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ABSTRACT

A COMPARISON OF THE ANATOMY AND NATURAL HISTORY OF COLUBOTELSON THOMSONI NICHOLLS, A SOUTH TEMPERATE, FRESH-WATER ISOPOD AND ASELLUS COMMUNIS SAY, A NORTH TEMPERATE, FRESH-WATER ISOPOD.

by Joseph George Engemann

Isopods of the family Phreatoicidae are commonly found inhabiting the detritus of shallow fresh-waters in Tasmania. Isopods of the family Asellidae are found in similar habitats in north temperate latitudes. The families are in separate sub-orders that have very distinct characteristics. There are no published life-histories of isopods in the Phreatoicidae.

Colubotelson thomsoni Nicholls, an isopod in the family Phreatoicidae, was studied in its natural environment, temporary pools on Mount Wellington, Tasmania, and specimens were collected for further study of life phenomena and preservation for anatomical and histological study. Asellus communis Say, an isopod in the family Asellidae, was also studied in its natural environment, a vernal pond in East Lansing, Michigan, and specimens

were collected for further study. Life cycles are determined by analysis of graphed length and date of collection data correlated with observations on the isopod's reproductive cycles. A comparison of the anatomy and natural history of the two species is then made.

Gross external anatomical differences between the two are due largely to (a) orientation of the pleural portion of the exoskeleton which gives C. thomsoni a laterally compressed appearance in contrast to the dorso-ventrally compressed appearance of A. communis, (b) reduction of the number of external abdominal segments and specialization of abdominal appendages in A. communis, and (c) a nearly uniform width of body regions of C. thomsoni in contrast to the anterior tapering of A. communis.

A close correspondence is present in cephalic and thoracic appendages of the two species.

A similar internal anatomy is noted with some differences including (a) a typhlosole present only in C. thomsoni, and (b) three pair of hepato-pancreatic glands in C. thomsoni, but only two pair in A. communis.

Embryos of A. communis develop a pair of dorsal thoracic appendages, with a histological resemblance to the adult pleopod, which disappears after they hatch.

Serial sections of C. thomsoni embryos have only a bulge in the position of the dorsal appendage of A. communis embryos.

C. thomsoni has only one reproductive period per year. Males may be paired with females for several months. Eggs are carried approximately six months before they hatch. Size data is interpreted to indicate two years are necessary to reach sexual maturity.

In contrast to the preceding, A. communis may have two or more reproductive periods per year. Pairing is of shorter duration and development requires approximately two weeks. Growth and development into maturity may occur in three months according to interpretation of size distribution data.

Major environmental differences observed between the two environments were higher summer temperatures, a greater abundance and diversity of other invertebrates, and a greater annual increment of detritus-forming leaf-litter in the vernal pond in Michigan. The lamellar structure of the vernal pond detritus caused by the abundance of leaves from deciduous trees, is considered to have been of possible significance in selecting the structural modification evolved in A. communis. The above

environmental differences, as well as a greater variety of aquatic vertebrates known from waters in Michigan which are capable of preying on aquatic isopods, are considered significant in the development of differences in life cycles, number of young produced, and growth rates.

Both species were able to survive the summer dry periods by remaining inactive in the moist bottom mud. Specimens collected in such a condition became active in less than a minute after water was added.

The taxonomic position of the two species is discussed. Also discussed is the possible role the differences in length of life cycle might have on speciation and evolution.

A COMPARISON OF THE ANATOMY
AND NATURAL HISTORY OF
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A SOUTH TEMPERATE, FRESH-WATER ISOPOD AND
ASELLUS COMMUNIS SAY,
A NORTH TEMPERATE, FRESH-WATER ISOPOD.

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INTRODUCTION

Fresh-water isopods are one of the most conspicuous and abundant groups of macroscopic crustaceans inhabiting the detritus in the shallows of many of the world's fresh waters. Most of the isopods are in the sub-order Aselloidea, but in the Southern Hemisphere species from the sub-order Phreatoicoidea are more common in many areas (Green, 1961). This thesis is a report of a study and comparison of a species from each of the sub-orders, one from the Southern Hemisphere, the other from a somewhat similar habitat in the Northern Hemisphere.

Colubotelson thomsoni Nicholls is an isopod of the sub-order Phreatoicoidea, family Phreatoicidae. It is restricted in distribution to fresh water on Mount Wellington, Tasmania, from altitudes of a few hundred feet to over 4,000 feet. Thus the specimens in this study were from the type locality (Latitude S., approx. 42° 54'; Longitude E., approx. 147° 17').

The sub-order Phreatoicoidea is a group of isopods with a remarkably similar facies (Nicholls, 1943). At present, members of the sub-order are found only in New Zealand, Australia, India and South Africa. Most species occur in Australia and they are found most abundantly and concentrated in the Australian island State, Tasmania. With the exception of one species in India, the distribution of the sub-order is restricted to the Southern Hemisphere. The specimens of C. thomsoni used in this study came from a population found in temporary pools of the North West Bay River on a sub-alpine flat, about 4,000 feet above sea level, near the summit of Mount Wellington.

Asellus communis Say is an isopod of the sub-order Aselloidea (Asellota), family Asellidae. It occurs in shallow aquatic environments in the Northeastern United States. The specimens used in this study came from a temporary roadside pool in Baker Woodlot on the campus of Michigan State University, East Lansing, Michigan (Latitude N. approx. 42° 45'; Longitude W. approx. 84° 30').

The original description of A. communis utilized general characteristics so that many aquatic isopods might be misidentified as this species. More precise analysis of morphological features has resulted in the description of many species within the family Asellidae. A. militaris Hay is similar but distinguishable from type locality specimens of A. communis. Richardson (1905) and Van Name (1936) synonymize A. militaris with A. communis. Records of the genus *Asellus* can be found in many areas around the North Temperate zone (Van Name, 1936; Racovitza, 1920; Nicholls, 1929; Mackin and Hubricht, 1938).

A fossil of a phreatoicid exists from the Triassic beds of Australia (Nicholls, 1943, p. 111). Although Australia has been separated from Asia since the Cretaceous, some transportation of phreatoicids on the feet of wading birds may have occurred. Aselloids and phreatoicids are probably more closely related to each other than to any other isopods. The close relationship is indicated by their similarity of anatomy and the presence of a pair of unique dorsal buds in the embryos of each (Barnard, 1927).

This study is a comparison of *C. thomsoni* and *A. communis*. Comparisons of anatomical structures are a very significant phase of evolutionary and phylogenetic studies. Snodgrass (1956, 1951, 1938) has worked extensively on comparative arthropod anatomy. Sanders (1957) has used comparative studies of crustacean appendages in his recent study of crustacean phylogeny. Many comparisons are either narrow in scope, to establish the nearest taxon to the taxon in question, or broad in scope, to establish systems of phylogeny. This study takes an alternative approach in its comparisons. The relationship of the animals studied is accepted as being rather remote within the same order (Chilton, 1894). The similarities and differences are used as a gauge of the relative rate of the evolutionary process on various aspects of the natural history of the two species. Since selective pressures of the environment are an important factor in most evolutionary change, the analysis of the life history and anatomy may aid in evaluating the more significant differences in the environment of the two species.

REVIEW OF THE LITERATURE

Colubotelson thomsoni was named by Nicholls (1944) at the time he erected the genus *Colubotelson*. Prior to Nicholls' monograph (1943, 1944) of the Phreatoicoidea, *C. thomsoni* was usually identified as the species *Phreatoicus australis* (Thomson, 1893; Smith, 1909; Barnard, 1914 and 1927; Sheppard, 1927) or *Phreatoicus tasmaniae* (Thomson, 1894a). Nicholls (1943, 1944) removed all the Australian species from the genus *Phreatoicus* Chilton because they had considerable differences from the genotype which was a rather specialized subterranean form. The Australian species have been placed by Nicholls (1943, 1944) in several genera.

There is no information in the literature on the life cycle of *C. thomsoni*.

Smith (1909) has a figure of a uropod of the Mount Wellington species in his figures of *Phreatoicus australis*. Nicholls (1944) has a description of the external anatomy as well as some illustrations of parts. He reported that it is morphologically intermediate between *C. joyneri* and *Metaphreatoicus magistri*. Barnard (1927) stated that specimens from Mt. Wellington (*C. thomsoni*) that he examined did not support Smith's (1909) statement that they possess a typhlosole.

Ecological notes about *C. thomsoni* are limited to those made by Thomson (1894b), Smith (1909), and Nicholls (1944).

The only major references not in the literature cited in Nicholls (1943, 1944) monograph containing information about the Phreatoicoidea are Hutchinson (1928), Barnard (1940), Nicholls (1946), Chopra (1947), Chopra and Tiwari (1950), Guiler (1952), Tiwari (1952), Guiler (1956), and Glaessner (1957). None contain significant new informatinn about *C. thomsoni*.

There are several very important works on the Phreatoicoidea. Chilton's (1894) paper contains a detailed anatomy of *Phreatoicus typicus* and a comparison of the then known phreatoicids with the Asellidae. Sheppard (1927) published a taxonomic monograph on the Phreatoicidae. Nicholls (1943, 1944) published a taxonomic monograph on the Phreatoicoidea. Barnard's (1927) paper includes a fairly comprehensive study on the life cycle and anatomy of the South African phreatoicids of the family Amphisopidae.

The literature on asellids is much more extensive than the literature on phreatoicids. The genotype, *Asellus aquaticus* (Linnaeus, 1761) Geoffroy St. Hilaire, 1746, is

abundant and widely distributed in Europe. Bovallius (1886) has twenty-seven literature citations for the species in his paper on the Asellidae. Since then papers on *A. aquaticus* have appeared more frequently as various aspects of its biology are explored. One worker, A. E. Needham (1937, *et seq.*) has over a dozen papers describing normal and experimental observations on *A. aquaticus*.

The species of *Asellus* here reported is *Asellus communis* Say, 1818, and is the first asellid described from North America. Say (1818) described *A. communis* as follows:

> "1. *A. communis*.* *Body* oblong oval, furnished with short rigid hairs; *interior antennae* equal to the peduncle of the exterior ones; *caudal appendices*, peduncle depressed.
> *Inhabits* small streams of fresh water, under stones.
> Cabinet of the Academy.
> Body oblong-oval, a little narrowed before, segments transverse, subequal, indistinctly emarginate on the edges each side, hairy; hairs very short on the disk, longer on the edges and feet; third and fourth segments linear, the anterior ones a little curved forwards and the posterior ones backwards; *head* narrower than the first segment, and not longer; *superior antennae* extending to the base of the tail; *inferior antennae* equal to the peduncle of the superior ones; *eyes* obovate, oblique, prominent, black; *tail* as broad as the segments of the body, transverse-suborbicular, equal to the last two segments conjunctly, depressed, and a little prominent between the appendices; *appendices*

> as long as the tail, laciniae subequal, peduncle dilated; anterior feet hardly longer, monodactyle, unarmed; thumb as long as the hand; hand oval; carpus triangular; remaining feet gradually longer to the hind pair, which is the longest, first and second joints suboval, gibbous above, third joint triangular, extended over the base of the succeeding one and tipped with long hairs, fourth and fifth linear; tarsi half as long as the preceding joint, simple acute.
> Length one fourth of an inch, breadth less than one tenth.
> A very common species in our fresh waters, particularly in rivulets under stones. It is frequently introduced with the Schuylkill water into Philadelphia. The female may be distinguished from the male by a valvular pectoral follicle in which the young are protected. In one of these I counted twenty-eight young ones."

Subsequent paper containing information about *A. communis* have been mostly redescriptions, distributional records and short notes on natural history (Milne-Edwards, 1840; Harger, 1874; Paulmier, 1905; Richardson, 1905; Fowler, 1912; Kunkel, 1918; Racovitza, 1920, and 1925; Johansen, 1920; Stammer, 1932; Van Name, 1936). A number of non-taxonomic papers exist. McMurrich (1895) has figured the early embryology of *A. communis* and his observations were similar to Rathke's (1834) more extensive observations on *A. aquaticus*. Forbes (1878) reported the occurrence of *A. communis* in the stomach contents of Illinois fishes. Richardson's (1904) work on natural history of isopods includes *Asellus* in genera discussed.

Allee (1912, *et seq.*) has probably done more work with *A. communis* than any other man. His work was ecological, physiological, and behavioral.

Further observations on *A. communis* have been published by Banta (1910), Shelford (1913), Hatchett (1947), Kenk (1949), and Ellis (1961). Extensive reports on the biology of species closely related to *A. communis* are those by Sars (1867, 1899), Kaulbersz (1913), Marcus (1930), and Ellis (1961). Waterman (1961) has cited many papers on the physiology of isopods.

Comparisons of anatomy of asellids and phreatoicids have been made by Chilton (1894), Thomson (1893), Barnard (1927), Sheppard (1927) and Nicholls (1943). Chilton (1894) noted the presence of coupling spines on the maxillipeds, the propodus of the gnathopod, male reproductive organs and spermatozoa were similar in *Phreatoicus* spp. and *Asellus* spp. He also noted a general similarity of cephalic and thoracic appendages while general body shape and pleon were markedly different in the two genera. Barnard (1927) noted the similarity of *Metaphreatoicus* spp. and *Asellus* spp. in the fourth male periopod, gastric mill, brood-pouch, presence of dorsal appendage in the embryo, and season the young are released. Sheppard (1927) noted the difference in the spine-row of *Asellus* spp. and phreatoicids, while there was a similarity of the coxal lobe of the maxilliped of ovigerous females and the condition of the coxopodites of the thoracic appendages of the two groups. Nicholls (1943) noted the differences between *Asellus* spp. and phreatoicids in the "subocular" area and relative development of mouthparts. Green (1961) has pointed out that the two groups are Northern and Southern Hemisphere counterparts. There are no publications with direct comparisons of *C*. *thomsoni* and *A*. *communis*.

That isopods are worthy of study can be inferred from reading Hynes (1960). He considers *Asellus* spp. an important member of the "pollution fauna" found on the surface of mud of "depositing" substrata where the isopods feed on dead leaves and bacterial growth. *Asellus* spp. are so important that he designates an *Asellus* Zone or an *Asellus*/*Cladophora* Zone in the recovering region of an organically polluted river.

METHODS

Qualitative sampling involved removing specimens from their environment with forceps, pipette, strainer, or other suitable means. An oversize pipette with a ¼ ounce bulb and no constriction in the end of the pipette was convenient for handling living specimens. Submerged objects were examined and specimens removed. Detritus and litter were concentrated by means of a common kitchen strainer with a diameter of about five inches and a mesh with about fifteen openings per inch, and then placed in a white 10 x 14 inch enamel pan for sorting. A small amount of water was added and the material was sorted. Specimens were removed as soon as they were located. Material was inspected individually in the pan. Then it was concentrated in clumps and left undisturbed for a short period. Eventually the animals would leave the clumps of debris and could be readily detected on the contrasting pan.

A special effort was made to secure every specimen in samples taken for use in determining population size class frequencies. The same pool was collected in repeatedly and in as nearly the same location as possible as a means of examining the same population for seasonal differences. A piece of fine brass screening with fourty-two openings per inch was occasionally used to check against the efficiency of the kitchen strainer. It was found that the kitchen strainer collected specimens of the smallest sizes found on the brass screen.

Material was usually taken to the laboratory in pint jars for a more thorough qualitative inspection. Most specimens were preserved while at the collecting site in 3" x 3/4" shell vials containing 70% ethyl alcohol. Other specimens selected for histological preparations were killed and fixed in either Bouin's Fluid or acetic-alcohol fixatives before preservation in 70% alcohol.

Macroscopic invertebrates from the area were collected and preserved in 70% ethyl alcohol. Observations on the activities of the macroscopic invertebrates were made in the field as the opportunity arose.

Temperature of the water, several inches below the water surface, was taken with an immersion type Fahrenheit thermometer.

The length of preserved specimens was measured from the anterior end of the head capsule to the posterior end of the telson. Specimens were straightened and shortened if necessary to eliminate any unpigmented intersegmental region.

Isopods were maintained in the laboratory in various glass containers. Water was kept at a low level, less than two inches deep, so that sufficient oxygen would be available. Greater depth was allowed in a series of rectangular glass tanks through which a continuous flow of water was siphoned (as diagrammed in fig. 1). For food, the Tasmanian isopods were provided with moss and liverworts. Michigan isopods were fed maple, elm, ash, beech, or oak leaves, which were partially decayed when taken from their natural habitat. Stacking finger bowls or covered containers proved more satisfactory than uncovered containers for growing _A_. _communis_. The rate of evaporation was reduced and formation of surface scum was inhibited in stacked, or covered, containers.

Appendages mounted in glycerine-jelly or CMC-10 were much more easily seen than ones mounted in balsam, which has a refractive index too similar to that of the appendages. Crystals frequently form in unringed slides made with CMC-10. Serial sections were prepared by the paraffin technique for observation of internal anatomy. Serial sections were routinely stained with hematoxylin and eosin. Photomicrographs were taken using Kodak Tri-X film and an AO Spencer phase contrast microscope with a trinocular body and a 35 mm. camera with a focal plane shutter. Outline drawings were prepared free-hand, by tracing photographs, and by the aid of a camera lucida.

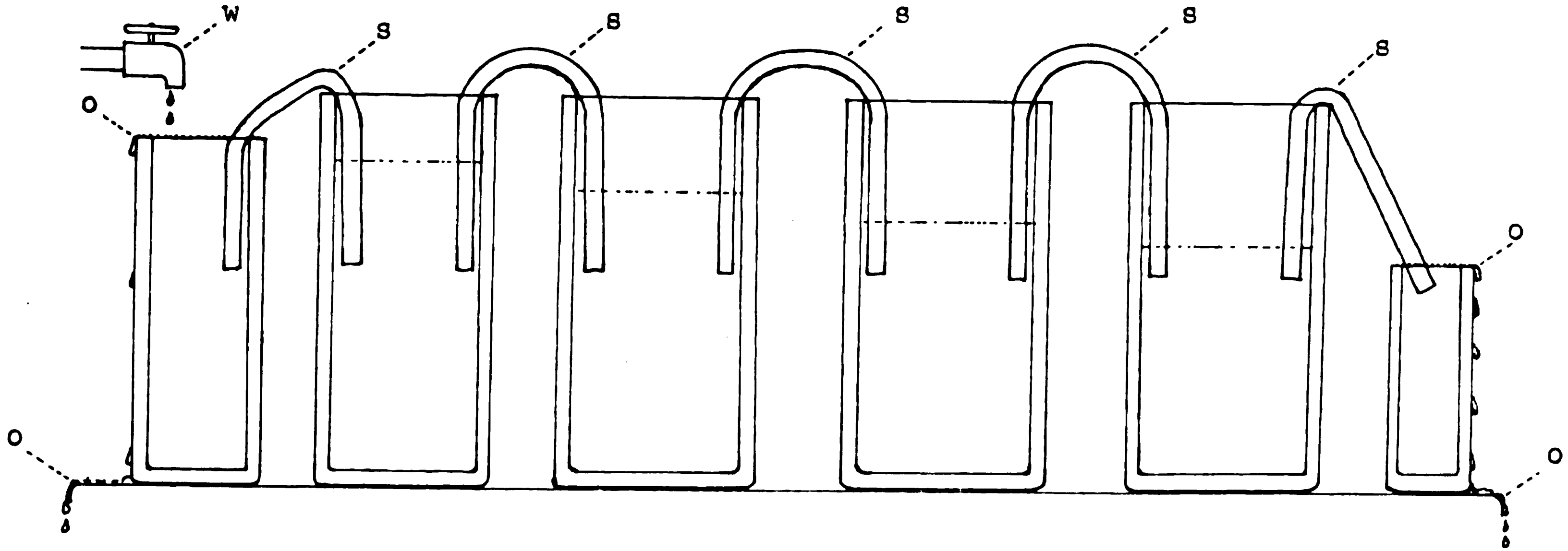


Fig. 1. Diagram of apparatus used to provide a constant flow of water for several groups of isolated isopods, or other bottom dwelling organisms. w, water supply; s, siphon; o, overflow. (Not to scale)

RESULTS

Anatomy of *C. thomsoni* and *A. communis*.

EXTERNAL ANATOMY

Length

Nicholls (1944) states the size of *C. thomsoni* as 12.5 mm. This is about the average length for males in my August 1957 collections. The longest male was 15 mm., the longest female 12 mm. After they reach 7 or 8 mm. the sexes can be differentiated. The smallest specimens collected were 2.5 mm. Length is approximately 7 times width in adult males and about 5 to 7 times width in females.

The length of individuals of *A. communis* used in this study was greater than the quarter inch of Say's (1818) specimens. The maximum length for males was 13½ mm., for females 10 mm. Most specimens over five millimeters long can be sexed. The smallest specimens collected were one millimeter long. The breadth of the organism is about one-fourth the length.

Cross-Sectional Shape

Cross-sections show the adults of both species of isopods are, more or less, circular in the intersegmental region.

The pleura and sterna of *C. thomsoni* project lateroventrally in regions where the legs are attached. The arrangement of the appendages and the downward elongation of the pleura of the abdominal segments results in a laterally compressed appearance.

