ONTOGENY OF THE FIRST AND SECOND PLEOPODS OF THE MALE CRAWFISH *ORCONECTES CLYPEATUS* (HAY) (DEDAPODA, ASTACIDAE)

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In all crawfishes of the family Astacidae, the appendages of the first and second abdominal segments of the male are modified for use as organs of sperm conduction from the deferent ducts of the male to the annulus ventralis (=seminal receptacle) of the female. Of these appendages, the first pair are the more highly modified showing a variety of forms which bear little resemblance to the generalized biramous condition found in the other abdominal appendages.

Although the gonopods of the male crawfish, and particularly the first pleopod, are of paramount importance in the taxonomy of the group, little is known of their growth and development. Andrews (1906) made an excellent study of the ontogeny of the annulus ventralis of the female but did not include information on the ontogeny of the gonopods of the male. Again, Andrews (1907) made a study of the young of the crawfishes *Pacifastacus leniusculus* and *Orconectes limosus* with emphasis upon their development immediately before and after hatching; however, this study did not include specific information on the development of the first and second pleopods of the male. Later, Andrews (1910, 1911) also made excellent studies of the anatomy, both internal and external, of the first and second pleopods of the crawfish *O. limosus* and gave an ontogenetic description of these appendages. He also noted that the sexes may be distinguished from one another in *O. limosus* after the third molt. Penn (1943) briefly described the development of the first pair of pleopods of *Procambarus clarki* (Girard) stating that "they appear as very small . . . 'knoblike' processes on the ventral transverse ridge of the first abdominal somite when the crawfishes are 4.5 mm cephalothorax length". He concluded that the first pair of pleopods of the very small males develop into the mature form by gradual growth and differentiation. Hobbs (1940, 1945) in his studies of the first pleopod of male Cambarinae, proposed a nomenclature to be followed in all taxonomic descriptions of crawfishes. Hart (1952, 1953) made excellent studies of the exokeleton, musculature, and serial homologies of the first three pairs of abdominal appendages of male *Cambarus longulus longulus* Girard and *Cambaroides japonicus* (DeHann). Suko (1953) made detailed studies on the development of secondary sexual characters in appendages of *Procambarus clarki*. He included notes on the development of the first and second pleopods of the male from their first appearance at a total body length of 4.7 mm to full development, and compared them with corresponding stages of the first and second pleopods of the female. Also included are drawings of the first and second pleopods of both male and female at critical stages in their development. Suko stated that the first pleopod made its first appearance on 4.7 mm individuals as a process from the epimeron lying between the pleuron and the sternum growing along the central bar of the sternum, and attained its full growth at the eleventh molt. The second pleopod appeared at the third instar and was completely formed at the eleventh instar. Finally, Hart (1956) gave a summary of the important changes in the first pleopod of *Cambarus l. longulus* from its appearance in the third instar to its mature form. He assumed that sexual maturity is attained when the crawfish has a cephalothorax length of between 14.0 and 17.5 mm. He also stated that at no time in the development of the first pleopod does it show any tendency toward a biramous condition so typical of the other pleopods.

Adult male crawfishes of the subfamily Cambarinae are peculiar in the possession of two distinct forms of the male sexual appendage. Those males capable of mating are designated as first form; those which are not capable of mating are designated as second form. First form males are distinguished from second form males by the presence of well-defined and corneous terminal processes of the first pleopods; the processes of the second form are poorly defined, blunt and never corneous. Also, the first form male possesses well-developed hooks on the ischiopodites of certain of the pereiopods, usually on the third or fourth pair, which are not present (or present but less developed) in the second form males. These distinguishing features of the two forms of the adult male crawfish were discussed at length by Hagen (1870), and more recently by Creaser (1933a), Hobbs (1942) and Hobbs and Marchand (1943).

Objectives of the Study

The objectives were threefold. First, to determine a growth increment for *Orconectes clypeatus.* This would make the determination of the instar of any individual possible and would permit the use of previously collected and preserved material in studying the ontogeny of the first and second pleopods of the male.

Second, to study the ontogeny of the first and second pleopods of the male from the earliest instar in which sexual dimorphism is apparent.

Third, to determine if the suture which was present between the basipodite and the endopodite of the first pleopod in juvenile males is recovered when the first form males return to the non-breeding condition after the close of the breeding season. The results of this study should show whether the second form is a seasonal condition or a developmental stage.

Materials and Methods

All or the specimens used were collected from a pineland ditch 2.4 miles south of Hickory, and a roadside ditch 2.5 miles south of Talisheek, St. Tammany Parish, Louisiana. During periods of drought when the ditches completely dried up, the crawfish were recovered from their burrows one to four inches below the surface of the ground as described previously by Smith (1953). At other times the crawfish were collected by means of a dipnet.

Growth increment.—The specimens which were used to determine the growth increment for each molt were kept individually in small, round, glass bowls 10 cm in diameter and 4 cm in depth. They were fed primarily on lettuce and the water was changed weekly. This crawfish survives well under laboratory conditions.

Some writers, notably Creaser (1933a) and Van Deventer (1937) questioned the validity of growth data gathered from laboratory raised animals; both writers preferred to collect large numbers of specimens at one place at stated time intervals throughout the year.

Any attempt to obtain growth data on particular individuals while allowing them to remain in their natural habitat is difficult because of the important part played by molting in the growth of crawfishes. This prevented the possibility of studying and measuring certain individuals, tagging them and releasing them in their natural habitat in the hope of recovering them at a later date for restudy and remeasurement. However, future workers should consider the method recently devised by Slack (1955) which apparently does not injure the crawfishes or alter their behavior, and which is not lost during the process of molting. The method involves injecting black numbering machine ink just beneath the exoskeleton.

In any study of growth, a measurement must be chosen which will show the true growth of the individual throughout the study. Total length is not considered a particularly valid measurement by most students of crawfish, although it has been used in some morphological studies such as those by Andrews (1907) and by Suko (1953). Andrews chose this measurement because of the extremely small size of the newly hatched individuals.

The length of the cephalothorax from the anterior tip of the acumen to the posterior edge of the carapace was chosen as the measurement which best fitted all requirements. Many writers, including Creaser (1933a), Van Deventer (1937), Tack (1941), Penn (1943) and Smith (1953), have used the length of the cephalothorax as a measurement of growth. This measurement has at once the advantage of being easily translated into terms of approximate total body length throughout the life span after the young become independent of the mother. Furthermore, it is not easily affected by the movement of the animal during the process of measurement since the exoskeleton of the cephalothorax is a rigid unit.

