

MARJORIE ESTELLF CARTER
and JANET M. BRADFORD

*Postembryonic Development
of Three Species of
Freshwater Harpacticoid
Copepoda*

SERIAL PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

The emphasis upon publications as a means of diffusing knowledge was expressed by the first Secretary of the Smithsonian Institution. In his formal plan for the Institution, Joseph Henry articulated a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This keynote of basic research has been adhered to over the years in the issuance of thousands of titles in serial publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Annals of Flight
Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in History and Technology

In these series, the Institution publishes original articles and monographs dealing with the research and collections of its several museums and offices and of professional colleagues at other institutions of learning. These papers report newly acquired facts, synoptic interpretations of data, or original theory in specialized fields. These publications are distributed by mailing lists to libraries, laboratories, and other interested institutions and specialists throughout the world. Individual copies may be obtained from the Smithsonian Institution Press as long as stocks are available.

S. DILLON RIPLEY
Secretary
Smithsonian Institution

INTERNATIONAL BOOK YEAR • 1972



SMITHSONIAN CONTRIBUTIONS TO
ZOOLOGY

NUMBER 119

*Marjorie Estelle Carter
and Janet M. Bradford*

Postembryonic Development
of Three Species of
Freshwater Harpacticoid
Copepoda

SMITHSONIAN INSTITUTION PRESS
CITY OF WASHINGTON

1972

ABSTRACT

Carter, Marjorie Estelle, and Janet M. Bradford. Postembryonic Development of Three Species of Freshwater Harpacticoid Copepoda. *Smithsonian Contributions to Zoology*, number 119, 26 pages, 14 figures. 1972.—The postembryonic development of three species of freshwater harpacticoid copepods from southern Georgia and southwestern Virginia has been studied. All of the larval stages (six nauplii and six copepodid stages) of *Elaphoidella bidens coronata* and *Bryocamptus zschokkei alleganiensis*, and all of the nauplii and two copepodid stages of *Moraria virginiana* were obtained, fully described, and figured. Where possible, the anatomical details were determined from the exuviae of a single individual.

A key to the identification of the six naupliar stages of harpacticoids is given as well as a chart summarizing the major features of each copepodid stage.

It is suggested that all life cycles of harpacticoid copepods in which fewer than six naupliar stages have been reported should be reexamined.

FOREWORD

This report represents the major portion of a dissertation submitted by Dr. Marjorie Estelle Carter to the faculty of the University of Virginia in partial fulfillment of the requirements for the Ph.D. degree that was awarded to her in June 1952. Her teaching duties at Valdosta State College and involvement in student affairs for some 16 years delayed the revision needed before submitting it for publication, and not until 1968, with the encouragement of Dr. Thomas E. Bowman and Miss Gayle A. Heron, did she begin work on a revised draft. Following her untimely death later in the year, the manuscript, together with her illustrations, was sent to me, and through the efforts of Dr. Janet M. Bradford, it has been brought up-to-date, and pertinent references to studies that have been made subsequent to Dr. Carter's investigations included.

As Dr. Carter's major professor, I should like to thank Dr. Bradford for her interest and the work that she has devoted to revising the copy supplied to her. I am sure that Dr. Carter would have concurred in my insistence that Dr. Bradford's name appear as a coauthor. I am also grateful to Dr. Bowman for his many helpful suggestions and his critical reading of the final draft. Thanks are also due Miss Margaret A. Daniel for arranging and refurbishing the figures.

The acknowledgments within the body of the text are quoted, almost verbatim, from the dissertation (original manuscript).

HORTON H. HOBBS, JR.

Library of Congress Cataloging in Publication Data

Carter, Marjorie Estelle, 1905-1968.

Postembryonic development of three species of freshwater Harpacticoid Copepoda.

(Smithsonian contributions to zoology, no. 119)

A revision of M. E. Carter's thesis—University of Virginia, 1952.

Bibliography: p.

1. *Elaphoidella bidens*. 2. *Bryocamptus zschokkei*. 3. *Moraria virginiana*. I. Bradford, Janet M., 1940— joint author. II. Title. III. Series: Smithsonian Institution. Smithsonian contributions to zoology, no. 119.

QL1.S54 no. 119 [QL444.C7] 591'.08s [595'.34] 72-277

Official publication date is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, Smithsonian Year.

Marjorie Estelle Carter
and Janet M. Bradford

Postembryonic Development of Three Species of Freshwater Harpacticoid Copepoda

Introduction

Few complete studies on larval and postlarval development of harpacticoid copepods have been made, and only three observations exist on the genera (*Elaphoidella*, *Bryocamptus*, and *Moraria*) considered here (Lang, 1948).

There is disagreement as to the number of naupliar stages in the development of harpacticoids. Although six naupliar stages have been found in some (Chappuis, 1916; Borutskii, 1925; Ewers, 1930; Johnson and Olson, 1948; Krishnaswamy, 1951; Grig, 1960; Fehrenbach, 1962; and Haq, 1965), only five naupliar stages have been described for the genera *Elaphoidella*, *Bryocamptus*, and *Moraria* (Chappuis, 1916; Borutskii, 1925; and Gurney, 1932).

The present report traces the postembryonic development in three species, two from the first naupliar stage through the adult, the other to the second copepodid stage.

All figures except those with individual scales are drawn to the scale indicated in the first component.

Systematic Status of Species Investigated

Elaphoidella bidens coronata (SARS, 1904).—I have followed Coker (1934) and Wilson (1956) in assigning the specimens used in this study to the subspecies *coronata*, described originally from the Hawaiian Islands. For a discussion of the somewhat involved

taxonomic status of North American specimens of *E. bidens*, see Wilson (loc. cit.).

In order that no confusion arise as to the identity of the animals used in the present investigation, detailed illustrations are given of the adult male (Figures 2*i*, *j*; 3*f*; 4*n*; 5*f*, *m*; 6*e*, *k*, *n*, *p*) and the adult female (Figures 2*g*, *h*; 3*g*, *m*; 4*d*, *j*, *o*, *s*; 5*g*, *n*; 6*f*, *j*, *o*, *q*).

Bryocamptus zschokkei alleganiensis COKER, 1934.—The harpacticoids used here agree, for the most part, with Coker's (1934:93) description of the subspecies *Bryocamptus zschokkei alleganiensis*. However, the number of segments of the endopods of the second and third legs of the female varies in individuals from the same locality. Some specimens have two segments as described by Coker, others have the endopod three-segmented on the second leg but only two-segmented on the third leg, and in some the endopods of both legs have three segments. Similar variations have been observed by Gurney (1932:148) and by Kiefer (1929:321).

The adult male (Figures 8*g*; 10*f*, *m*; 11*f*, *m*) and female (Figures 8*f*, 9*a-c*, *j*; 10*g*, *n*; 11*e*, *n*) are figured.

Moraria virginiana CARTER, 1944.—This species was described (Carter, 1944) from only two specimens, both female. Drawings of the hitherto undescribed male and most of its appendages are included here (Figures 13*e*, 14*c*, *g*, *h*, *j-p*).

Materials and Methods

The animals used in this study were obtained from several localities. *Elaphoidella bidens coronata* was

Marjorie Estelle Carter, Valdosta State College, Valdosta, Georgia (deceased 1968). Janet M. Bradford, Collaborator, Division of Crustacea, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

collected from two localities in the vicinity of Valdosta, Lowndes County, Georgia. Late in 1948, I collected several females and a single male from a small artificial pool on the campus of the Valdosta State College. The next year, I could find no harpacticoids in this habitat but found them abundant in a small stream at the north end of town. No males were taken from the stream, but several females with eggs were found, and from one of these I succeeded in rearing three generations of females parthenogenetically.¹

Bryocamptus zschokkei alleganiensis is found in abundance in nearly every small stream in the vicinity of Mountain Lake, Giles County, southwestern Virginia, and is usually associated with growths of algae and moss. Animals from several locations around the Mountain Lake Biological Station were collected and reared. Those used in the drawings and descriptions were reared from individuals taken from a small stream that flows into Little Stony Creek, about two miles from the Station, while those taken from other localities were used for comparison.

Moraria virginiana was originally collected from a small group of springs, locally known as Twin Springs, near the Mountain Lake Biological Station (Carter, 1944). Since then, I have taken many animals, both male and female, from swampy places where there is a heavy growth of sphagnum moss along the trail leading from the Station to Twin Springs.

Adult animals were collected by taking small amounts of water and debris from the bottom of small streams and pools. This material was examined with the aid of a wide-field stereoscopic microscope, and the animals placed in culture dishes where they could be observed more easily. Females with eggs were isolated in culture dishes until the eggs hatched, whereupon some of them were isolated, and others were left in the dish with the mother. When only one species of harpacticoid was found in a collection, the water and detritus contained in it were strained through bolting silk and placed in culture dishes, and the larvae and adults introduced into the filtrate seemed to thrive. In some instances, an artificial cul-

ture medium, similar to that used by Banta (1921) in raising *Daphnia*, was used.

Square watch glasses were most convenient for culturing the copepods, but small chemical watch glasses, placed in Syracuse dishes to support them, were satisfactory. All culture dishes were covered with small squares of glass and kept in a moist chamber.

The entire larva is difficult to study when stained, and most of my observations are based on the exuviae. This procedure enabled the development of a single individual to be followed through its various stages. Although the tests are very difficult to find in the culture dishes because of their transparency, I found that directing light on a mirror on which the culture dish had been placed reflected just enough light on the tests so they could be seen more readily. The adults and the larvae which died were treated with 5 to 10 percent potassium hydroxide in order to remove the tissues.

The adults and copepodid larvae, stained with alum cochineal, provide satisfactory material for mounting; however, Reynold's Stain gives better results. The test of the naupliar stages are difficult to stain because of the very thin cuticle; best results were obtained when the larvae were left in acid fuchsin for 24 to 48 hours and then treated with glacial acetic acid and clove oil before mounting in balsam. The adults and copepodids were mounted in glycerine sealed with paraffin so that they could be removed for dissection.

Drawings were made with the aid of a camera lucida, and the figures of all stages were made, insofar as possible, from the exuviae of a single individual.

Postembryonic Development

Elaphoidella bidens coronata (Sars)

First Naupliar Stage

FIGURE 1a, g

Body inflated, with subcircular and characteristically ornamented dorsal shield. Two median lobes present posterior to midlength; anterior lobe semicircular with posteromedian emargination; posterior lobe bearing posteromedian knob (Figure 1g).

Labrum subspatulate, very narrow anteriorly; anterior margin distinctly emarginate. Narrow portion

¹ A discussion of the rearing of this species parthenogenetically is given by Roy (1931), and the scarcity of males reported by Lang (1948).

of labrum lying between first antennae; posterior to first antennae, lateral margins abruptly diverging before turning posteriorly. Posterior margin fringed with fine hairs and with tuft of longer median hairs.

ANTENNA I.—Segment 1 short and naked. Segment 2 about twice length of proximal segment, bearing three terminal spinules and three setae: proximal and median setae short and rather delicate; subterminal seta heavy and extending beyond end of terminal segment. Segment 3 about two-thirds length of segment 2, bearing one subterminal group of spinules and two subterminal and one terminal seta; latter about three times length of subterminal setae.

ANTENNA II.—Coxopodite broader than long with semicircular row of spinules on distoventral surface, its proximopostaxial angle produced into curved acute process, bordered by dentations from apex to beginning of curve, projecting above posterior portion of labrum. Basipodite broader than long but narrowing into short postaxial protuberance bearing one seta. Exopodite three-segmented; segment 1 almost as long as combined length of distal segments, bearing short postaxial seta at midlength and terminal seta nearly four times length of segment; segment 2 one-third length of segment 1, naked; segment 3 with subterminal seta slightly exceeding length of segment and terminal seta more than twice length of entire exopodite. Endopodite consisting of one long segment bearing very delicate seta at midlength, group of subterminal spinules, and two terminal setae; one of latter narrow and very short, other stout, almost as long as segment, and apparently movably articulated at its base.

MANDIBLE.—Coxopodite dorsal to basipodite, its median border produced into rounded lobe. Basipodite subrectangular with two oblique rows of spinules on ventral surface and plumose spine on proximoventral surface. Exopodite two-segmented: segment 1 slightly longer than basipodite, bearing small spine at midlength and subterminal seta; segment 2 about one-third length of segment 1, bearing short subterminal seta and terminal seta, latter about three-fourths length of entire animal. Endopodite one-segmented, bearing two curved serrate spines and four slender setae.

Ventral plate (Figure 1a) about one-third broader than long with two rows of spinules across ventral surface, one near midlength and other on caudal margin. Caudal margin rounded but produced postero-

laterally in paired protuberances, each terminating in single fine seta.

Second Naupliar Stage

FIGURE 1b

Second nauplius differing from first in following respects: ornamentation of dorsal shield indistinct except for retention of anterior median lobe.

ANTENNA I.—Segment 3 with additional group of spinules just distal to midlength, and subterminal seta about one-third length of terminal seta present in first nauplius.

ANTENNA II.—Segment 1 of exopodite with additional spine on preaxial surface near midlength, its size similar to that of corresponding postaxial spine. Large simple terminal seta of endopodite with two small spinules at midlength.

MANDIBLE.—Basipodite with second seta, slenderer than first, on postaxial surface. Endopodite with one additional spine lateral to those present in first nauplius.

MAXILLA I.—First maxillae, absent in first nauplius, represented by pair of feathered setae on anterior third of ventral plate. Ventral plate emarginate caudally; posterior rows of spinules lacking but replaced by short lateral spinules.