The dorso-ventrally flattened appearance of *A. communis* is caused by the lateral extension of the terga and epimera to the attachment of the legs.

External Sexual Differences.

Both species have several sexual differences in common. The gnathopods of the males are more robust than those of the female. The males have a slightly modified fourth walking leg. The pene through which the vas deferens opens extends medio-ventrally from the coxa of the seventh male periopod. Both males have modified second pleopods (figs. 26 and 27). Females of both have oostegites extending medially from the coxa of the first four pairs of legs. The oostegites of gravid females are so enlarged that they overlap to form a marsupium. Males of both have a larger maximum size.

The female of *A. communis*, especially the gravid female, is proportionally wider in the anterior thoracic region than the male. The *A. communis* female has only four pairs of pleopods.

The Head.

The head of *C. thomsoni* has a rounded capsular appearance

dorsally and the mouthparts extend ventrally occupying as much space as the head proper. The anterior margin of the head is smoothly excavate. The head is as wide as the rest of the organism.

The head of A. communis is excavate anteriorly, wider than long and rounded laterally. There is a postero-lateral process which is not prominent unless the head is rotated slightly. The head is the narrowest region.

The Eyes.

The eyes are flush with the surface of the head. Each eye of C. thomsoni has approximately 20 ocelli, and is located near the anterior of the head in a lateral position. There are approximately 12 ocelli in the eyes of A. communis and they are located midway along the lateral margins of the head.

The Antennules (First Antennae).

The antennule of C. thomsoni is slightly shorter than the peduncle of the antenna. It is immediately dorsal and medial to the antenna. If the first three articles (segments) are considered peduncle, it then has a five articled flagellum. The segments are of about equal length but are variable in different individuals. The terminal segment is always much smaller. In addition to typical hair-like setae, the distal articles contain a number of specialized setae which have a terminal half blunt, slightly enlarged and cylinder-like (fig. 2). These correspond to the "olfactory cylinders" of Chilton (1894, p. 188, and Pl. XVI, fig. 2) on Neophreatoicus assimilis.

The antennule of A. communis is also slightly shorter than the peduncle of the antenna. It is immediately dorsal to the antenna. The basal segment is about as wide as long. The second segment is of smaller diameter but it is the longest segment of the antennule. The third is of still smaller diameter and is second in length. There are eleven segments in the flagellum which are of the same diameter and shorter than the three most proximal segments which form the peduncle. The first three segments have a few long setae, the rest a few short setae. Some of the setae on the distal segments are blunt with the distal part forming a cylinder distinct from the basal part (fig. 3). Perhaps these correspond to the olfactory tubes (Bovallius, 1886) of the European asellids. They are very similar, in construction, to the specialized setae on the antennule of C. thomsoni.

The Antennae (Second Antennae).

The antennae, in both species, are attached immediately in front of the eyes. Both have antennae with five-segmented peduncles. The flagellum is twice as long as

Fig. 2. Tip of antennule, 13 mm. male C. thomsoni. O, "olfactory setae." x 180.

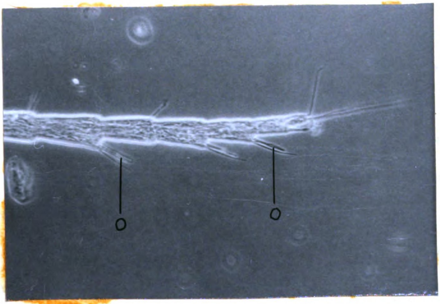


Fig. 3. Tip of antennule, 9 mm. female Asellus communis. O, "olfactory setae." x 180.

the peduncle. The segments of the peduncle and the flagellum have setae at their distal ends. Setae of the peduncle are longest and their length equals the diameter of the peduncle. Segments of the flagellum are shorter than wide at the proximal end and grade unto ones that are three (_C_. _thomsoni_) or four (_A_._communis_) times longer than wide distally. The change in relative dimensions is due to a distal reduction in diameter of the flagellum, while the actual segment length increases only slightly.

The first two segments of the antennal peduncle of _C_. _thomsoni_ are each shorter than wide, and as long together as the third or fourth. The fifth segment is longest but shorter than the third and fourth together. The flagellum has from 18 to 23 articles. Antenna length is much less than the combined length of head and thorax.

The first three segments of the antennal peduncle of _A_. _communis_ are each shorter than wide. The two distal peduncular segments are each equal to the length of a body segment, the most distal being slightly the longer. The flagellum has approximately 60 articles. Antenna length is equal to the combined length of head and thorax.

Mouth Parts.

The Labrum.

The labrum (figs. 4 and 5) of both species is shaped like an inverted dome. The ventral margin is densely fringed with short, stout setae. The asymmetry of the labrum of *C. thomsoni* observed by Nicholls (1944) is apparently due to the posture of the setae.

The Mandibles.

Both species have mandibles with a definite asymmetry. The right mandible lacks a *lacinia mobilis*. The left mandible has a *lacinia mobilis* between the incisor process and the spine-row (fig. 6). The *lacinia mobilis* has three teeth (or less in *A. communis*). The palps are three segmented. The two distal segments have on their distal half a series of pectinate setae. The hairs forming the pectination are only on the terminal end of the setae. The setae of the terminal segment form a dense curved brush. The palp projects anteriorly beneath the peduncles of the antennae.

C. thomsoni has a double row of spines in the spinerow directed toward the molar process when the mandibles are closed. The arrangement assists the inward movement of food and prevents its escape from the molar process (fig. 7). The molar process has a roughly square grinding surface with twenty striated rows on its surface.

The spine-row of *A. communis* is composed of plumose setae, rather than spines as in *C. thomsoni*. The molar process is somewhat circular and has over thirty striations visible on it. The setae on the two terminal segments of the palp somewhat oppose each other leaving a sub-circular opening between them.

The Labium.

The labium of *C. thomsoni* is deeply cleft. The sides of the cleft diverge at almost a right angle to each other (fig. 8). Halfway along the inner margin of the side of the cleft is an indentation which separates the margin into an inner part, forming the notch of the V and bearing very tiny setae and an outer half bearing a dense brush of larger setae which are directed medially.

The labium of *A. communis* is deeply cleft (fig. 9). Distally there is a dense fringe of setae which are progressively shorter in the cleft in contrast to the abrupt transition from large setae to small setae along the cleft of *C. thomsoni*.

The Maxillae.

The paired first maxillae (maxillula of Nicholls) of *C. thomsoni* have two rami (fig. 10). The medial ramus is

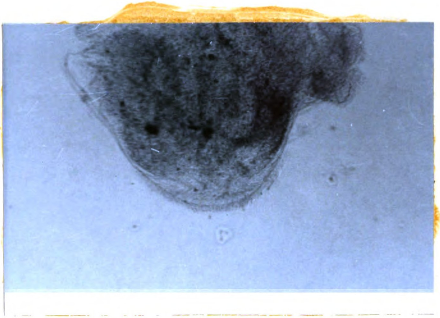


Fig. 4. Labrum of 9 mm. female A. communis. x 180.

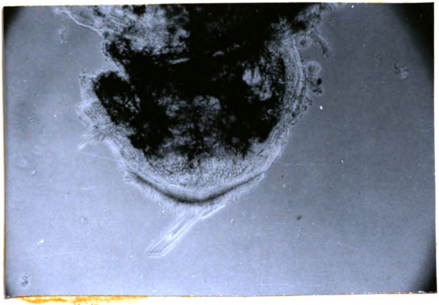


Fig. 5. Labrum of 13 mm. male C. thomsoni. x 180.

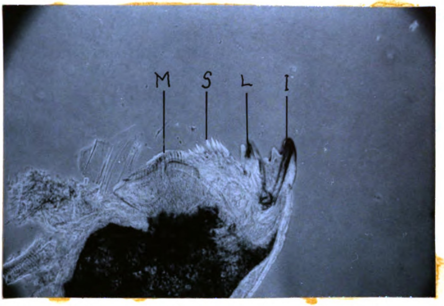


Fig. 6. Left mandible of 13 mm. male C. thomsoni. I, incisor; S, spine row; M, molar process; and L, lacinia mobilis. x 80.

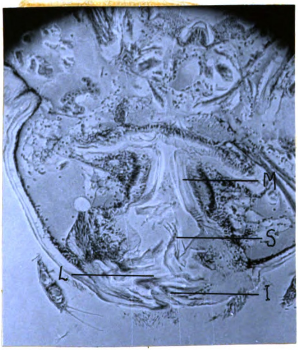


Fig. 7. Section through mandibles of female C. thomsoni showing opposing action of right and left incisive and molar processes with inwardly directed spine row. I, incisor; S, spine row; M, molar process; and L, lacinia mobilis. x 80.

shorter, narrower and bears four stout plumose setae terminally. The lateral ramus bears about a dozen tooth-like terminal setae, one of which is usually a plumose setospine, and two sub-terminal plumose setae. Both curve so that their ends are directed somewhat medially.

The second maxilla of *C. thomsoni* is more leaf-like with three lobes. The middle lobe is frequently difficult to distinguish. The medial margin of the medial lobe bears a double row of setae. The setae of one row are plumose to some extent. At the distal end are several stouter setae which are pectinate along their medial margin. Between the right and left maxillae is a small curved median process of unknown function.

The first maxilla of *A. communis* has two rami (fig. 11). The medial ramus bears five stout plumose setae. The lateral ramus bears over a dozen pectinate or forked spines in which most of the teeth are near the terminal end and are blunt. The spines are in three rows. The second maxilla is three lobed and more leaf-like. The inner ramus is the widest and bears two terminal rows of setae, one row is of simple setae, one is of pectinate setae on which the teeth point laterally. The outer two lobes, or rami, bear long setae which curve medially and on the medial surface of the

Fig. 8. Labium of 13 mm. male C. thomsoni. x 80.

Fig. 9. Labium of 9 mm. female A. communis. x 80.

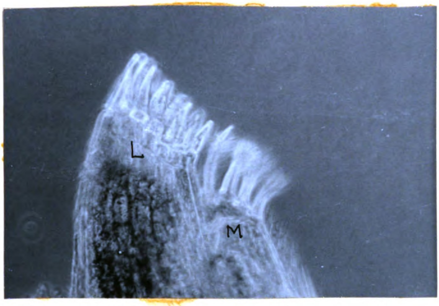


Fig. 10. Maxillula of 13 mm. male C. thomsoni. M, medial ramus; L, lateral ramus. x 180.

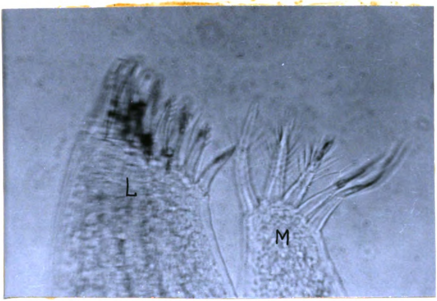


Fig. 11. First maxilla of 9 mm. female A. communis. M, medial ramus; L, lateral ramus. x 360.

distal end they bear many short uniform teeth.

The Maxillipeds.

The maxillipeds of C. thomsoni are the most postero-ventral mouth parts with palps that extend to the area near the incisive processes of the mandibles. The epipodites of the maxillipeds are broad and plate-like, arising from the coxae and covering the basal portions of the maxillae. The palp on the latero-distal margin of the basis possesses a large plumose setae which Nicholls (1943, p. 16) states probably represents the point where the exopodite once was carried. The basis also gives rise to a plate projecting antero-dorsally and provided with several coupling hooks (fig. 12) on the medial side. The plate of the basis has a simple setae on its proximal dorsal margin grading into pectinate setae terminally. The coupling hooks are apparently derived from this series of setae. The four remaining segments of the palp are progressively smaller and provided with simple setae which are more abundant along the medial margin. Projecting posteriorly from the coxal segment in the female is a lobe provided with several long setae.

The maxillipeds are considered the first thoracic appendages. Slightly in advance of the posterior margin of the head of *C. thomsoni* is the cervical groove which represents the fusion of the maxilliped segment with the primary head (Nicholls, 1943).

The maxillipeds of *A. communis* are also the most postero-ventral of the mouth parts. They possess plate-like epipodites which cover the bases of the maxillae laterally. There is a five-segmented palp, as in *C. thomsoni*, which extends as far as the mandibles. Along the midline is an anterior extension of the basis with a dorsally extending side. This process is provided with plumose setae. Five coupling spines (fig. 13) extend medially with their distal end toothed. A lobe of the coxal segment of the female extends posteriorly and is tipped with plumose setae. The setae of the palp and epipodite are simple.

Walking Legs (Legs or Pereiopods).

The seven pairs of walking legs and their component segments are of similar construction in both species.

Legs of C. thomsoni.

C. thomsoni has two pairs of legs at the posterior of the thorax which are longer than the preceding pairs. The first leg (gnathopod) is sub-chelate, i.e. the dactyl is folded down upon a raised palmar area on the propod (figs. 16 and 17). The palmar area is provided with approximately nine stout denticulate spines. The dactyl possesses very fine spines on the surface opposing the palm. In the adult male the gnathopod is more robust. The fourth leg of the male is also modified in possessing one or two stout spines on the propod and a dactyl which is distinctly more curved (fig. 20), than those of the other legs.

Each leg has the coxal segment fused with the body segment, but less definitely so in the posterior legs. A leg is illustrated by fig. 22. The basal segment is the largest and longest segment. A keel, bearing a few long setae on its dorsal edge (the side opposite that to which the dactyl is directed), is well developed on the basal segment of the posterior three pairs of legs. The keel, which contains no appreciable musculature (fig. 23), is directed forward in the first four pair of legs and backward in the last three pair. The ischial segment is shorter than the basos to which it is attached. There is a slight keel on this segment also.

There are stout setae which arise from the ventral distal portion of the basos and extend outward near the ischios. The ischios has median and terminal tufts of the

Fig. 12. Section through mouthparts of *C. thomsoni* showing coupling spines of maxillipeds. C, coupling spine; M, maxillary gland. x 80.

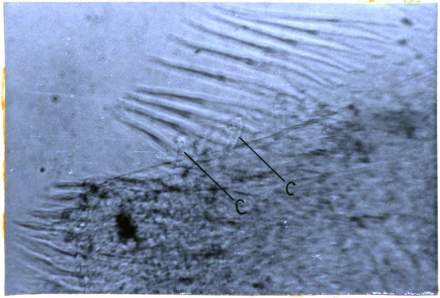
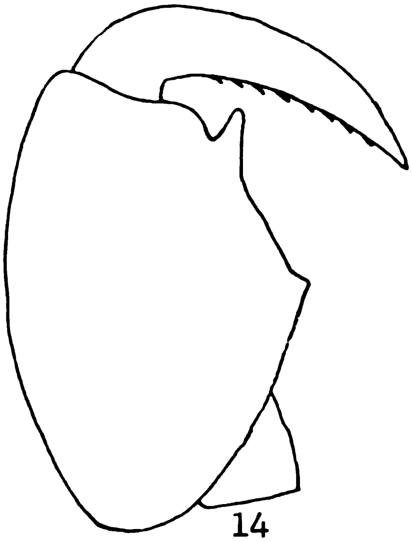


Fig. 13. Coupling spines (c) of maxilliped of 11½ mm. male *A. communis*. x 360.



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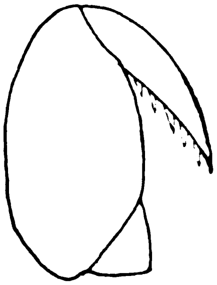

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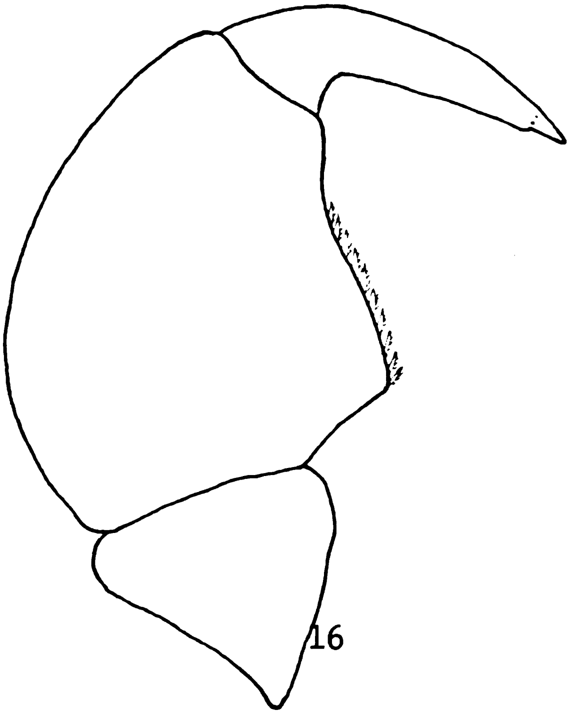
Fig. 14. Gnathopod carpus, propod and dactyl of male <u>Asellus communis</u>. x 58.

Fig. 15. Gnathopod carpus, propod and dactyl of female <u>A</u>. <u>communis</u>. x 58.



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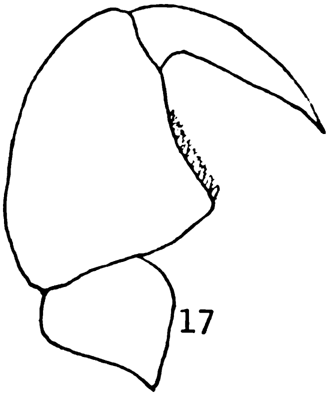

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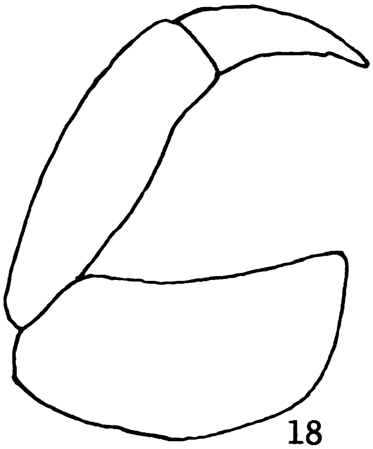
Fig. 16. Gnathopod carpus, propod and dactyl of male <u>C</u>. <u>thomsoni</u>. x 58.
Fig. 17. Gnathopod carpus, propod and dactyl of female <u>C</u>. <u>thomsoni</u>. x 58.

same type of setae. Both tufts are oriented in the same direction on the same side of the segment. Somewhat similar distal tufts are present also on the meros, carpus, and propod. In general the tufts are most highly developed on the side opposite the direction of flexion of the joint by which they are located.

The meros arches dorsally to extend a process over its distal joint. This arch serves as the origin of muscle fibers which converge to their insertion on the carpus. The carpus and propod tend to be straight cylindrical segments. However, in the gnathopod the carpus is triangular. The gnathopodal propod is enlarged and possesses a palmar process as mentioned before. Close examination of the dactyl shows a few subterminal setae around the claw-like end which may be just a stout terminal spine.

The leg flexes dorsally at the joint between basos and ischios as well as at the one between ischios and meros. The meros and carpus are usually held in line. The flexure is ventral at the junctions of carpus and propod, and propod and dactyl.

In the female the oostegites extend medially from the coxa of the first four pair of legs. The oostegites of gravid females are so enlarged that three or four overlap



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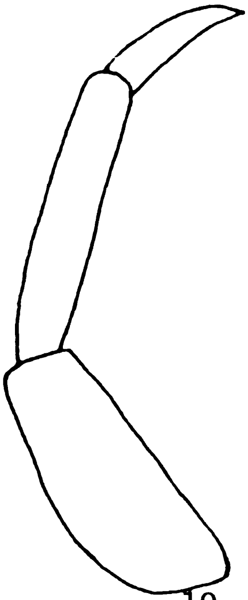

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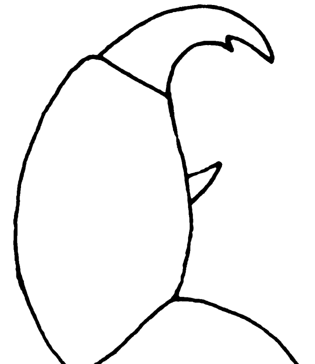

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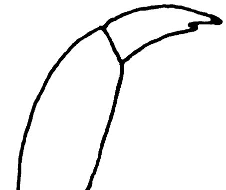

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Fig. 18. Carpus, propod and dactyl, fourth leg, 11½ mm. male *A*. *communis*. x 58.
Fig. 19. Carpus, propod and dactyl, fourth leg, 9 mm. female *A*. *communis*. x 58.
Fig. 20. Carpus, propod and dactyl, fourth leg, 13 mm. male *C*. *thomsoni*. x 58.
Fig. 21. Carpus, propod and dactyl, fourth leg, 10 mm. female *C*. *thomsoni*. x 58.

