectodermal proliferations were converted into ommatidia. Then up to the tenth stage the eyes bulged laterally from the head surface and became more prominent. Development of eyestalks was completed between the seventh and tenth stage. After that developments of the eyes involved elongation of the eyestalks and increase in the size of the pigmented portion; this was complete in the eighteenth stage.

Movement of the eyes was controlled by two oblique muscles and one transverse muscle (not shown in my figure) as described by Claus (1886) for *Branchipus stagnalis*. The two oblique muscles originated from the median tendon of the head, one from the anterior tendon of the head (used for raising the eye in the forward position); the second set originated from the posterior tendon, crossed the oblique muscles at the base of the eyestalk, and were inserted at the distal end of the eyestalk. It functioned to move the eyestalk anteroposteriorly. The transverse muscle originated from the median tendon and was inserted near the posterior base of the retinal nerve cells; it was used to move the eye posteroventrally and ventrodorsally.

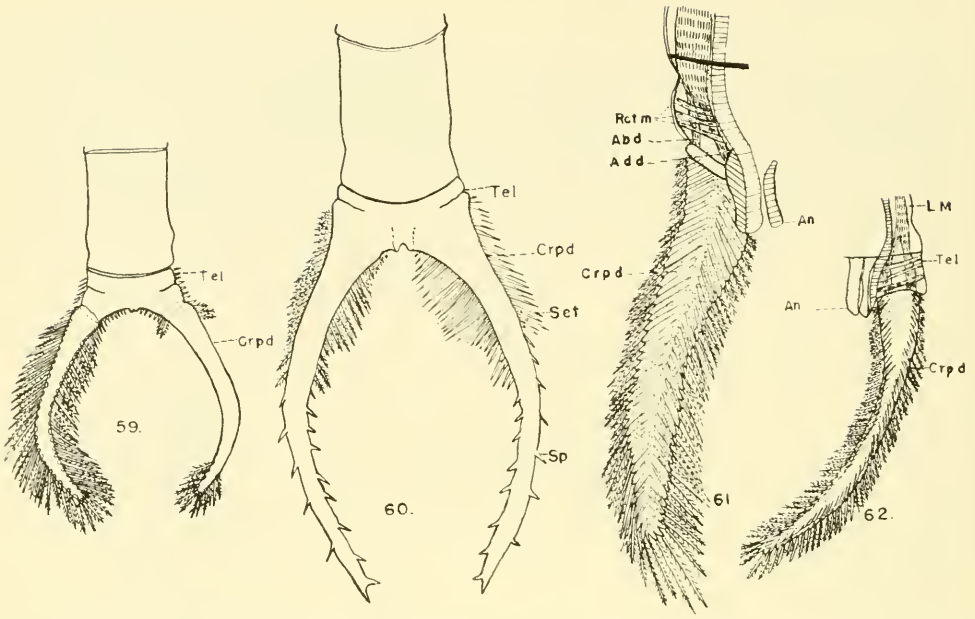
D. Thoracic Appendages and Their Musculature

Rudiments of the thoracic appendages appeared in the second larval stage (fig. 2, *Th app bd*). They developed progressively from the anterior end of the postcephalic region; therefore several stages of appendage development were represented in each larval stage. In the second stage each of the three thoracic segments had a group of cells branching out laterally from the ventrolateral ectoderm. In subsequent stages (figs. 3-5, 7) the appendages expanded to fuse loosely with the anterior haemocoelomic cavity. During subsequent stages (figs. 37, 38) several lobes were added to the ventral side of the appendage bud to form the exopodite (*Fl*), two lobes to the anterior side to form one distal epipodite (*Epd*), and one praeepipodite (*prpd*) with a notch on its outer margin. The setae produced on the distal end of the exopodite and the endopodite (1-6) were at first very few in number. Subsequently they increased in number and contained setules in the adult.