Third Naupliar Stage

FIGURE 1c

Third nauplius differing from second in following respects:

ANTENNA I.—Segment 3 with two additional subterminal setae proximally about half length of subterminal seta of second nauplius; distalmost subterminal seta subequal in length to terminal seta.

ANTENNA II.—Protuberance on postaxial margin of postaxial extension of coxopodite bearing short feathered seta instead of tuft of hairs characteristic of second nauplius. Segment 3 of exopodite bearing subterminal seta approximating length of terminal seta. Endopodite with additional group of spinules at about midlength.

Ventral plate lengthened, with posterior part of body extending well beyond dorsal shield; caudal margin of plate with second pair of protuberances mesial to first pair.

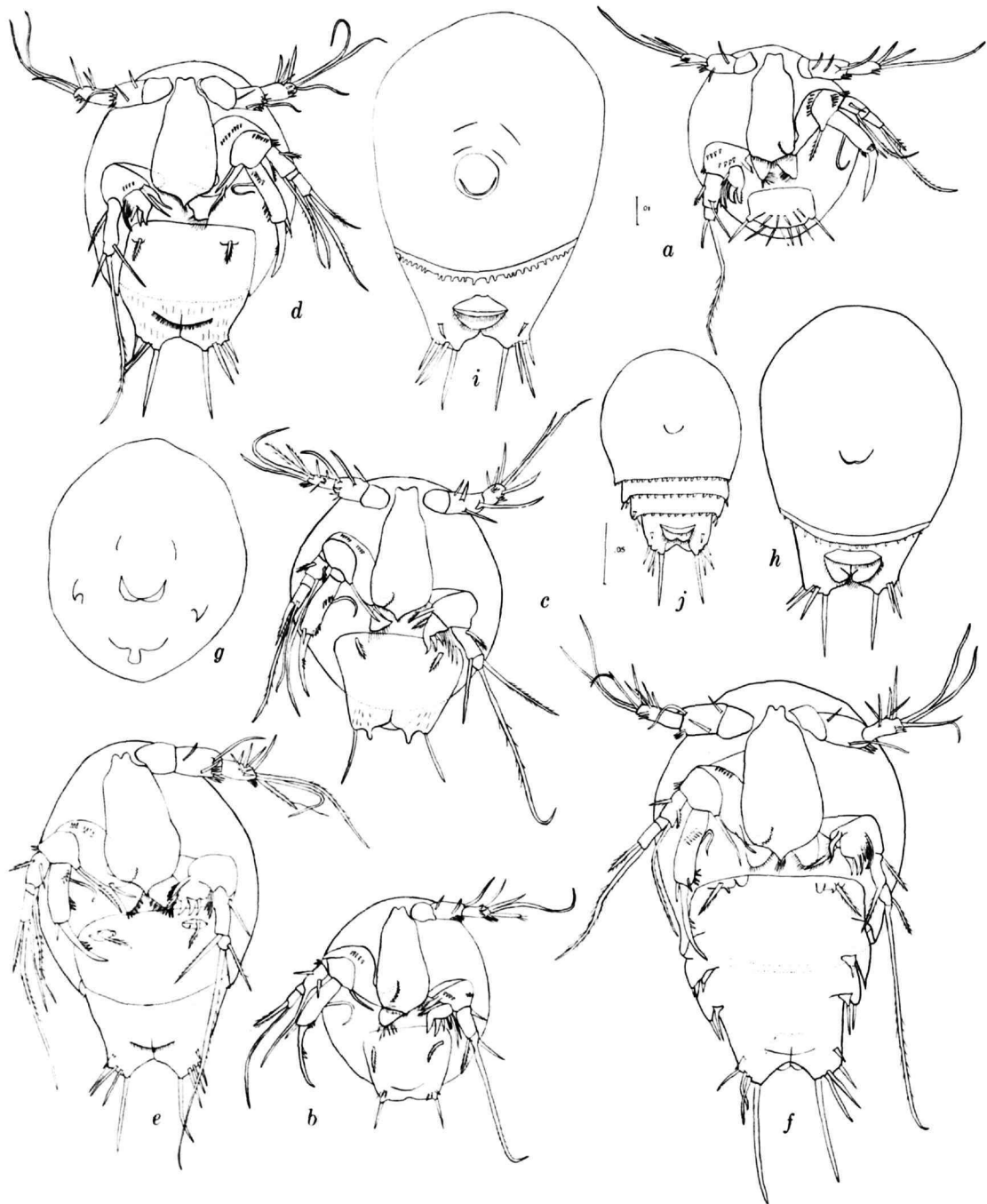


FIGURE 1.—*Elaphoidella bidens coronata*: a, first nauplius, ventral view; b, second nauplius, ventral view; c, third nauplius, ventral view; d, fourth nauplius, ventral view; e, fifth nauplius, ventral view; f, sixth nauplius, ventral view; g, first nauplius, dorsal view; h, fourth nauplius, dorsal view; i, fifth nauplius, dorsal view; j, sixth nauplius, dorsal view.

Fourth Naupliar Stage

FIGURE 1d, h

Fourth nauplius differing from third in following respects: Antenna I with segment 3 bearing additional small seta. Ventral plate with single pair of lobes bearing seta of first maxilla. Posterior region of body longer, its caudal margin bearing two setae lateral to each of original pair; pair of prominent setae present on protuberances first appearing in third nauplius. Anal plate with fine spinules along posterior border.

Fifth Naupliar Stage

FIGURE 1e, i

Fifth nauplius differing from fourth in following respects: Antenna I with segment 3 bearing one additional seta; maxilla I with lobe more clearly delineated, and bearing small protuberances. Pygidial area with additional ventral seta on each side.

Sixth Naupliar Stage

FIGURE 1f, j

Sixth nauplius differing from fifth in following respects: Ventral plate bearing small seta on lobe of second maxilla; rudiment of maxilliped represented by lobe. Posterior region consisting of two segments indicated by two pairs of swimming legs and by dentate margins dorsally, and pygidial area.

First Copepodid Stage

FIGURES 2a,b; 3a,h; 4a,e,k,p; 5a,h

Body consisting of cephalothorax and four free segments.

ANTENNA I (Figure 3a).—As in sixth naupliar stage except segment 3 bearing 11 setae.

ANTENNA II (Figure 3h).—Similar to that of adult: segment 1 very short, naked, about one-third length of following segment; segment 2 bearing palp with one subterminal and three terminal setae; segment 3 with three groups of spinules—one proximally, another at midlength, and third subterminally—also one subterminal and three terminal setae.

MANDIBLE (Figure 4a).—As in adult.

MAXILLAE AND MAXILLIPEDS (Figure 4e,k,p).—Similar to those of adult.

FIRST LEG² (Figure 5a).—Basipodite with lateral protuberance bearing short seta; preaxial surface with two groups of spinules. Exopodite one-segmented with three lateral spines and three terminal setae; groups of spinules present at bases of lateral spines; distal row of spinules extending obliquely nearly to mesiodistal border of preaxial surface. Endopodite one-segmented, bearing four spinules on lateral border, group of spinules proximally on mesial border, two terminal setae, and short subterminal spine on mesial border.

SECOND LEG (Figure 5h).—Basipodite bearing short lateral seta with group of spinules at base and row of spinules near mesiodistal border. Exopodite one-segmented, bearing two lateral spines, both as long as exopodite, one subterminal lateral spine slightly longer than exopodite, one laterodistal seta more than twice length of exopodite, and mesiodistal seta more than three times length of exopodite. Endopodite one-segmented, bearing four lateral spinules, two terminal setae, one subterminal seta on mesial border, and two groups of spinules on proximomesial border.

THIRD LEG (Figure 2a).—Represented by lobe with three setae on second free segment.

Second Copepodid Stage

FIGURES 2c; 3b,i; 4b,f,l; 5b,i; 6a

Second copepodid differing from first in following respects:

Body consisting of cephalothorax and five free segments.

ANTENNA I (Figure 3b).—Five-segmented.

FIRST LEG (Figure 5b).—Exopodite two-segmented: segment 1 bearing one laterodistal spine; segment 2 with lateral margin bearing one spine at midlength, one subterminally, one terminally, and two terminal setae. Endopodite two-segmented: segment 1 bearing oblique row of spinules on lateropreaxial surface and

² Each pair of legs joined together by copula extending between coxopodites. Exopodites of all legs have group of spinules situated at bases of lateral spines, and all segments of both exopodites and endopodites have oblique subterminal row of spinules extending onto preaxial surface.

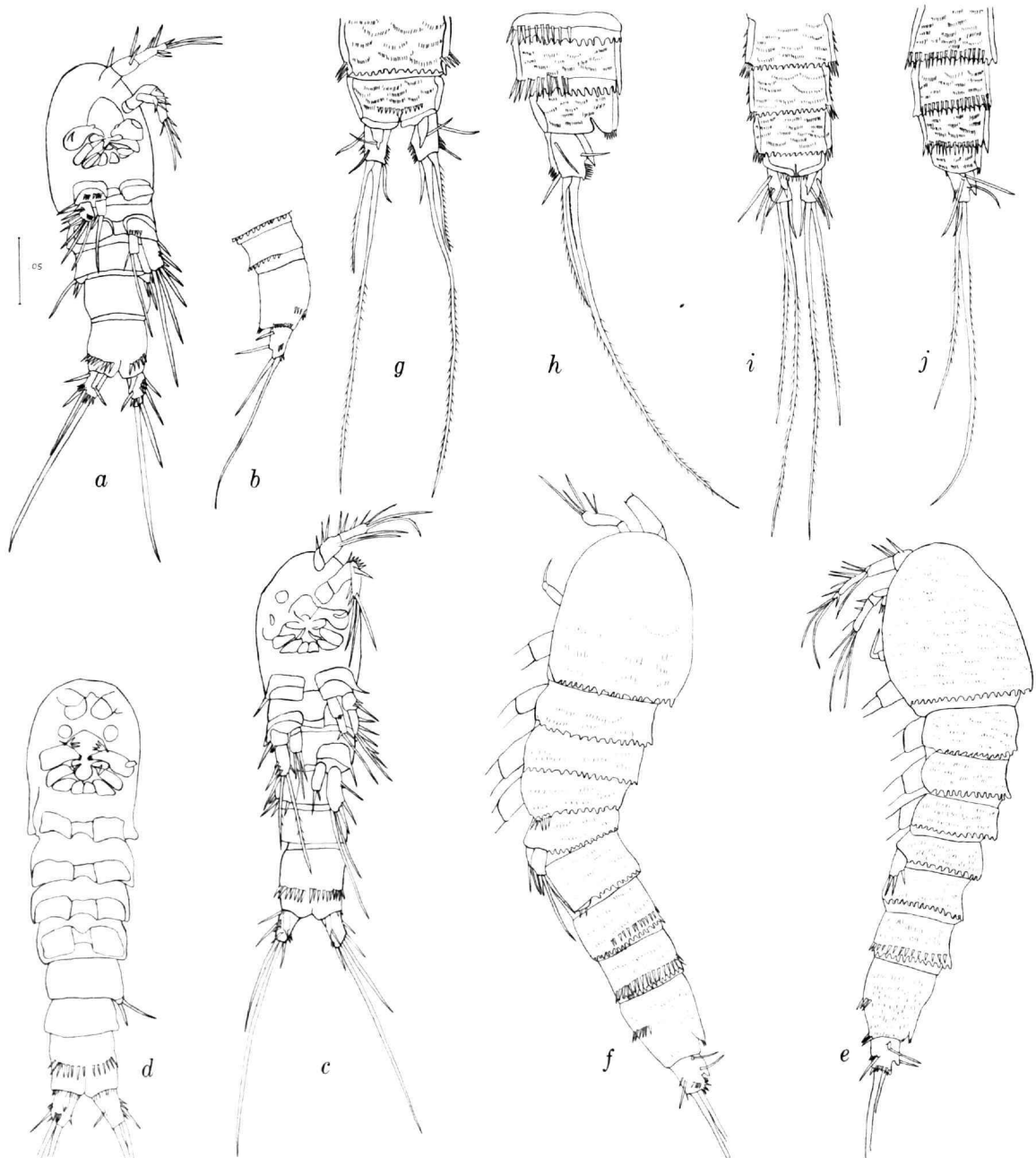


FIGURE 2.—*Elaphoidella bidens coronata*: *a*, first copepodid; *b*, posterior of first copepodid, lateral view; *c*, second copepodid; *d*, third copepodid; *e*, fourth copepodid; *f*, fifth copepodid; *g*, posterior of adult female, dorsal view; *h*, posterior view of adult female, lateral view; *i*, posterior of adult male, dorsal view; *j*, posterior of adult male, lateral view.