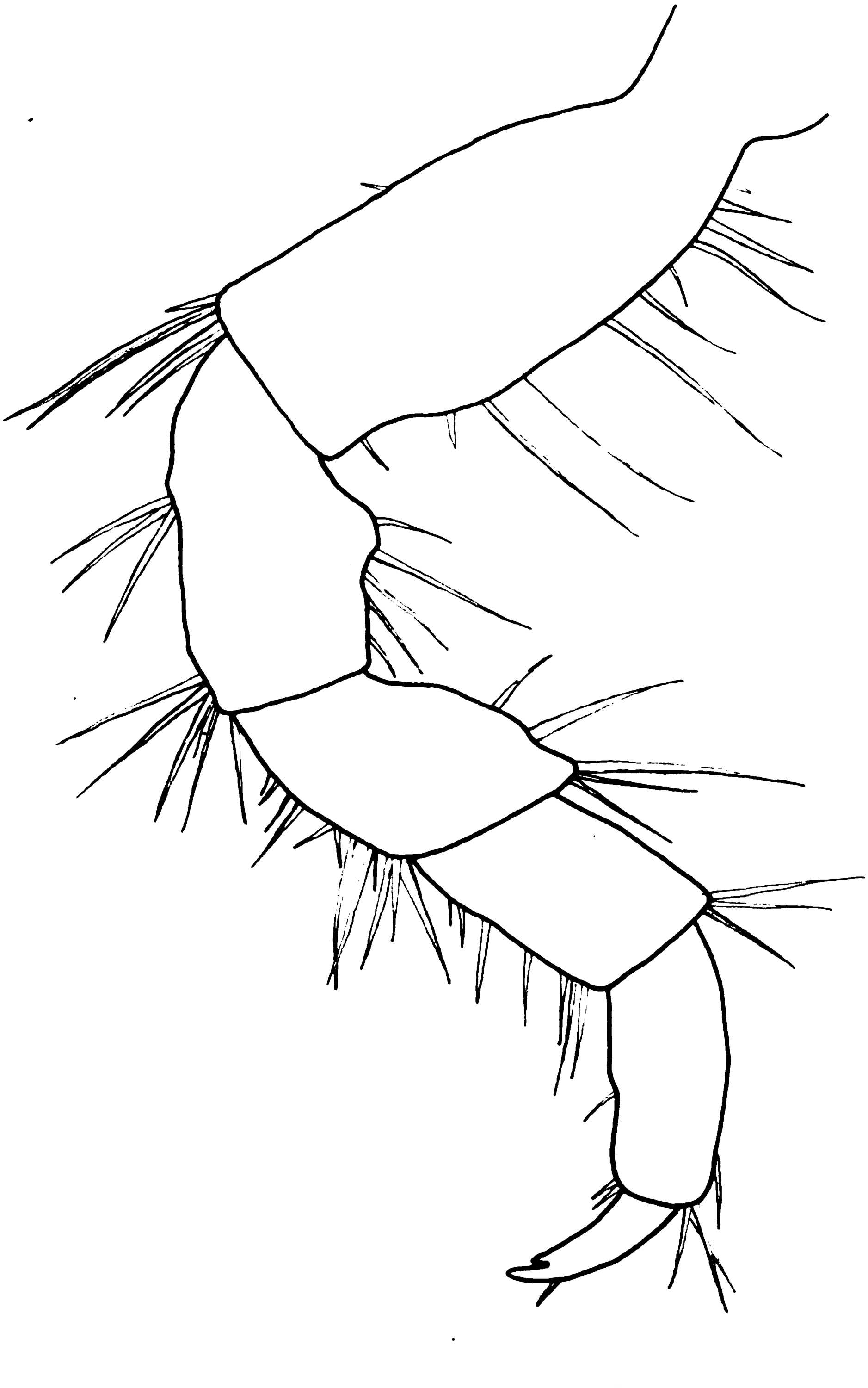

Fig. 22. Third leg of 13 mm. male C. thomsoni. x 58.

Fig. 23. Basis of seventh leg of male <u>C</u>. <u>thomsoni</u>. Note how musculature does not extend into keel.

at most locations along the ventral midline of the marsupium.

The pene through which the vas deferens opens extends medio-ventrally from the coxa of the seventh male periopod.

Legs of A. communis.

The legs are successively longer toward the posterior. In the male the fourth leg is as short as the first (gnathopod) however. The legs are similar except the first (subchelate gnathopod) of both sexes (figs. 14 and 15) and the male's fourth leg (fig. 18). The male gnathopod has two processes (fig. 14) and a row of setae on the palm. The larger process arises in the middle of the palm and slants toward the articulation of the dactyl. The small process is a low hump between the other process and the dactyl. The basis is the largest segment of a leg and the first movable one. The basis of the leg is only slightly keeled on the dorsal surface, the musculature sometimes extending into the dorsal expansion.

The ischium resembles the basis but is smaller. The merus is shorter than the other segments but has a long arching process which is tipped with long, stout spines extending over the carpus. The carpus is of smaller diameter than the preceding segments but of approximately

the same length as the ischium. The propod is as long as the basis but of smaller diameter. The dactyl is less than half the length of the propod except on the gnathopod. There, the dactyl on the palmar surface has short stiff setae giving a toothed appearance to the dactyl (fig. 14). The other legs have fewer, but longer, setae on the corresponding surface of the dactyl. There are a few setae on the dorsal and ventral ridges of the segments and on the distal ends. A leg is illustrated in fig. 24.

The Pleopods.

The pleopods of C. thomsoni are biramous (fig. 25). The exopodite is fringed with setae most of which are plumose. The exopodite is two lobed except on the first pleopod. The endopodite is posterior to the exopodite and resembles the basal lobe of the exopodite but lacks setae. On the second male pleopod is a penial stylet of no known function (fig. 26). It is a curved cylindrical structure along the medial side of the endopodite. The penial stylet is provided with about four terminal setae plus some proximal ones on the medial side. There are numerous muscles inserting on the lateral side of the stylet's articulation with the base of the pleopod. The stylet could easily reach the opening of the vas deferens if directed toward it. Since a penial s

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stylet does not occur in the female it is probably reasonable to assume that it is used in sperm transfer. The posterior three pair of pleopods have epipodites developed into small lamellae which are also fringed with setae.

The pleopods of _A_. _communis_ are primarily respiratory in function. Modification has occurred on the third pleopod which has the exopodite developed as a protective cover with a distinctive suture or fold angled across its middle. The second pleopod of the male is not primarily respiratory but has the endopodite modified for sperm transfer (Van Name, 1936, p. 19). In the male the first pleopod is two-segmented and very small with a few small setae fringing its tip. The second pleopod of the male has a fringe of long setae on the exopodite, whereas the endopodite is small and curved (fig. 27), being only about two-thirds the length of the exopodite.

The female lacks one pair of pleopods. Needham (1938, 1941) states that the first pair are lacking in females of _A_. _aquaticus_ and _A_. _meridianus_. The only pair present anterior to the modified cover-like pair in _A_. _communis_ females is the pair of small plates fringed with setae. The exopodites of the remaining pleopods have at least a few setae on

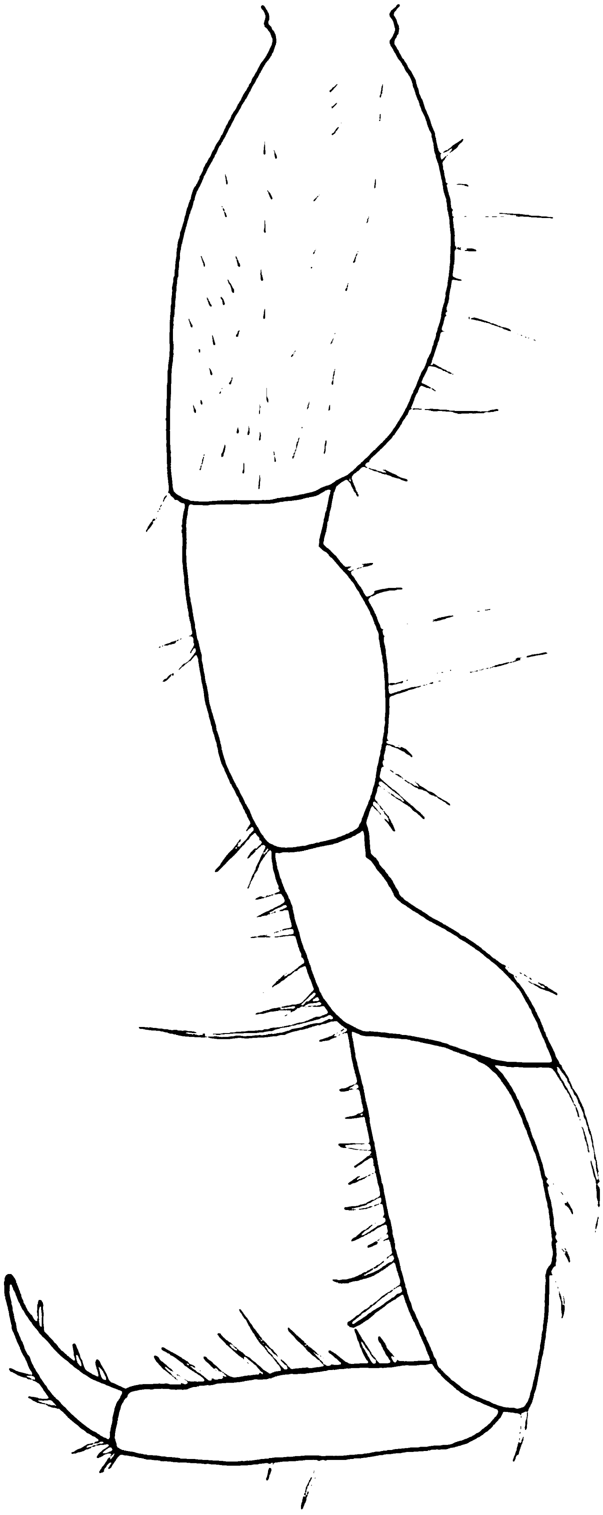


Fig. 24. Third leg of 11½ mm. male A. communis. x 58.

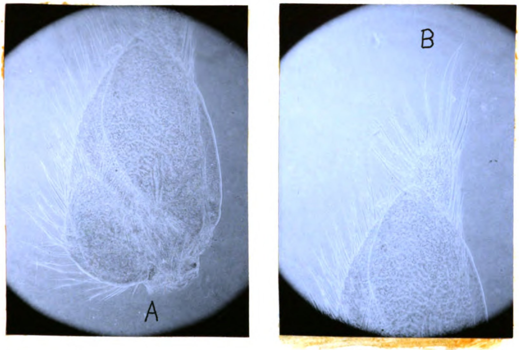


Fig. 25. Fifth pleopod of 10 mm. female C. thomsoni. A, proximal end; B, distal end. x 50.

Fig. 26. Endopodite of second pleopod of 13 mm. male C. thomsoni. M, muscle fibers; P, penial stylet. x 50.

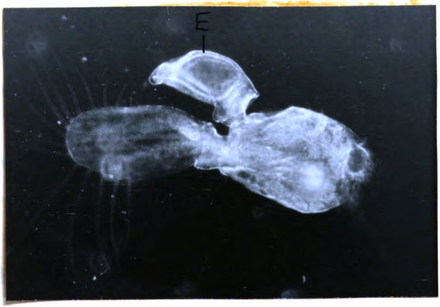


Fig. 27. Second pleopod of 11½ mm. male A. communis. E, endopodite. x 80.

their lateral proximal margin. The third has the most plus a row proximal to the angling fold. In addition to the setae the fourth pleopod's exopodite has a fringe of fine hairs along the proximal lateral portion.

Telson and Uropods.

The ventral margins of the telsonic pleura of C. thomsoni bear a series of stiff setae which have short terminal branches (fig. 28). The telsonic apex is small, upturned, and bears four stout setae and several finer ones. Lateral to this is a lobe bearing a stout seta. The uropods are inserted along the latero-ventral margin. Each uropod has a large basal segment and two rami. Between the rami is a small process with several terminal spines (fig. 29). The rami are lateral and medial in arrangement but their greatest thickness is in the dorso-ventral plane. There are two tufts of setae located ventrally on the basal segment, and several dorsal spines. Although not much movement was observed in the uropods during laboratory observations on locomotion they are well supplied with muscles.

A. communis does not have a distinct telson on the abdomen. The uropods are inserted along the posterior edge of the abdomen with a space between about equal to the length of a thoracic segment. They have a flattened appearance, especially in the male. The endopodite is

Fig. 28. Spines of margin of telsonic pleura of 13 mm. male C. thomsoni. x 110.

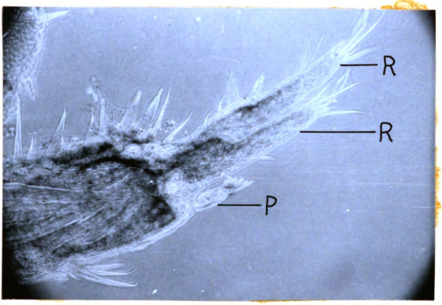


Fig. 29. Uropod of 10 mm. female C. thomsoni showing small, spinous process (P) between the rami (R). x 80.

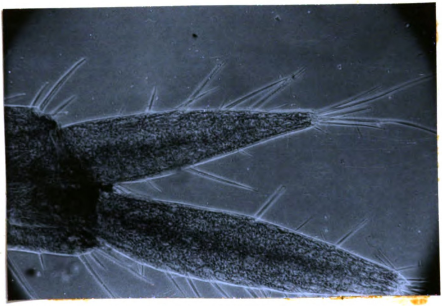


Fig. 30. Uropod of 9 mm. female A. communis. x 80.

longer than the exopodite (fig. 30). Each has a tuft of apical setae. Individual setae are spaced along the margins. The exopodite and endopodite are lateral and medial in position. The majority of their setae are also lateral and medial in position.

Locomotion of *C. thomsoni*.

Normal locomotion is by walking or crawling and includes a variety of possibilities. Each leg has an anterior-posterior plane of normal movement. They can also be moved laterally. The gnathopod is most median in position. Subsequent legs move in a plane lateral to the immediately preceding leg until the sixth leg is reached. Leg six is mesial in position to leg five, and leg seven is mesial to leg six. Thus despite close points of attachment legs can move rather freely. For movement over a glass surface by captive animals the first, second, third and seventh legs have the most effect. Legs four and six may undergo only token movement, rarely contacting the surface or they may be used with seeming efficiency. Leg five is essentially stationary and occupies a position nearly horizontal, often flexing dorsally if the animal is tipped on its side and thus may be used in righting itself. Leg three and sometimes leg two may be less useful

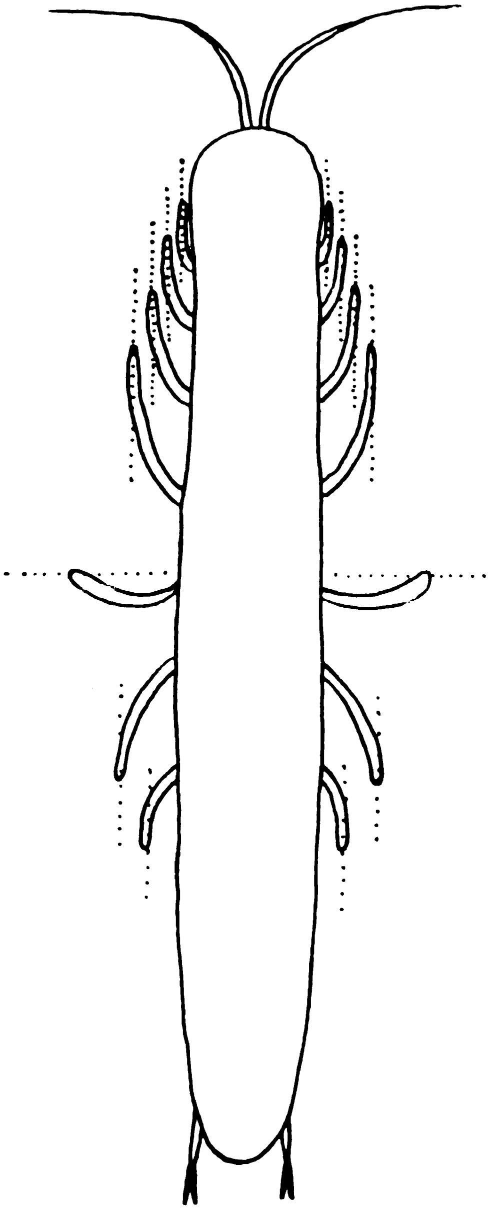


Fig. 31. Plane of movement of legs of C. thomsoni.

in some females with brood pouches; they are then sometimes arched so that only legs one and seven are in contact with the substrate. The plane of movement is indicated in fig. 31.

Legs one through four are usually well synchronized. The beginning of movement seems to be initiated by the first or second leg. When under motion leg four reaches forward and pulls backward slightly in advance of leg three and so on until the motion reaches the front. Legs six and seven commonly move at a slower rate than legs one through four. The right and left corresponding legs are usually in the same phase of movement or nearly so in legs one through four, while legs of pairs six and seven may move alternately or in phase.

Main points of bending the legs are at the distal end of the coxa and at the distal end of the basis. In the gnathropod the dactyl is also extended and brought back to supplement the movement of the leg.

Pleopods are not used for locomotion by undisturbed individuals. Pleopodal beating may provide a water current to aid movement of irritated specimens.

Uropods usually trail travois-style but the abdomen is frequently flexed then extended causing the uropods to

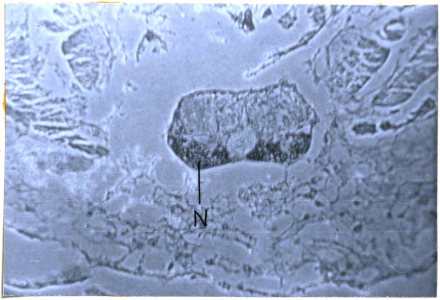


Fig. 33. Ganglion of C. thomsoni showing concentration of neurons (N) in the ventral region. x 180.

provide some thrust. This movement is usually sporadic and sometimes very infrequent. When disturbed, speed can be increased by an increase in the magnitude and rapidity of this flexing and extending movement which produces a water current giving additional thrust. Usually speed at room temperature is approximately one-half to one centimeter per second. When climbing, speed is slower and movement more deliberate. They will often continue to walk for hours at a time around the containers they are in and at the speed they travel could be expected to cover approximately one-half mile in a day.

The antennae extend forward and apart at an ever increasing angle until at the end the filaments form an angle that is usually over forty-five degrees from the anterior-posterior midline. Usually the right and left antennae are alternating as they are waved up and down. Antennules are projected out and up in a fairly constant position.

Locomotion of A. communis.

A. communis has a rate of sustained movement that is approximately the same as that of *C. thomsoni*. However, *A. communis* more frequently moves with spurts separated by stationary periods than by sustained movement.

The abdominal appendages are not used for locomotion. The uropods are usually positioned at an angle to the main axis of the animal and the rami are widely spread, giving a large area of coverage, perhaps for sensory purposes.

Normal locomotion involves movement of the thoracic appendages only. The position of the first four pairs of legs is such that each succeeding leg moves in a plane lateral and somewhat caudad to the preceding leg. The fifth and sixth legs have ranges of movement that do not ordinarily overlap the position of other legs. The seventh leg is moved very little during normal locomotion. The plane of movement of the legs is diagrammed in fig. 32.

INTERNAL ANATOMY

Nervous System

C. thomsoni has a large supraesophageal ganglion or "brain" in the head capsule. Smaller segmental ganglia occur at intervals along the paired tracts of the ventral nerve cord. The cell bodies of neurons of a ganglion are concentrated in the ventral part of the ganglion (fig. 33). Lateral nerves arise from the ganglia. The nerve and ganglia are located above the exoskeleton of the sternum.

The circumesophageal connectives of *A*. *communis* extend abruptly from the supraesophageal ganglion. The cell bodies of the neurons of the posterior ganglia are located in the ventral part of the ganglia.

Digestive System.

The hepato-pancreatic glands and the intestine (fig. 34) fill most of the body cavity of *C*. *thomsoni*. The hepato-pancreatic glands open into the ventral surface of the stomach. They are paired tubular glands. Two short pair, one of which is very short, extend anteriorly. Three pair extend posteriorly most of the length of the animal. All open at the base of the gastric mill. The ventral and lateral tube of one side join, then their common tube receives the dorsal tube before entering the stomach. This is similar to the condition found in *Mesamphisopus capensis* by Barnard (1927), whereas Smith (1909) found *Phreatoicopsis terricola* to have two pair. My dissection of a specimen of *P*. *terricola* indicated there may be a third short pair extending only about half the length of the other two pair.

The intestine posterior to the stomach is of a uniform structure. It is connected to the anus by the short rectum. The large absorptive cells of the intestine contrast sharply

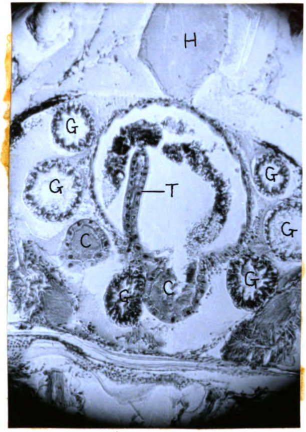


Fig. 34. Cross-section of abdominal region of female C. thomsoni showing hepato-pancreatic glands (G), abdominal cecae of intestine (C), heart (H), and typhlosole (T). x 80.