The animals after being brought to the laboratory from the field were measured and placed in glass bowls. Such data as cephalothorax length, sex, and date of collection were kept for each specimen. Measurements were taken by means of a vernier caliper and were recorded to the nearest

0.1 mm. Approximately twenty-four hours after each molt, the newly molted crawfish was remeasured. The time interval between molting and remeasurement was necessary to allow the exoskeleton to harden. Juveniles and adults of both sexes were used in the increment determination.

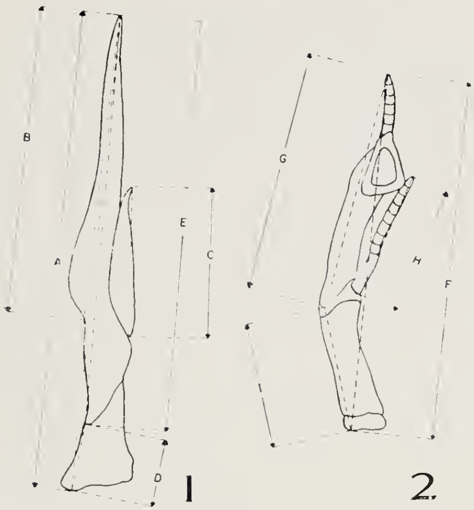
Ontogeny.—To show clearly the expected allometric growth of the first and second pleopods, the animals to be studied were divided into size groups, measurements made of significant characters and such measurements treated statistically. The animals were separated first according to whether they were first form or second form. They were further arranged in groups with a cephalothorax length range of 0.4 mm, since this had been found to be the average increase in cephalothorax length per molt. For example, the males measuring 5.3 mm in cephalothorax length were arbitrarily assigned to the size group 5.0 to 5.4 mm. Ten specimens for each size group were selected randomly from the preserved material for study. This number was selected as being small enough to be convenient yet large enough to handle statistically with fair accuracy. In some cases where more than ten specimens in one size group were accidentally studied, all were included to eliminate personal bias. Lack of sufficient material prevented the inclusion of size groups of first form males below 11.5 mm in cephalothorax length and above 17.4 mm (Table 1). Likewise, 5.0 mm and 17.9 mm cephalothorax length represent the minimum and the maximum sizes of second form males studied (Table 2). All measurements, with the exception of the cephalothorax length, were made with an ocular micrometer calibrated for an American Optical Company's stereoscopic microscope and were recorded to the nearest 0.1 mm. In each case the right pleopod was removed for measurement except when injured. The measurements chosen for study on the first pleopod (fig. 1) were (A) total length, (B) length of the central projection, (C) length of the mesial process, (D) length of the basipodite, and (E) length of the endopodite. In first form males the latter two measurements were omitted because of the obliteration of the suture between the basipodite and the endopodite. The measurements on the second pleopod (fig. 2) were (F) total length, (G) length of the endopodite, (H) length of the exopodite, and (I) length of the protopodite. To better compare the growth rates of the various organs, the measurements were all expressed as ratios of the measurements to the length of the cephalothorax, unless otherwise stated, rather than as absolute measurements. Standard deviation and standard error of the mean were computed without grouping according to the method outlined by Cazier and Bacon (1949).

TABLE 1.
First form males used in ontogeny study

No. of Specimens	Cephalothorax Length Range	Mean
12	11.5-11.9	11.73
12	12.0-12.4	12.21
12	12.5-12.9	12.66
13	13.0-13.4	13.10
13	13.5-13.9	13.58
11	14.0-14.4	14.08
10	14.5-14.9	14.57
10	15.0-15.4	15.08
10	15.5-15.9	15.68
10	16.0-16.4	16.20
11	16.5-16.9	16.65
10	17.0-17.4	17.35

TABLE 2.
Second form males used in ontogeny study

No. of Specimens	Cephalothorax Length Range	Mean
11	5.0- 5.4	5.39
10	5.5- 5.9	5.81
11	6.0- 6.4	6.21
11	6.5- 6.9	6.70
10	7.0- 7.4	7.21
11	7.5- 7.9	7.58
10	8.0- 8.4	8.20
11	8.5- 8.9	8.60
10	9.0- 9.4	9.10
10	9.5- 9.9	9.81
13	10.0-10.4	10.22
11	10.5-10.9	10.75
10	11.0-11.4	11.28
10	11.5-11.9	11.70
10	12.0-12.4	12.20
10	12.5-12.9	12.64
10	13.0-13.4	13.13
12	13.5-13.9	13.60
10	14.0-14.4	14.12
12	14.5-14.9	14.63
10	15.0-15.4	15.21
10	15.5-15.9	15.56
11	16.0-16.4	16.10
10	16.5-16.9	16.58
10	17.0-17.4	17.21
11	17.5-17.9	17.75



Figures 1-2. Illustrations of measurements used in the ontogeny study. **1**, Mesial view of first pleopod of second form male: (A) length of pleopod, (B) length of central projection, (C) length of mesial process, (D) length of basipodite, (E) length of endopodite. **2**, Mesial view of second pleopod of second form male: (F) length of pleopod, (G) length of endopodite, (H) length of exopodite, (I) length of protopodite.

Growth Increment

Between January 24, 1956 and June 18, 1957, 153 molts from 132 specimens were recorded. These showed an average increment of 0.41 mm. Standard deviation and standard error of the mean were ± 0.1821 and ± 0.1288 respectively. Several increment averages were taken during this period and none varied more than 0.02 mm from this final figure after the first fifty molts were recorded. The scatter diagrams, showing correlation between increment and cephalothorax length (figs. 3-6) indicate that there is very little correlation between the growth increment per molt and cephalothorax length. The regression lines show that the second form males that molted and remained second form (fig. 3) tended to increase in cephalothorax length slightly more per molt with increased size (positive correlation), whereas, the second form males that molted to second form (fig. 6), the first form males that molted to second form (fig. 5), and the females (fig. 4) tended to increase in cephalothorax length slightly less per molt with increased size (negative correlation). However, these positive and negative correlations are not considered significant. Thus *O. clypeatus* tends to increase in cephalothorax length approximately the same amount per molt regardless of sex or size.

The smallest recorded sexually mature *O. clypeatus* (first form) measured 10.8 mm in cephalothorax length (Smith, 1953). With an average increase of 0.4 mm cephalothorax length, and using a modified version of Van Deventer's (1937) formula, the approximate number of molts for any individual may be calculated.