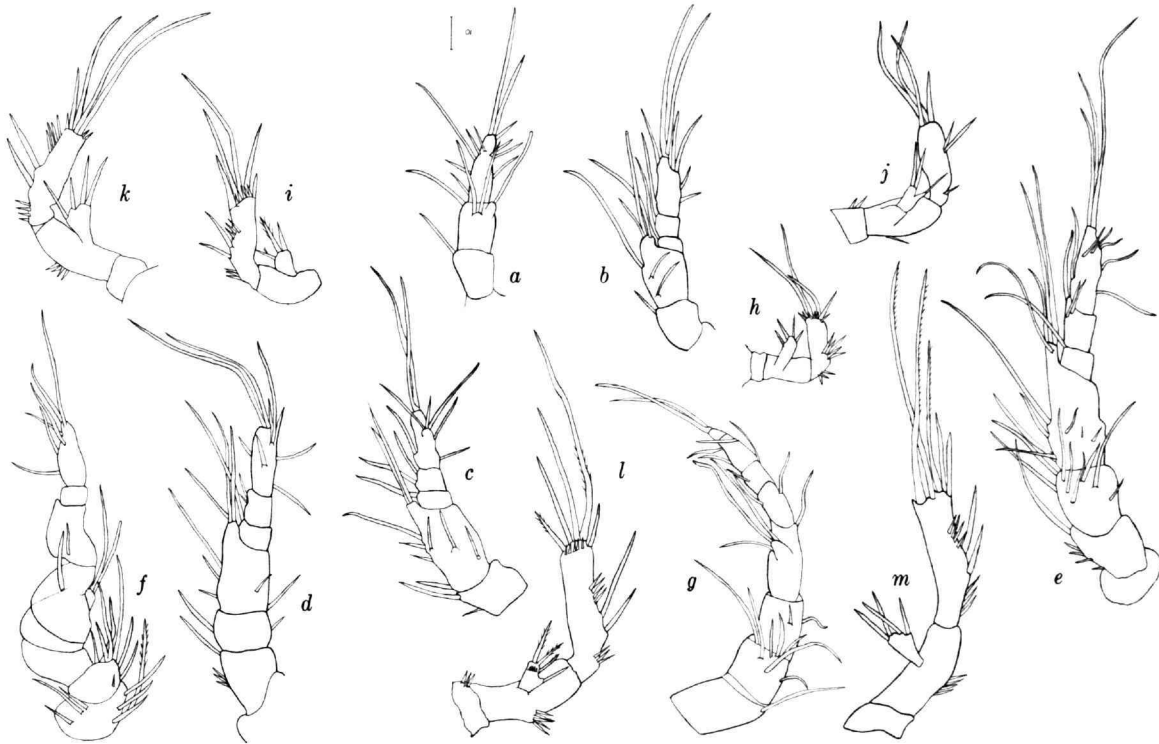


FIGURE 3.—*Elaphoidella bidens coronata*, a-g, antenna 1: a, first copepodid; b, second copepodid; c, third copepodid; d, fourth copepodid; e, fifth copepodid; f, adult male; g, adult female. h-m, antenna 2: h, first copepodid; i, second copepodid; j, third copepodid; k, fourth copepodid; l, fifth copepodid; m, adult female.

group of very small spinules on mesial border at mid-length; segment 2 with oblique row of spinules on lateropreaxial surface and one spine, one very long seta, and one short spine terminally.

SECOND LEG (Figure 5i).—Exopodite two-segmented: segment 1 bearing lateral spine at mid-length; segment 2 with one lateral spine, one mesial spine, one subterminal spine, and two terminal setae. Endopodite two-segmented: segment 1 naked; segment 2 with four spinules on lateral border, one terminal spine and one terminal seta, and mesial border with one subterminal spine and short spine near mid-length.

THIRD LEG (Figure 6a).—Basipodite bearing one lateral seta. Exopodite one-segmented, with two lateral spines, subterminal spine, terminal spine, and terminal seta. Endopodite one-segmented, bearing three terminal spines.

FOURTH LEG (Figure 2c).—Represented by lobe bearing four spines.

Third Copepodid Stage

FIGURES 2d; 3c,j; 4g; 5c,j; 6b,g

Third copepodid differing from second in following respects:

Body consisting of cephalothorax and six free segments.

FIRST LEG (Figure 5c).—Basipodite with additional spine on mesiodistal border.

SECOND LEG (Figure 5j).—Segment 2 of exopodite bearing additional lateral spine slightly smaller than, and proximal to, lateral spine present in second copepodid stage, and additional very small spine on mesial border. Segment 1 of endopodite with small spine on mesial border.

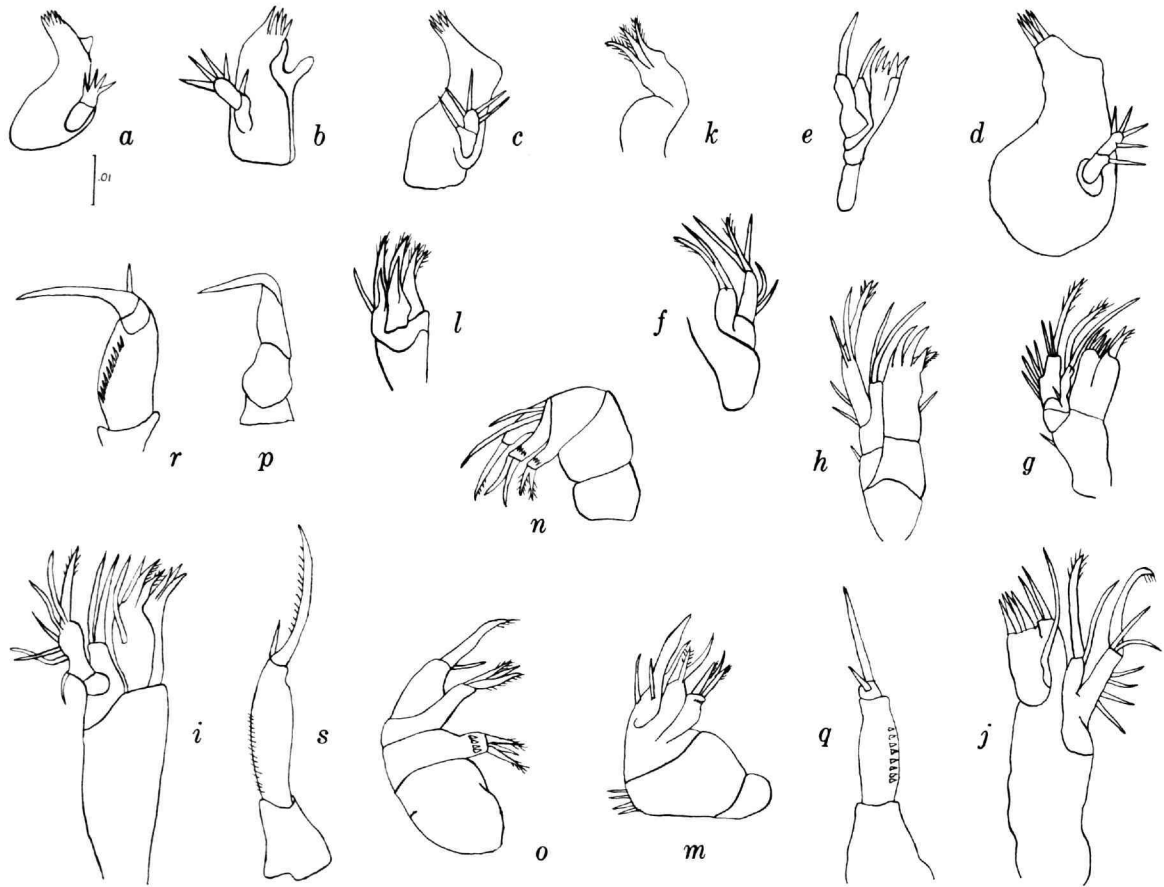


FIGURE 4.—*Elaphoidella bidens coronata*, a-d, mandible: a, first copepodid; b, second copepodid; c, fourth copepodid; d, adult female. e-j, maxilla 1: e, first copepodid; f, second copepodid; g, third copepodid; h, fourth copepodid; i, fifth copepodid; j, adult female. k-o, maxilla 2: k, first copepodid; l, second copepodid; m, fifth copepodid; n, adult male; o, adult female. p-s, maxilliped: p, first copepodid; q, fourth copepodid; r, fifth copepodid; s, adult female.

THIRD LEG (Figure 6b).—Exopodite two-segmented; segment 1 bearing lateral spine and oblique row of spinules distally; segment 2 with one lateral spine, one subterminal spine, two terminal setae, and two mesial spines. Exopodite two-segmented: segment 1 naked; segment 2 with three terminal setae and subterminal spine on mesial border.

FOURTH LEG (Figure 6g).—Exopodite one-segmented, bearing two lateral spines and three terminal spines. Endopodite one-segmented, with two terminal setae.

FIFTH LEG (Figure 2d).—Represented by small lobe on caudolateral margin of fourth free segment bearing two setae.

Fourth Copepodid Stage

FIGURES 2e; 3d,k; 4c,h,q; 5d,k; 6c,h,l

Fourth copepodid differing from third in following respects:

Body consisting of cephalothorax and seven free segments.

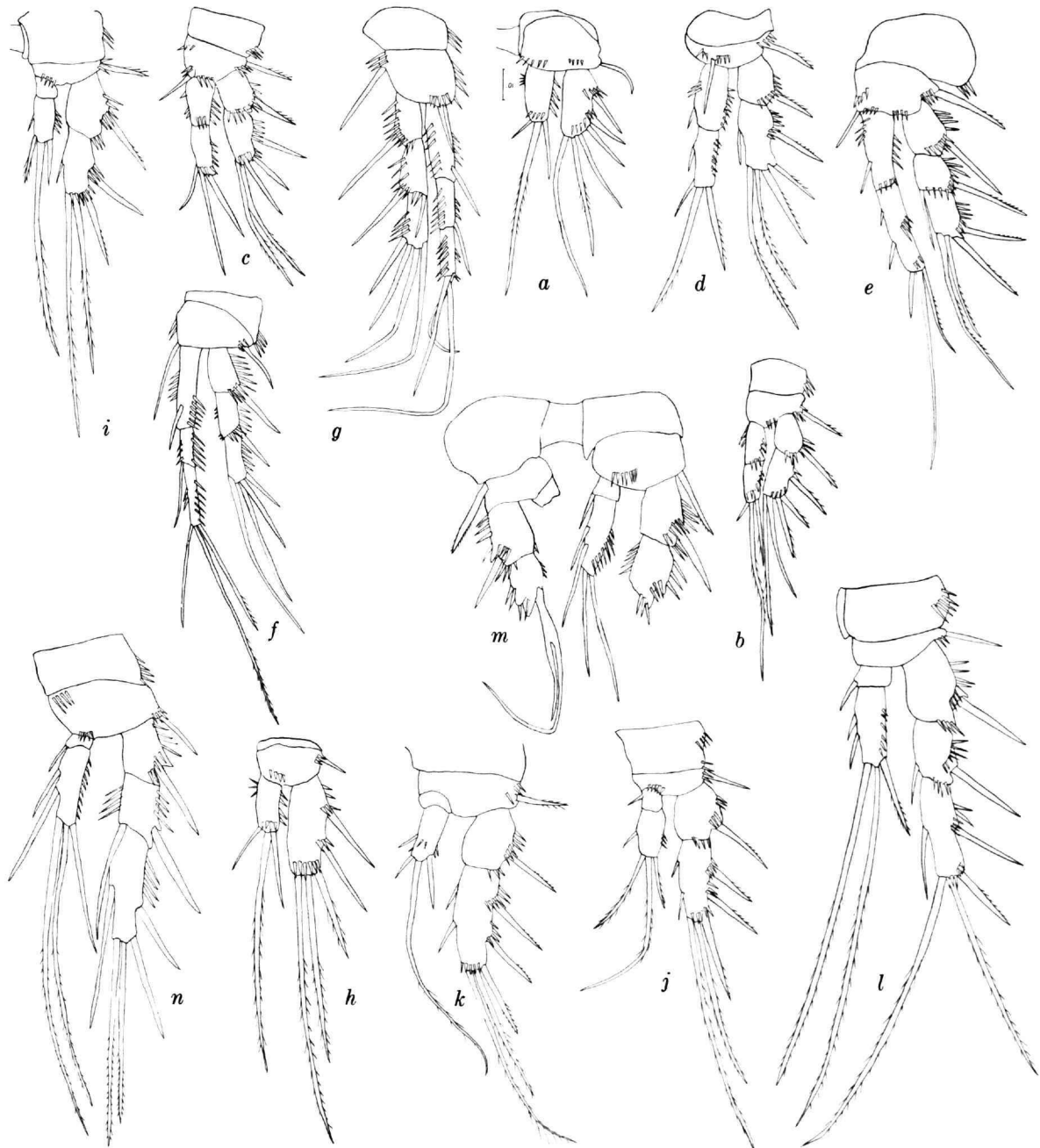


FIGURE 5.—*Elaphoidella bidens coronata*, a–g, first leg: a, first copepod; b, second copepod; c, third copepod; d, fourth copepod; e, fifth copepod; f, adult male; g, adult female. h–n, second leg: h, first copepod; i, second copepod; j, third copepod; k, fourth copepod; l, fifth copepod; m, adult male; n, adult female.

ANTENNA I (Figure 3*d*).—Six-segmented.

FIRST LEG (Figure 5*d*).—Segment 2 of exopodite bearing spine on mesial border at midlength. Both segments of endopodite with mesial spine.

THIRD LEG (Figure 6*c*).—Segment 2 of exopodite bearing additional spine on lateral border and one spine on mesial border.

FOURTH LEG (Figure 6*h*).—Exopodite two-segmented: segment 1 with one spine laterally and row of spinules distally; segment 2 bearing two lateral spines, one distal spine, two terminal setae, one subterminal mesial spine, and two small mesial spines. Endopodite two-segmented: segment 1 naked; segment 2 with one terminal spine, one terminal seta, and one small mesial spine.

FIFTH LEG (Figure 6*l*).—Represented by three lobes; mesial lobe with one small spine, large lobe lateral to it with two spines and three setae, and lateral lobe bearing long seta.