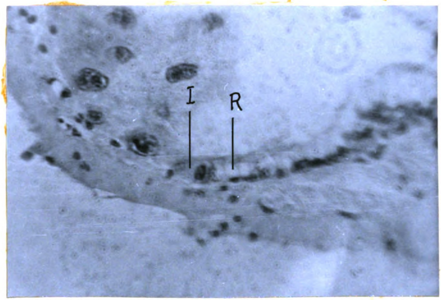


Fig. 35. Junction of intestine (I) and rectum (R), cross-section of male C. thomsoni. x 360.

at each end of the intestine with the small cells of the stomach or rectum as shown in fig. 35. The cells of the intestinal lining possess very large nuclei and are of the simple cuboidal type. The cells of this layer are thrown intoa ventral loop extending dorsally into the lumen as the typhlosole. This structure is not an artifact of preservation. Fig. 36 shows the inner circular and outer longitudinal muscle fibers of the intestinal wall do not follow the intestinal lining cells forming the fold of the typhlosole. In some instances the muscles do follow the fold which is much more open. The Mount Wellington specimens examined by Barnard (1927) when he stated they do not have one must have been of the latter type since the typhlosole of those could resemble a wrinkle produced by preservation. Thus Smith's (1909) statement is substantiated regarding the presence of a typhlosole that was questioned by Barnard (1927). The cells of the lining make up most of the thickness of the intestinal wall. They are of regular arrangement (see fig. 37). In P. terricola they can be seen to present a rectangular appearance arranged in rows visible to the unaided eye. Some specimens of C. thomsoni have a few paired ventral or lateral cecae in the abdominal region (fig. 34).

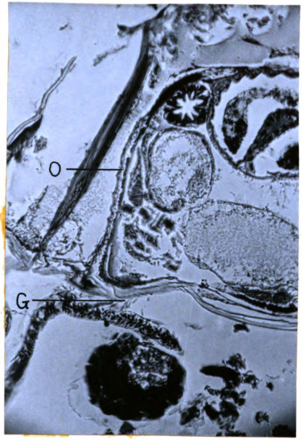


Fig. 36. Cross-section of female C. thomsoni through oviduct (O) and genital opening (G). x 80.

In A. communis there are two pair of hepato-pancreatic glands that arise ventrally near the posterior end of the gastric mill. There is a short median pocket extending back from the common atrium of the hepato-pancreatic glands.

The intestine of A. communis lacks a typhlosole and is round in cross section. It has an inner circular muscle layer and an outer longitudinal muscle layer. The lining is a single layer of large cells with prominent nuclei.

Circulatory System.

Dorsal to the intestine of C. thomsoni is the "heart" or dorsal blood vessel extending through abdomen and thorax. The position of the valves indicates the "heart" is filled through the ostia (fig. 38). There are a number of paired arteries (fig. 39) connected to the heart.

The heart of A. communis lies in a blood sinus in the posterior thoracic region.

Excretory System.

The contorted tubular maxillary glands are considered excretory structures of isopods by Needham (1942a). The glands are prominent structures in the head.

Exoskeleton.

The exoskeleton of a gravid female C. thomsoni was 16 microns thick. The exoskeleton of a female, from a

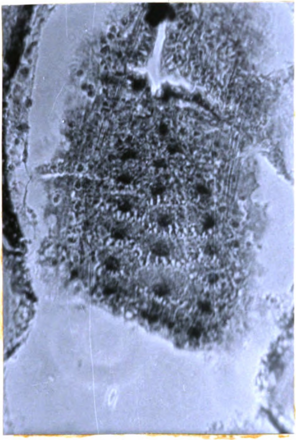


Fig. 37. Tangential section of gut wall of C. thomsoni showing regular arrangement of cells.

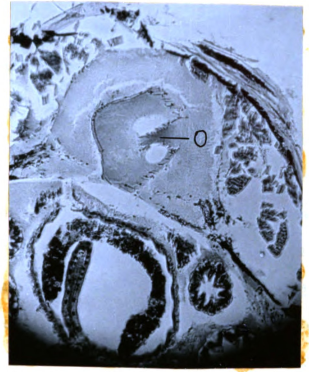


Fig. 38. Section through ostium (O) in heart of female C. thomsoni. x 80.

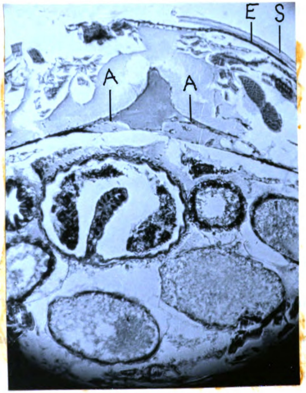


Fig. 39. Section through arteries (A) leaving heart of female C. thomsoni. E, hypodermis; S, exoskeleton. x 80.

breeding pair of A. communis, was 8 microns thick. In both species the exoskeleton is colorless.

Coelom, Muscles, and Coloration.

Coelomic spaces extend through most portions of the organisms. Striated muscles run in many directions through the spaces. They underlie the hypodermis in many regions. The hypodermis contains much brown pigment, especially on the dorsum (fig. 39) of both species. C. thomsoni is darker brown, although some specimens in a late pre-molt condition have a banded appearance with a slight irridescence which partially obliterates the brown. Such specimens are usually in vegetation or on the surface of the bottom, but rarely in the bottom mud.

No pigment occurs where the muscle fibers pass through the hypodermis to insert, or originate, in the exoskeleton. That, Needham (1942b) has shown, is the cause of pigment pattern in the English species of Asellus.

Reproductive System.

The paired tubular testes of the male C. thomsoni are located dorsolateral to the intestine. The vas deferens descends from the posterior end of the testes to open through the pene on the coxa of the seventh periopod. The ovaries of the female occupy a position similar to the testes of the male. The oviducts of the gravid female descend from the posterior of the ovaries to open (fig. 36) within the brood pouch near the posterior of it.

Eggs.

The eggs of *C. thomsoni* are large (750 microns in diameter), spherical, yellow, and few in number. From 11 to 17 were found in brood pouches of females. A 12 mm. female that was dissected had 18 eggs packed in two columns extending from mid-abdomen to the third thoracic segment. They were in the position of the ovaries. The gut was empty and her exoskeleton was in a pre-molt stage. She was collected May 18, 1957.

The eggs of *A. communis* are smaller (350 microns in diameter), pale yellow, and more numerous. Brood pouches contained from 95 to 168. Those dissected did not remain intact for counting.

Developmental Stages and the Dorsal Appendage.

No dorsal appendage was observed in whole eggs and embryos of *C. thomsoni* that were examined with a dissecting scope. Position of the embryo in the egg was somewhat variable. In general they were sharply folded upon themselves in the region of the last two thoracic appendages of the embryo. The folding brought the dorsal surface of the posterior region into contact with the dorsal surface of the anterior region. Variation involved folding similar in position but with the lateral surface in contact, or an intermediate position. However, the ventral surface always faced the outer portion of the egg membrane, thus the developing appendages took a position at one end of the egg or as a band enveloping it. Serial sections revealed a protrusion which represents the dorsal appendage. The dorsal appendage is yolk filled and does not project much beyond the circumference of the egg (figs. 40 and 41). The chorion encloses the appendage without following its contours. Thus except for position the embryo is much like that of *Mesamphisopus capensis* figured by Barnard (1927). The material from which Barnard prepared his figure was very generously loaned to me by the South African Museum and shows some sections (fig. 42) in which the dorsal appendage is even more prominent than in his figure.

The developmental stages of *A. communis*, as well as the general internal anatomy, agree with that figured in Sars (1867) for *A. aquaticus*. The dorsal appendage is a prominent feature on the egg in the late stages of development and is shown in fig. 43. Histologically the appendage is identical to the adult pleopod. The ventral surface

with the developing appendages of the embryo occupies the surface position. The folding along the dorsal side causes the dorsal appendages of the embryo to appear at opposite sides of the egg. Sars (1867) has shown that the chorion has disappeared from the egg of *A. aquaticus* at this stage.

The newly hatched young of both *A. communis* and *C. thomsoni* have a general resemblance to the adults but have only six pairs of walking legs.

An adult female of *C. thomsoni* is illustrated in fig. 44.

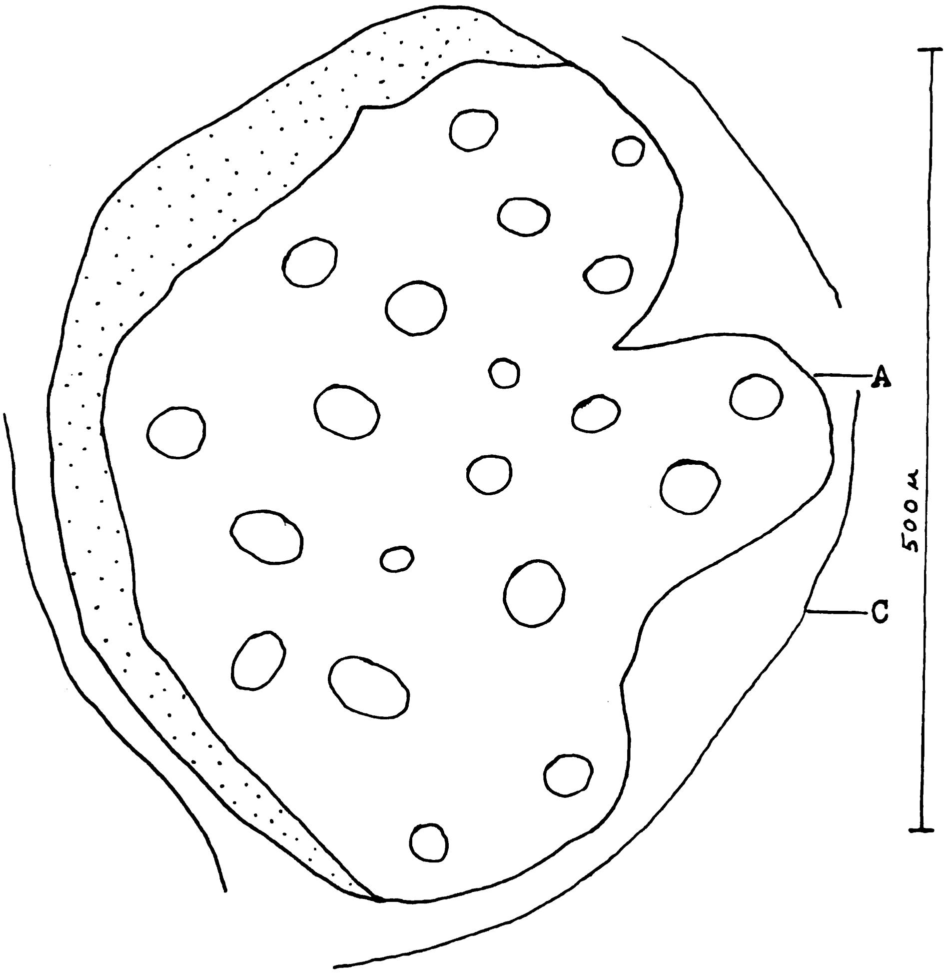


Fig. 40. Drawing of an embryo of C. thomsoni (longitudinal section). Stippling, cellular area; circles, yolky area; A, dorsal appendage; C, chorion. Drawn with the aid of a camera lucida.

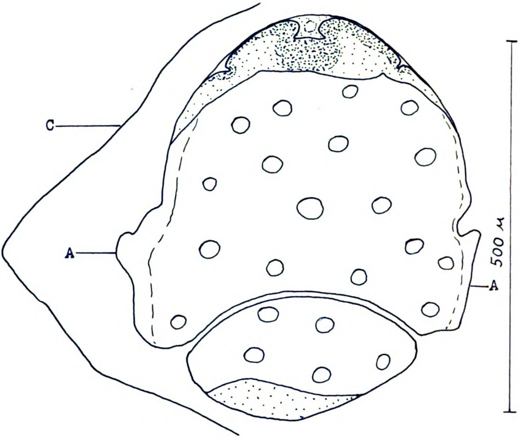


Fig. 41. Drawing of an embryo of C. thomsoni (cross-section). Stippling; cellular area; circles, yolky area; A, dorsal appendage; C, chorion. Note that both dorsal appendages are visible and that embryo appears in two portions due to folding. Drawn with the aid of a camera lucida.

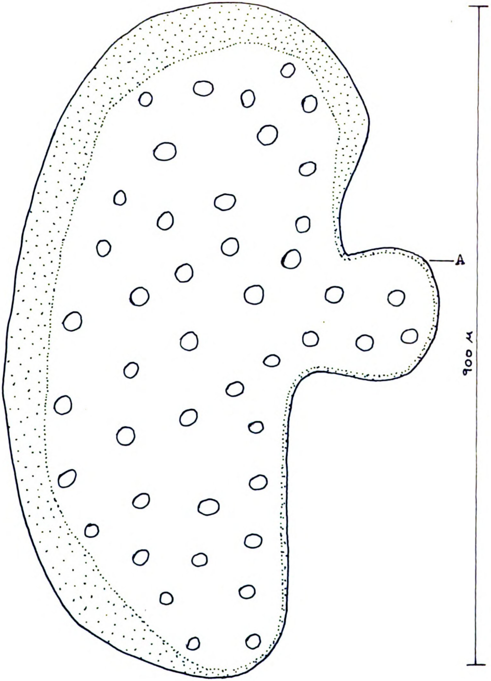


Fig. 42. Drawing of an embryo of M. capensis (longitudinal section). Stippling, cellular area; circles, yolky area; A, dorsal appendage. Drawn with the aid of a camera lucida from a slide prepared by K. H. Barnard on 20/12/13; on loan from the South African Museum.

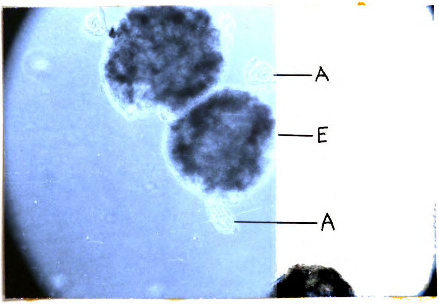


Fig. 43a. Dorsal appendage (A) of A. communis showing relationship to egg (E). x 80.

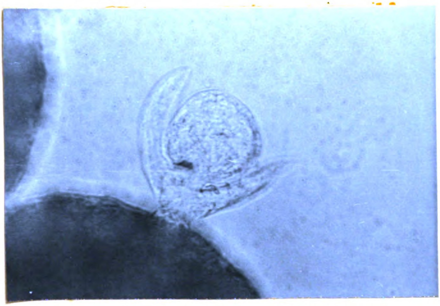


Fig. 43b. Dorsal appendage of A. communis. x 360.

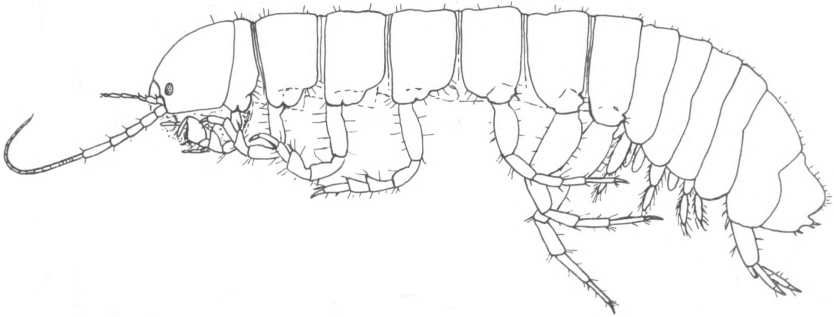


Fig. 44. Lateral view drawing of adult, non-gravid female C. thomsoni.

NATURAL HISTORY OF COLUBOTELSON THOMSONI

Size Distribution.

Examination of collections usually showed three size classes. This is partially evident in the graph (fig. 45) of the size classes of collections. Specimens were measured for length when flattened along a straight edge in a manner such that the intersegmental membranes did not show. Measurement was to the nearest one-half millimeter from the anterior edge of the head capsule to the posterior end of the telsonic projection. From the graphs (fig. 45 and fig. 46) it is obvious that I tended to gauge length as being closer to the nearest millimeter than to the fractional measurement. The presence of three distinct size classes (fig. 47) is more obvious than the modes in fig. 45 indicate.

Laboratory Rearing.

Specimens maintained in glass tanks in the laboratory had a high mortality. No young were reared to maturity. Those that hatched in the laboratory did so at an earlier time than occurred in nature. Perhaps higher laboratory temperatures speeded some developmental processes faster than others with reduced vitality as a result. Laboratory

Fig. 45. Size distribution of C. thomsoni. Ordinate, number of individuals; abscissa, length in mm. Diagonal ruling, males; stippling, females; clear, sex undetermined.

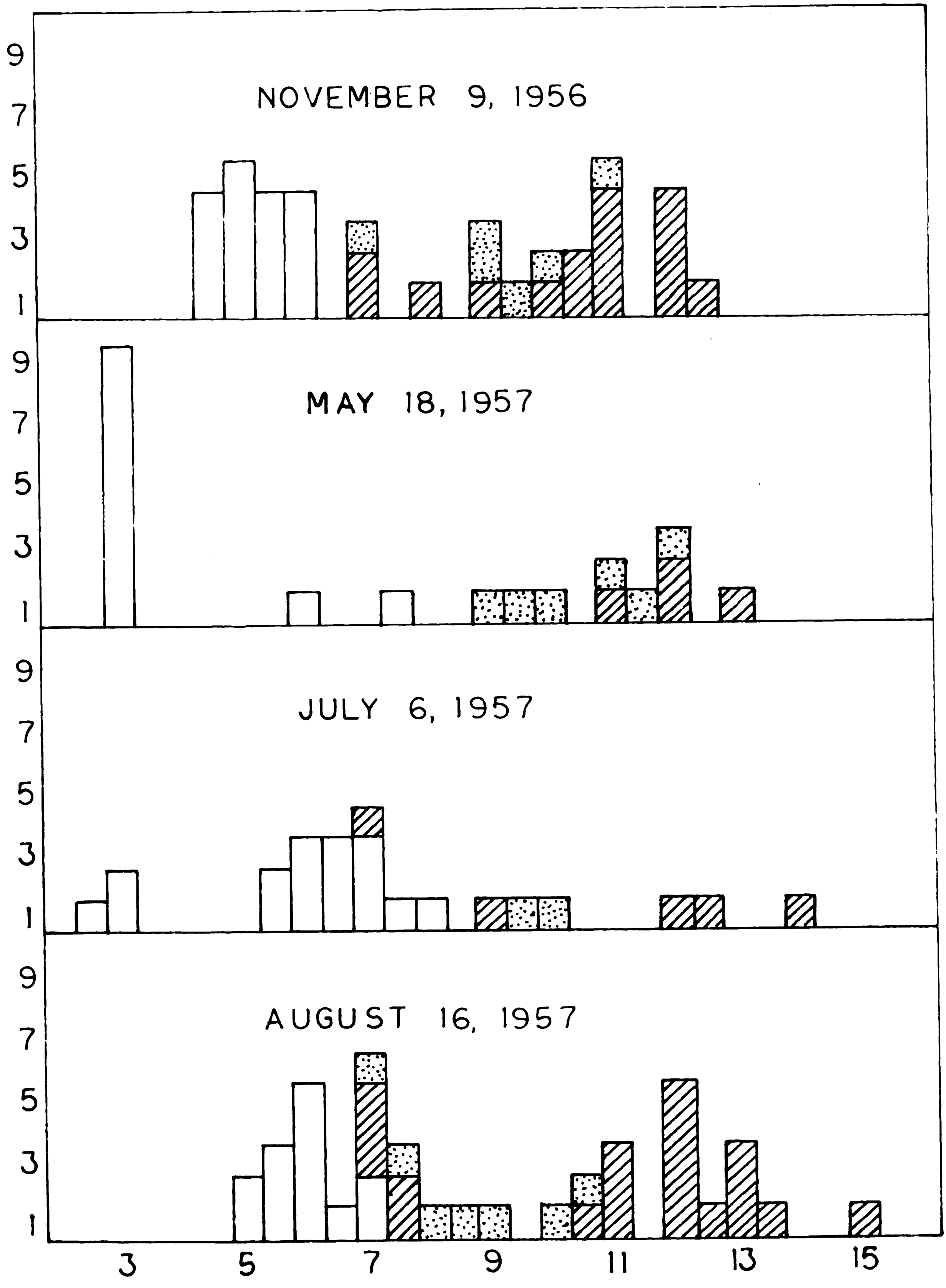

NOVEMBER 9, 1956
MAY 18, 1957
JULY 6, 1957
AUGUST 16, 1957
1
3
5
7
9
3
5
7
9
11
13
15

Fig. 45.

Fig. 46. Size distribution of Metaphreatoicus magistri collected on Bruny Island, Tasmania on February 19, 1957. Ordinate, number of individuals; abscissa, length in mm.