In the third stage five rudimentary appendage buds had developed. A seta was present on the first four. In the fourth stage there were seven thoracic appendicular buds; in the fifth stage, nine buds; and in the sixth stage eleven thoracic appendages in various stages of development had differentiated. In this stage two genital segments (1st and 2nd abdominal) had also developed. All thoracic appendages had setae with setules on their distal ends. The number of setae on the sixth endites and the flabella increased progressively from the first stage to the adult. In the sixth stage, the eleventh thoracic appendage had one seta each on the flabellum and the sixth endite. That number increased to 45 and 26 respectively in a fully grown fairy shrimp. From the seventh stage, the larvae were differentiated by the number of setae on the flabella and the sixth endites of the eleventh thoracic appendage as suggested by Heath (1924) for *Branchinecta occidentalis*. In the ninth stage the structures of the thoracic appendages were adult-like except for the number of setae on the flabellum and the sixth endite (fig. 37). The endopodite consisted of six endites; the sixth endite had a row of 19 setae. The exopodite had a flabellum at the distal end with a row of 39 setae with setules. The exopodite included one epipo-



Figures 52-58. **52.** Lateral view of female genitalia of fourteenth larval stage. **53.** Lateral view of female genitalia of sixteenth larval stage. **54.** Ventral view of cercopod of eighth larval stage. **55.** Ventral view of abdomen and cercopods of ninth larval stage. **56.** Ventral view of abdomen and cercopods of tenth larval stage. **57.** Ventral view of right cercopod of eleventh larval stage. **58.** Ventral view of last abdominal segment and cercopods of fourteenth larval stage of the male.



Figures 59-62. **59.** Ventral view of last abdominal segment and cercopods of eighteenth larval stage of the male. **60.** Ventral view of last abdominal segment and cercopods of fully grown male. **61.** Ventral view of left cercopod of thirteenth larval stage of female. **62.** Ventral view of left cercopod of adult female.

dite on the posterolateral side of the flabellum, and one praeepipodite posterior to the epipodite. The last two were membranous and had no setae. The praeepipodite had serrations around its margin with a notch on its middle.

The musculature of the thoracic appendage is complicated. Interpretation of thoracic musculature is presented according to Preuss (1957) (fig. 38). In the seventh stage the muscle pattern was clearly established. In each appendage there were four main dorsal muscle strands spread into a fan-like shape in an anteroposterior sequence. These muscles originated along the dorsolateral body wall and were inserted along the inner side of the wall of the appendage. Similarly a series of ventral muscle strands originated on the ventral body wall near the base of the appendage and were inserted along the appendage wall. Two sets of axial and longitudinal muscles were developed in each segment; one set of these three individual strands ran laterally (fig. 39, *Lt m*) to the nerve trunk along the base of the appendage. There was also a set of several dorsal and lateral muscle strands located between the epidermis and the intestine. Each axial muscle (*Sp ne m, Su ne m*) extended a little posteriorly into the next segment, where it overlapped with its corresponding muscle. When these muscles were contracted unilaterally the axial muscles caused the thorax to flex in any direction, and on simultaneous contraction the entire thorax was shortened while the segments were telescoped into one another. The ultimate differentiation of the musculature in the subsequent stages involved only the appearance of striations and increase in size.

The muscles of the trunk region of adult fairy shrimp are shown in Figures 39 and 40 in the longitudinal and the transverse sections through the thoracic region. The terminology for the muscles of the trunk follows the description given by Cannon (1926) for *Chirocephalus diaphanus.*

E. Genital Ogans and Their Musculature

The anlagen of the external genital organs in both sexes appeared in the sixth stage, but could not be distinguished from the thoracic segmental anlagen. The primordia of the two genital segments were formed posterior to the eleventh thoracic appendage (fig. 42, *Rd gentl*) and devel-

oped into male and female genitalia respectively by the fusion of these two segments in the subsequent stages. The segmental rudiments were developed from the ventral ectoderm in a way similar to that of the thoracic segments. In the eighth stage the fused genital segments had shown growth only in length in the axial direction. In the tenth and eleventh stages the genitalia became distinctly male and female externally. The genital segments attained adult form in the fifteenth stage (fig 47) in both sexes. The gonads developed in the eleventh stage on either side of the intestine and extended back into the abdomen.