Fifth Copepodid Stage

FIGURES 2*f*; 3*e,l*; 4*i,m,r*; 5*e,l*; 6*d,i,m*

Fifth copepodid differing from fourth in following respects:

Body consisting of cephalothorax and eight free segments.

FIRST LEG (Figure 5*e*).—Exopodite three-segmented: segment 1 bearing lateral spine and semicircular row of subterminal spinules; segment 2 with lateral spine, row of spinules, and one seta on mesiodistal border; segment 3 bearing lateral subterminal spine, terminal spine, and two terminal setae. Endopodite two-segmented, one-fourth longer than exopodite: segment 2 with additional small spine on mesial border.

SECOND LEG (Figure 5*l*).—Exopodite three-segmented; segment 2 bearing two subterminal spines, one laterally and one mesially, and distal row of spinules; segment 3 with one lateral, one mesial, and one subterminal spine and two terminal setae. Endopodite two-segmented: segment 2 with additional spine on mesial border.

THIRD LEG (Figure 6*d*).—Exopodite three-segmented: segment 2 bearing two subterminal spines, one laterally and one mesially, and row of subterminal spinules; segment 3 with one lateral spine, one subterminal spine, two terminal setae, one subterminal

seta on mesial border, and one mesial spine near midlength. Endopodite two-segmented: segment 1 bearing one small mesiodistal spine; segment 2 with two additional mesial spines.

FOURTH LEG (Figure 6*i*).—Exopodite three-segmented: segment 2 bearing two subterminal spines, one laterally and one mesially, and distal row of spinules; segment 3 with one lateral spine, one distolateral spine, one terminal spine, one terminal seta, one distomesial spine, and one mesial spine at midlength. Endopodite two-segmented: segment 2 bearing one terminal spine, one terminal seta, and two very thick mesial spines.

FIFTH LEG (Figure 6*m*).—Three lobes large, appearing as distinct segments, mesial lobe bearing three additional spines.

SIXTH LEG (Figure 6*m*).—Represented by distinct lobe bearing two setae on fifth free segment. Leg not discernible in adult female.

Bryocamptus zschokkei alleganiensis Coker

First Naupliar Stage

FIGURE 7*a*

Dorsal shield subcircular, smooth, with anterior portion often broken in exuviae.

Labrum subspatulate, very narrow anteriorly. Narrow portion lying between bases of first antennae, margins diverging posterolaterally posterior to antennae; fine hairs bordering posterior margin and with tufts of longer hairs on median line.

ANTENNA I.—Segment 1 short and naked; segment 2 about twice length of segment 1, bearing three subterminal spinules and three setae, proximal and median setae short and delicate, terminal seta rather heavy and about twice length of segment 2; segment 3 about two-thirds length of segment 2 bearing two long terminal setae, one subterminal seta about half length of terminal setae, and two groups of spinules, one group situated at midlength, other subterminally.

ANTENNA II.—Coxopodite broader than long with semicircular row of spinules on lower distal surface; proximopostaxial angle produced into curved acute process bearing hairs along postaxial margin from apex to beginning of curve, process projecting dorsally above posterior portion of labrum. Basipodite wider than long, narrowing postaxially forming short

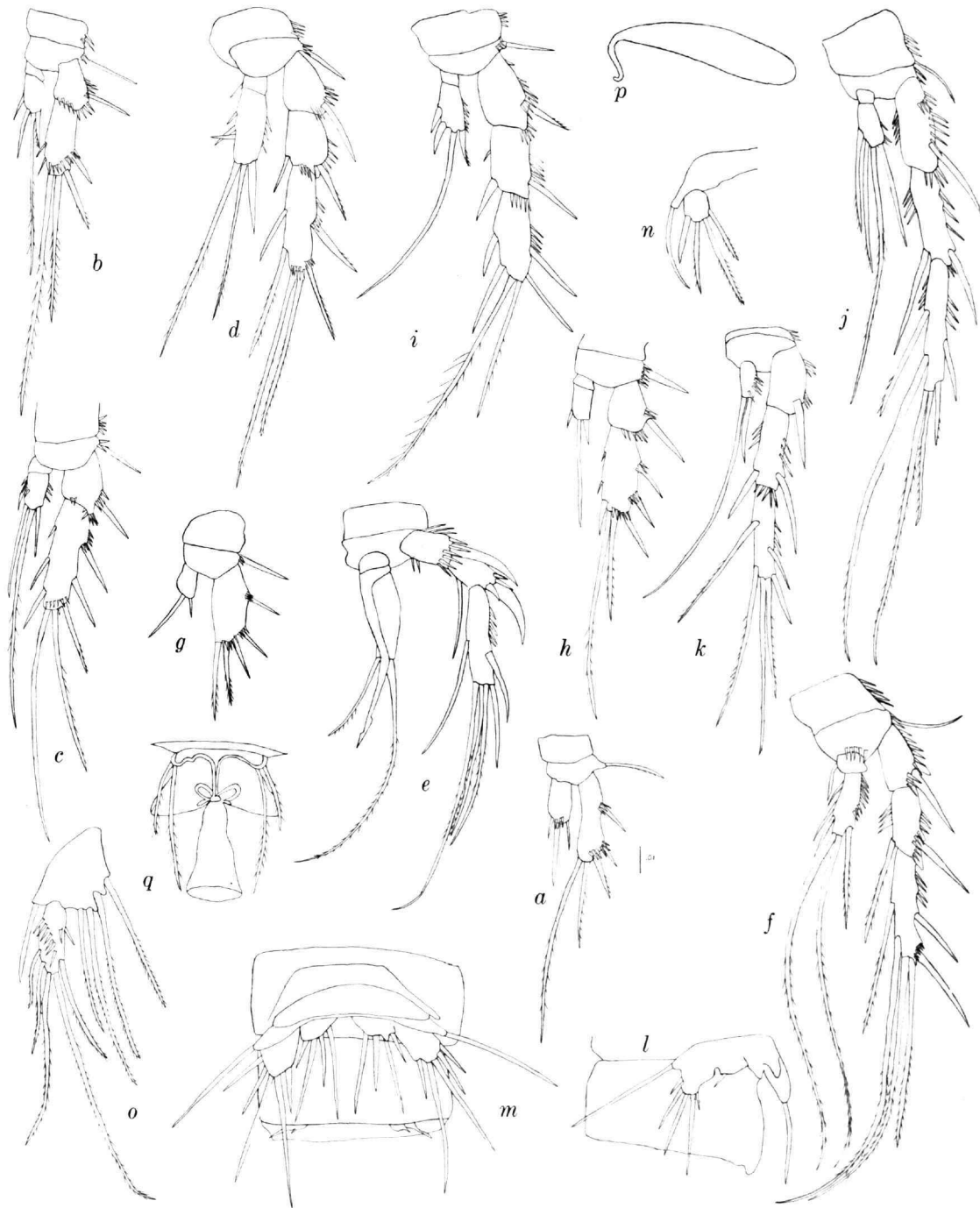


FIGURE 6.—*Elaphoidella bidens coronata*, a-f, third leg: a, second copepodid; b, third copepodid; c, fourth copepodid; d, fifth copepodid; e, adult male; f, adult female. g-k, fourth leg: g, third copepodid; h, fourth copepodid; i, fifth copepodid; j, adult female; k, adult male. l-m, fifth leg and sixth lobe: l, fourth copepodid; m, fifth copepodid. n-o, fifth leg: n, adult male; o, adult female. p, spermatophore; q, seminal receptacle.

protuberance bearing three terminal setae. Exopodite three-segmented: segment 1 subequal in length to basipodite, bearing one short postaxial seta at midlength and terminal seta nearly four times length of segment; segment 2 one-half length of segment 1 and bearing one distal seta subequal in length to exopodite; segment 3 two-thirds length of segment 1, bearing one short subterminal seta and another terminally about one and one-half times length of exopodite. Endopodite one-segmented with group of spinules near distal end, very delicate seta at midlength, and two terminal setae; one of latter very short and narrow, other almost as long as endopodite, very stout, and articulated basally.

MANDIBLE.—Median border of coxopodite produced into rounded lobe. Subrectangular basipodite bearing semicircular row of spinules preaxially and plumose seta on proximomesial surface. Exopodite two-segmented: segment 1 slightly longer than segment 2, bearing small spine at midlength and seta terminally; segment 2 about one-third length of segment 1, bearing short subterminal seta and another terminally about three-fourths length of entire animal. Endopodite one-segmented with two curved spines and four setae.

Ventral plate about one-third wider than long, bearing two rows of long, slender spinules across ventral surface, one row near midlength and other near caudal margin. Caudal margin with paired protuberances, each terminating in single fine seta.

Second Naupliar Stage

FIGURE 7b

Second nauplius differing from first in following respects:

ANTENNA I.—Segment 3 with additional group of spinules and single short, stout, tufted seta subterminally.

ANTENNA II.—Coxopodite bearing protuberance with small tuft of hairs on postaxial margin of postaxial extension. Exopodite with additional small seta on preaxial surface of segment 1 near midlength. Endopodite one-segmented with additional group of spinules proximally.

MANDIBLE.—Endopodite with one additional spine lateral to two present in first nauplius.

MAXILLA I.—Represented by pair of plumose setae on anterior third of ventral plate.

Caudal portion of ventral plate emarginate and posteromedian row of spinules lacking but replaced by short lateral spinules.

Third Naupliar Stage

FIGURE 7c,g

Third nauplius differing from second in following respects:

ANTENNA I.—Segment 3 with two additional small setae at midlength.

ANTENNA II.—Protuberance on postaxial margin of postaxial extension of coxopodite with one plumose seta instead of tuft of hairs found in second nauplius. Segment 3 of exopodite with additional slender seta immediately proximal to, and about twice as long as, subterminal seta.

Caudal margin of ventral plate bearing second pair of setae anteromesial to first pair about one-third their length, and pair of protuberances mesial to setae. Plate considerably lengthened with posterior region of body extending well beyond dorsal shield.

Fourth Naupliar Stage

FIGURE 7d

Fourth nauplius differing from third in following respects:

ANTENNA I.—One additional seta on segment 3.

MAXILLA I.—Represented by bifurcate lobe with two setae on mesial lobe and one very small seta on smaller lateral lobe.

Posterior region of body lengthened, its caudal margin bearing two delicate setae lateral to setae present in third naupliar stage; median protuberances of third naupliar stage lacking. Anal plate with very fine spinules along posterior border.

Fifth Naupliar Stage

FIGURE 7e

Fifth nauplius differing from fourth in following respects:

ANTENNA I.—An additional very small seta present on segment 3.

MAXILLA I.—Setae larger and lobe more prominent and two-segmented.

MAXILLA II.—Represented by small lobe caudal to maxilla I.

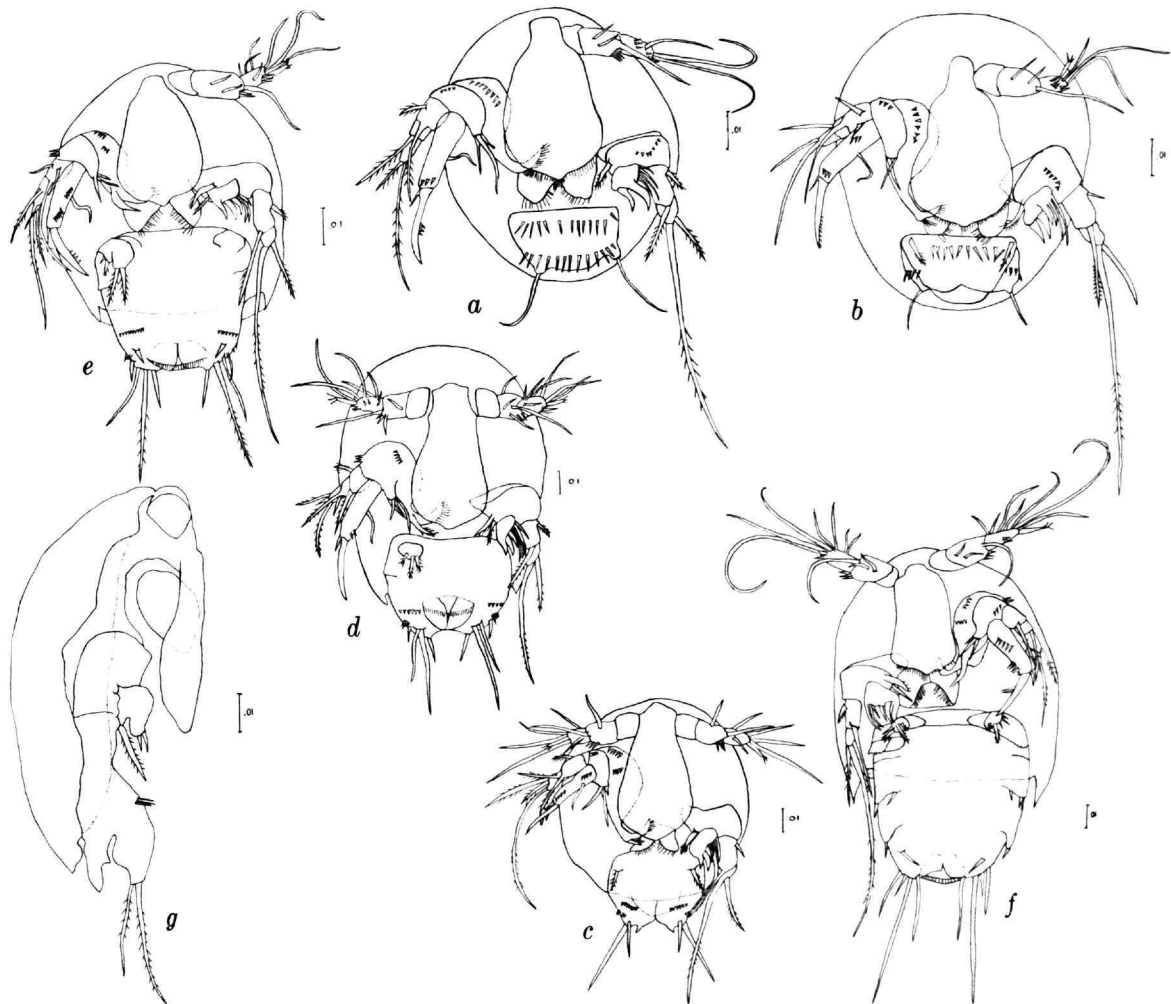


FIGURE 7.—*Bryocamptus zschokkei alleghaniensis*: a, first nauplius, ventral view; b, second nauplius, ventral view; c, third nauplius, ventral view; d, fourth nauplius, ventral view; e, fifth nauplius, ventral view; f, sixth nauplius, ventral view; g, third nauplius, lateral view.