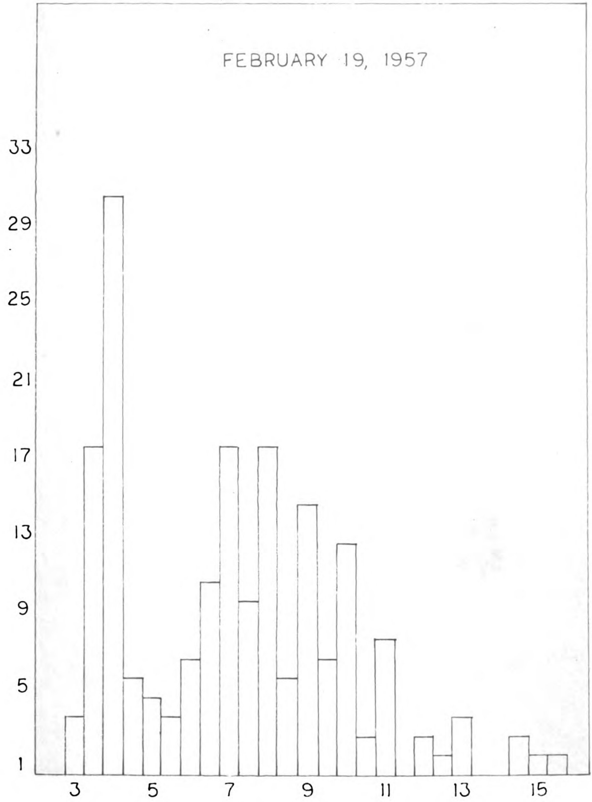


Fig. 46.

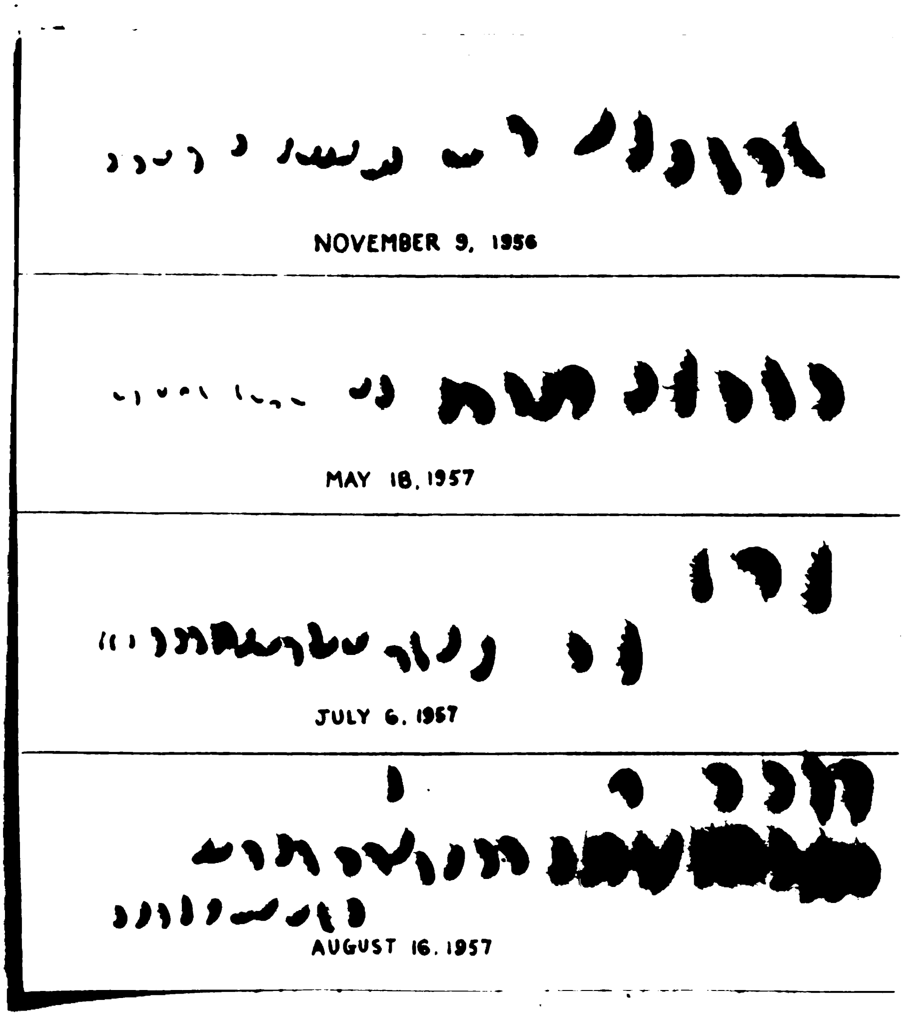


Fig. 47. Photograph of specimens used for size distribution in figure 45. x 5/7.

Table 1. Reproductive cycle of *C. thomsoni* on Mt. Wellington, Tasmania.

	3 Sep 1956	22 Sep 1956	6 Oct 1956	30 Oct 1956	9 Nov 1956	2 Jan 1957	14 Jan 1957	15 Feb 1957	6 Mar 1957	15 Apr 1957	18 May 1957	6 Jul 1957	16 Aug 1957
Breeding pairs collected	no	no	no	no	no	no	no	yes	yes	yes	yes	one pair	no
Gravid females collected	yes	yes	yes	yes	yes	no	yes	no	no	no	yes	yes	yes

Supplementary notes.

November 9, 1956. Three females with marsupia eventually molted and on Dec. 29, 1956 were bearing small oostegal plates which did not form marsupia.

January 14, 1957. Two females with young in marsupia were collected and kept alive. The next day the young, except two in one female, had left the marsupia.

February 15, 1957. Four pairs were kept alive in the laboratory. Three pairs were still present the next day, two pairs the following day and for two additional days. On Feb. 20 one pair was still together but later separated after the male had curled around the female. On Feb. 21, 1957 three of the pairs were paired again.

March 6, 1957. Specimens collected at this time were inactive in the dried-up pool bottom. When water was added to the paired specimens, as well as other specimens, they became active in less than a minute. One female had an empty marsupium.

May 18, 1957. Of paired specimens kept alive in the laboratory, two pair were still together on May 27, 1957, but the females of three pair which had separated had marsupia.

temperatures ranged from 42° F. to 92° F. while midday water temperatures in their native pool on Mt. Wellington were from 32°F. to 70° F.

Reproductive Cycle.

Table 1 contains data showing only one breeding cycle per year in *C. thomsoni*. Pairing begins in February and is a prolonged process which even the dormancy of a dry period did not stop. The fourth walking legs of the male are used to carry the female beneath him. Pairing may last three months. Following mating, eggs are laid about June and are carried for months until the miniature adults hatch and are released about December.

With such a long reproductive cycle, in which all members are at about the same stage, there can be only one large influx of small individuals into the population per year. Thus each major peak in the curve should be chiefly individuals released at the end of the yearly reproductive cycle. The sudden influx of the smallest size class at the end of the cycle is obviously from the most recent year, the next larger size class those from the previous year, and so on. Inspection of the data reveals at least three size classes. Thus it takes a minimum of three years for *C. thomsoni* to reach maturity. Mortality and slower growth of the larger sizes could obscure what is possibly a longer cycle of life. Barnard (1927) used a similar analysis of size classes of

collections of Mesamphisopus capensis in South Africa and found that member of the Amphisopidae took approximately two years to reach full size.

Paired specimens were first collected on February 15. Specimens were still collected in the paired condition as late as May 18, with one pair being found on July 6. Pairs brought into the laboratory would not always remain paired. Two pair brought in on May 18 were still paired nine days later. Females from other pairs brought in at the same time had separated from the males, completed their molt, and developed marsupia by May 27. Data in Table 1 indicates that copulation occurs in April or May.

Incubation.

The eggs are carried through the winter and well into the summer before they hatch. Many gravid females were collected on September 3. All of them died by October 9, probably from the high temperatures which occurred in the laboratory. Development of the eggs seemed to occur more rapidly than in the natural habitat. None were reared successfully. The few that did hatch died shortly after hatching. A considerable quantity of yellow material, presumably unabsorbed yolk, could be seen in the thoracic region of the young which are unpigmented when hatched.

As with other isopods, the young resemble the adults but have one fewer pair of legs and fewer antennal segments,

as well as lacking the brown marbling seen in the adults. Of two females with marsupia collected on January 14, one had an empty marsupium and the young from the other had nearly all left by the next day. Nearly all eggs develop successfully.

Ecdysis.

After the young escape, the subsequent molt of the female replaces the large oostegal plates forming the marsupium with small plates similar to those of the pre-reproductive period. The exuvia of the youngest specimens are shed in such a fragmented filmy condition that the parts are not distinguishable from the debris the isopods must be fed to maintain them. The larger specimens molt and leave an exuvium which is usually in two pieces. The break usually occurs behind the fourth thoracic segment. Specimens are seldom found exposed in their natural environment but are usually in the mud, under rocks, or in vegetation. However, numerous exuvia could be seen on the surface of some moss in which they were reasonably abundant. One was observed once kicking at its head with its uropods, until its molting was complete. Specimens are often found in which the anterior half is a lighter silvery-brown color due to the presence of the front half of the exuvium. It would be impossible to calculate the

number of molts from size classes as can be done for Tardigrades (Higgens, 1959) and Ostracod instars (Kesling, 1951) since the isopods' segmentation makes the measurement of length so variable.

Life Cycles of Related Species.

Limited data (fig. 46) indicates *Metaphreatoicus magistri* may have a life cycle similar to the closely related *C. thomsoni*. There was an absence of gravid females at the same time in each population and the graph of the population size classes shows peaks indicative of a three year life cycle. This occurs in a markedly warmer habitat with no freezing temperatures. Other species collected in other parts of Tasmania seemed to be at the same phase of their reproductive cycle as *C. thomsoni*. Barnard (1927) in his study of *Mesamphisopis capensis* made the only previous investigation of the general biology of a phreatoicid. There are several differences between the life cycle of *C. thomsoni* and the life cycle of *M. capensis* (Barnard) Nicholls, 1942.

Barnard interpreted his data as indicating the South African phreatoicid matures in less than two years. He also found that the mating, or pairing, began much later (in early May) but lasted even longer (about six months).

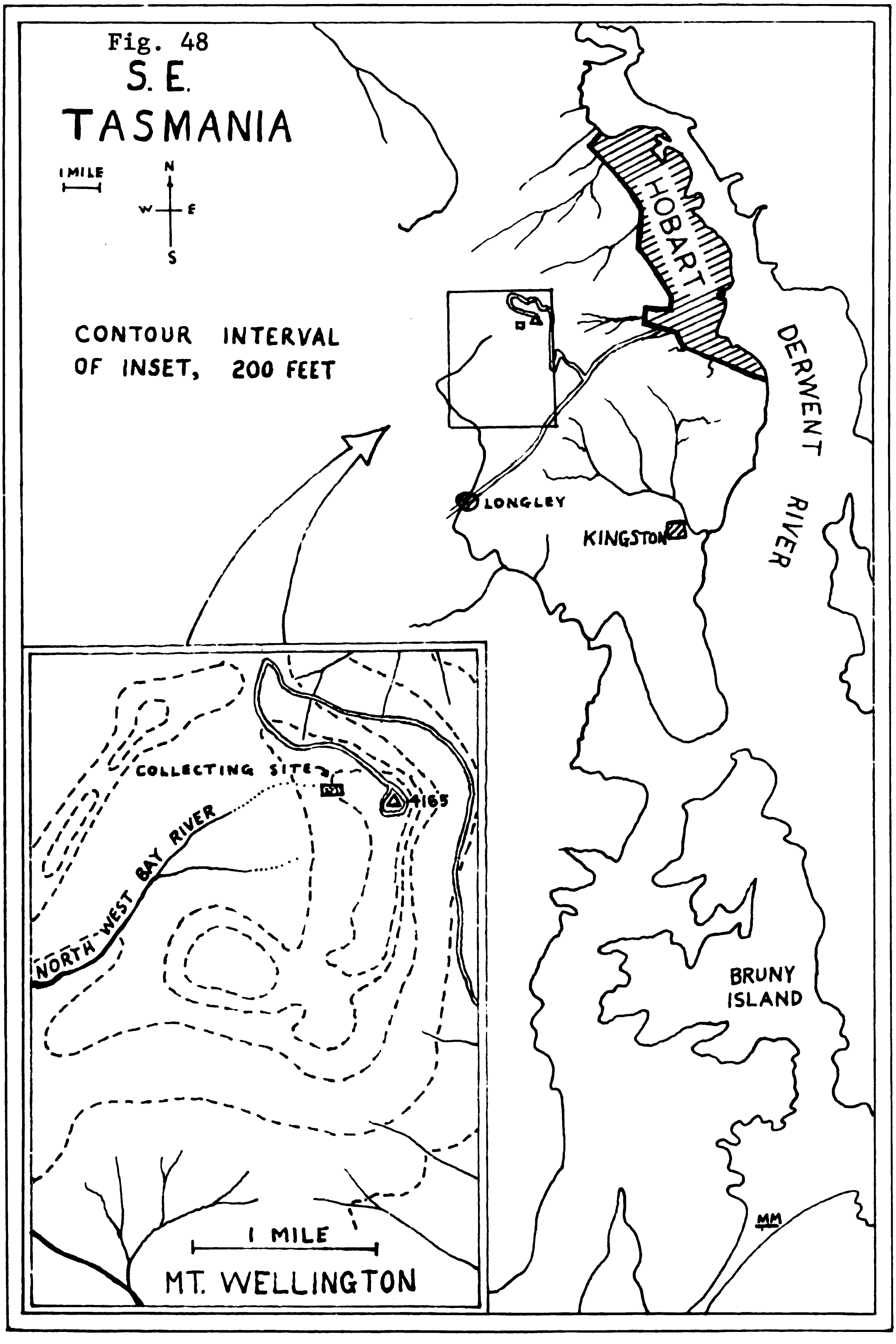
However, the eggs were deposited in the marsupium and hatched before two months had passed after pairing. Their release occurred in late December which is comparable to the time of release of *C. thomsoni*. They produce 7 - 15 eggs but usually fewer (5-12) reach maturity. Barnard concluded that the female produces only one brood on the basis of size data and the absence of females among the young and males shortly after hatching. He was not successful in rearing them under laboratory conditions for more than a month and frequently gravid females died before the eggs hatched.

Sex of specimens reported in figure 45 includes 45 males and 21 females with 57 too immature to sex.

General Ecology of C. thomsoni.

The pools on Mount Wellington in which *C. thomsoni* was taken were clear and shallow, mostly less than one foot in depth, and in only a few places wider than one could step across. The collecting site is indicated on the map of Mount Wellington (fig. 48). The water supply from rain and melting snows percolates down through the scanty vegetation and high-moor soil covering the dolerite peak. The flow of water is slow in most places due to the slight slope, rock obstructions, and the bolster plant (*Abrotenella Fosterioides*) which by its damming gradually

Fig. 48


S. E.
TASMANIA
1 MILE
N
W
E
S
CONTOUR INTERVAL OF INSET, 200 FEET
HOBART
DERWENT RIVER
LONGLEY
KINGSTON
BRUNY ISLAND
MM
COLLECTING SITE
4165
NORTH WEST BAY RIVER
1 MILE
MT. WELLINGTON

alters the flow pattern of the water (Martin, 1940). The rainfall is about fifty-five inches per year, with monthly means ranging from 3.36 inches in February to 6.04 inches in October. The temperature of the air at a location 1,600 feet below the collecting site has a mean maximum of 52.4° F. and a mean minimum of 39.6° F. For February, the means are 61.7 and 45.7, for October 52.2 and 38.0. July has the lowest means, 43.9° F. and 34.9° F. Thus with the seasons having a six months lag or advance in the Southern Hemisphere, the higher insolation of summer with a slightly lower rainfall and higher temperatures frequently causes the pools to dry up during January, February, or March. During 1957 the pools were nearly dry on January 2. On January 14 some pools were still present but there was no appreciable current left. By February 15 the situation was still similar. On March 6 they were dry with the mud still moist but not wet. The filled pool is shown in fig. 49 and the same area is shown in fig. 50 during a dry period. During the dry period the mud remained at least slightly moist although cracks appeared on the surface. Inactive specimens were found in the dry mud. Some were in small chambers not much larger than the individual. No structural material other than the mud could be found forming the wall of the chamber. The isopods

Fig. 49. Mount Wellington collecting site with pool full.

Fig. 50. Mount Wellington collecting site with dried pool bottom.

Fig. 50a. Mount Wellington collecting site showing dried pool bottom.

Fig. 50b. Mount Wellington collecting site as viewed from Battery Point, Hobart.

Table 2. Temperature of pool, Mt. Wellington and remarks about collection of _C. thomsoni_.

Date	Temperature of water, °F.	Remarks
Sept. 3, 1956	--	Sunny, snow on ground, phreatoicids found in moss, under cushion plant, under stones, etc.
Sept. 12, 1956	34°	None found. Some unmelted snow in pools.
Sept. 22, 1956	39°	Found in moss.
Oct. 6, 1956	42°	Mostly gravid females in cushion plant.
Oct. 17, 1956	44°	Males found in loose moss.
Oct. 30, 1956	45°	Gravid females in cushion plant and moss.
Nov. 9, 1956	56°	Gravid females mainly in moss. All others chiefly in mud.
Jan. 2, 1957	65°	Found in mud. Pool nearly dry.
Jan. 14, 1957	70°	No current left. Specimens found under rocks, with a few in moss and mud.
Feb. 15, 1957	54°	Many paired in moss.
Mar. 5, 1957	--	Pool dry, none collected.
Mar. 6, 1957	--	Dormant specimens found in damp mud and under cushion plant.
Apr. 15, 1957	44°	Some still paired under cushion plant. Others in mud.
May 4, 1957	42°	Large ones found in pool ten feet from summer low point.
May 18, 1957	40°	Paired specimens under cushion plant.
July 6, 1957	32°	Pool ice-covered. Few phreatoicids found.
Aug. 16, 1957	33°	Pool ice-covered. Fairly abundant in mud.

collected under these conditions were moist but exhibited no activity. When they were placed in water they became active within a minute and were not noticeably different in behavior than the ones collected in wetter circumstances.

By April 15 the water level was back to normal. The pools were usually ice-covered during July, August, and September. Data regarding temperature of the pool is in Table 2. Further information regarding rainfall variability is provided by Scott (1956). Davies (1958) discusses the surface geology of Mount Wellington. Martin (1940) treats the physical factors as well as the vegetation of Mount Wellington. Aquatic vegetation was of only two species. One, Drepanocladus sp. in some areas made extensive beds which frequently contained mature phreatoicids. The other, a tiny leaf liverwort, Jungermannia sp., occurred in much smaller patches which occasionally contained phreatoicids. The phreatoicids, apparently, were feeding on the periphyton. In the laboratory the Drepanocladus was left fairly much intact, although its periphyton was removed by the feeding phreatoicids. In the process of feeding on the liverwort, Jungermannia sp., leaves were usually separated from the stem. The bolster plant, Abrotenella Fosterioides grew in and at the edge of the pools with its base in the water. On the underside of clusters of them I have found paired adults and at other times gravid females. *Astelia alpina* made up most of the remaining vegetation of the edge not occupied by *A. Fosterioides*, but it was less in the water and I found no association between it and phreatoicids. In addition to the moss and vegetation there were other habitats for the phreatoicids. Sometimes an individual would be found crawling along the bottom. Often they could be found on the undersides of rocks. But most frequently they could be found in the soft organic mud which filled the lower spots where the current was slow. The mud was fine, black and almost flocculent. All sizes (but few gravid females) could be sifted from such mud on most occasions. Immature forms were rarely found in places other than the mud. Phreatoicids were seldom found in mud denser with inorganic particles. No leaf litter occurred on the pool bottoms. Many broad leafed plants occurred nearby but were of the evergreen type so the seasonal accumulation of leaf litter did not occur. This is probably a widespread condition in the Southern Hemisphere areas where the Myrtaceae is the most important woody plant family. Other species are commonly found among submerged vegetation and roots or under rocks. More unusual locations have been crayfish burrows (*Hypsimetopus intrusor*, Sayce, 1902); wooden reservoir pipe (*Colubotelson setiferus*, Nicholls, 1944); wells (Chilton, 1894); a hot, saline bore (*Phreatomerus latipes*, Chilton, 1922); subterranean burrows (*Phreatoicopsis terricola*, Spencer and Hall, 1896); and the stomach of trout (*Mesacanthotelson decipiens*, Nicholls, 1944). *Phreatomerus latipes* was taken swimming in the hot, saline bore, and to my knowledge is the only record of a swimming phreatoicid. *Colubotelson thomsoni* was never observed swimming under either field or laboratory conditions.

Animals associated with *C. thomsoni* were mostly of the type common to vernal ponds and small bodies of water throughout the world. However, there were perhaps fewer species and fewer individuals present. Those collected at the collecting site are listed in Table 3. There was a notable absence of larger predators. The red-spotted frog *Crinia tasmaniensis* of Mount Wellington has been found to have phreatoicids in its stomach during the breeding season by John Hickman (personal communication). Although I have found the frog and tadpoles in pools on Mount Wellington, I have never found it in the sample area. There were no mollusks in the pools. *Anaspides tasmaniae* is found in the deeper pools farther down the Northwest Bay River on Mount Wellington, but I have never collected them in the study area either, although the literature indicates they occurred there in other years.

Table 3. List of the taxa of invertebrates, other than *C. thomsoni*, having examples observed in the sample pool on Mt. Wellington, Tasmania.