In the male the posterior portion of the first genital segment ultimately developed into a pair of ventrolateral, finger-like outgrowths called penes (figs. 44-48), each consisting of a chitinous fixed part and an eversible membranous tube with spines on its inner side. These both developed from the ectodermal part of the two genital segments. At the distal end of the protruded penis the vas deferens opened to the exterior.

In the development of the female genitalia (figs. 49-53), the mid-ventral parts of the genital segments and the primordia of the oviducts were fused. At the point of fusion a continuity was established with the distal end of the oviduct. The uterus was developed medially from the rudiment of the second genital segment. At the distal end of the developing egg pouch a large opening connected the developing uterine cavity with the outside. In subsequent stages the yolk and shell glands were developed. In the seventeenth stage of the female the yolk and the shell glands filled most of the empty space in the egg pouch and the ventral portion of the fused genital segments. The eggs in various stages of development were also observed in this stage.

The muscles of the genital segments are homologous to the muscles of the thoracic segments except for the absence of the appendicular muscles. In the male the penis was supplied with three powerful posterior muscles called the retractors (fig. 44, *Retr*) of the penis, and the other two muscle strands called the anterior and posterior extensor muscles (*Extr pen*). These five muscle strands were inserted on the vas deferens and were used for its constriction (fig. 47, *Retro vd*). Two well developed segmental muscles were also inserted on the penis, originating from the inner dorsal wall of the genital segments (transverse and oblique descending muscles), and were used for the retraction of the genitalia.

In the female the segmental muscles (transverse and oblique descending (fig. 52, *obl m*) were attached to the egg pouch at the anterior and posterior positions. The uterus, shell and yolk glands, and oviductal portion in the egg pouch were supplied with several muscle bands (fig. 52, *extra ovi, Rot ovi, Flx ovi*) used for the etxension, retraction, and rotation of these organs.

F. Abdominal Segments and Their Musculature

In the first five larval stages there was no distinction of the abdominal segments. The abdomen was present in these early stages as a cylindrical, unsegmented trunk located between the developing thoracic segments and the anal opening. The external rudiments of the first two true abdominal segments (14th and 15th body segments) appeared in the sixth stage when the body length was 1.78 mm. In the ninth stage the 16th, 17th, 18th, and 19th trunk segments (fig. 55, *Abdo*) were differentiated. On the lateral side of each segmental joint a pair of minute hairs was developed. Their sensory function was indicated by the attachment of the nerve fiber at their bases. These sensory hairs persisted to the fifteenth stage; they degenerated in subsequent stages. The adult form of the abdominal segments was attained in the ninth stage (fig. 55) when the body length was 3.67 mm. During the subsequent gradual development of the abdominal segments there was only an increase in size.

The rudiment of the musculature was formed soon after the anlagen of the abdominal segments appeared. In the fully developed segment there were two sets of longitudinal muscles, dorsal and ventral bundles on each side (fig. 41). The gonads were developed between the dorsolongitudinal and ventrolongitudinal muscles. The abdominal nerve trunks were developed medial to the ventral strands.

The musculature of the abdomen in the adult fairy shrimp consisted of segmental muscles as observed in the thoracic and genital segments; appendicular muscles were lacking (fig. 41). The muscles of the abdomen consisted of a set of dorsal and ventral longitudinal bands (*DLM, VLM*) run-

ning throughout the abdominal segments. There was also a pair of muscles joining dorsal and ventral longitudinal muscle bands. Two pairs of inner and outer dorsoventral muscles (*I dvm, O dvm*) were developed, which originated from the inner dorsal and lateral body wall, and were inserted into the tendinous fiber at the ventral side of the ventrolongitudinal muscle bands, likewise located dorsal to the abdominal nerve. The abdominal muscles functioned to push the eggs or sperm from the gonads to the genitalia, and also help to steer the body during swimming.