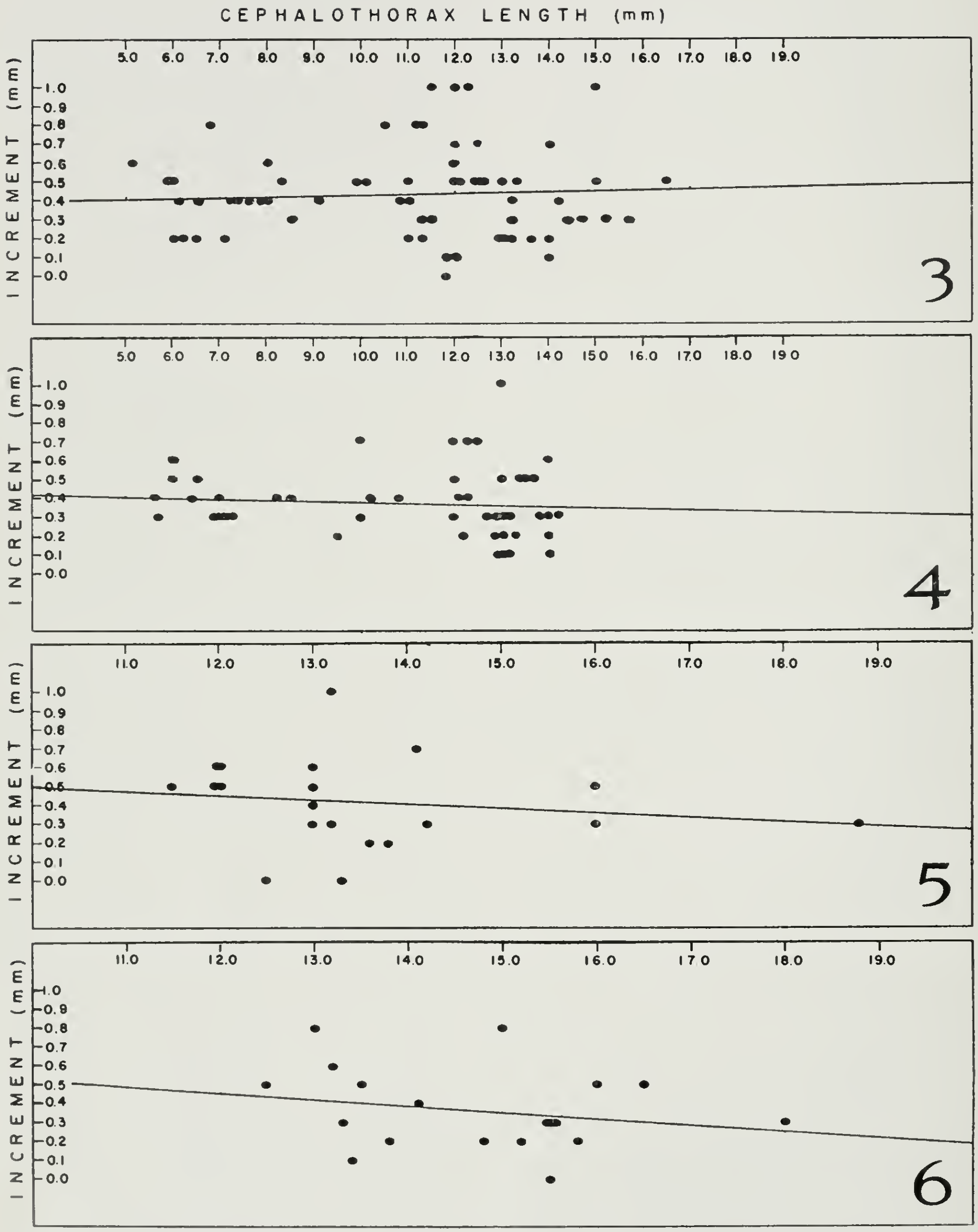
$$\frac{x - y}{0.41} + 2 = z$$

Where:

x = cephalothorax length of individual
y = average cephalothorax length of juvenile crawfish when it first becomes free-living (i.e., 2.5 mm according to Smith)
0.41 = average growth increment at each molt
2 = number of molts undergone by crawfish before it becomes free-living
z = total number of molts undergone

Hence, *O. clypeatus* requires approximately twenty-two molts before reaching the minimum size for sexual maturity. Van Deventer (1937) stated that a cephalothorax length of 20.0 mm marked the boundary of sexual maturity in males of *Orconectes p. propinquus* (Girard), and that approximately eight to nine molts were required by *O. p. propinquus* males before reaching sexual maturity. Based upon fifty-nine actual molt increments, Penn (1943) found that the average increase in cephalothorax length of all sizes of *Procambarus clarki* was 2.6 mm per molt. He also stated that males attained sexual maturity at approximately 31.0 mm cephalothorax length, indicating *P. clarki* passes through approximately 12 molts before reaching sexual maturity. Also, Suko (1953) reports a first form male in the eleventh instar. Tack (1941) did not determine an increment for *Orconectes immunis* (Hagen); however, he raised a pair of males in the laboratory which survived the eighth molt and still had juvenile form sexual appendages.

Thus, *O. clypeatus* has a comparatively low average increase in cephalothorax length



Figures 3-6. Scatter diagrams showing correlation between growth increment and cephalothorax length. **3.** Males molting from second form to second form. **4.** Females. **5.** Males molting from first form to second form. **6.** Males molting from second form to first form.

per molt, and also requires a higher number of molts before attaining sexual maturity. Possibly this is due in part to the small size of *O. clypeatus,* and also to unknown environmental and physiological differences, as well as inherent genetic growth factors.

Ontogeny of the First and Second Pleopods

The study of the ontogeny of the first and second pleopods of male *O. clypeatus* was somewhat hampered by the early egg-laying season in the fall of 1956. According to Smith (1953), the egg maturation and embryonic development extends from October through January. However, during the period of the present study several extensive collections produced only two egg-bearing females (collected September 17, 1956) and the eggs were shed and eaten by the females after two days in captivity. In February after rains had refilled the collecting site, hordes of juveniles were collected, but these already ranged from 5.3 to 7.0 mm cephalothorax length. These circumstances prevented the study of the young from the time of their hatching until they were in approximately the twelfth instar. One preserved collection consisting of two females bearing young (range: 1.8 to 2.5 mm cephalothorax length) was of importance in giving an insight into the first appearance of the sexual appendages.