Setae on caudal margin of ventral plate larger; one additional small seta present anteromesial to most lateral seta of distal group.

Sixth Naupliar Stage

FIGURE 7f

Sixth nauplius differing from fifth in following respects:

MANDIBLE.—Usually no apparent difference but in one shed (with distinct intersegmental sutures across entire body), coxopodite with teeth on median lobe as in copepodids and adult.

MAXILLA I.—Lobes distinct; intersegmental suture present laterally between lobes of first maxilla and those of second maxilla.

Body posterior to maxillae divided laterally into two distinct segments with rudiments of first two pairs of swimming legs and pygidial area.

First Copepodid Stage

FIGURES 8a; 9e; 10a,h

Body consisting of cephalothorax and four free segments.

ANTENNA I (Figure 9e).—As in sixth nauplius but segment 2 with distal lobe bearing one seta and one asthete.

FIRST LEG (Figure 10a).—Basipodite bearing lateral protuberance with one spine and two rows of spinules on lateral surface. Exopodite one-segmented, bearing two lateral spines, one subterminal spine, one terminal spine, and one terminal seta. Groups of

spinules present at bases of lateral spines, and distal row of spinules extending obliquely on preaxial surface. Endopodite one-segmented, with four pairs of spinules along lateral border, row of subterminal spinules, one terminal spine, and one terminal seta.

SECOND LEG (Figure 10h).—Basipodite bearing one lateral spine with group of spinules at base and row of spinules near mesiodistal border. Exopodite one-segmented, bearing two lateral and two terminal spines. Endopodite one-segmented, with four pairs of spinules along lateral border, one terminal spine, and one terminal seta.

THIRD LEG (Figure 8a).—Represented by caudolateral lobe with two spines on second free segment.

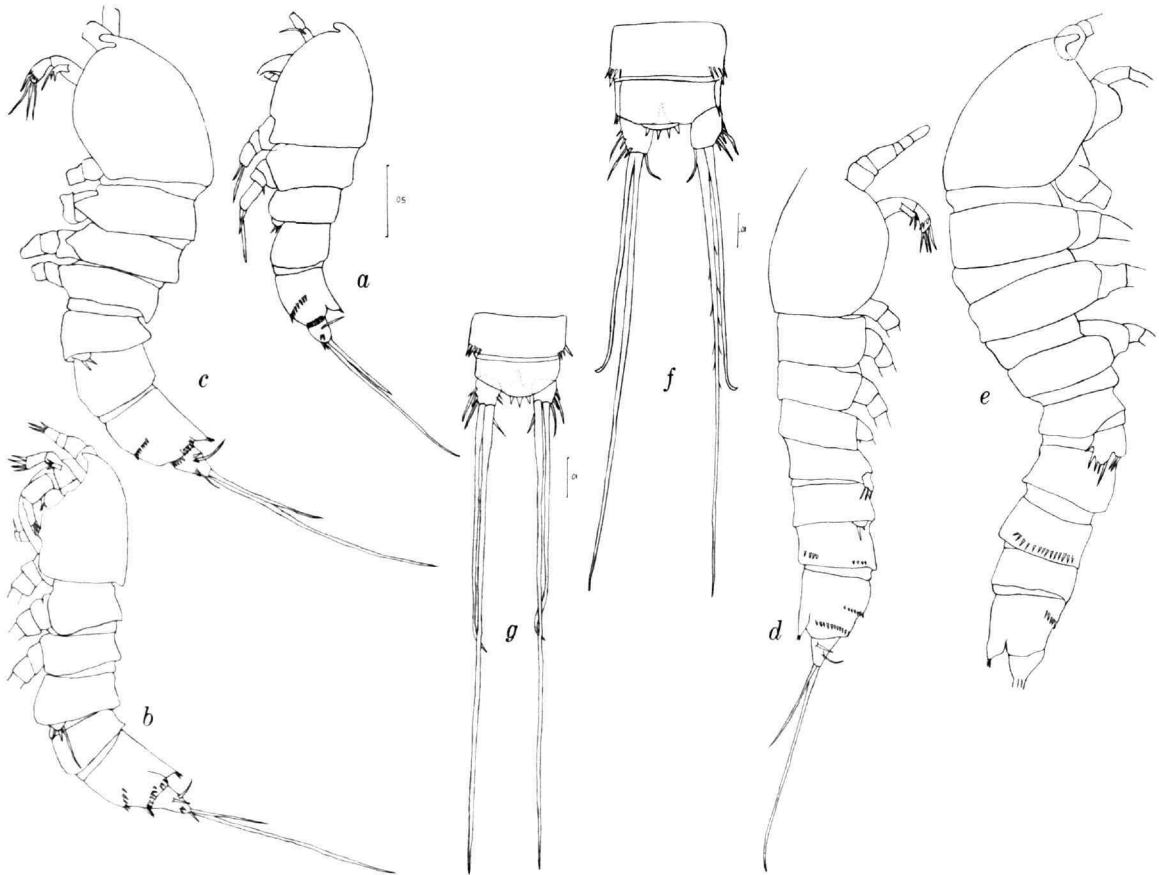


FIGURE 8.—*Bryocamptus zschokkei alleganiensis*: a, first copepodid; b, second copepodid; c, third copepodid; d, fourth copepodid; e, fifth copepodid; f, posterior of adult female, dorsal view; g, posterior of adult male, dorsal view. Figures 8a–e are on scale indicated on Figure 8a.

*Second Copepodid Stage*FIGURES 8*b*; 9*f*; 10*b*,*i*; 11*a*

Second copepodid differing from first in following respects:

Body consisting of cephalothorax and five free segments.

ANTENNA I (Figure 9*f*).—Five-segmented.

FIRST LEG (Figure 10*b*).—Basipodite bearing additional spine on mesiodistal surface. Exopodite two-segmented: segment 1 with lateral spine near distal end; segment 2 with lateral spine at midlength, one subterminal spine, one terminal spine, and two terminal setae. Endopodite two-segmented: segment 1 bearing row of spinules on lateral border; segment 2 with lateral row of spinules, one terminal spine and terminal seta.

SECOND LEG (Figure 10*i*).—Exopodite two-segmented: segment 1 with laterodistal spine; segment 2 bearing lateral spine, two terminal spines, and one small terminal seta. Endopodite two-segmented: segment 1 naked; segment 2 with three pairs of spinules

on lateral border, one subterminal spine, and two terminal setae.

THIRD LEG (Figure 11*a*).—Basipodite bearing one lateral seta and laterodistal group of spinules. Exopodite one-segmented, bearing lateral spine near midlength, one subterminal spine, and three terminal spines. Endopodite one-segmented, with four lateral spinules and three terminal spines.

FOURTH LEG (Figure 8*b*).—Represented by lobe bearing two spines and one seta.

*Third Copepodid Stage*FIGURES 8*c*; 9*g*; 10*c*,*j*; 11*b*,*g*

Third copepodid differing from second in following respects:

Body consisting of cephalothorax and six free segments.

SECOND LEG (Figure 10*j*).—Segment 2 of exopodite with one additional lateral spine proximal to lateral spine present in second copepodid, one additional very small spine on mesial border, and mesio-

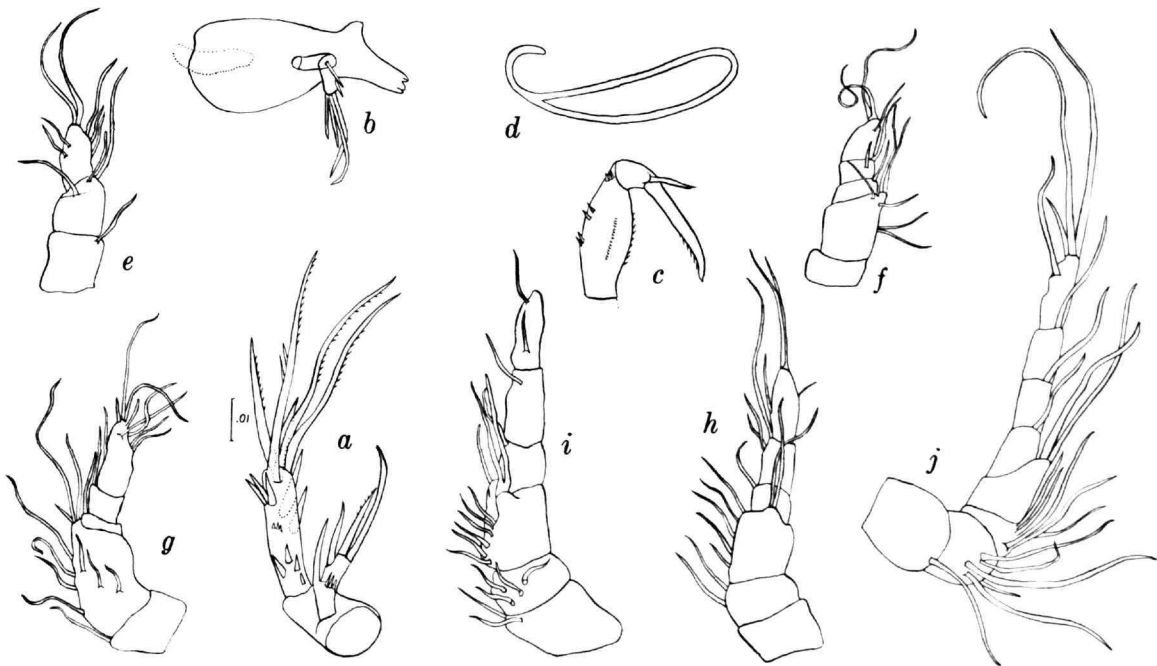


FIGURE 9.—*Bryocamptus zschokkei alleganiensis*: *a*, adult female, antenna 2; *b*, adult female, mandible; *c*, adult female, maxilliped; *d*, spermatophore. *e*-*j*, antenna 1: *e*, first copepodid; *f*, second copepodid; *g*, third copepodid; *h*, fourth copepodid; *i*, fifth copepodid; *j*, adult female.

distal seta more than four times length of that of second copepodid.

THIRD LEG (Figure 11*b*).—Exopodite two-segmented: segment 1 bearing laterodistal spine; segment 2 with one lateral spine, one subterminal spine, one terminal spine, one terminal seta, and one small mesial spine. Endopodite two-segmented: segment 1 naked; segment 2 bearing one subterminal spine, two terminal setae, and two lateral spinules.

FOURTH LEG (Figure 11*g*).—Exopodite one-segmented, with one lateral spine and four terminal spines. Endopodite one-segmented, bearing two terminal spines and one terminal seta.

FIFTH LEG (Figure 8*c*).—Represented by small lobe bearing two small spines on caudolateral margin of fourth free segment.

Fourth Copepodid Stage

FIGURES 8*d*; 9*h*; 10*d,k*; 11*c,h,j*

Fourth copepodid differing from third in following respects:

Body consisting of cephalothorax and seven free segments.

ANTENNA I (Figure 9*h*).—Six-segmented.

FIRST LEG (Figure 10*d*).—Segment 2 of exopodite bearing one spine on mesial border at midlength. Segment 2 of endopodite with two stout terminal spines.

THIRD LEG (Figure 11*c*).—Segment 2 of endopodite bearing two additional terminal setae, subterminal spine enlarged into very stout, terminally rounded spine equivalent in length to that of segment.