G. Telson, Cercopods and Their Musculature

In the first larval stage there were no seta around the anus. In the second stage, at the posterior end of the unsegmented part of the postcephalic region, a pair of setae projected on each side of the anus. In the third stage another pair of setae developed on the lateral to the previous pair of setae. In the fifth stage one more pair of setae projected posteriorly on the inner side of the previous two pairs of setae which had become longer. In the seventh stage the cercopods first appeared (fig. 7, *Crpd*). According to Hsŭ (1933) the last abdominal segment, which was smaller than the others was the telson, and the two rami with setae on either side developed into the cercopods. In this stage each ramus or developing cercopod had five setae with setules. In the eighth stage (fig. 54) of both sexes each developing cercopod had eight setae with setules; then in the ninth stage (fig. 55) the number increased to fourteen on each cercopod. Following this there were twenty setae in the tenth stage (fig. 26), twenty-six in the eleventh stage (fig. 57), fifty in the twelfth stage, sixty in the thirteenth stage (fig. 61), and seventy in the seventeenth stage in both sexes. In the adult female (fig. 62) the number of setae with setules increased to eighty-five and that number was retained throughout life. In the male the increase in the number of the setae was not so rapid after the seventeenth larval stage. In the eighteenth stage the male had seventy to seventy-five setae on each cercopod, and some of these were degenerated at their distal ends with their bases showing development of the chitinous spines of the mature adult (fig. 60). In the fully grown male each cercopod had about sixteen spines distally and fifty-six setae with setules proximally. During this stage there was a gradual increase in the length of each cercopod and the number of setae with setules. In the fully grown male each cercopod was fused with the telson and had only a faint line indicating the fusion.

The telson contained four transverse muscle strands originating on the lateral walls and inserted on sides of the rectum (fig. 57, *Rct m*). These muscles were used for dilation of the rectum.

There were two muscles attached to each cercopod; they originated from the posterior end of the ventrolongitudinal muscle bands and were inserted on the proximal and distal ends of the cercopods. The outer muscle (fig. 61, *Abd*) of each cercopod was used to pull the cercopod away from the body, while the inner one (fig. 61, *Add*) pulled the cercopod towards the body. The bases of the setae projected internally and were attached to minute muscle fibers. The latter were continuations of the abductor and the adductor muscles of the cercopods. These minute muscle fibers were used to move the setae in an upward and downward direction.

H. Growth Rate

Observations made on the growth rate of the different parts of the body were more or less similar to those of *Artemia salina* as described by Weisz (1946). In the development of the thoracic segments, when a new segment was differentiated, the preceding segment increased in length and width. The longer thoracic appendages were located anteriorly. As the eleventh thoracic segment appeared in a rudimentary stage, the fifth segment and its appendages were completely developed, and at the same time the rudiment of the nineteenth trunk (6th abdominal) segment appeared. At the advanced sixth stage the segments of the abdomen, which had retained constant length during the development of the thoracic segments and their appendages, started to grow rapidly in length. The genital segments (12th and 13th) developed in equal length and remained equal throughout their later development. The genital segments were longer than the eleventh thoracic segment but became progressively shorter in relation to the fourteenth and other abdominal segments. When the nineteenth abdominal segment