Description of the First and Second Pleopods of a First Form Male

The first pleopod, which reaches the coxopodite of the first pereiopod when in normal position, consists of three fused segments: coxopodite, basipodite, and endopodite. The exopodite is lost. The endopodite bears two conspicuous, terminal rami: the central projection which is very long, slender, subcylindrical and corneous and the mesial process which is considerably shorter (between one-third and one-half the length of the central projection) and also acute and non-corneous. The central projections of the right and left first pleopods are curved mesially and cross each other slightly at the tips when held in a resting position.

The second pleopod consists of four segments: a coxopodite, basipodite, exopodite and endopodite, and overlaps the basal portion of the first pleopod. The exopodite is slender, segmented and slightly offset from the endopodite, while the endopodite bears a terminal segmented process and a triangular-shaped outgrowth on the mesiodorsal side. This process, called the "triangle" by Andrews (1911), and later described by Hart (1953) as the centrocephalic process, is partly sclerotized and partly membranous and fits snugly into the space between the first pleopods.

Significant Stages in the Development of the First and Second Pleopods of the Male

First pleopod.—The first pleopods of the male appear as small papillae, widely separated on the sternum and pointing mesially toward each other when the crawfish are approximately 2.0 mm (second instar) in cephalothorax length (fig. 7). At this stage the rami of the endopodite are undifferen-

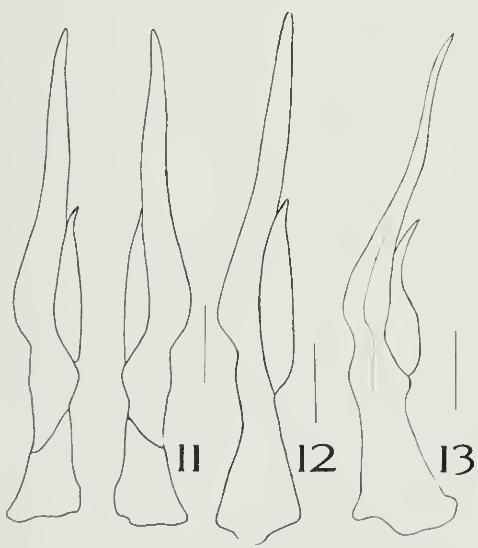
Figures 7-10. Outline drawings of caudal view of first pleopod. Vertical lines = 1.0 mm. **7.** Juvenile, 2.0 mm cephalothorax length. **8.** Juvenile, 5.3 mm cephalothorax length. **9.** Juvenile, 8.7 mm cephalothorax length. **10.** Second form, 13.0 mm cephalothorax length.

tiated. As the crawfish increases in size, the first pleopods tend to be relatively closer together, with the sternal sclerite from which they arise developing into a heavy, calcified, transverse ridge.

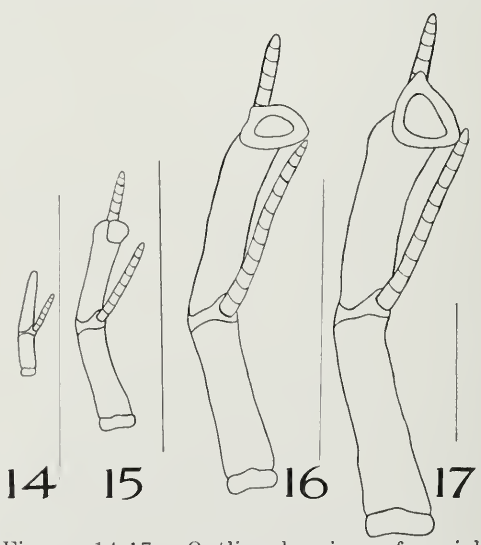
The mesial process is barely visible as a slight groove on the lower portion of the endopodite in approximately the 5.0 mm stage (fig. 8), but not until approximately the 10.0 mm stage (fig. 9) does the mesial process appear as a completely separate process.

After maturity is reached there are no significant changes in the first pleopod (figs. 10-12), other than a gradual increase in size which is approximately proportional to the increase in size of the cephalothorax length with each molt, except those resulting from the change from second form to first form (fig. 13) and from first form to second form. Except for various individual differences, the first pleopod of the second form male which has never undergone the change from second form to first form is identical to the first pleopod of a specimen of the same size which has molted from second form to first form and then returned to the second form condition following the breeding season. This pleopod shows at no time in its development any tendency toward a biramous condition. This agrees with the findings of Hart (1956) in his study on the ontogeny of the first pleopod of *Cambarus l. longulus* Girard.

Second pleopod.—In comparing the development of the second pleopod, one must keep in mind that whereas the first pleopod never at any time closely resembles any of the other pleopods, the second pleopod is present as early and is at first identical to the unspecialized pleopods. It becomes specialized through the course of its development by the addition of an outgrowth and not by the loss of parts. As previously mentioned, no first instar specimens were available to the writer for study; however, Andrews (1911) mentions that the pleopods of the second, third, fourth and fifth somites of both males and females of *Orconectes limosus* are represented at the time of hatching and are remarkably similar. Thus, the writer assumed that the second pleopod of *O. clypeatus*, of the same genus, appears at approximately the same time as the third, fourth and fifth pleopods, since these four pleopods were all of the same size in the smallest observed specimens. The second pleopod appears in the 2.0 mm stage

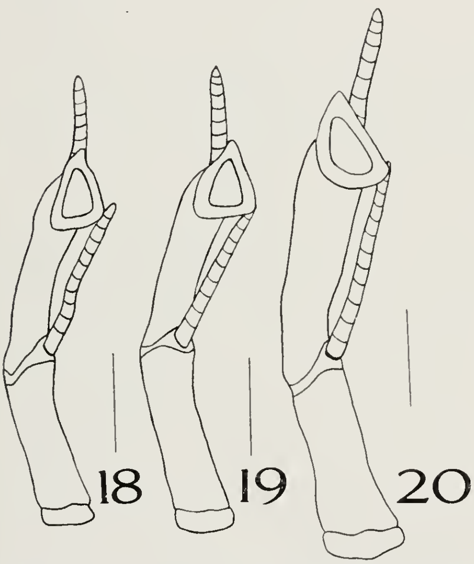


Figures 11-13. Outline drawings of the first pleopod (caudal view unless otherwise indicated). Vertical lines = 1.0 mm. **11.** Cephalic and caudal views, second form, 15.0 mm cephalothorax length, with complete suture. **12.** Second form, 15.0 mm cephalothorax length, without suture. **13.** First form, 16.5 mm cephalothorax length.