Protozoa	
Peritrichida.	*Vorticella* sp.
Platyhelminthes	
Tricladida.	Planariidae.
Anellida	
Oligochaeta.	
Plesiopora.	Naididae. *Pristina* sp.
Prosopora.	Lumbriculidae.
Arthropoda	
Crustacea	
Cladocera.	
Copepoda.	*Cyclops albicans* Smith.
Ostracoda.	Cypridae.
Amhpipoda.	*Neoniphargus montanus* (Thompson).
Insects	
Collembola.	Hypogastrura?
Trichoptera.	Limnephilidae.
Coleoptera.	Helodidae. Dysticidae (two species).
Diptera.	Tendipedidae. Tipulidae?
Arachnida	
Acarina.	Hydrachnellae.

A. tasmaniae and *C. thomsoni* would seldom be in direct competition if both were present due to different feeding preferences. The amphipod *Neoniphargus montanus* (Thompson) occurs abundantly in the pools. *N. montanus* is much smaller than *C. thomsoni* and more active, spending much of its time in the open. In contrast to *C. thomsoni* which is a dull brown-black, the color of the mud, the amphipod is yellowish-orange. A small ostracod with bluish-green valves is common on the surface of the mud. A copepod was frequently found in the moss. A light red mite with dark markings was found in the pool during the summer. Adult and immature dytiscid beetles were common. Only one large (over ½ inch) adult dytiscid was found. When it was placed in the tank with a phreatoicid the phreatoicid was found dead the next day with many of the dorsal tergites missing. Small adult dytiscids (less than ¼ inch) were common. On one occasion one was observed to bump the posterior of a small phreatoicid just at the surface of the mud. The phreatoicid spurted forward as if he had been stung. Trichoptera larvae were sometimes present. Tendipedid larvae were abundant. A long red oligochaete was very abundant in the more compact bottom sediments which seldom contained phreatoicids. The flocculent, phreatoicid containing sediments also had two species of colorless small oligochaetes. A planarian, Dugesia sp., was abundant until summer. It was grey-black with round auricular sense organs and the pair of eyespots were posterior to the area between the auricles of the triangular head. The phreatoicids and the large red oligochaete were the dominant animals in the pool. Each appeared to prefer a different type of bottom sediment. The planarian and the amphipod were at times abundant in the area above the bottom mud. One interesting point regarding the isopods, amphipods, and ostracods of the pool was that they were never observed to swim in either field or laboratory, but always crawled or burrowed. Thus the only forms observed swimming were the adult dytiscids and the few copepods. Vorticella sp. was sometimes very abundant as epizooites on specimens maintained in the laboratory. Occasionally laboratory specimens would develop a dense growth of Saprolegnia sp. around them within a day of death. The rapid growth of the mold made it appear that the mold was established before death and perhaps caused death. Dead specimens, not removed immediately from aquaria, were often filled with many Euglena sp., Colpoda? sp., and bacteria. Specimens of C. thomsoni put in an enamel tray for sorting from debris would usually remain motionless and curled for some time. In fact, curling seemed a more frequent response to disturbance than escape movements.

Isopods, in closed vials of water, increased the frequency and magnitude of pleopodal beating in the early stages of asphyxiation. When *C. thomsoni* and *N. montanus* were placed in the same vial the amphipods would succumb before the isopods. The isopods could be revived more readily than the amphipods when placed in open containers with little water.

There was an incomplete correlation between pools which appeared suitable for phreatoicids, and the presence of phreatoicids. Incomplete observations indicate that pools containing isppods may have been pools with greater resistance to drying during drought periods.

NATURAL HISTORY OF ASELLUS COMMUNIS

Size Distribution.

Collections of *A. communis* were of one size class, two size classes, or a wide range of sizes. The smallest sizes were collected in May and August, larger sizes were present in all collections (Table 4). The adults of the spring population were easily distinguishable from the juveniles of the spring population by a minimum size difference of 3 mm. Most young were added to the population in early May. The young of the spring were the major part of the late June population; adults were then very rare. More juveniles were added to the population in August.

Pairing and Egg Deposition.

Pairing of adults was relatively short and probably was of less than a month's duration. A large number of breeding pairs were found in the spring (the juveniles of the May collection were the progeny resulting from that breeding period).

Laboratory observations confirmed the speed of their reproductive process. Paired specimens were seldom together long after being brought into the laboratory. They soon separated and the females molted to produce a marsupium which they filled with eggs.

Following are observations made on April 2, 1958. A pair was isolated at 3 p.m. The male was considerably larger than the female and held her with his fourth periopods between her third and fourth periopods on the thorax. During more than half an hour of observation at 15X magnification with a binocular microscope, he attempted to, and perhaps did, fertilize her from each side by arching his body in the posterior thoracic region and bending his posterior around to her side. His first and second pleopods would often quiver violently and move back and forth rapidly but no transfer of material could be seen. This was repeated several times, usually first on one side and then the other in rather quick succession and then a longer rest afterward. At times he would bend his head down sharply over and in front of her. At least once, he was observed holding the base of an antennae of hers with his gnathopod. The antennal base seemed to fit between the two palmar processes. At times she would vibrate up and down beneath him. At least some of the time, he was causing the vibration with his fourth periopod. That was apparent because there was some slack in his grip with greater movement of his periopod than her body. He moved very little at the time. I thought that he was being unsuccessful and would keep trying *ad infinitum*

Table 4. Size distribution of *A. communis* in collections from Baker Woodlot pool.

Length in millimeters.	Apr 25	May 2	May 9	May 30	Jun 6	Jun 14	Jun 20	Jun 27	Jul 4	Jul 11	Jul 25	Aug 1	Aug 8	Aug 15	Aug 22	Aug 29	1959 Oct 18	Nov 6	1960 Apr 16	May 25
																				+
13																				+
12																				
				+															+	
11																			+	
10			+ ●									+								●●
												+								●
9	+			●●●●		●		●											●	●●●
				●									+				+	+	●●	●
8			●●	●	●●	●						●	●			+++	+		●●●●	●
	●	●●●●	●●											+			+			
7		+●●	++●		●						●	+++ ●	●	+	+	+	++●●	●●	●	
	+	++●	●							++		+		+	+++ +++ ●●	++	+ ●● ●●			
6		+1	++●									++	+	++++ +++	+++ ++++ ●●	+++ +++ 1 ●●	1●●	1 ●	●	
	+++	+1●	++●						+	4		++	+	●	++ +++ ●	+ ++ ●	+●●●		●	
5	●●●	+1					2	+++	+2	+2	1		2	+ ++ 1 ●●	+++ ●●● +++5 ●●	++ ●●● ++ ●●●	3●●	1		
		1				5	6	+4	1	5			1	+4	8 ●● ●●	3●	3			
4	●					11	5	+7●	6		2		1	3	3	4				
				1	4	9	4	6	4	3	2		1	2	1					
3				3	4	16	5	4	4	2	2			1	4	2			2	
				4	1	11	1	3	5				1		4	3				
2				8	11	3										2				3
				2	1											1				2
			117	1																

Plain numbers = sex undetermined; + = male; ● = female.

so I stopped observing. Seven hours later they were separated. The anterior part of an exuvium was present and presumably belonged to the female for the male did not appear to be changed. Her brood pouch was already full of eggs, none were seen on the bottom of the dish. She still possessed both antennae and uropods.

Specimens are frequently found with an antenna or a uropod missing. Loss of an antenna could easily result from mating. Eggs are frequently dropped from the marsupia of specimens being reared in the laboratory. A female with an empty marsupium was isolated. Seven hours later the marsupium was full but the lamellae of it were ruffled to one side although no opening was visible. On the bottom of the finger bowl were 36 to 40 eggs. The eggs in the marsupium seemed tightly packed in.

Incubation and Growth.

Observations on the incubation period were in fair agreement with Ellis (1961). He found *A. militaris* (i.e., *A. communis*) had an incubation period of 10 or 11 days and *A. intermedius* 12 or more days, depending on temperature. I found *A. communis* had completed incubation in 15 days at room temperature and one day later had no marsupium, i.e., the largest oostegal plates were replaced with small ones by a post-incubatory molt. Table 4 indicates the wild population grows to parental size in approximately three months during the period of May to August. The pool was dry during September and the larger sizes seemed to survive this period best. I do not interpret my data to indicate a growth during this period as suggested by Kenk (1949). On September 5th I was able to find seven gravid females in moist depressions in the dry pond. The females became active when placed in water. Along with them were four tiny specimens about one millimeter long which were the same size as others in the brood pouches. On September 19, 1959 one came out of a sample of dirt to which water was added.

A female collected through the ice early in winter was placed in a jar in the refrigerator with several other isopods. Although inadequately fed to produce normal yolk filled eggs, she had a marsupium at the time in the spring when they were most common in the natural population.

Specimens maintained in the laboratory had variable growth rates depending on the amount of food supplied. Thus specimens with little food exhibited little or no growth but resumed rapid growth with adequate food. Thus it would seem that the slow growth reported by Johansen (1920) was the result of an inadequate food supply.

Number of Broods.

Examination of the size distribution in Table 4 indicates that only one brood was produced in the spring breeding season since the period when the shortest size was collected in was of such short duration with no recurrence of that size until August. Apparently the August broods came predominantly from the young of the year as indicated by the declining size of gravid females in the fall (Table 5) and the sparsity of large size females in July collections (Table 5). But examination of the results in Table 5 indicates that females may produce a second brood since the majority of larger females in the June-July period were gravid. Their numbers were small and of minor importance in the population. These observations agree with Allee (1912b) on number of broods, but the size distribution indicates it is doubtful that any adults from the spring survived to the following year as he stated they may. Paris and Pitelka (1962) found a somewhat similar pattern of brood production in the terrestrial isopod, Armadillidium vulgare.

Table 5. Data of collections containing *A. communis* females over 6½ mm. long.

	Apr 25 1959	May 2 59	May 9 59	May 30 59	Jun 6 59	Jun 14 59	Jun 27 59	Jul 25 59	Aug 1 59	Aug 8 59	Aug 22 59	Sep 5 59	Oct 18 59	Nov 6 59	Apr 16 60	May 25 60
Number of females over 6½ mm. long	1	8	7	6	3	2	1	1	2	2	2	4	6	2	8	8
Number of gravid females over 6½ mm.	0	4	6	5	3	1	1	1	0*	2	1*	4	0	0	0	2
% of females over 6½ mm. that were gravid	0	50	86	83	100	50	100	100	0	100	50	100	0	0	0	25
Size range (in mm.) of gravid females	-	7-9	7-10	8-9	7-8	8	9	7	-	7-8	6½	6-7	-	-	-	9½-10
Total number of specimens in the collection	10	19	133	26	24	57	31	8	12	11	64	11	27	6	14	15

* this collection contained one with an empty marsupium not included in the number recorded.

Brood Size.

Ellis (1961) found that brood size was proportional to length of parent in *A. intermedius*. Hatchett (1947) made similar observations on *A. communis*. Two selected *A. communis* with apparently undisturbed, full marsupia had brood sizes that were within the size ranges they found in *A. intermedius* and *A. communis*. One 9 mm. long had 168 embryos, one 7½ mm. long had 95 eggs. Ellis (1961) found gravid females from less than 5 mm. to almost 13 mm. in length. The size range of gravid females for *A. communis* has less variability in my data (see Table 5). The range is from 6 mm. to 10 mm. In the spring the length is nearer the median value, whereas in the fall they were mostly 6½ or 7 mm. long. Hatchett (1947) found that brood size ranged from 53 to 235 in females varying from 7 to 11½ mm. long. Within the same brood all eggs, or embryos, were very close to the same stage of development. Non-developing eggs were never observed in marsupia. I suspect that under natural conditions a very high proportion of eggs retained in the marsupia hatch.

Sex Ratio.

Sex of specimens determined from 13 months collecting beginning April 25, 1959 included 113 males and 107 females with 388 immatures.

General Ecology of *A. communis*.

The vernal pond from which the specimens of *A. communis* used in this study were taken had maximum dimensions of over 100 feet by over 60 feet in the spring when its greatest depth was over three feet due to flooding by melting snow and heavy spring rains. This size was not maintained long and a more natural level appeared to about two feet of depth which gave dimensions of about 60 feet by about 40 feet (The area in zones B and C of fig. 51). Following foliation of the trees and the resulting transpiration the level dropped rapidly until the depth was approximately one foot, except for occasional partial refilling by heavy rains. The last foot of water was quite persistent until prolonged hot dry periods came and the water disappeared. In the year of 1959 the pool became dry in mid-July for a short period and again during September and early October.

As Allee (1912b) stated, specimens can be found in the mud during droughts. Specimens which I found during such periods were in depressions filled with leaves and mud. They were inactive but became active shortly after water was added to the container in which they were placed. The specimens thus recovered on September 5, 1959 were all gravid females. Litter and mud from the same depression also harbored many *Chaoborus* sp. larvae, many aquatic oligochaetes, and some tendipedid larvae which became active when water was added.

From December 1959 to April 1960 the pond was ice-covered. During this period the water developed a discoloration and foul smell. The few live asellids collected then were in a rather sluggish condition. On the thirty-first of January, 1960, there were about three inches of snow cover. There were three inches of surface ice over about five inches of water which covered a second layer of ice similar to the condition Kenk (1949) encountered in his Pond I.

Temperatures encountered in the pond are recorded in Table 6. Average monthly temperatures and precipitation recorded in Table 6 are from stations located a few miles from the collecting site in Baker Woodlot. The pond was shaded most of the day by the canopy provided by trees which are predominantly American elm, swamp white oak, black ash, and silver maple. These also contributed the majority of the leaf litter along with a strong admixture of beech and maple leaves from the trees on higher ground around. No rooted aquatic plants occurred in the pond. A slight algal growth consisted principally of <u>Spirogyra</u> spp. The central, more persistent portion of the pond (Zone C, fig. 51) had no herbaceous vegetation when the pond was dry. In addition to the small trees which are indicated on

Table 6. Temperature of Baker Woodlot pond and temperature and precipitation records taken at the Horticulture Farm, East Lansing (Hort. Farm records reported in the U. S. Dept. of Commerce annual summary of climatological data for Mich.).

1959 Month	Day	East Lansing Horticulture Farm Inches of Precip.	Evap.	Aver. Temp. °F. Air	Water in pan Max.	Min.	Baker Woodlot Pond °F.
Jan		1.95		18.6			
Feb		1.76		22.7			
Mar		1.83		32.6			
Apr		4.24	4.09	47.8	61.5	39.0	
May		2.74	6.31	62.7	78.2	54.4	
	2						72
	9						66
	30						70
Jun		2.16	8.16	69.0	85.9	60.9	
	6						70
	14						60
	20						67
	27						76
Jul		5.59		71.4	88.4	62.7	
	4						73
	11						65
	18						(dry)
	25						68
Aug		4.54	5.87	74.7	89.7	67.3	
	1						67
	8						68
	15						76
	22						77
	29						77
Sep		2.76	4.93	65.7	79.9	56.2	
	5						(dry)
Oct		5.10	2.28	50.3	59.2	43.2	
	3						(dry)
	18						47
Nov		2.72		34.9			
	6						41
Dec		1.88		32.6			

the map there were a few grape vines and small oak seedlings. Zone B supported a sparse growth of seedlings, moss, and dandelions after the water receded. Zone A, which was inundated for only a short time in the spring, had a luxuriant growth of grasses and herbs as well as much poison ivy. The litter in the pond, which provided the cover for A. communis, came principally from the elm, oak, ash, and maple canopy of the pond.

Rotting leaves from the pool were used as a source of food for asellids kept in the laboratory. Maple leaves were utilized rapidly and oak leaves only slightly. Gibbons (1960) reported that aerial spraying of DDT reduced the population of insects that he was studying in Baker Woodlot. DDT may partially have caused the changes that have occurred since field work for this study was done. Isopods have been harder to find and algae more abundant during recent checks on the pond. Since this is not a quantitative study this cannot be verified. An ecological study was done in the area by Wacasey (1961). His study of salamanders from rather similar nearby ponds which also contained asellids revealed no Asellus spp. among the food items used by either Ambystoma maculatum or Ambystoma jeffersonianum. Vertebrates were rarely observed in the pond in which the asellids of this study were collected,

Fig. 51. Map of vernal pond at edge of Baker Woodlot.

⬚	Bottom depth below surface, 0 to 1 foot when pond is full (Zone A).
░	Bottom depth below surface, 1 to 2 feet when pond is full (Zone B).
▒	Bottom depth below surface, 2 to 3 feet when pond is full (Zone C).
+–+–+–+→	Fence.
A	American elm.
B	Black ash
C	Swamp oak.
D	Silver maple.
E	<u>Carya</u> sp.
F	Dead oak.
'	2 to 6 inches in diameter.
"	6 to 12 inches in diameter.
'''	12 or more inches in diameter.

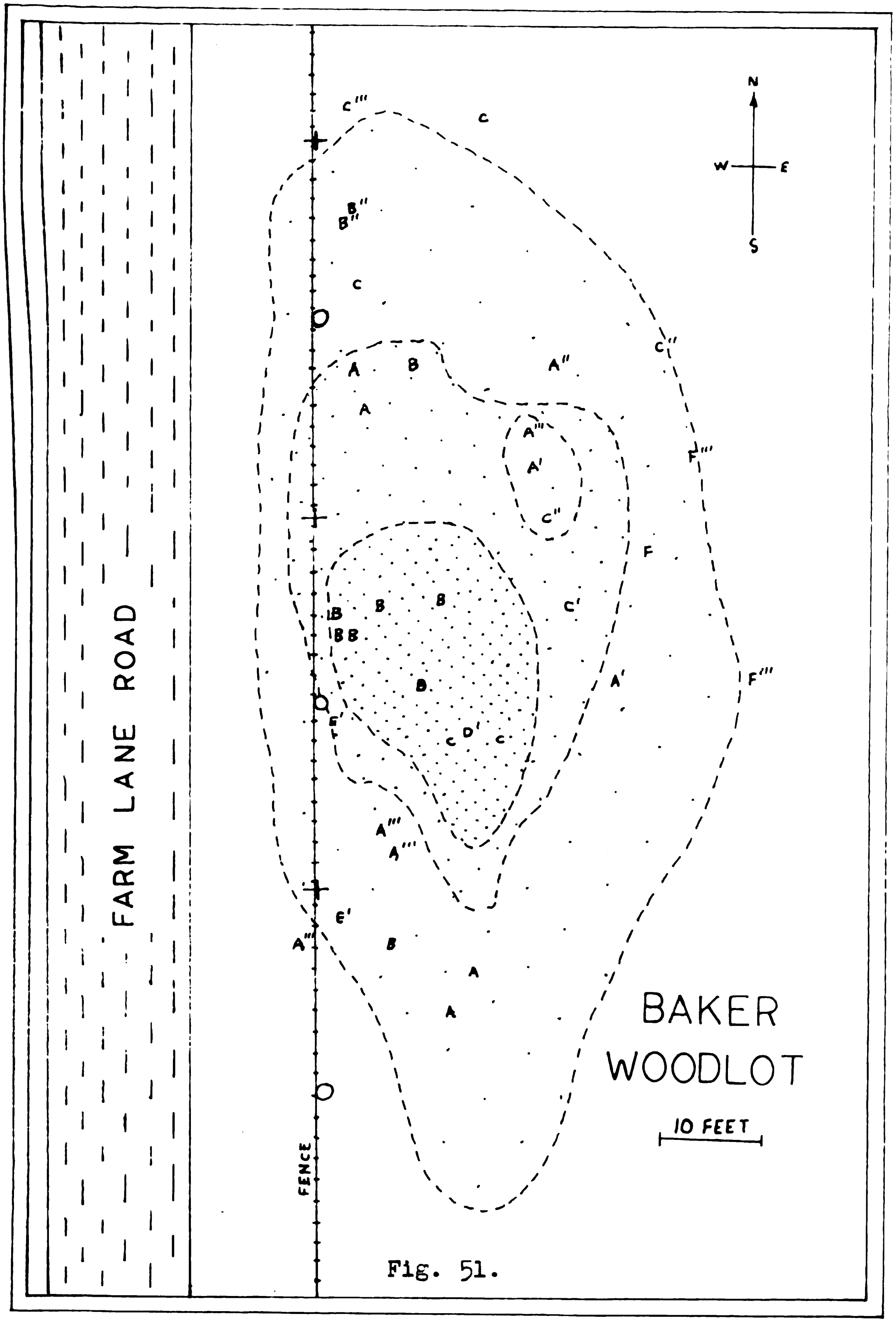

FARM LANE ROAD
FENCE
N
W
E
S
BAKER
WOODLOT
10 FEET
C'''
C
B''
B''
C
A
B
A''
C''
A
A'''
A'
F'''
C''
F
B
B
B
B
B B
C'
B
A'
F'''
E'
C
D'
C
A'''
A'''
E'
A'''
B
A
A

Fig. 51.

only the leopard frog and the green frog and many unidentified tadpoles were observed. The invertebrates found in the pond are listed in Table 7. The planarians were very abundant (usually many specimens in a sample) in the spring but disappeared in the summer. Daphnia sp. was very abundant in the spring as well as smaller copepods and ostracods. A member of the lumbriculidae was usually very abundant among the litter and bottom mud. Lymnaea sp. was abundant on the surface until later in the year. Immature aquatic insects were usually present but the adults were most prominent in the springtime. Water mites, leeches, hydras, and rotifers were sometimes very abundant. Large predaceous aquatic insects were present but were never observed preying upon asellids. Allee (1929) has stated that dytiscids and crayfish feed on asellids. Dytiscids were abundant (i.e., present in most samples) in the springtime as adults although larvae never became very abundant. A larval dytiscid was placed in a finger bowl of water with a male asellid on April 13, 1958; on April 14, only the dytiscid remained. Only one small crayfish was observed in the pond. A possible instance of cannibalism was noted as follows. The male and female which had been observed during the fertilization process were left in the same finger bowl. Since the ages of the female's

Table 7. List of taxa represented in the observed biota of Baker Woodlot roadside pond, **other than *A. communis*.**

Chlorophyta
Siphonales. *Vaucheria* sp.
Zygnematales. *Zygnema* sp. and *Spirogyra* spp.
Protozoa
Testacida. *Arcella discoides* E. and *Difflugia oblonga* E.
Peritrichida. *Zoothamnium* sp.
Coelenterata
Hydrozoa. *Hydra* sp.
Platyhelminthes
Rhabdocoelida. *Dalyellia* sp.
Tricladida. *Planariidae.*
Rotifera. *Sinantherina* sp.
Annelida
Oligochaeta
Plesiopora. *Aeolosoma variegatum* Vejd.
Prosopora. *Lumbriculidae.*
Hirudinea
Rhynchobdellida. *Helobdella stagnalis* L.
Arthropoda
Crustacea
Cladocera. *Daphnia longispina* (O.F.M.)
Copepoda. *Cyclops?*
Ostracoda. *Cypridae.*
Conchostraca.
Decapoda. Cambarinae.
Insecta
Odonata. Lestidae.
Hemiptera. Corixidae and Gerridae.
Megaloptera. *Chauliodes* sp.
Coleoptera.
Hydrophilidae. *Berosus* sp.
Dytiscidae. *Coptotomus* sp., *Bidessus* sp., *Laccophilus* sp., and *Hydroporus?*
Diptera.
Culicidae. *Culex tarsalis?*, *Anopheles* sp., and *Chaoborus* sp.
Tendipedidae, Tendipedinae.
Arachnida
Acarina.
Hydrachnellae. *Limnochares* sp. and others.
Mollusca
Gastropoda
Pulmonata. *Lymnaea* sp. and *Aplexa hypnorum* (L.).
Chordata
Amphibia
Anura. *Rana clamitans* Latreille and *R. pipiens pipiens* Schreber.

eggs were known they were being removed at intervals and preserved for later study. But six days after fertilization the female was gone, two pleopods were floating on the surface, and a few exoskeleton parts were on the bottom. Presumably the male ate her since the exoskeleton normally remains intact on dead specimens.