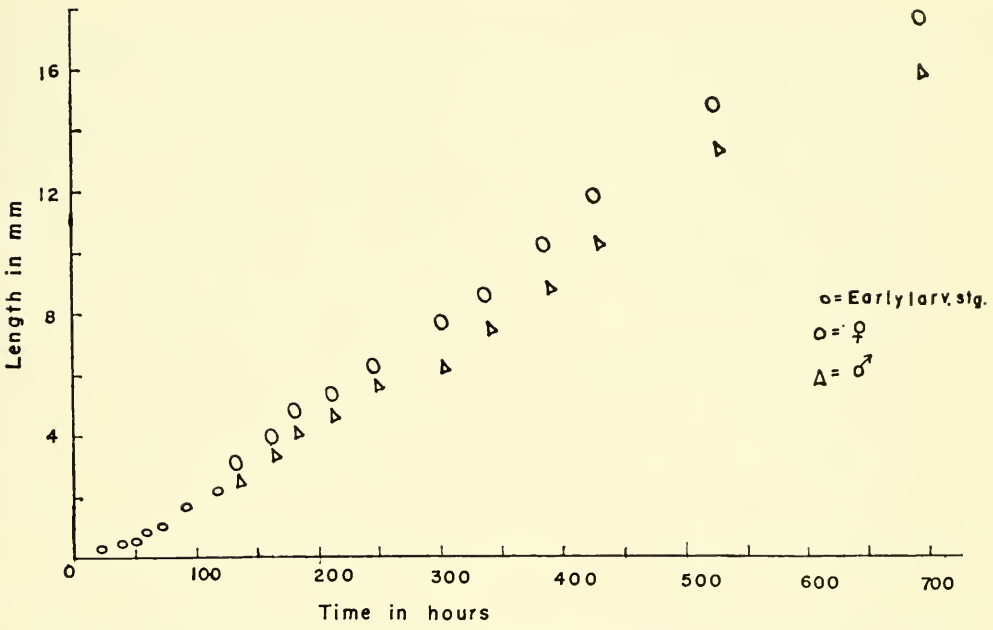


Figure 63. Growth rate of male and female larval stages of *Streptocephalus seali.*

appeared as a rudiment, the eleventh thoracic segment reached the mature stage.

As the graph shows (fig. 63), the growth rate was rapid up to the seventh stage at which time there was no distinction in sex. From the eighth stage the sex of the larvae was differentiated and rate of growth of the females were more rapid. In comparison to the female, growth of male larvae was slower between the tenth and eleventh stages; then there was a slight increase, but growth rate decreased again between the twelfth and thirteenth stages. In subsequent stages up to the adult and even after the adult stage the rate of growth in the males and females was nearly constant.

I. Abbreviations Used in Figures

Abd—Abductor muscle
Abdo—Abdomen
Abdo seg—Abdominal segment
Acl gl—Accessory gland
Add—Adductor muscle
An—Anus
Ant—Antenna
Ant ext—Anterior extensor muscle
Antl—Antennule
Asd m—Ascending muscle
Bsl seg—Basal segment of the antenna
Bspd—Basipodite
Ce—Compound eye
Chi spr—Chitinous spur
Cir m—Circular muscle
Con m—Connective muscle
Crpd—Cercopod
Dhb ptpd—Distal hook bristle of the protopodite
DLM—Dorsal longitudinal muscle
Dpr—Depressor muscle
Dsd m—Descending muscle
D seg—Distal segment of the antenna
Egp—Egg pouch
Endp—Endopodite
Epd—Epipodite
Evs pen—Eversible penis
Ex gl—Excretory gland
Expd—Exopodite
Extr—Extensor muscle
Fl—Flabellum
Fl fm—Flabelliformis muscle
Flx—Flexor muscle
Fr app—Frontal appendage
Gen d—Genital duct
Gl—Gland
Gt—Gut
Gt m—Gut muscle
Ht—Heart
Infl pr end—Inflexor of protenditis
I dvm—Inner dorsoventral muscle
Intm—Intermediate segment of the antenna
Larv stg—Larval stage
L lp—Lower lip of the egg pouch
L lm—Longitudinal muscle of the labrum
Lm—Labrum
LM—Longitudinal muscle
Lm M—Labral muscle
Lt m—Lateral muscle
Lt shr—Lateral sensory hairs
Lv—Levator muscle
Lv prend brc—Levator protenditis brevis
Lv prend long—Levator protenditis longus