Figures 14-17. Outline drawings of mesial view of second pleopod. Vertical lines = 1.0 mm. **14.** Juvenile, 2.0 mm cephalothorax length. **15.** Juvenile, 5.3 mm cephalothorax length. **16.** Juvenile, 8.7 mm cephalothorax length. **17.** Second form, 13.0 mm cephalothorax length.

(second instar) as a flattened, translucent, typically biramous appendage with the endopodite slightly longer than the exopodite (fig. 14). The exopodite shows segmentation, whereas segmentation in the endopodite is absent or, at best, obscure. The distinctive centrocephalic process first appears in the 5.0-5.4 mm size groups (fig. 15) as a small protuberance on the mesial side of the endopodite near the distal end. At this stage the endopodite is prominent with the exopodite decidedly smaller. The exopodite which begins as a short, club-like ramus, becomes relatively narrower and longer with each succeeding molt (figs. 14-20) until the specimen molts into the first form condition. By the time the cephalothorax length of the specimen is 8.7 mm, the centro-



Figures 18-20. Outline drawings of mesial view of second pleopod. Vertical lines = 1.0 mm. **18.** Second form, 15.0 mm cephalothorax, with complete suture on first pleopod. **19.** Second form, 15.0 mm cephalothorax length, without suture on first pleopod. **20.** First form, 16.5 mm cephalothorax length.

cephalic process has taken on much of its final appearance (fig. 16). As might be expected, the change from second form to first form does not affect the second pleopod as extensively as it does the first pleopod, the chief difference being that portions of the endopodite, especially the centrocephalic process, are more sclerotized in the first form condition.

Ontogenetic Variation

The first and second pleopods of *O. clypeatus* undergo a very rapid growth rate in early life; however, in later life their growth rates tend to parallel that of the cephalothorax. In the second form males all five of the measurements of the first pleopod (length, length of the central projection, length of the mesial process, length of the endopodite and length of the basipodite) show an initial growth rate that closely parallels the growth rate of the cephalothorax. Then between 6.0 and 10.0 mm the growth rates of these parts increase rapidly. On the other hand, all four of the measurements of the second pleopod (length, length of the protopodite, length of the exopodite and length of the endopodite) show a rapid, steady increase in growth rate from the smallest size measured (5.0 mm) to 10.0 mm (fig. 21).

Another character is expressed as a ratio of the length of the central projection to the length of the mesial process, and shows that the proportional growth rates of the two parts are almost identical (figs. 23 and 24). Little change of significance is to be noted throughout the life span.

The growth rate of the first and second pleopods and their component parts in the first form males tend to parallel closely that of the cephalothorax length and may be considered isometric (fig. 21).

Significance of the First Form and Second Form Conditions

The existence of two forms in the mature male crawfishes of the subfamily Cambarinae has aroused much interest and speculation as to the explanation of this phenomenon. Much has been written describing the two forms in various species, but little is known of the actual position of the second form in the life history of any species.

Previous Studies

Hagen (1870), who was the first to publish on the eixstence of the two forms in the male crawfish, gave a detailed description of the two forms and conjectured that the second form was merely a sterile individual. Faxon (1884) conducted a simple experiment in which he kept several first form males and mature females of *Orconectes rusticus* together in the laboratory. After breeding, three of the males molted;

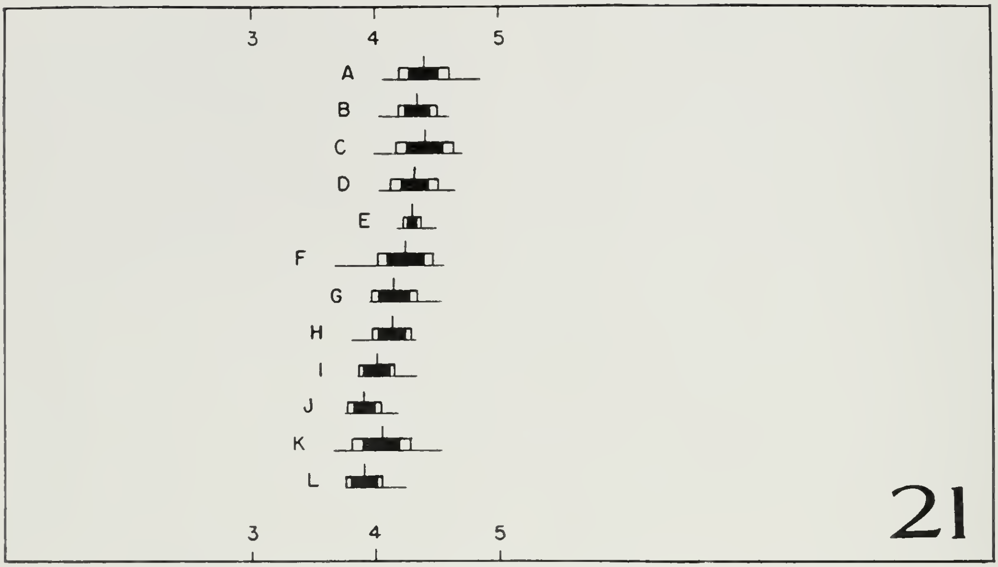


Figure 21. Ontogenetic variation in length of endopodite of second pleopod of first form male. Size groups (cephalothorax length) indicated to left of line as follows: **A** = 11.5-11.9 mm, **B** = 12.0-12.4 mm, **C** = 12.5-12.9 mm, **D** = 13.0-13.4 mm, **E** = 13.5-13.9 mm, **F** = 14.0-14.4 mm, **G** = 14.5-14.9 mm, **H** = 15.0-15.4 mm, **I** = 15.5-15.9 mm, **J** = 16.0-16.4 mm, **K** = 16.5-16.9 mm, **L** = 17.0-17.4 mm.

their exuviae were of the first form whereas the soft-shelled specimens were of the second form. Faxon concluded from this observation that the two forms represented alternating periods in the life of the individual male crawfish; the first form being the form assumed during the breeding season, the second form that assumed during the intervals between.