Although asellids were an important invertebrate group in the study pond, they never reached the concentration reported in Ellis (1961) or Allee (1929). Ellis found them as numerous as 15,600 per sq. foot based on a 9 sq. inch sample area. In a larger sample area (exact size not determined) I found a maximum of 133 individuals.

TAXONOMICAL DISCUSSION

Colubotelson thomsoni Nicholls, 1944, is morphologically distinct and allopatric with related species. The species of the genera *Colubotelson* and *Metaphreatoicus* form a closely related complex in the sub-family Paraphreatoicinae. Nicholls (1944) uses only the morphology of the tailpiece to separate the two genera. He states that *C. thomsoni* "closely resembles *C. joyneri*, but in the condition of the tailpiece seems intermediate between that species and *M. magistri*." The limited generic descriptions he has provided are insufficient to determine the genus of *C. thomsoni* which has intermediate generic characteristics. The specimens, described as *C. thomsoni* in this thesis, fit the species description of *C. thomsoni* and are from the type locality of *C. thomsoni*. The latter two facts indicate the identification is correct although the generic descriptions of *Colubotelson* and *Metaphreatoicus* need improvement. Since the species of the two genera almost form a continuum, with respect to the distinguishing features of the genera, it is unlikely that a satisfactory generic description can be written to differentiate between those close to each other but separated by the generic boundary.

Asellus communis Say, 1818 is a somewhat plastic species that is widely distributed in the United States and Canada. The specimens in this study are probably similar to those referred to as *A. militaris* by Ellis (1961), Kenk (1949), and others. *A. militaris* was described by Hay (1878). Later he (Hay, 1882) referred to it as *A. communis* with the following statement:

> "I am now pretty well convinced that the form that I described as cited above is the same as the Eastern species. It differs certainly from the Eastern specimens in the armature of the hand, in the form of the genital plates, in size, and in some other respects; but I do not believe that these characters are sufficiently marked and constant to enable us to found species on them."

Since then both major monographs on the Isopoda of the United States (Richardson, 1905; Van Name, 1936) have treated it as a synonym of *A. communis*.

C. thomsoni is in the isopod sub-order, Phreatoicoidea. *A. communis* is in the isopod sub-order, Asellota. The relationship to some other crustacean taxa is shown in fig. 52.

	Bopyroidea	Oniscoidea	Asellota	Phreatoicoidea	Valvifera	Flabellifera
Only one distinct abdominal segment			X		X	
Male opening on first abdominal segment					X	
Body not greatly flattened				X	X	
Uropoda styliform	X	X	X	X		
Uropoda terminal	X	X	X			
Uropoda flattened and hinged to side of telson					X	X
Pleopoda fitted for air breathing		X				
Mostly parasitic	X					

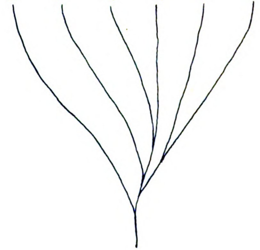


Fig. 52. Diagram of Isopod Relationships. Modified after Richardson (1904), Hale (1929), and Nicholls (1943).

DISCUSSION

Anatomical Comparison.

An understanding of some principles underlying anatomy is desirable before embarking on a comparison of the anatomy of these two related animals. The structure, or anatomy, of an organism is the expression of its genotype under the influence of its environment. Even identical genotypes may result in different forms under different conditions as the cyclomorphosis in the helmet shapes of cladocerans illustrates. Thus with acknowledged differences in the environment of the two species of isopods under comparison, it would be pointless to repeatedly contrast the many minor variations that might occur.

Each species comes from a different distinct group with many other species. One of the groups is proven ancient by the fossil record. Similarities could indicate similar selective processes have resulted in the retention (parallel evolution) or development (convergent evolution) of similar structure. That the retention of the similarities, rather than the development of them, has occurred is indicated by the little change in phreatoicids since Triassic times. Thus general similarities are useful indicators of the parts of the organisms that have been subject to similar selective pressures of a relatively unchanged type. Such pressures would be capable of preserving genetic configurations derived from their common ancestor, whoever it may have been. Conversely, differences of a major nature probably indicate the long term operation of different environmental pressures. Environment may include the internal environment of the organism.

Form is related to function. This statement is documented in a general sort of way by Thompson (1961) and will be further demonstrated in this study.

Gross Anatomy

Table 8 is provided for easy comparison of some features of *A. communis* and *C. thomsoni*. The gross aspect of phreatoicid and asellid is markedly different due to the dorso-ventral flattening in the asellids contrasting to the somewhat lateral compression of the phreatoicid (Chilton, 1894). The lateral compression of phreatoicids is an amphipod-like characteristic that caused confusion in the first concepts of their phylogeny. The different direction of flattening is a consistent external difference although it is not accompanied by much internal difference. The difference in the direction of flattening is primarily due to a change in the position, or rather angle, of the pleura. The rotation of the asellid pleura to a more horizontal position may be an expression of the influence of the habitat in the following respect. The leaf litter of asellid habitats studied consists partially of flattened leaves which give a lamellar structure to part of the substrate of temperate woodland pools during the greater portion of the year. Thus the flattened asellid would have his legs pressed against the solid portion of the substrate as he made his way among them motivated by his negative phototaxis or search for food. The phreatoicid with his shape and habit of curling up isopod-style would have a difficult time keeping his legs in solid contact with the substrate for efficient locomotion. Conversely, the more equidimensional cross-section of the phreatoicid would have a generally greater efficiency for movement in random or fasicularly arranged branches of moss, etc. or the amorphous flocculent detritus it commonly inhabits.

The thicker exoskeleton of the slow-moving phreatoicid would offer greater protection needed with its habit of curling up when disturbed. The reduced protection provided by the thinner exoskeleton of the asellid may have hastened the selection of the speedier asellids. The

Table 8. Tabular comparison of *C. thomsoni* and *A. communis*, differences.

	C. thomsoni	*A. communis*
longest male	15 mm.	13½ mm.
longest female	12 mm.	10 mm.
smallest individual	2½ mm.	1 mm.
orientation of pleura	extend ventrally	extend laterally
head width	equals rest of body	narrowest body region
head appendages	-------------grossly similar----------------	
ocelli per eye	20 (approx.)	12 (approx.)
thoracic appendages	-------------grossly similar----------------	
palm of male gnathopod	9 denticulate spines	2 or 3 processes
pleon segments	separate	fused
1st and 2nd pleopods	size similar to 3rd, 4th and 5th	smallest pleopods (one pair missing in female)
exopodite of 3rd pleopod	similar to others	modified as a protective cover
uropods	stout, short, and locomotory	slender, long, and sensory
typhlosole	present	absent
hepato-pancreatic glands	3 pair	2 pair
thickness of exoskeleton	16 microns	8 microns

Table 8 (continued).

	C. thomsoni	*A. communis*
diameter of egg	750 microns	350 microns
dorsal appendage of embryo	3 flat lobes, prominent	variable bulge within egg membranes
number of embryos (max. noted)	17	168
incubation period	one-half year	approx. two weeks
age at sexual maturity (approx.)	two years (minimum)	three months (minimum)

reverse could as well be true, increased speed may have reduced selective pressure for a thick exoskeleton.

The shape of *A. communis*, narrow anterior and wider posterior with antennae-like uropods, may aid the isopod in escape from enemies which may have mistaken front for back.

Appendages

Extremely close correspondence is shown in the appendages. Some modifications have occurred but the similarities are even more remarkable. There is even a great similarity in their setation. Most impressive are the existence of similar specialized setae, e.g., on the antennule are olfactory setae (figs. 2 and 3), the lateral lobes of the second maxilla have pectinate setae which bear their teeth and curve in the same direction, the maxillipeds (Chilton, 1894) have stout coupling spines (figs. 12 and 13). In addition, general chaetotaxy is remarkably similar (compare figure 22 with figure 24).

Some divergence is shown in the following aspects of the appendages. *A. communis* has large processes instead of spines on the palmar surface of the propod of the gnathopod (the general similarity of gnathopod was noted by Chilton, 1894). The gnathopods of female asellids are much less chelate. The first two pair of pleopods are greatly reduced in *A. communis*, while the third pair has the exopodite modified as a protective cover. The uropods of *A. communis* are less robust, more movable, proportionally longer, and are attached caudally rather than lateroventrally as in *C. thomsoni*.

The difference in the gnathopod is difficult to explain. The processes on the gnathopod of the asellid male provide a grasping mechanism for holding the female's antennae during coitus. The phreatoicids have their palm well supplied with spines in both male and female. Since the *A. communis* females have nearly lost the chelate condition of the gnathopod, perhaps the chelate condition of the gnathopod is primarily of sexual importance and of little value for feeding or locomotion.

Chilton (1894) noted the pleon in the Asellidae was small, flattened, and usually of only one segment in contrast to large segmented pleon of a phreatoicid.

The condition of the abdominal appendages is probably related to the flattened aspect taken on by *A. communis* as is the absence of segmentation for most of the pleon. First, the flattening reduced the protection provided for the delicate pleopods by the downward projecting abdominal pleura of the phreatoicids (see fig. 35). The development of the protective function of the third pleopod allowed the second pleopod of the male to remain free to continue its reproductive function. Reduced size of the two pair of exposed pleopods probably had selective advantage for preventing serious injury to them. Flattening caused reduced structural strength of the sort needed for rapid flexing and extension of the pleon. Without the ability to flex in this manner the locomotory function of the abdomen is minimized and associated locomotory structures are no longer under selective pressure to maintain their locomotor efficiency. Thus the uropods of asellids have retained and probably improved their sensory function at least as far as mobility and coverage is concerned since they no longer need the strength demanded of a structure bearing the load of an amphipod-like kick. This has allowed development of their slender uropods. The loss of unneeded segmentation would be rapidly selected for if the chance of injury to intersegmental regions is as great as the infolded non-sclerotized membranes would indicate.

The brood pouch and coxal lobe of the maxilliped of ovigerous females are similar. This was reported by Barnard (1927) and Sheppard (1927).

Developmental Stages

The dorsal appendage represents an extremely interesting cenogenetic characteristic. In the phreatoicoidea it is not much more than a yolk filled bulge on the dorsal surface of the embryo. Its integument is very thin in contrast to the limb primordia which are formed by a high concentration of cells. The appendage encloses, or stores, yolk that cannot be contained in the embryo as it develops its peculiar folds within the limiting membranes of the egg. Since the chorion encloses the appendage without following its contours closely the appendage is of limited value for diffusion of dissolved gases, wastes, etc.

In _A_. _communis_ the dorsal appendage is a highly organized structure which projects far beyond the outer surface of the egg. The histological structure of the appendage is similar to the respiratory portion of the adult pleopods. The appendage does not appear to be yolk filled. The respiratory function could allow a more rapid metabolism for the speedy development which occurs in _A_. _communis_.

The qualitative change involved in evolving from a storage organ to a respiratory organ is remarkable in that it occurs in an embryonic structure.

_A_. _communis_ has more eggs than _C_. _thomsoni_. _C_. _thomsoni_ has larger eggs than _A_. _communis_. Volume of eggs produced appears to have a close correspondence. The same amount of egg material would obviously produce bigger eggs if the material were distributed to fewer eggs. More eggs could be an answer to a higher mortality rate. Smaller eggs could allow more rapid development in response to the same pressure. The phreatoicid, *Phreatomerus latipes*, of Central Australia, produces up to 109 eggs (Nicholls, 1943). The life cycle of *P. latipes* has not yet been described. Perhaps *P. latipes* has a more rapid development than *C. thomsoni* since size of egg and rate of development are often inversely related. A change in the rate of development might be accompanied by the modification of the dorsal appendage. Nicholls remarks about the large size of *P. latipes* marsupium. That might be an indication that there was no reduction of egg size with increase in number of eggs. If there were no reduction of egg size I would not expect more rapid development on the basis of the inverse relationship noted above.

Sensory structures are similar. The antennules of both bear olfactory cylinders or specialized setae (fig. 2 and fig. 3), of small size which have a short basal portion and short blunt terminal portion. The eyes of each are composed of a small number of ocelli set nearly flush with the integument.

Both are dark brown; a color similar to the substrate they usually inhabit.

The internal anatomy is grossly similar. Barnard (1927) noted the similarity of the gastric mill in the two groups. *A. communis* has only four hepatic cecae, whereas *C. thomsoni* has eight.

The absence of a typhlosole in the asellid is probably not the result of a modification of the asellid, as most differences were interpreted to be. Since the presence of a typhlosole is not a characteristic of all the Phreatoicoidea, the typhlosole appears to be a character evolved since the divergence of the Asellota and Phreatoicoidea. If the typhlosole had been a character of the ancestral type it would probably have had a selective value due to the greater surface provided for alimentary functions.

Cell bodies of the neurons occupy the ventral portion of the ganglia in both species.

Life Cycles.

The most obvious difference in life cycles is the relatively long time it takes *C. thomsoni* to rear young and for them to mature. *A. communis* reproduces rapidly and perhaps would rear more broods in a year's time under favorable conditions than the probable minimum of two broods a year. One factor in the shorter incubation time of *A. communis* could be the smaller egg size (half the diameter) which accompanies the larger brood size. Unfortunately, nothing is known about the life cycle of phreatoicids such as *Paramphisopus palustris* and *Phreatomerus latipes* which have larger brood sizes than *Colubotelson thomsoni*. In a stable population replacement must equal mortality. Thus is seems that individuals of *A. communis* are subject to greater predation or are physiologically less well suited to the environment. Since most eggs in each species hatch successfully it must be that the mortality comes later and that *A. communis* requires more individuals to carry it through the unfavourable season. Since a maximum of 17 eggs was observed in the brood pouch of *C. thomsoni*, and *A. communis* had an average of 117 eggs (Hatchett, 1947) at a pace six times as frequent as *C. thomsoni*, it is evident that *A. communis* has a reproductive potential over 40 times as great as *C. thomsoni*. With a large population it is more likely that enough of the population will be in the depressions most suited, to retaining sufficient moisture for life during dry periods, to maintain the population. Since many of the isolated pools further from the main stream on Mount Wellington contained no phreatoicids, though otherwise indistinguishable from pools containing them, the phreatoicids may have been unable to weather the dry spell in them. Higher population levels may have enabled them to exist there by increasing the probability of some being in the moister part during the dry season.

Barnard (1927, p. 152) considered the time of year the young emerged as important. He stated as a general rule that young of animals are produced during the season most favorable to their further growth. Thus the life cycle of *A. communis*, *C. thomsoni*, and the South African phreatoicids have the following in common. Maximum production of young following the cool season and before the dry period. Thus the young have time to develop sufficient vitality for successful aestivation. Although the period of greatest reproductive activity of *A. communis* does conform to this the recovery of such a large percentage of aestivating gravid females may represent an abnormal circumstance.

Sexual Differences.

Niiyama (1956) has demonstrated an XO sex mechanism in the isopod, *Tecticeps japonicus*, and stated that Dworak had reported one from *Asellus aquaticus* with a male diploid number of 17 chromosomes. Such a mechanism would give an expected sex ratio of one male to one female. Barnard (1927, p. 151) inferred the existence of such a ratio in *M. capensis* because of the absence of single males or females during the period of pairing. Allee (1929) found approximately equal sex numbers during collecting at periods and places other than those with the large aggregations which were predominantly male. Sexes reported among the phreatoicid species show great variability in ratios of males to females. Males predominate in the collections I made but some types of collecting areas yielded more females. Probably the gravid females avoid the mud, which was used for population samples, and thus cause the unequal sex ratio. Sexual differences in habitat selection by M. capensis were probably a cause of Barnard's (1927) observations of great fluctuation in sex ratios in many collections, some of which were mostly gravid females. Thus the absence of females after emergence of young was attributable to death of the females, but may have been due to other causes. Collections of A. communis in this study were made in an area of considerable uniformity which presented fewer sampling problems, thus the ratio reported comes close to the theoretical one to one.

Why the gravid female of C. thomsoni perfers to remain in places other than detritus is not certain.

A trait common to both groups is the method of pairing in which the male uses his fourth walking leg to carry the female until she is ripe for fertilization. The only

considerable difference noted about this process was the longer time the whole event takes for C. thomsoni. This appears to be a very primitive characteristic since it is quite similar to the activities of members of the Gammaridae in the order Amphipoda, another pericaridan order.

Both C. thomsoni and A. communis seem to be able to produce more than one brood since post-gravid females were able to molt their large oostegal plates and return to the small size oostegal plates of the non-gravid female.

Both share the isopodan characteristic of larvae with six legs. As far as was observed, both have similar methods of molting.

Comparison of the Pools.

Temperature in both pools followed an annual cycle with cold temperatures and ice cover in the winter and high temperatures in the summer. The Michigan pond had a warmer summer temperature. Probably the slight flow in the Tasmanian pool helped keep the pool cooler in the summer.

The higher altitude of Mt. Wellington tended to counteract the general maritime climate of Tasmania. Fluctuations more comparable to the pond in continental-climated Michigan occur in Mt. Wellington waters than occur in waters of lower altitude in Tasmania. Since there is less than nine minutes of latitude difference in their distance from the equator they have comparable day lengths. Higher altitude results in less atmospheric filtration of light at the Tasmanian location. The Tasmanian pools were not shaded by a tree canopy. The greater insolation falling on the pool bottom may have raised the micro-environmental temperature of the detritus closer to the temperature of the pond occupied by <u>A</u>. <u>communis</u>. The differences in light and temperature are slight and the dry periods seem comparable in the two areas.

The vernal pond, since it lacks an outlet, is probably much richer than the Tasmanian pools in nutrients for production of a rich microbiota in the detritus and forming the aufwuchs which are the sources of much isopod food. Its richness would result from its lack of an outlet for particulate matter and a greater annual increment of detritus forming organic matter from the surrounding deciduous trees. This factor and the flow factor made the vernal pond richer in planktonic life than the mountain pool. The flow supplying the pool came from the rocky sparsely vegetated top of Mt. Wellington in contrast to the run-off the vernal pond received from the richer nearby beech-maple forest in periods of high rainfall. This probable difference in trophic structure at a primary level may mean that the long life cycle of *C. thomsoni* represents an adaptation to a habitat poor in nutrients more than the short life cycle of *A. communis* indicates an adaptation to high mortality rates since life cycles of small aquatic invertebrates of comparable size rarely take more than a year to complete.