Md—Mandible
Me—Median eye
Mx 1—First maxilla
Mx 2—Second maxilla
Mx br—Maxillary brush
N—Nerve
Nc—Nerve cord
Obl m—Oblique muscle
Ovi—Oviduct
O dvm—Outer dorsoventral muscle
Pen—Penis
Phb Ptpd—Proximal hook bristle of the Protopodite
Pl end—Pleuro-endopoditis
Plp—Palp
Pl pepd—Pleuro-Praaeepoditicus
Pl ped ref—Pleuro-pedalis refigens
Post ext—Posterior extensor muscle
Pri intri—Prior internus
Prmt—Promotor muscle
Prpd—Praeepipodite
Prtpd—Protopodite
Pt ram ma pref—Post ramus major praefigens
Rct m—Rectal muscle
Rd gentl—Rudimentary genitalia
Ref—Refigens muscle
Retr vd—Retractor muscle of the vas deferens
Rmt fl—Remotor of flabellum
Scl—Sensory cells
Set—Seta
Shrs—Sensory hairs
Sp—Spine
Sp ne m—Supra-neural muscle
S sp md—Sensory spine of the mandible
Su ne m—Sub-neural muscle
Tel—Telson
Th app bd—Thoracic appendage bud
Tntl pr—Tentacular process
Tr ext ref—Transverse externus refigens
Tr int—Transverse internus muscle
U lp—Upper lip of the egg pouch
V lb—Ventral lobe of the genital segment
VLM—Ventral longitudinal muscle
Vd—Vas deferens
1-11—Thoracic appendages
12-13—Genital segment

IV. Discussion

Studies were made on the postembryonic larval stages of the fairy shrimp *Streptocephalus seali* Ryder to determine the number of larval stages, and when the development of individual structures and their musculture took place.

Distinctions of the larval stages were made according to the method of Weisz (1947). The number of stages was determined by the number of body segments and the body length. The total length of any one larval stage was nearly the same regardless of the number of ecdyses (mean $\pm$ 2). The constant conditions in the laboratory and the above-mentioned method of identification minimized the influence of external factors such as variance in salinity, temperature, pH, etc. Thus, I agree with Weisz (1947) that his method of identification of larval stages was more reliable than identifying them by molting cycles as employed by Heath (1924).

For the complete development of *Streptocephalus seali,* eighteen larval stages were involved. After the eighteenth stage there was only an increase in the body length, and in the apical segment (hand) of the male antenna. The distinction in sex was observed from the eighth larval stage. The basis for that distinction was the rudiment of the developing projection from the protopedite of the male antenna, which later developed into the apical segment or the hand. From the eighth stage the development was gradual, faster in the females than in the males. In the tenth stage the setae on the antennal exopodite of the male and female degenerated and the antennae moved gradually toward the anterofrontal side of the head.

The first few larval stages of *S. seali* had structures, especially antennae, more or less similar to those described by Packard (1883) for *Streptocephalus texanus,* and for *Branchipus stagnalis;* and by Oehmichen (1921) for *Branchipus grubei.* The similarities were the development of the saber-shaped hook bristle on the inner and ventral side of the protopodite or first basal segment of the second antennae. This hook bristle (figs. 1-7, 20) at first was naked, then became beset with two rows of fine setules in the first larval stage; later, in the second stage it split into two flat branches possessing setules at the distal end of each branch. The second segment of the second antenna also had a long, flat and curved inward hook bristle which though first naked had setules in the advanced first larval stage. At the distal end of the antennae there were two branches each of which had three long setae; but, *S. texanus,* according to Packard (1883) had five setae on the exopodite of the antenna. In the ninth stage, the antennal setae were completely degenerated; the same was described by Packard (op. cit.) for *S. texanus.* Similarly the antennal exopodite had thirteen long setae in *S. seali,* but in *S. texanus* had fifteen.