Steele (1902) drew several conclusions concerning the changes of the first and second forms after various laboratory experiments with *Orconectes nais* (called *Cambarus virilis* by Steele). She pointed out that during the late fall and winter the primary reproductive organs of the second form males were smaller and less developed than the same organs in the first form males. She also noted that males with imperfect or no chelae continue to molt into second form until the chelae have reached a size normal for the size of the animal. This was probably only an sssumption, as pointed out by Creaser (1933a), because several first form males of *O. nais* with imperfectly developed chelae were observed by him in Missouri in September and October.

Harris (1903) considered the two forms of the male in detail. He reviewed the works of Hagen and Faxon and gave the results of his own observations and experiments on *O. nais* and *O. immunis*. He noted that first form males of *O. immunis* collected in the middle of April soon molted into the second form condition. However, contrary to the conclusions of Hagen, Faxon and Steele, Harris reported observing spermatozoa in the same quantity and apparently in the same condition in the testes of both first and second forms, and concluded that the second form males were not sterile. He also mentioned a communication from W. P. Hay who reported seeing second form males in the act of copulation. This report has been the source of controversy in more recent works.

Creaser (1933a) studied a single population of *Orconectes p. propinquus* making collections at stated intervals during the year and noting seasonal changes in the male population. He concluded that the second form of the sexual appendage might be regarded as a developmental rather than a seasonal condition. He further concluded that after breeding, the older crawfishes die and do not, for the most part, if at all, revert to the second form condition. He explained the presence of second form males

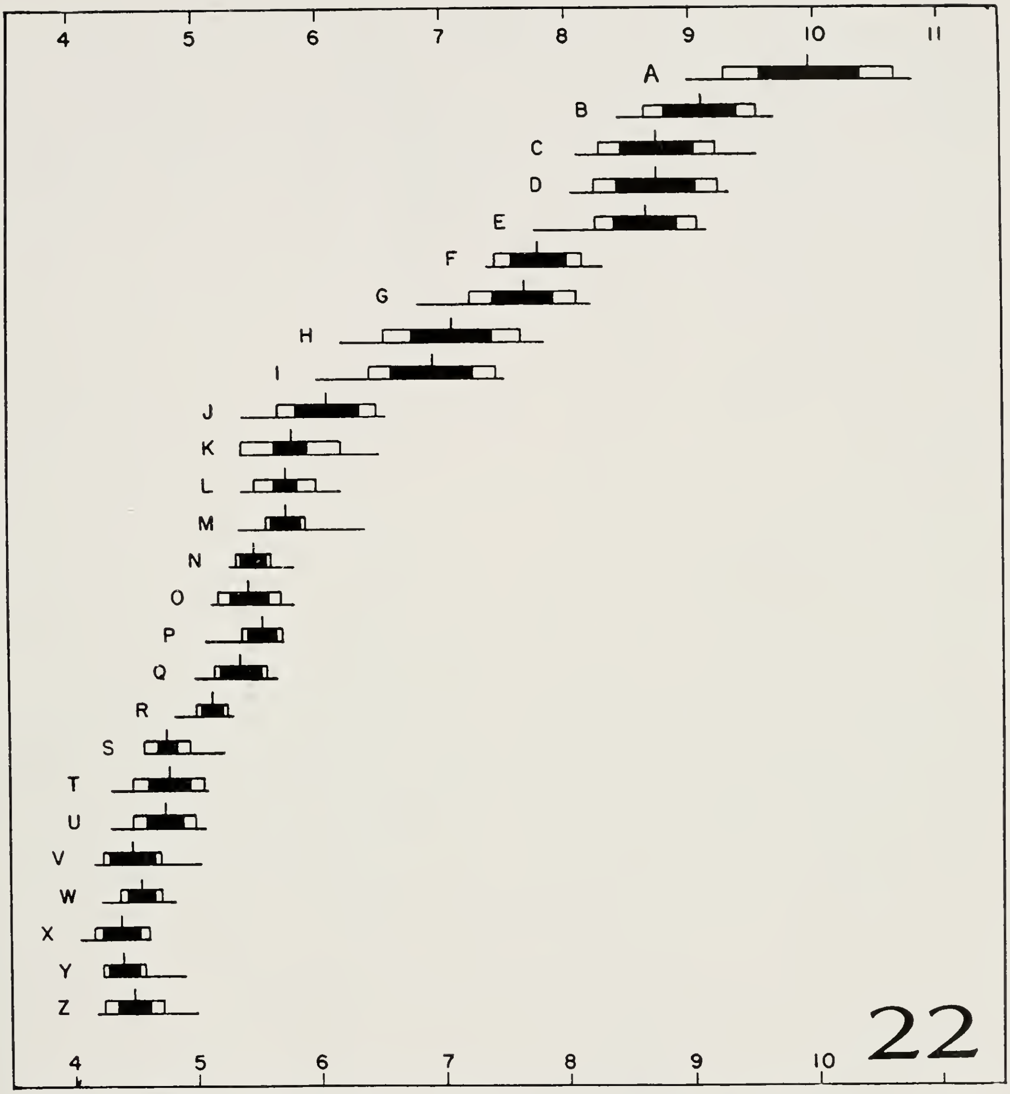


Figure 22. Ontogenetic variation in length of endopodite of second pleopod of second form male. Size groups (cephalothorax length) indicated to left of line as follows: **A** = 5.0-5.4 mm, **B** = 5.5-5.9 mm, **C** = 6.0-6-4 mm, **D** = 6.5-6.9 mm, **E** = 7.0-7.4 mm, **F** = 7.5-7.9 mm, **G** = 8.0-8.4 mm, **H** = 8.5-8.9 mm, **I** = 9.0-9.4 mm, **J** = 9.5-9.9 mm, **K** = 10.0-10.4 mm, **L** = 10.5-10.9 mm, **M** = 11.0-11.4 mm, **N** = 11.5-11.9 mm, **O** = 12.0-12.4 mm, **P** = 12.5-12.9 mm, **Q** = 13.0-13.4 mm, **R** = 13.5-13.9 mm, **S** = 14.0-14.4 mm, **T** = 14.5-14.9 mm, **U** = 15.0-15.4 mm, **V** = 15.5-15.9 mm, **W** = 16.0-16.4 mm, **X** = 16.5-16.9 mm, **Y** = 17.0-17.4 mm, **Z** = 17.5-17.9 mm.

in the population which were larger than some of the first form specimens on the assumption that not all of the young of the first year transform into the first form during the fall breeding season but overwinter in the second form condition.

Hobbs (1942) mentioned that the adult male crawfish exhibits two distinct and usually alternating morphological forms. Moreover, he stated that the first form is the breeding stage and that the two forms are deifnitely associated with the reproductive cycle.