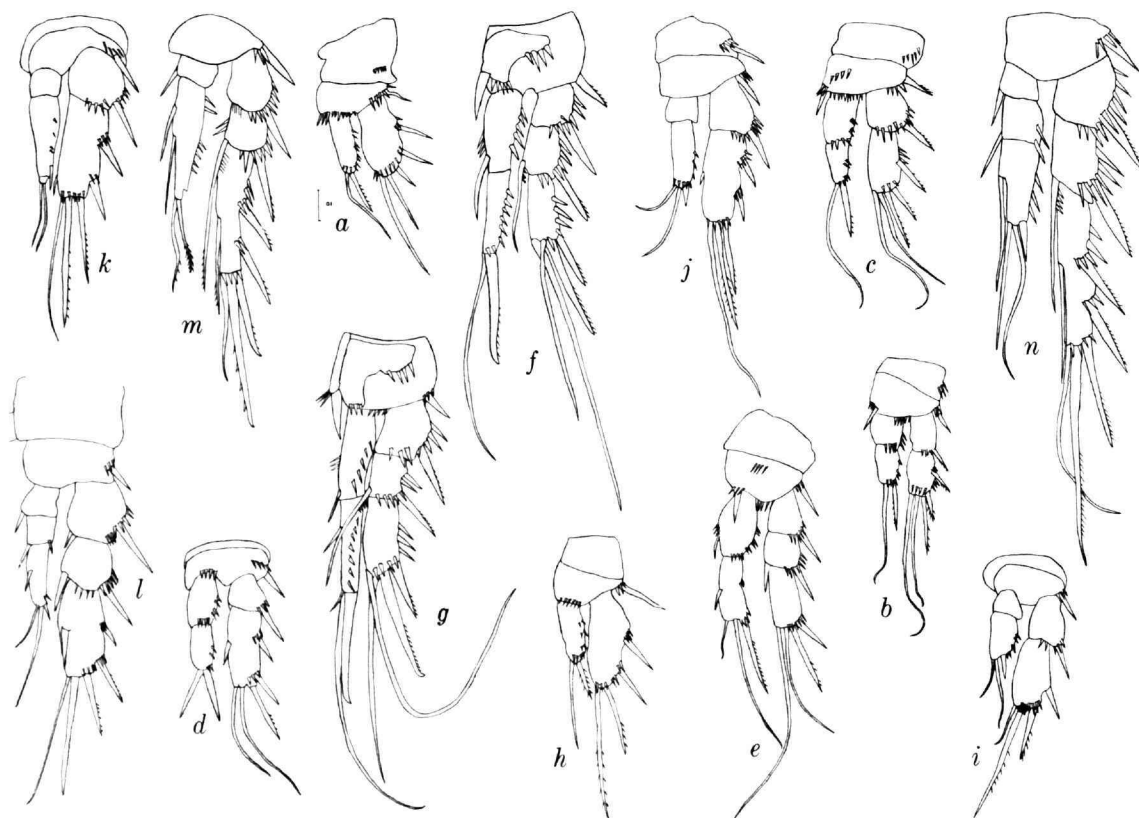


FIGURE 10.—*Bryocamptus zschokkei alleganiensis*, a–g, first leg: a, first copepodid; b, second copepodid; c, third copepodid; d, fourth copepodid; e, fifth copepodid; f, adult male; g, adult female. h–n, second leg: h, first copepodid; i, second copepodid; j, third copepodid; k, fourth copepodid; l, fifth copepodid; m, adult male; n, adult female.

FOURTH LEG (Figure 11*h*).—Exopodite two-segmented: segment 1 bearing one laterodistal spine; segment 2 with two lateral spines, two distal spines, one terminal seta, and one subterminal mesial spine. Endopodite two-segmented: segment 1 naked; segment 2 bearing one subterminal spine, one terminal spine, and one terminal seta.

FIFTH LEG (Figure 11*j*).—Represented by three lobes: mesial lobe bearing two small spines, large lobe lateral to it with three spines and two setae, and

lateral lobe bearing single long seta.

SIXTH LEG (Figure 11*j*).—Represented by pair of small lobes on caudolateral margins of fifth free segment, each bearing one spine and one seta.

Fifth Copepodid Stage

FIGURES 8*e*; 9*i*; 10*e,l*; 11*d,i,k,l*

Fifth copepodid differing from fourth in following respects:

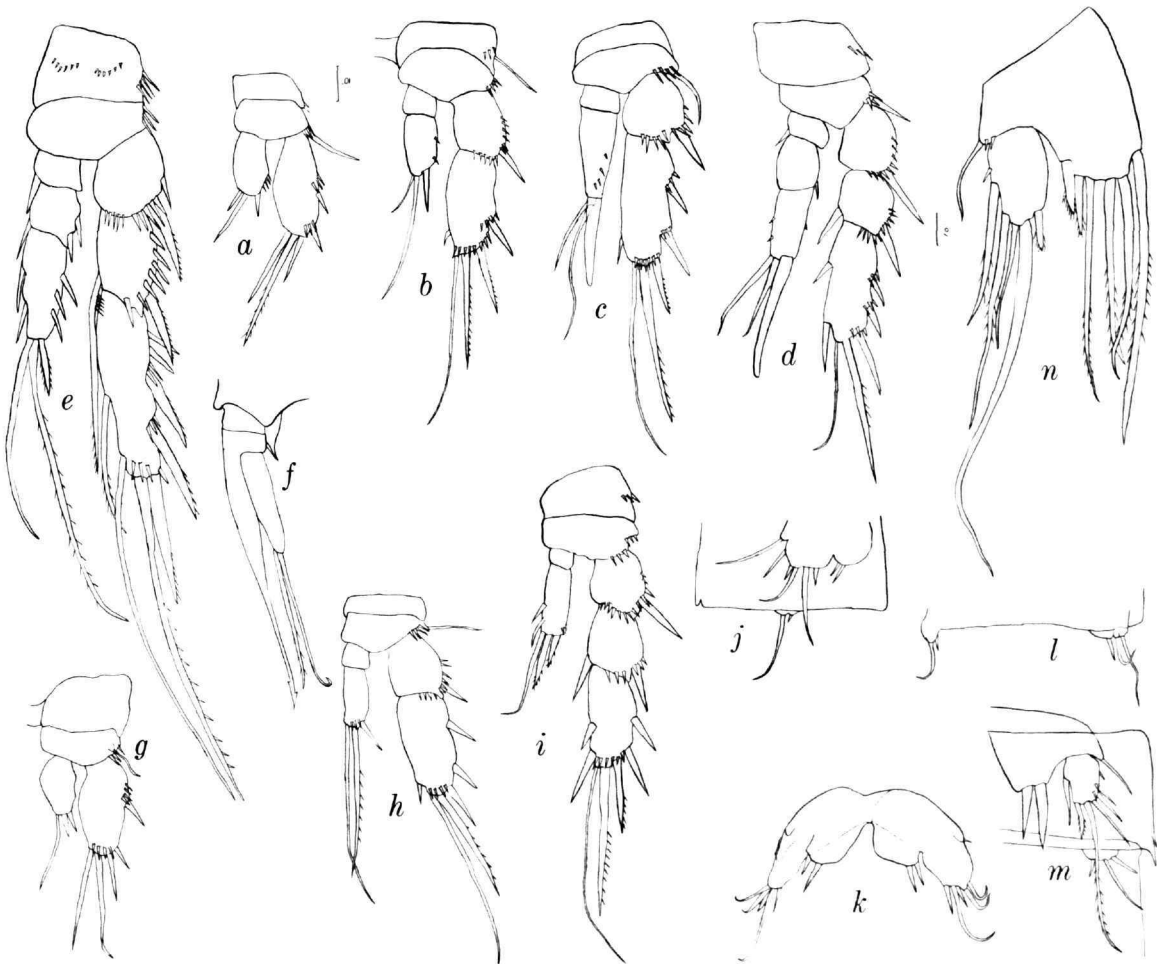


FIGURE 11.—*Bryocamptus zschokkei alleganiensis*, *a-f*, third leg: *a*, second copepodid; *b*, third copepodid; *c*, fourth copepodid; *d*, fifth copepodid; *e*, adult female; *f*, adult male. *g-i*, fourth leg: *g*, third copepodid; *h*, fourth copepodid; *i*, fifth copepodid. *j*, fourth copepodid, fifth and sixth legs; *k*, fifth copepodid, fifth legs; *l*, fifth copepodid, sixth leg; *m*, adult male, fifth and sixth legs; *n*, adult female, fifth leg.

Body consisting of cephalothorax and eight free segments.

FIRST LEG (Figure 10e).—Basipodite bearing one mesiodistal spine. Exopodite three-segmented: segment 2 with one laterodistal spine and one mesiodistal spine; segment 3 with one subterminal spine, one terminal spine, and two terminal setae. Endopodite two-segmented: segment 1 bearing one mesial spine, group of spinules on mesial border proximal to spine, and three pairs of spinules on lateral border; segment 2 with one terminal spine, two terminal setae, one spine on mesial border at midlength, and two spinules on lateral border at midlength; segment appearing to be divided at midlength.

SECOND LEG (Figure 10l).—Exopodite three-segmented: segment 1 bearing one laterodistal spine and one mesiodistal spine; segment 2 with one laterodistal spine and one mesiodistal spine; segment 3 bearing one lateral and one subterminal spine, two terminal spines, one terminal seta, and one mesial spine. Endopodite³ three-segmented: Segment 1 bearing one mesiodistal spine; segment 2 with one laterodistal and one mesiodistal spine; segment 3 bearing two subterminal spinules, one terminal spine, two terminal setae, and one mesial spine at midlength.

THIRD LEG (Figure 11d).—Exopodite three-segmented: segment 2 bearing one laterodistal and one mesiodistal spine; segment 3 with two lateral spines, one subterminal spine, one terminal spine, one terminal seta, one subterminal mesial spine, and one small spine on mesial border at midlength. Endopodite three-segmented: segment 1 bearing one mesiodistal spine; segment 2 with one laterodistal spine; segment 3 bearing one lateral and two mesial spinules, stout subterminal spine longer, and two terminal setae thicker at their bases.

FOURTH LEG (Figure 11i).—Exopodite three-segmented: segment 2 bearing one laterodistal and one mesiodistal spine; segment 3 with one lateral spine, one subterminal spine, two terminal spines, one terminal seta, and two mesial spines. Endopodite two-segmented: segment 1 bearing two lateral spinules,

two terminal spines, one terminal seta, and two mesial spines.

FIFTH LEG (Figure 11k).—Two mesial lobes larger and more distinct.

SIXTH LEG (Figure 11l).—Represented by pair of small lobes on caudolateral margins of fifth free segment, each lobe bearing one spine and two setae. Leg not present in adult female.

Moraria virginiana Carter

First Naupliar Stage

FIGURE 12a,b

First nauplius inflated, bearing subcircular dorsal shield characteristically ornamented: one dorsomedian lobe with four points projecting caudodorsally, one pair of pointed lateral lobes, and one pair of lobes posterior to median lobe.

Labrum subspatulate, very narrow anteriorly with paired lobes on anterolateral angles, posterior margin bordered by fine hairs with tuft of longer hairs projecting from lobe on median line. Narrow portion situated between bases of antennae, from which margins diverging posterolaterally.

ANTENNA I.—Segment 1 short and naked. Segment 2 about twice length of segment 1, bearing distal group of long spinules, proximal group of shorter spinules, and three setae: distal seta long and slender, remaining two short, stout, and tufted with fine hairs distally. Segment 3 about two-thirds length of segment 2, bearing two terminal setae, one subterminal seta, and two subterminal groups of very long spinules.

ANTENNA II.—Coxopodite broader than long, bearing semicircular row of spinules on ventral surface; proximopostaxial angle produced into slightly curved extension ending in tuft of hairs, extension also bearing protuberance with one plumose seta. Basipodite wider than long, narrowing postaxially forming short protuberance bearing two setae. Exopodite three-segmented: segment 1 with one preaxial seta; segment 2 bearing one subterminal seta on short protuberance; segment 3 with two terminal setae. Endopodite one-segmented, bearing one delicate seta at midlength, group of subterminal spinules, and two terminal setae: one short and slender, other almost as long as segment, stout, and movably articulated with segment.

³Adult females from the same locality also have three-segmented endopods on the second and third legs; however, from other localities, some adults have two-segmented endopods on both second and third legs while others have the second endopod two-segmented and the third three-segmented. Similar variations have been observed in the adults by Kiefer (1929:321) and Gurney (1932:148).

MANDIBLE.—Preaxial median border of coxopodite produced into small rounded lobe. Basipodite bearing row of spinules on lower surface and one plumose seta on proximal lower surface. Exopodite two-segmented: segment 1 slightly longer than basipodite, bearing one small spine at midlength and one terminal seta; segment 2 with one short subterminal seta and one terminal seta about twice length of exopodite. Endopodite one-segmented, bearing two curved spines and several delicate setae.

Ventral plate bearing two rows of very long slender spinules across ventral surface, one row near midlength and other near caudal margin. Caudal margin rounded but bearing paired lateral protuberances each with single fine seta.

Second Naupliar Stage

FIGURE 12c,d

Second nauplius differing from first in following respects:

ANTENNA I.—Segment 3 of first antenna bearing one additional subterminal, very stout, and tufted seta.

ANTENNA II.—Endopodite with additional group of spinules proximally.

MANDIBLE.—Basipodite with one additional seta on mesial border.

MAXILLA I.—Represented by one pair of lateral lobes on anterior surface of ventral plate.

Caudal portion of ventral plate emarginate, median posterior row of spinules replaced by two groups of very long, slender, hairlike spinules situated at base of caudal protuberances.

Third Naupliar Stage

FIGURE 12e,f

Third nauplius differing from second in following respects:

ANTENNA I.—Segment 3 bearing one additional seta.

ANTENNA II.—Segment 1 of exopodite bearing one additional seta. (Endopodite absent in single test examined.)

MAXILLA I.—Each lobe present in second nauplius bearing one plumose seta.

Caudal margin of ventral plate with one pair of

protuberances mesial to lobes present in second nauplius, median anterior row of spinules replaced by lateral spinules.

Fourth Naupliar Stage

FIGURE 12g,h

Fourth nauplius differing from third in following respects:

ANTENNA II.—Postaxial extension of coxopodite bearing one additional lobe, and lobe present in third nauplius with one plumose seta.

MAXILLA I.—Bearing one additional seta. Intersegmental suture present posterior to maxillary lobes.

MAXILLA II.—Represented by one pair of indistinct lobes anterior to intersegmental suture.

MAXILLIPED.—Represented by one pair of indistinct lobes posterior to maxillary lobes.