Considerable controversy had existed regarding the number of segments in the male antenna. Baird (1852), Claus (1873, 1886),

Cissler (1883), and Daday (1910) explained that the antennae of the male have three segments with joints; namely, basal segment, intermediate curved segment, and apical segment (or hand). Barnard (1929) and Linder (1941) favored the idea that the male antennae of *Streptocephalus* species have only two segments as in other families of the fairy shrimp. From my observations on the development of the male antenna, I concluded that the male antenna consisted of three segments. This conclusion was based on observation of the development of the apical lobe of the antenna of the male from the eighth stage to the adult. The apical lobe or the tentacle-like process (fig. 10) became the intermediate segment; from its distal end in the eleventh stage the third segment (or hand) developed with distinct demarcations of the joints. The spur or the hook (remnant of the earlier exopodite) was just the continuation of a process from the basal segment of the antenna.

The development of the frontal appendage has been described by several authors. Grube (1853) traced the development of the frontal appendage from the basal segment of the male antenna in *Streptocephalus proboscideus*. Daday (1910) stated that the frontal appendage in *S. purcelli* arose from the head. Evans (1915) in *S. texanus* traced its origin from the union of the basal parts of the antennae which had separated from the antennae and fused with the head. In *Chirocephalus grubei* Oehmichen (1921) showed that the rudiment of the frontal appendage arose from the distal part of the protopodite although in the adult its position was rather proximal; a similar origin was described by Heath (1924) in *Branchinecta occidentalis* and by Hsŭ (1933) in *C. nankinensis*. Claus (1886) described the origin of the frontal appendage in the Streptocephalidae and stated that during larval development the paired rudiments of the frontal appendage migrated from the male antennae to the head where they coalesced and formed a common structure. The twofold origin of the frontal appendage was disclosed by a notched tip at the distal end. I found that in *S. seali* the origin of the frontal appendage was similar to that described for the family Strepotocephalidae by Evans (1915) and Linder (1941).

During the development of the larval stages, there was a gradual degeneration of the mandibular palp with its setae. The sensory spine originated on the posterior side of the coxopodite of the jaw, and curved towards the mouth. This spine also degenerated completely in the later stages. Nothing has been mentioned in the literature about this sensory spine of the mandible except by Spangenberg (1875) and Oehmichen (1921) who stated that in the adult this spine was a remnant of the mandibular palp. But, in the early larval stages I found that this sensory spine originated independently and separately from the palp. Also, no description had been given in the literature concerning the function of this spine, except that Oehmichen (1921) gave it the name "sensory spine". I presumed that when the palp was a swimming appendage in early larval stage, this spine with setules was a sensory organ, but later both degenerated and the sensory function was taken over by the second maxillae. The complete degeneration of the palp and the sensory spine of the mandible was accomplished in the twelfth stage of *S. seali*. Heath (1924) maintained that the remnant of the palps was present in adult *B. occidentalis*, while Hsŭ (1933) observed that the palps had completely degenerated in *C. nankinensis* when the larva was 3.6 mm long.

Development of the first and second maxillae was followed in detail up to the fifth larval stage. Beyond that stage the changes in both pairs of maxillae were comparatively slight and limited mainly to an increase in size and addition of more setae possessing setules on the first maxillae.

Formation of the different parts of each thoracic appendage was gradual and each part was differentiated from a rudimentary stage to the adult form during development. Considerable confusion has existed in the literature regarding the interpretation of the appendicular components. Proximally near the epipodite a lamelliform lobe-like structure developed; this was called the praeepipodite by Linder (1941) while other authors such as Daday (1910) referred to it as a bract. The terminology used by Linder seemed to be more convincing, thus, I have followed it in the present description of all parts of the appendage. During the development of the appendage the rudiment of the praeepipodite originated as a single lobe and was envaginated from the anlage of the appendage. In the adult the margin of the

praeepipodite was serrated and had a notch on the mediolateral side. According to Linder (1941) and others, the notch represented the fusion point of two praeepipodites to the adult stage, but during the whole developmental course I did not find any indication of the division of the praeepipodite, except a minute notch in the adult.