Results

Preserved exuviae of each individual and the molted specimens were eaxmined for

TABLE 3.
Results of the suture study

Condition of Suture Prior to Molting	Complete Suture	Mesial Suture	Complete Suture	Mesial Suture	No Suture	No Suture
Form	II-II	II-II	II-I	II-I	I-I	I-II
Complete Suture Retained	23					
Suture Retained Mesially		6				
Suture Lost			10	5		
Complete Suture regained		1				8
Mesial Suture Regained						5
Suture Not Regained					1	4

the presence or absence of a suture between the basipodite and endopodite of the first pleopod. The writer at first anticipated that, after losing the suture when molting into the first form condition, the specimen would not regain the suture when it molted into the second form condition following the breeding season. Thus, this lack of suture on the first pleopod would clearly delineate the "true" second form male from the larger juveniles.

However, the examination of the exuviae and molted specimens showed immediately that this was not the case (Table 3). Four

Figure 23. Ontogenetic variation in ratio of central projection/mesial process in first form male. Abbreviations for size groups as in fig. 21.

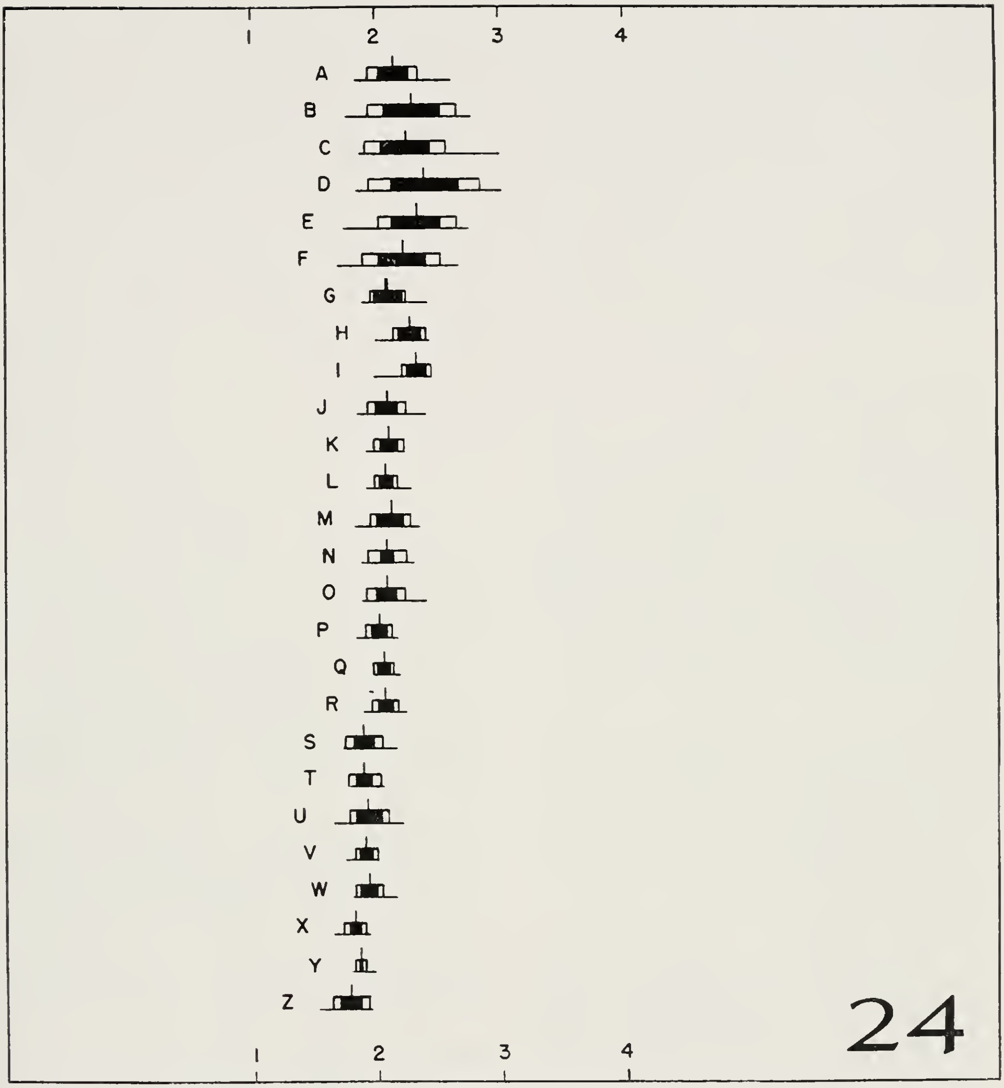


Figure 24. Ontogenetic variation in ratio of central projection/mesial process in second form male. Abbreviations for size groups as in fig. 22.

of the seventeen specimens (23.5%) which molted from first form to second form did not regain the suture between the basipodite and the endopodite of the first pleopod. However, five of the seventeen (29.4%) regained the suture on the mesial side of the pleopod, and eight of the seventeen (47.1%) completely regained the suture. All of the second form males which molted into the first form condition lost the suture completely; the second form males possessing a complete suture without exception retained the complete suture in the next instar; and one specimen which molted from first form to first form failed to regain the suture.

One particular individual is worth mentioning. This specimen when captured was in the second form condition with a suture on the mesial surface of the first pleopod. Following its molt to first form it had lost the suture completely. Later, when it molted back into second form it had regained the suture mesially. Finally, the complete suture was regained following the next molt which was from second form to second form.

Thus, the results of this study are in line with the general summary presented by Hobbs and Marchand (1943) and clearly demonstrates that in *O. clypeatus* the second form condition cannot be considered to be a developmental rather than a seasonal (reproductive) condition.

Comparison of Results with Previous Studies

The occurrence of second form individuals with only a mesial suture seems to further confuse the problem. Furthermore, as noted above, the majority of individuals molting from first form to second form regained the suture completely. Thus, this method is not a sure means of separating second form males of *O. clypeatus* which have never molted into first form from those which have molted into first form and then returned to the second form. Hagen (1870) mentioned the same phenomenon in his discussion on the second form of males of *Cambarus acutus* (probably *Procambarus blandingi acutus*). He stated that occasionally, both in younger and in full-grown specimens, the articulation between the basipodite and the endopodite was partly gone, but its remains were still visible on the upper margin; and that in most cases the articulation had entirely disappeared.