Caudal portion of body produced into two large prominences corresponding to caudal rami of adult, each prominence bearing four setae: lateral and mesial setae on caudal margin, remaining two setae on lobe just anteroventral to posterior margin.

Fifth Naupliar Stage

FIGURE 12i,j

Fifth nauplius differing from fourth in following respects:

ANTENNA I.—Segment 3 bearing nine setae, two of which short, blunt, and plumose.

LABRUM.—Broader posteriorly than anteriorly, broader portion bearing short hairs along lateral and caudal margins.

MAXILLA I.—Lobes more prominent, setae longer, and one additional very small spinule present mesial to other two setae.

Caudal margins of caudal prominences directed caudolaterally instead of caudally, resulting in four setae on each side appearing on lateral instead of posterior border.

Sixth Naupliar Stage

FIGURE 12k,l

Sixth nauplius differing from fifth in following respects:

ANTENNA I.—Additional small seta on segment 3.



FIGURE 12.—*Moraria virginiana*: *a*, first nauplius, ventral view; *b*, first nauplius, dorsal view; *c*, second nauplius, dorsal view; *d*, second nauplius, ventral view; *e*, third nauplius, ventral view; *f*, third nauplius, posterior part of dorsal shield; *g*, fourth nauplius, ventral view; *h*, fourth nauplius, dorsal view; *i*, fifth nauplius, ventral view; *j*, fifth nauplius, posterior part of dorsal shield; *k*, sixth nauplius, posterior part of dorsal shield; *l*, sixth nauplius, ventral view.

MAXILLA I.—Additional seta lateral to two setae present in fifth nauplius.

MAXILLA II.—Lobes more prominent and intersegmental suture posterior to lobes no longer evident.

MAXILLIPED.—Represented by two pairs of lobes: one pair near median line, and other situated lateral to first pair and just mesial to second maxillae.

Posterior part of body divided, by incomplete in-

tersegmental sutures, into two segments: anterior with rudiments of first two pairs of swimming legs, and posterior constituting pygidial area. Setae of large caudal prominences longer.

First Copepodid Stage

FIGURES 13a,b; 14a,d

In the two available tests of the first copepodid, the cephalic appendages are so poorly preserved that they cannot be described or figured.

Body consisting of cephalothorax and four free segments.

FIRST LEG (Figure 14a).—Basipodite bearing one lateral spine and three rows of spinules on distal border. Exopodite one-segmented, bearing two lateral

spines, one subterminal spine, one terminal spine, and two terminal setae. Endopodite one-segmented, bearing subterminal spine, one terminal spine, one terminal seta, and two lateral spinules.

SECOND LEG (Figure 14d).—Basipodite bearing one lateral spine with group of spinules at its base and one row of spinules on its distal border. Exopodite one-segmented, with one lateral spine, one subterminal spine, and three terminal spines. Endopodite one-segmented, bearing three terminal spines.

THIRD LEG (Figure 13a).—Represented by one pair of caudolateral lobes on second free segment, each lobe bearing two setae. Caudal segment with ventral surface bearing two rows of spinules extending from lateral border almost to median line; dorsal surface with slightly rounded and toothed anal plate.

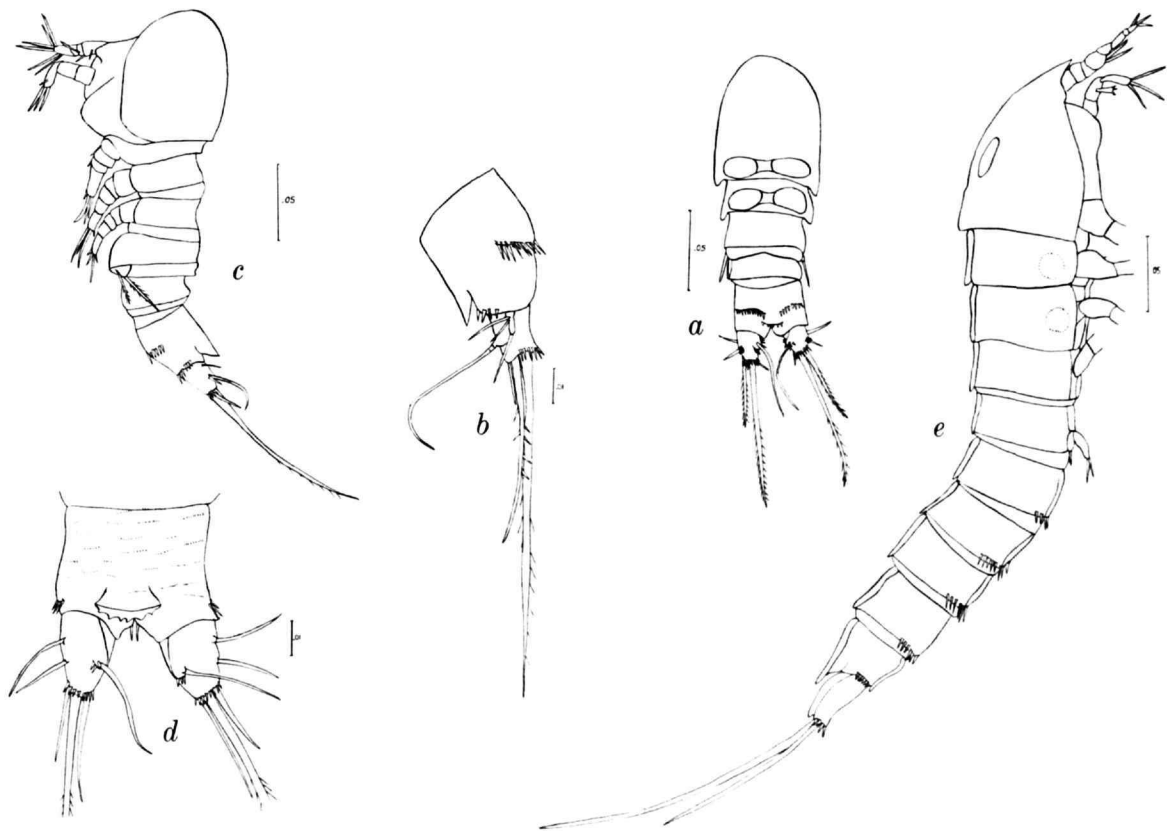


FIGURE 13.—*Moraria virginiana*: a, first copepodid; b, posterior part of first copepodid, lateral view; c, second copepodid, lateral view; d, posterior part of second copepodid, dorsal view; e, adult male, lateral view.

Caudal ramus with dorsal protuberance bearing one slender seta about three times length of ramus, two lateral setae, one row of subterminal spinules, and three terminal setae: mesial seta very short, middle one about half length of entire body, and lateral seta half length of middle one.

Second Copepodid Stage

FIGURES 13*c,d*; 14*b,e,f,i*

Body consisting of cephalothorax and five free segments.

ANTENNA I.—Five-segmented: segment 1 bearing one seta; segment 2 with five setae and one esthete;

remaining three segments bearing total of twelve setae.

FIRST LEG (Figure 14*b*).—Basipodite bearing one laterodistal and one mesiodistal spine, with spinules at bases of each, and two rows of subterminal spinules. Exopodite two-segmented: segment 1 bearing one lateral spine near distal end; segment 2 with one lateral spine at midlength, one subterminal spine, one terminal spine, and two terminal setae. Endopodite two-segmented: segment 1 bearing one subterminal row of spinules; segment 2 with two terminal spines and one terminal seta.

SECOND LEG (Figure 14*e*).—Basipodite bearing one lateral spine near distal border with group of spinules

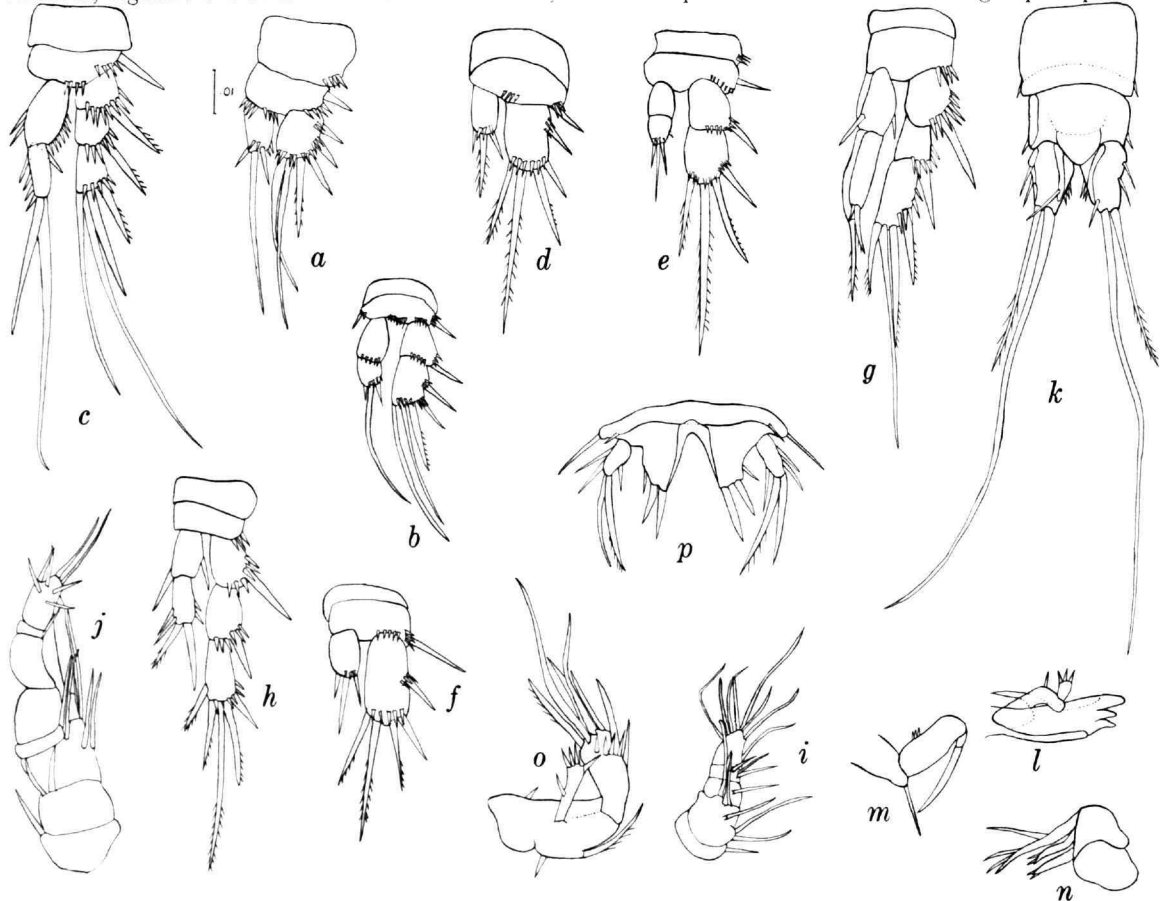


FIGURE 14.—*Moraria virginiana*, *a-c*, first leg: *a*, first copepodid; *b*, second copepodid; *c*, adult male. *d-e*, second leg: *d*, first copepodid; *e*, second copepodid. *f-g*, third leg: *f*, second copepodid; *g*, adult male. *h*, adult male, fourth leg. *i-j*, antenna 1: *i*, second copepodid; *j*, adult male. *k*, posterior part of adult male, dorsal view; *l*, adult male, mandible; *m*, adult male, maxilliped; *n*, adult male, maxilla 2; *o*, adult male, antenna 2; *p*, adult male, fifth leg.

at its base and one row of subterminal spinules. Exopodite two-segmented: segment 1 bearing one laterodistal spine; segment 2 with one subterminal spine and three terminal spines. Endopodite two-segmented: segment 1 naked; segment 2 bearing one lateral spinule and three terminal spines.

THIRD LEG (Figure 14f).—Basipodite bearing one lateral spine with group of spinules at its base and one subterminal row of spinules. Exopodite one-segmented, bearing one lateral spine and four terminal spines. Endopodite one-segmented, bearing three terminal spines and three subterminal spinules.

FOURTH LEG (Figure 13c).—Represented by lobe bearing two setae.

Anal plate more round than that of first copepodid, teeth on margin less prominent.

Caudal rami similar to those of first copepodid but innermost terminal seta much longer.

Discussion

Most early reports on the stages in postembryonic development of harpacticoids are based on the association of one or two larval stages with adults, and few investigators attempted to rear an individual from the first nauplius to the first copepodid stage as did Dietrich (1915) for *Canthocamptus staphylinus*. More recently (Fraser, 1936; Johnson and Olson, 1948; and Haq, 1965), attempts were made at rearing the larvae of harpacticoid copepods to study their development, and some success was achieved during the present study in recording the development of a single individual.

The Naupliar Stages

Several workers have reported five or fewer naupliar stages for a number of harpacticoid copepods (Dietrich, 1915; Tesch, 1915; Chappuis, 1916; Brian, 1922; Borutskii, 1925; Gurney, 1932; and Fraser,

1936) but other work, much of it more recent, indicates six naupliar stages (Chappuis, 1916; Borutskii, 1925; Ewers, 1930; Johnson and Olson, 1948; Krishnaswamy, 1951; Grig, 1960; Fahrenbach, 1962; and Haq, 1965).

Six naupliar stages are characteristic of the development of all three species considered in the present study: *Elaphoidella bidens coronata*, *Bryocamptus zschokkei alleganiensis*, and *Moraria virginiana*.