Both locales had seasonal dry spells resulting in dried up pool bottoms. That these two animals, found living in areas subject to such conditions, have the ability to wait for rain in an inactive state is not surprising. If they didn't, a yearly reinvasion would be necessary.

Faunal Differences.

In general, the fauna of the Tasmanian site seemed rather depauperate. Only amphipods were present there in abundance, but absent in the Michigan pond. Perhaps the low number of asellids may have been one reason for the absence of large numbers of amphipods and mayfly larvae, since Minckley (1962) and Brown (1961) have noted the importance of asellid feces in detritus fed upon by these forms.

On the other hand, the vernal pond had two snails and a fingernail clam compared to no mollusks in the mountain pool. It was also the only place to have hydra, leeches, and a crayfish.

Both had planarians in abundance in the springtime although the vernal pond had two more species during the summer. Both had a variety of aquatic insects although the vernal pond had greater variety (Table 3 and Table 7). They were primarily dytiscid beetles and tendiped larvae in Tasmania while the Michigan site had, additionally, other dipterous larvae and hemipterans. Both had water mites, cladocerans, copepods and ostracods as well as small, colorless oligochaetes and a larger red-blodded one. Frogs are known from both areas, one small species on the mountain and several species in the woods, two of which were found in the pond. In both areas frogs are known to eat aquatic isopods.

In summary, the effect of the fauna in Michigan would probably have a greater impact on *A. communis* because of competition and predation, particularly competition since the numbers, sizes, and variety of competitors (i.e., the fauna) are greater. Direct competition for food seems quite low in both areas, particularly in Michigan where a surplus of leaves is evident. Because of its habits *C. thomsoni* would be less exposed to predation by frogs than A. communis.

Since both areas were covered by glaciation in the Pleistocene, both forms must be relatively recent arrivals in their respective areas. Invasion routes would probably have been rivers for the most part, unless passive transport by birds, etc., is more common than active migration.

C. thomsoni would only have to go upstream a short distance since that area had only mountain glaciation. In such waters C. thomsoni would have been exposed to a lesser variety of fish, amphibians, reptiles, since Tasmania is notably poor in fresh-water native fish, has only eleven species of frogs (Moore, 1961), and no salamanders, turtles, or aquatic snakes. In contrast, North America has a rich fresh-water fish fauna, and many frogs, salamanders, turtles, and aquatic snakes. Many of these may be capable of preying on such organisms as Asellus spp. Ellis and Gowing (1957) have demonstrated a preference for Asellus intermedius by brown trout (an introduced species) in Michigan. Forbes (1878) found Asellus spp. in the stomachs of native fish in Illinois. Most faunal differences are long standing ones and could have placed a premium on high reproductive potential for Asellus spp. Thus many eggs, rapid development, and early maturity may have enabled them to survive. Their speed, coloration, retiring habits, and head-like posterior would reduce the fatalities from predation. The dorsal appendage of the embryo may have speeded developments sufficiently to allow survival, or it may have permitted development in an environment that is subject to periods of low oxygen due to decomposition of abundant decaying organic matter.

Evolutionary Considerations.

The effect of evolutionary change on the asellids would seem to have been much greater than on the phreatoicids if Glaessner (1957) is correct about the phylogenetic position of the phreatoicids. Actively meiotic cells are more subject to mutation than resting cells. Thus the asellids, with reproductive periods at least six times as frequent as the phreatoicids, would seem to be more subject to mutation. Also the opportunity for recombination would be six times as frequent. Thus selective pressure could be effective on new genetic combinations six times more often.

Another factor which might affect evolution within the phreatoicids is the small size of the breeding population. The immature stages make up a large proportion of the phreatoicid population over the year, whereas at some periods the asellid population is nearly all mature individuals. A small breeding population can carry fewer genetic combinations than a large one. Thus the possibility of loss of factors of low frequency appears to be greater in the phreatoicids. At any rate, the Triassic phreatoicid indicates changes in the group have been very slow.

Since phreatoicids were already extant in the Triassic, 100,000,000 years would be a conservative estimate of the length of time the phreatoicids and asellids have been pursuing a separate evolution. In the last chapter we saw that some morphological characteristics had undergone a parallel evolution or remained unchanged. Other morphological characteristics diverged greatly. Most characteristics underwent an intermediate amount of divergence. Characteristics of physiology and behavior have undergone a similar range of changes. Similar are food preference, habitat preference, and method of pairing. Different are reaction to disturbance, duration of pairing, and speed of movement. Somewhat modified are use of walking legs as well as other structures which have undergone structural modifications.The fact that behavorial characteristics cannot be visualized, as structures can, does not mean they are less important as an integral part of the whole organism. Both types of characteristics have been the product of long periods of selection and in a stable environment should have high adaptive value.

Temporal Reproductive Isolation and Speciation.

An interesting situation exists in the phreatoicids. It is possible that three genetic lines could be estab-

lished in the sympatric population. There would be complete reproductive isolation of the three lines _if_ there were no success in breeding the fourth year of their life and none matured and bred the second year. A longer reproductive life would not necessarily make the gene flow between the lines complete since the mortality would probably restrict gene flow with a direct proportionality. Thus speciation could occur without geographic or niche separation. It is in effect a temporal isolation. The existence of several species in Great Lake, Tasmania (Nicholls, 1944) may be a result of this ability. Of course, a similar situation occurs in cicadas and other insects with a long life cycle. Alexander and Moore (1962) point out that, although the genus _Magicicada_ has speciation aided by temporal isolation, due to long life cycles the rate of speciation is slow.

Marine Relatives.

There is no evidence of marine forms among the phreatoicids. The one from brackish wells in Central Australia is perhaps more closely related to marine forms than those found within sight of the sea. The family Janiridae in the Aselloidea has marine members which strongly resemble _Asellus_ spp. So do members of the family Stenetriidae. The relict nature of the phreatoicids and the variety within the asellots hide their origin. However a fresh-water origin appears more likely in the light of over fifty species of phreatoicids still extant in fresh water. Thus marine Asellota may represent a return to that environment from fresh-water ancestors.

SUMMARY

1. *Colubotelson thomsoni* is shown to have a long life cycle, with pairing and development of eggs taking several months each, with growth to maturity taking at least two years.
2. Frequency of brood production in *C. thomsoni* is shown to be a yearly phenomena.
3. A general description of the environment of *C. thomsoni* and its relation to it is presented. Seasonal sexual differences in habitat selection as the cause of aberrant sex ratios is indicated.
4. Various features of the external and internal anatomy of *C. thomsoni* have been presented and the controversy about its typhlosole resolved.
5. Aspects of the biology of *Asellus communis*, corresponding to those presented for *C. thomsoni*, are presented based on the literature and original observation.
6. Their taxonomic positions are discussed and their general phylogeny presented.
7. Aspects of the anatomy, natural history, and ecology of each are compared and discussed. Some mechanisms of evolution are suggested.

8. The comparison of the differences in the two animals is interpreted as indicating the following environmental differences have exerted the most effective selective pressure.

a. _A_. _communis_ is in a structurally different environment caused by the annual addition of leaves from deciduous trees.

b. _A_. _communis_ is subject to greater predation.

c. _C_. _thomsoni_ lives in an area with a poorer trophic structure.

LITERATURE CITED

Alexander, R. D., and T. E. Moore. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, Magicicada). Misc. Publ., Mus. Zool., Univ. Mich., 121:1-59.

Allee, W. C. 1912a. Seasonal succession in old forest ponds. Trans. Ill. Acad. Sci., 4:126-131.

_______. 1912b. An experimental analysis of the relation between physiological states and rheotaxis in Isopoda. Jour. Exp. Zool., 13:269-344.

_______. 1913a. The effect of molting on rheotaxis in isopods. Science, 37:882-883.

_______. 1913b. Further studies on physiological states and rheotaxis in Isopoda. Jour. Exp. Zool., 15:257-295.

_______. 1914. Certain relations between rheotaxis and resistance to potassium cyanide in Isopoda. Jour. Exp. Zool., 16:397-412.

_______. 1917. The salt content of natural waters in relation to rheotaxis in Asellus. Biol. Bull., 32:93-97.

_______. 1923. The effect of potassium cyanide on metabolism in two fresh-water Arthropods. Am. J. Physiol., 63:499-502.

_______. 1929. Studies in animal aggregations: natural aggregations of the isopod, Asellus communis. Ecology, 10:14-36.

_______. 1931. Animal Aggregations. Univ. of Chicago, Chicago.

_______. 1938. The Social Life of Animals. Norton, New York.

Banta, A. M. 1910. A comparison of the reactions of a species of surface isopod with those of a subterranean species.Jour.Exp. Zool., 8:243-310, 439-488.

Barnard, K. H. 1914. Description of a new species of *Phreatoicus* (Isopoda) from South Africa. Ann. S. Afr. Mus., 10:231-240.

_______. 1927. A study of the freshwater isopodan and amphipodan Crustacea of South Africa. Trans. Roy. Soc. S. Afr., 14:139-215.

_______. 1940. Contributions to the crustacean fauna of South Africa. XII. Ann. S. Afr. Mus., 32:381-543.

Bovallius, C. 1886. Notes on the family Asellidae. Bihang Till K. Svenska Vet. -Akad. Handlingar., Band. 11. N:o 15.

Brown, D. S. 1961. The food of the larvae of *Chloeon dipterum* L. and *Baetis rhodani* (Pictet) (Insecta, Ephemeroptera). J. Animal Ecology, 30:55-75.

Chilton, C. 1894. The subterranean Crustacea of New Zealand; with some general remarks on the fauna of caves and wells. Trans. Linn. Soc. Lond., 6:163-284.

_______. 1922. A new isopod from Central Australia belonging to the Phreatoicidae. Trans. Roy. Soc. S. Aust., 46:23-33.

Chopra, B. 1947. First record of occurrence in India of the ancient sub-order Phreatoicoidea (Crustacea: Isopoda). Proc. Indian Sci. Congr. 34 (III, 7):176.

Chopra, B. and K. K. Tiwari. 1950. On a new genus of phreatoicid isopod from wells in Banaras. Rec. Indian Mus., 47:277-289, Pls. XVII-XX.

Davies, J. L. 1958. The cryoplanation of Mount Wellington. Pap. Proc. Roy. Soc. Tas., 92:151-154.

Ellis, R. J. 1961. A life history study of *Asellus intermedius* Forbes. Trans. Am. Micro. Soc., 80:80-102.

Ellis, R. J. and H. Gowing. 1957. Relationship between food supply and condition of wild brown trout, *Salmo trutta* Linnaeus, in a Michigan stream. Limnol. and Oceanog., 2:299-308.

Forbes, S. A. 1878. The food of Illinois fishes. Ill. State Lab. Nat. Hist. Bull., 1:71-89.

Fowler, H. W. 1912. The Crustacea of New Jersey. Rep. N.J. Mus., 1911:29-650, Pls. I-CL.

Gibbons, C. F. 1960. Some observations on the life history and biology of *Buccalatrix ainsliella* Murt. in a Michigan woodlot. Master's Thesis, Mich. State Univ., East Lansing.

Glaessner, M. F. 1957. *Palaeocrangon*, a Permian isopod crustacean. Rec. S. Aust. Mus., 13:143-145.

Green, J. 1961. A Biology of Crustacea. Witherby, London.

Guiler, E. R. 1952. A list of the Crustacea of Tasmania. Rec. Queen Vict. Mus., Launceston, 3:15-44.

_______. 1956. Supplement to a list of the Crustacea of Tasmania. Rec. Queen Vict. Mus., Launceston, N.S., no. 5:1-8.

Hale, H. H. 1929. The Crustaceans of South Australia. Harrison Weir, Adelaide.

Harger, O. 1874. *In*: Smith, S. I. The Crustacea of the fresh waters of the United States. Rep. U. S. Comm. Fish. 1872 and 1873., 637-665, Pls. I-III.

Hatchett, S. P. 1947. Biology of the Isopoda of Michigan. Ecol. Mon., 17:47-79.

Hay, O. P. 1878. Description of a new species of *Asellus*. Ill. State Lab. Nat. Hist. Bull., 1:90-92.

_______. 1882. Notes on some fresh-water Crustacea, together with descriptions of two new species. Am. Nat., 16:241-243.

Higgens, R. P. 1959. Life history of *Macrobiotus islandicus* Richters with notes on other Tardigrades from Colorado. Trans. Am. Micro. Soc., 78:137-154.

Hutchinson, G. E. 1928. On the temperature characteristics of two biological processes. S. Afr. J. Sci.,25:338-339.

Hynes, H. B. N. 1960. The Biology of Polluted Waters. Liverpool Univ. Press, Liverpool.

Johansen, F. 1920. The larger freshwater Crustacea from Canada and Alaska. Canad. Field-Nat., 34:145-148.

Kaulbersz, G. I. 1913. Biologische Beobachtungen an Asellus aquaticus. Zool. Jahrb., Abt. Zool. Physiol., Bd. 33, 3 Heft: 287-360.

Kenk, R. 1949. The animal life of temporary and permanent ponds in Southern Michigan. Misc. Publ. Mus. Zool., Univ. Mich., 71:1-66.

Kesling, R. V. 1951. The morphology of ostracod molt stages. Ill. Biol. Mon., 21:1-324.

Kunkel, B. W. 1918. The Arthrostraca of Connecticut. Conn. State Geol. Nat. Hist. Survey Bull. No. 26.

Mackin and Hubricht. 1938. Records of distribution of species of isopods in Central and Southern United States, with descriptions of four new species of Mancasellus and Asellus (Asellota, Asellidae). Am. Mid. Nat., 19:628-637.

Markus, Henry C. 1930. Studies on the morphology and life history of the isopod, Mancasellus. Trans. Am. Micro. Soc., 49:220-237.

Martin, D. 1940. The vegetation of Mt. Wellington, Tasmania. Pap. Proc. Roy. Soc. Tas., 1939:97-124, Pls. XIV-XVI, map.

McMurrich, J. P. 1895. Embryology of the isopod Crustacea. Jour. Morph., 11:63-154, Pls. V-IX.

Milne-Edwards. 1840. Histoire Naturelle des Crustaces, comprenant l'anatomie, la physiologie et la classification de ces animaux; Tome Troisieme. Paris.

Minckley, W. L. 1962. Studies of the ecology of a spring stream: Doe Run, Meade County, Kentucky. Ph.D. Dissertation, Univ. of Louisville, Louisville.

Moore, J. A. 1961. The frogs of Eastern New South Wales. Bull. Am. Mus. Nat. Hist., 121:149-386.

Needham, A. E. 1937. On relative growth in *Asellus aquaticus*. Proc. Zool. Soc., 107A:289-313.

________. 1938. Abdominal appendages in the female and copulatory appendages in the male *Asellus*. Quart. J. Micro. Sci., 81:127-150.

________. 1941. Abdominal appendages of *Asellus*. II. Quart. J. Micro. Sci., 83:61-89.

________. 1942a. The structure and development of the segmental excretory organs of *Asellus aquaticus*. Quart. J. Micro. Sci., 83:205-243.

________. 1942b. Micro-anatomical studies on *Asellus*. Quart. J. Micro. Sci., 84:49-72, Pl. 2.

________. 1943. On relative growth in *Asellus aquaticus*. II. Proc. Roy. Soc., A113:44-75.

________. 1945. Peripheral nerve and regeneration in Crustacea. Jour. Exp. Biol., 21:144-146.

________. 1946a. Ecdysis and growth in Crustacea. Nature, 158:667-668.

________. 1946b. Peripheral nerve and regeneration in Crustacea. II. Jour. Exp. Biol., 22:107-109.

________. 1949a. Formation of melanin in regenerating limbs of a crustacean. Nature, 164:717-718.

________. 1949b. Growth and regeneration in *Asellus aquaticus* (L.) in relation to age, sex and season. Jour. Exp. Zool., 112:49-78.

________. 1953. The central nervous system and regeneration in Crustacea. Jour. Exp. Biol., 30:151-159.

________. 1954. Physiology of the heart of *Asellus aquaticus* L. Nature, 173:272.

_______. 1956. Nitrogen output and ecdysis in Crustacea. Nature, 178:495-496.

Nicholls, G. E. 1929. A new species of Asellus (A. nipponensis) from Japan. Arch. Zool. Exp. Gen. Notes et Rev., 68:33-38.

_______. 1943. The Phreatoicoidea (Part I). Pap. Proc. Roy. Soc. Tas., 1942:1-145.

_______. 1944. The Phreatoicoidea (Part II). Pap. Proc. Roy. Soc. Tas., 1943:1-157.

_______. 1946. A summary of Tasmanian phreatoicids: a contribution to the biological survey of Tasmania. Pap. Proc. Roy. Soc. Tas., 1945:55-61.

Niiyama, H. 1956. Cytological demonstration of an XO sex-mechanism in males of Tecticeps japonicus, an isopod Crustacea. Cytologia, 21:38-43.

Paris, O. H. and F. A. Pitelka. 1962. Population characteristics of the terrestrial isopod Armadillidium vulgare in California grassland. Ecology, 43:229-248.

Paulmier, F. C. 1905. Higher Crustacea of New York City. New York State Mus., Bull. 91:117-189.

Racovitza, E. G. 1920. Notes sur les Isopodes. Arch. Zool. Exp. Gen., Notes et Rev., 58:79-115.

_______. 1925. Notes sur les Isopodes. Arch. Zool. Exp. Gen., 63:533-622.

Rathke, H. 1834. Recherches sur la formation et le development de l'Aselle d'eau douce (Oniscus aquaticus, Linn.) Annal. des Sci. Nat., 2me ser., 2:139-157, Pl. II.

Richardson, H. 1904. Contributions to the natural history of the Isopoda. Proc. U. S. Nat. Mus., 27:1-89.

_______. 1905. Monograph on the Isopoda of North America. Bull. U. S. Nat. Mus., 54:i-liii, 1-727.

Sanders, H. L. 1957. The Cephalocarida and crustacean phylogeny. Syst. Zool., 6:112-128, 148.

Sars, G. O. 1867.Historire naturelle des Crustaces d'eau douce de Norvege. Christiana.

_______. 1899. An account of the Crustacea of Norway. Vol. II, Isopoda. Bergen Museum, Bergen.

Say, Thomas. 1818. An account of the Crustacea of the United States. Jour. Acad. Nat. Sci. Phila., 1:423-441.

Sayce, O. A. 1902. A new genus of Phreatoicidae. Proc. Roy. Soc. Vict., 14:218-224.

Scott, Peter. 1956. Variability of annual rainfall in Tasmania. Pap. Proc. Roy. Soc. Tas., 90:49-57.

Shelford, V. E. 1913. Animal communities in temperate America as illustrated in the Chicago regions. Bull. Geogr. Soc. Chicago, No. 5:1-362.

Sheppard, E. M. 1927. Revision of the family Phreatoicidae (Crustacea), with a description of two new species. Proc. Zool. Soc. London, 1927(pt. 1):81-124.

Smith, G. W. 1909. The freshwater Crustacea of Tasmania, with remarks on their geographical distribution. Trans. Linn. Soc. London, 2:61-92.

Snodgrass, R. E. 1938. Evolution of the Annelida, Onychophora, and Arthropoda. Smith. Misc. Coll., 97:1-159.

_______. 1951. Comparative Studies on the Head of Mandibulate Arthropods. Comstock, Ithaca.

_______. 1956. Crustacean metamorphoses. Smith. Misc. Coll., 131:1-78, +iii.

Spencer, B. and T. S. Hall. 1896. Description of a new genus of terrestrial Isopoda allied to the genus Phreatoicus. Proc. Roy. Soc. Vict., 9:12-21.

Stammer, H. J. 1932. Zur Kenntniss der Verbreitung und Systematik der Gattung Asellus, insbesondere der mitteleuropaischen Arten (Isopoda). Zool. Anzeiger, 99:113-131.

Thompson, D'Arcy. 1961. On Growth and Form. Ed. by J. T. Bonner. Cambridge, London.

Thomson, G. M. 1893. Notes on Tasmanian Crustacea, with descriptions of new species. Proc. Roy. Soc. Tas., 1892:45-76.

_______. 1894a. On a new species of *Phreatoicus* from Tasmania. Ann. Mag. Nat. Hist. (6)13:349-351, Pl. XI.

_______. 1894b. On a freshwater schizopod from Tasmania. Trans. Linn. Soc. London, 2nd ser., 6:285-303, Pls. 24-26.

Tiwari, K. K. 1952. The morphology of *Nichollsia kashiense* Chopra and Tiwari (Crustacea: Isopoda Phreatoicoidea). Proc. Indian Acad. Sci., 35B2:69-77.

Van Name, W. G. 1936. The American land and fresh-water isopod Crustacea. Bull. Am. Mus. Nat. Hist., 71:1-535.

Wacasey, J. W. 1961. An ecological study of two sympatric species of salamanders, *Ambystoma maculatum* and *Ambystoma jeffersonianum*, in Southern Michigan. Ph.D. Thesis, Mich. State Univ., East Lansing.

Waterman, T. H. 1961. The Physiology of Crustacea. Vol. II. Academic Press, New York.