Several conclusions about *O. clypeatus* may be drawn from the results of this study. First, all the males lose the suture between the basipodite and the endopodite of the first pleopod following the molt into first form regardless of the condition of the suture prior to molting. Second, the majority of the first form males molt into the second form condition following the breeding season, thus disproving the idea that the second form is merely a developmental condition. Third, the presence or absence of a suture between the basipodite and the endopodite of the first pleopod of the second form male is not a sufficiently reliable character to be used as a means of distinguishing second form males which have not been in the first form previously, from those which have been in the first form.

Summary

O. clypeatus was found to have an average growth increment of 0.41 mm cephalothorax length per molt. This increment is constant throughout the life span of the individual.

The length of the carapace of *O. clypeatus* tends to increase approximately the same amount per molt regardless of sex or size.

The first and second pleopods of *O. clypeatus* undergo a very rapid allometric growth rate between the size ranges 5.0 and 10.4 mm cephalothorax length; however, above this size range their growth rates tend to parallel the growth rate of the cephalothorax in both first and second form males.

The growth rate of the first and second pleopods and their component parts tends to parallel closely that of the cephalothorax length in the first form males of all sizes and may be considered isometric.

All the males of *O. clypeatus* lose the suture between the basipodite and the endopodite of the first pleopod following the molt into first form regardless of the condition of the suture prior to molting.

First form males of *O. clypeatus* molt into the second form following the breeding season, thus disproving the idea that the second form is merely a developmental condition.

In *O. clypeatus* the presence or absence of a suture between the basipodite and endopodite of the first pleopod of the second form male is not a sufficiently reliable character to be used as a means of distinguishing second form males which have not been in the first form condition previously from those which have.

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References Cited

Andrews, E. A. 1906. Ontogeny of the annulus ventralis. *Biol. Bull.*, 10(3): 122-137.

———— 1907. The young of the crayfishes *Astacus* and *Cambarus*. *Smithson. Contrib. Knowl.*, 35: 1-79.

———— 1910. The anatomy of the stylets of *Cambarus* and *Astacus*. *Biol. Bull.*, 18(2): 79-97.

———— 1911. Male organs of sperm transfer in the crayfish *Cambarus affinis:* their structure and use. *Jour. Morph.*, 22(2): 239-297.

Cazier, Mont A. and Annette L. Bacon 1949. Introduction to quatitative systematics. *Bull. Amer. Mus. Nat. Hist.*, 93(5): 343-388.

Creaser, Edwin P. 1933a. Seasonal changes in the male population of *Faxonius propinquus* (Girard). *Occ. Pap. Mus. Zool. Univ. Mich.*, No. 253: 1-9.

———— 1933b. Descriptions of some new and poorly known species of North American crayfishes. *Occ. Pap. Mus. Zool. Univ. Mich.*, No. 275: 1-21.

Faxon, Walter 1884. On the so-called dimorphism in the genus *Cambarus*. *Amer. Jour. Sci.*, 27(Ser. 3): 42-44.

Hagen, Hermann August 1870. Monograph of the North American Astacidae. *Illustr. Cat. Mus. Comp. Zool.*, 3: 1-109.

Harris, J. A. 1903. An ecological catalog of the crayfishes belonging to the genus *Cambarus*. *Kans. Univ. Sci. Bull.*, 2: 51-187.

Hart, C. W., Jr. 1952. The exoskeleton and musculature of the appendages of the first three abdominal segments of *Cambarus longulus longulus* Girard. *Va. Jour. Sci.*, 3(1): 39-48.

———— 1953. Serial homologies among three pairs of abdominal appendages of certain male crayfish. *Jour. Morph.*, 93(2): 285-300.

———— 1956. The postembryonic development of the first pleopod of *Cambarus longulus longulus* Girard. *Va. Jour. Sci.*, 7(1): 9-13.

Hobbs, Horton H., Jr. 1940. On the first pleopod of the male Cambari. *Proc. Fla. Acad. Sci.*, 5: 55-61.

———— 1942. The crayfishes of Florida. *Univ. Fla. Publ., Biol. Sci. Ser.*, 3(2): 1-179.

———— 1945. Notes on the first pleopod of the male Cambarinae. *Quart. Jour. Fla. Acad. Sci.*, 8(1): 67-70.

Hobbs, Horton H., Jr. and Lewis J. Marchand 1943. A contribution toward a knowledge of the crayfishes of the Reelfoot Lake area. *Jour. Tenn. Acad. Sci.*, 18(1): 6-35.

Penn, George Henry 1943. A study of the life history of the Louisiana red-crawfish, *Cambarus clarkii* Girard. *Ecology*, 24(1): 1-18.

———— 1952. The genus *Orconectes* in Louisiana. *Amer. Midl. Nat.*, 47(3): 743-748.

Slack, Keith V. 1955. An injection method for marking crayfish. *Prog. Fish Cultur.*, 17(1): 36-38.

Smith, Elsie Wayne 1953. The life history of the crawfish *Orconectes (Faxonella) clypeatus* (Hay). *Tulane Stud. Zool.*, 1(7): 79-96.

Steele, Mary 1902. The crayfish of Missouri. *Univ. Cincinnati Bull.*, 2 (Ser. 2): 1-54.

Suko, T. 1953. Studies on the development of the crayfish. I. The development of secondary sex characters in appendages. *Sci. Rept. Saitama Univ.*, 1B(2): 77-96.

Tack, Peter Isaac 1941. The life history and ecology of the crayfish *Cambarus immunis* Hagen. *Amer. Midl. Nat.*, 25(2): 420-446.

Van Deventer, William Carl 1937. Studies on the biology of the crayfish *Cambarus propinquus* Girard. *Ill. Biol. Monogr.*, 15(3): 1-67.

Abstract

The crawfish, *Orconectes clypeatus*, was found to have an average growth increment of 0.41 mm cephalothorax length per molt. This increment was established under laboratory conditions and is apparently constant throughout the life span of the individual.

The first and second pleopods undergo a very rapid growth rate in early life exceeding the growth rate of the cephalothorax, however, after maturity the growth rates of the pleopods tend to parallel that of the cephalothorax.

The majority of the first form males kept in the laboratory molted into the second form condition following the breeding season, thus disproving the idea that the second form is merely a developmental condition.

In *O. clypeatus* the presence or absence of a suture between the basipodite and the endopodite of the first pleopod of the second form male is not a sufficiently reliable character to be used as a means of distinguishing second form males which have not been in the first form condition previously from those which have.