In the reports in which only five nauplii have been observed in the life history of harpacticoids, there is no uniformity as to which stage is lacking. This lack of consistency seems particularly significant in view of the following: (1) Few of the investigators have based their reports on the exuviae of a single individual, and only a few workers have isolated and reared the nauplii of a single species. (2) The fourth and fifth stages are so similar that had not the exuviae of an isolated individual been obtained in the present study, these two nauplii probably would not have been distinguished.

If it may be assumed that all freshwater harpacticoids have six naupliar stages in their life cycles and that the features exhibited by each stage of the species observed in the present study (Figures 1, 7, 12) are characteristic, then in most instances it seems apparent that the fourth or fifth nauplius was overlooked (e.g., Dietrich, 1915; Borutskii, 1925, and others); however, in the description of the naupliar development of *Canthocamptus pygmaeus*, Gurney (1932: 89–92) probably failed to obtain the third nauplius.

In light of the careful work of Ewers and others, my own observations, the fact that six nauplii are characteristically present in the life cycles of all calanoids and many cyclopoids, and that few detailed studies have been made of the naupliar development of harpacticoids, it seems desirable that the postembryonic development of all species in which fewer than six stages have been reported should be re-examined.

Key to the Naupliar Larvae of Harpacticoids Having Five Molts Preceding the First Copepodid Larva

- | | |
|---|------------------------|
| 1. Caudal margin rounded and bearing row of hairs | First Nauplius |
| Caudal margin not rounded and without row of hairs | 2 |
| 2. Caudal margin emarginate and bearing groups of hairs on posterolateral margin. | Second Nauplius |
| Caudal margin cleft and bearing no hairs | 3 |

Key to the Naupliar Larvae of Harpacticoids Having Five Molts Preceding the First Copepodid Larva—Continued

- | | |
|---|------------------------|
| 3. Caudal margin with slight median cleft and with fingerlike lobe on each side of cleft. | <i>Third Nauplius</i> |
| Caudal margin with deep median cleft and fingerlike lobes lacking | 4 |
| 4. Each caudal lobe bearing four setae | <i>Fourth Nauplius</i> |
| Each caudal lobe bearing five setae | 5 |
| 5. No trace of swimming legs | <i>Fifth Nauplius</i> |
| Two pairs of swimming legs represented by setae-bearing lobes | <i>Sixth Nauplius</i> |

The naupliar stages of each of the three species of copepods treated in this study are similar in most respects. Differences were noted in the second antennae and in the development of the maxillae and of the maxillipeds.

On antenna II, the postaxial extension of the coxopodite of *E. bidens coronata* is dentate, but bears hairs in *B. zschokkei alleganiensis* and *M. virginiana*. This extension bears two lobes in *M. virginiana* but only one in the other two species. The setae on the protuberance of the basipodite vary in number: one in *E. bidens coronata*, three in *B. zschokkei alleganiensis*, and two in *M. virginiana*. The first maxilla of the second nauplius is evident in *E. bidens coronata* and *B. zschokkei alleganiensis* as a single seta; however, in *M. virginiana*, there is a distinct naked lobe, and setae are not present until the third stage. The second maxilla does not appear until the fifth stage in *E. bidens coronata* and *B. zschokkei alleganiensis*, whereas there is a distinct lobe in the third stage of *M. virginiana*. This lobe is more distinct in the fifth stages of *B. zschokkei alleganiensis* and *M. virginiana* than in the sixth nauplius of *E. bidens coronata*.

The rudiments of the maxillipeds are scarcely evident until the sixth stage of *E. bidens coronata*, but a lobe is present in the fifth stage of *B. zschokkei alleganiensis* and in the fourth stage of *M. virginiana*.

The caudal margin of the third nauplius bears two pairs of setae in *B. zschokkei alleganiensis*, but only the original pair are present in that of the other two species.

Except for slight variations and discrepancies between some accounts, there appears to be a remarkable degree of uniformity, even in details in the naupliar development of freshwater harpacticoid copepods. In many instances, the similarities are so marked that distinction between the early nauplii of different species and even between some genera, would appear to be difficult, if not impossible. Be-

cause the naupliar stages of so few species in a single genus have been studied, it is impossible at present to distinguish between the nauplii of different genera with any degree of assurance.

Harpacticoid nauplii may be distinguished from nauplii of other groups by the following characteristics which have been compiled from my work and the studies of others: the first antennae directed laterally when at rest; the large spatulate labrum; the stout, prehensile seta on the endopodite of the second antenna; the pincerlike spines on the endopodite of the mandible; and the long terminal spine on the exopodite of the mandible.

The Copepodid Stages

All free-living copepods, insofar as is known, undergo six molts following the last naupliar stage, the last of which gives rise to the adult. These latter immature stages, the copepodid larvae, resemble the adult in their general facies, and the adult cephalic appendages are only slightly modified from those of the first copepodid. Some attempts have been made (Brian, 1922; Gurney, 1932; Krishnaswamy, 1951; and others) to trace the later larval development of harpacticoids. Gurney's account of the copepodid development, as expressed in his chart, applies equally as well to the two copepods, *Elaphoidella bidens coronata* and *Bryocamptus zschokkei alleganiensis*, of which I have a complete series of stages, and to the first two stages I obtained of *M. virginiana*.

The following chart presents a complete resumé of the pattern of development as it occurs in *Elaphoidella bidens coronata*, *Bryocamptus zschokkei alleganiensis*, and the first two stages of *M. virginiana*. Although Gurney's report for *C. staphylinus* is not so complete, there is agreement between the features he mentioned and those cited here.

TABLE 1.—Segmentation in body and appendages of copepodids I–VI

Stage Copepodid	segs. Body	I Ant. segs.	Segments of exopodite				Segments of endopodite						
			P ₁	P ₂	P ₃	P ₄	P ₁	P ₂	P ₃	P ₄	P ₅	P ₆	
I	12	3	1	1	rud.		1	1	rud.				
II	13	5	2	2	1	rud.	2	2	1	rud.			
III	14	5	2	2	2	1	2	2	2	1			
IV	15	6	2	2	2	2	2	2	2	2	rud.	rud.*	
V	16	6	3	3	3	3	2	2**	2**	2	rud.	rud.	
adult female	16	8	3	3	3	3	3	2**	2**	2	present		
adult male	17	8	3	3	3	3	3	2	3	2	present		

* Sixth leg of fourth copepodid in *E. bidens coronata* represented by very small lobe.

** Endopodites of second and third legs of *B. zschokkei alleghaniensis* sometimes consisting of three segments.

The copepodid stages can be distinguished by counting the number of free segments; i.e., those not included in the cephalothorax. The first copepodid stage has four, the second five, the third six, the fourth seven, the fifth eight, and the adult male nine. The adult female has only eight visible segments; although another is added posteriorly, the fourth and fifth from the caudal end are fused, either partly or completely. The fifth copepodid stage can be distinguished from the adult by the presence of a long segment at the posterior end of the abdomen, whereas the long segment in the adult female is the fourth anterior to the caudal rami.

The addition of segments in the first antenna progresses more irregularly so that while there are three in the first copepodid larva, there are five in the second and third, six in the fourth and fifth, and eight in the adult. It is also noteworthy that the addition of segments in this appendage occurs both distally and proximally. The fourth segment from the proximal end in the adult, which may be recognized in all of the stadia by the presence of a protuberance on which is borne a seta and an esthete, corresponds to the second of the three-segmented appendage of the first copepodid. Thus there are two additional segments added basally: the first segment appears in the fourth copepodid larva, and the second segment appears in the adult.

Because of the difficulty of locating the exuviae in the culture dishes, and because of the variation in the rate of development, the time between each stage has not been accurately determined. However, the time

required for the newly hatched nauplius to reach the first copepodid stage is approximately 10 days, and the time required for the first copepodid stage to reach the adult is about 20 days.

Acknowledgments

It is with great pleasure that I express my appreciation to Dr. Horton H. Hobbs, Jr., for his help and guidance, for his corrections of the manuscript, and for his encouragement which has made this work possible. I also wish to acknowledge my indebtedness to the late Dr. B. D. Reynolds, Director of the Mountain Lake Biological Station, for sending me materials; to Dr. J. Rappaport of the Miller School of Biology for translation of difficult passages in German; to Dr. Beatrice Nevins and Miss Betty Gunter of Valdosta State College for their assistance in arranging the drawings and reading of the manuscript; and to the faculty and members of the Miller School of Biology for their help and encouragement.

Literature Cited

- Banta, A. M.
1921. A Convenient Culture Medium for Daphnids. *Science*, new series, 53(1381):557-558.
- Borutskii, E. V.
1925. [Larvae of Freshwater Harpacticoida (Copepoda)]. *Trudy Kosinskoi Biologicheskoi Stantsii*, 3:49-60.
- Brian, A.
1922. *L'Altheutha depressa* Baird (copepodo harpacticoida) e i suoi larvali. *Monitore Zoologico Italiano*, 33:8-14.

- Carter, Marjorie E.
1944. Harpacticoid Copepods of the Region of Mountain Lake, Virginia. *Journal of the Elisha Mitchell Scientific Society*, 60(2):158-166, plates 65-67.
- Chappuis, P. A.
1916. Die Metamorphose einiger Harpacticidengenera. *Zoologischer Anzeiger*, 48(1):20-31.
1931. Copepoda Harpacticoida der Deutschen Limnologischen Sunda-Expedition. *Archiv für Hydrobiologie*, Suppl. Bd. 8:512-584.
- Coker, R. E.
1934. Contribution to Knowledge of North American Freshwater Harpacticoid Copepod Crustacea. *Journal of the Elisha Mitchell Scientific Society*, 50(1-2):75-141, plates 1-15.
- Dietrich, W.
1915. Die Metamorphose der freilebenden Süßwasser-Copepoden 1. Die Nauplien und das erste Copepodidstadium. *Zeitschrift für wissenschaftliche Zoologie*, 113(2):252-325.
- Ewers, Lela A.
1930. The Larval Development of Freshwater Copepoda. *Contribution, Franz Theodore Stone Laboratory, Columbus, Ohio*, 3:1-30, 13 plates.
- Fahrenbach, W. H.
1962. The Biology of a Harpacticoid Copepod. *La Cellule*, 62(3):303-376, plates 1-9.
- Fraser, H. J.
1936. The Occurrence Ecology and Life History of *Tigriopus fulvus*. *Journal of the Marine Biological Association of the United Kingdom*, 20:523-535.
- Grig, R. E.
1960. [Development of some Harpacticoida of the Black Sea.] *Trudy Cevastopol'skoi Biologicheskoi Stantsii*, 13:68-77.
- Gurney, R.
1932. *British Freshwater Copepoda*. Volume II. Ray Society, London, ix+336 pages, 1195 figures.
- Haq, S. M.
1965. Development of the Copepod *Euterpina acutifrons* with Special Reference to Dimorphism in the Male. *Proceedings of the Zoological Society of London*, 144(2):175-201.
- Johnson, M. W. and J. B. Olson
1948. The Life History and Biology of a Marine Harpacticoid *Tisbe furcata*. *Biological Bulletin*, 95:320-32.
- Kiefer, F.
1929. Beiträge zur Copepodenkunde (XII). *Zoologischer Anzeiger*, 83(11-12):319-25.
- Krishnaswamy, S.
1951. Development of a Harpacticoid Copepod, *Macrosetella gracilis*. *Madras University Journal*, 21B(2):256-271.
- Lang, K.
1948. *Monographie der Harpacticiden*. Håkan Ohlssons Boktryckeri, Lund. 1682 pages, 610 figures.
- Roy, J.
1931. Sur l'existence de la parthénogenèse chez une espèce de Copépodes (*Elaphoidella bidens*). *Comptes rendus des séances de l'Académie des Sciences*, 192:507-508.
- Tesch, J. J.
1915. Quantitative Untersuchungen über das Vorkommen der Copepoden und ihrer Entwicklungsstadien im Plankton bei Haaks-Feuerschiff 1912, mit einem Anhang: Die Nauplien und Copepoditen von *Euterpina acutifrons* (Dana). *Rapporten en Verhandlungen Ryksinstitut*, 1:269-307.
- Wilson, Mildred S.
1956. North American Harpacticoid Copepods. 1. Comments on the Known Fresh-water Species of the Canthocamptidae. 2. *Canthocamptus oregonensis* n. sp. from Oregon and California. *Transactions of the American Microscopical Society*, 75(3):290-307.

Publication in Smithsonian Contributions to Zoology

Manuscripts for serial publications are accepted by the Smithsonian Institution Press, subject to substantive review, only through departments of the various Smithsonian museums. Non-Smithsonian authors should address inquiries to the appropriate department. If submission is invited, the following format requirements of the Press will govern the preparation of copy.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½" top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 pages, including typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index*, if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys*, number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy*, use the short form (taxon, author, date:page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within an entry, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in, or at the end of, the entry. For *references within the text*, use the author-date system: "(Jones 1910)" and "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910:122, pl. 20: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of, or in addition to, the English system.

Illustrations (line drawings, maps, photographs, shaded drawings) can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed *Plates*, and individual components should be lettered (Plate 9*b*) but may be numbered (Plate 9: figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork. An instruction booklet for the preparation of illustrations is available from the Press on request.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." For capitalization of titles in foreign languages, follow the national practice of each language. Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

For *free copies* of his own paper, a Smithsonian author should indicate his requirements on "Form 36" (submitted to the Press with the manuscript). A non-Smithsonian author will receive 50 free copies; order forms for quantities above this amount with instructions for payment will be supplied when page proof is forwarded.