A confusion in the naming and the interpretation of the number of the endites exists in the literature. Packard (1883), Calman (1909), Linder (1941), and Nourisson (1958) identified six endites considering the gnathobase or first endite to consist of only one endite, while the last or sixth endite was considered to be adjacent to the flabellum. Cannon and Leak (1933), Lowndes (1933), and Borradaile (1959), on the other hand, counted seven endites, considering the first to be composed of two fused endites; thus the endite adjacent to the flabellum was considered the seventh endite. Claus (1873) and Hsŭ (1933) labelled the first endite as the foot lobe or gnathobase, the second endite as the first foot lobe or endite and the endite adjacent to the flabellum called fifth endite. Claus labelled the flabellum as sixth endite, but Hsŭ called it an exite. My observations on the development of the thoracic appendage indicated there were only six endites, one flabellum which was a part of the exopodite, one epipodite, and one praeepipodite. The gnathobase or first endite consisted of only one endite and not two as implied by others. Claus' (1873) interpretation of the flabellum as the sixth endite seemed to be wrong. From the external as well as the internal structure of the appendage and also from a description of other authors, I think that the flabellum is the exopodite.

Two interpretations regarding the origin of the genital segments have been published. Nitsche (1875), Packard (1883), Claus (1886), Sars (1896), Hsŭ (1933), and Linder (1941) hypothesized that the genital segments were the modified first two abdominal segments, and from their ventral side the external genitalia were developed. Borradaile (1959) stated that the genital segments included a twelfth thoracic and the first abdominal segment. My observations indicate that the genital segments should be regarded as the first two abdominal segments. The basis for this contention is that the development of the genital segments was more or less similar to the development of the abdominal segments. The sensory hairs on posterolateral side near the abdominal and genital segmental joints were present up to the 15th larval stage, and degenerated together after that stage. In addition to that the musculature of the genital and abdominal segments showed more similarity to each other than to the musculature of the thoracic segments. Though the genital segments contained more muscles than other abdominal segments, the segmental muscle pattern was the same in both.

Spangenberg (1875) observed that the genitalia developed as two independent outgrowths from the ventral side of the twelfth and thirteenth trunk segments in *Branchipus stagnalis*. I observed a similar origin of the genitalia in *S. seali*.

V. Summary and Conclusions

1. A review of the literature on the biology of fairy shrimp was made.

2. Eighteen larval stages occurred in 29 days; their distinction was based on the increase in the number of the segments and the body length.

3. Studies were made on the external development, the musculature of the head, the thoracic segments, and their appendages, genitalia, abdominal segments, and cercopods.

4. The origin and the development of the frontal appendages and the male antenna were traced. The conclusion was reached that the frontal appendage originated from the basal segment of the male antenna, which then coalesced with the head and fused medially; also, that the male antenna was composed of three segments.

5. The conclusion was reached that the sensory spine of the mandible of the early stages was not the remnant of the palp but a separate structure and both degenerated in preadult stage. Also, the thoracic appendage was composed of six endites and one praeepipodite besides other structures of the appendage. The genital segments were modified from the first two abdominal segments.

6. A brief study was made to observe the rate of growth of the larval stages and their structures at various periods. The rate of growth in the female larva was faster than in the male.

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ABSTRACT

The postembryonic larval stages of the fairy shrimp *Streptocephalus seali* Ryder were studied. Eighteen larval stages completed in 29 days are described from the first stage to adult. The development of the head appendages, thoracic appendages, genitalia, abdominal segments, and cercopods are described. The development of the male antenna and frontal appendage with their musculature is detailed especially due to their importance in the taxonomic studies of fairy shrimps. The various parts of the head appendages, thoracic appendages, and the genital segments are described and interpreted.

Conclusions were reached that male antenna have three segments; the frontal appendage originated from the basal segments of the male antennae; the sensory spine of the mandible was not the remnant of the mandibular palp; and, the two genital segments were the modified first two abdominal segments. The development of the musculature of the various structures of the fairy shrimps was described.

The growth rate of the early male and female larval stages was described. The female larval stages showed a faster growth rate than those of males.

To elaborate the development of the postembryonic larval stages and various developing structures, sixty-three figures are included.