

## TASMANIAN TEMNOCEPHALIDEA

By

V. V. HICKMAN

(With 38 figures and 1 plate)

## ABSTRACT

W. A. Haswell has described from Tasmania three species of *Temnocephala*, namely, *T. quadricornis*, *T. tasmanica* and *T. aurantiaca*. The descriptions are very brief. In the present paper they have been amplified. In addition three new species, *T. cita* and *T. fulva* from *Parastacoides tasmanicus* (Erichson) and *T. pygmaea* from *Astacopsis gouldi* (Clark), are described. Observations on the eggs, period of incubation, rate of growth and survival apart from the hosts are given. At ordinary temperatures the eggs of *T. cita* hatch in 67 days, *T. tasmanica* in 35-70 days, *T. quadricornis* in more than 196 days, *T. pygmaea* in 31-32 days, *T. aurantiaca* in more than 56 days and *T. fulva* in more than 60 days. The times taken to reach adult size by those species, which were hatched in the laboratory and reared apart from their hosts, are as follows: *T. tasmanica* 233 days, *T. pygmaea* 152 days and *T. aurantiaca* 117 days. In the case of *T. quadricornis* the rate of growth is such that adult size should be attained in about 190 days.

Most of the species, when removed from the host and kept under laboratory conditions, exhibit marked powers of survival. Thus specimens of *T. tasmanica* have lived for 707 days, *T. quadricornis* 76 days, *T. pygmaea* 59 days, *T. aurantiaca* 245 days. Young specimens hatched in the laboratory adapt themselves to the conditions more readily and often survive much longer than those removed from the host. Even in the absence of adequate aeration and food some species survive for lengthy periods. Thus, for example, an adult specimen of *T. tasmanica* placed in 3.0 ml. of water in a small tube, which was then firmly corked, lived for 100 days. *T. aurantiaca* treated in the same way lived for 70 days. During the period the animals decreased from adult size to that of a newly hatched specimen.

## INTRODUCTION

Three species of *Temnocephala* have been recorded from Tasmania. They are *T. quadricornis* Haswell (1893), *T. tasmanica* Haswell (1900) and *T. aurantiaca* Haswell (1900). In a study of the

family Temnocephalidae Pereira & Cuocolo (1941) placed the three species in a new genus, *Temnomonticellia*. Baer (1953) considers the establishment of the new genus not justified.

Haswell's descriptions of the three species are very brief and Baer (1931) expressed the opinion that a more thorough study of the three forms would undoubtedly justify uniting them in a single species. However, the present investigation shows that they are sufficiently distinct for them to be regarded as separate species.

Three new Tasmanian species are described, namely, *T. pygmaea* from the large fresh-water crayfish, *Astacopsis gouldi* (Clark), *T. cita* from the burrowing crayfish, *Parastacoides tasmanicus* (Erichson) and *T. fulva* also from *Parastacoides tasmanicus* (Erichson). A key distinguishing the Tasmanian *Temnocephala* from one another and from other Australian species is provided.

Some of the species have been maintained apart from their hosts for long periods. Observations on the incubation of the eggs, rate of growth of the young and survival under laboratory conditions are recorded.

A study of the literature on the Temnocephalidae reveals much difference of opinion concerning the function and naming of certain parts of the male and female reproductive systems. Fyfe (1942) calls the bulbous enlargement immediately preceding the base of the penis the granular vesicle and states that Haswell (1893) names it the coecal pouch. This, however, is not the case. Haswell gives the name coecal pouch or ejaculatory sac to the structure, which Fyfe designates the seminal vesicle, and the name cirrus bulb to the structure, which she calls the granular vesicle. The organ which Haswell and most other authorities call the seminal vesicle is termed by Fyfe the seminal duct. The organ which Haswell (1893) calls the coecal pouch or ejaculatory sac is termed an accessory bladder by Merton (1922) and prostate by Baer (1953). Table I indicates the equivalence of the terms used by the authors mentioned above.

TABLE I.

Haswell, 1893	Merton, 1922	Fyfe, 1942	Baer, 1953
Seminal vesicle	First seminal vesicle	Seminal duct	Seminal vesicle
Ejaculatory sac or coecal pouch	Accessory bladder of second seminal vesicle	Seminal vesicle	Prostate
Cirrus bulb	Second seminal vesicle	Granular vesicle	Ejaculatory vesicle

The terminology and functions of the bladder-like structure, usually called the *vesicula resorbiens*, have been fully discussed by Haswell (1924). It may be pointed out that the name is due to Merton (1913). Fyfe (1942) states incorrectly that it is due to Haswell. Incidentally the word *resorbiens*, which is in general use, should be *resorbens*, since it is derived from the Latin verb *resorbere*.

### MATERIALS AND METHODS

Fresh-water crayfish collected in various parts of Tasmania and found to be carrying *Temnocephala* were brought back alive in water to the laboratory. The *Temnocephala* were then carefully removed from their hosts and placed in fresh water in glass dishes. They were fed on small particles of the internal organs of flies and other insects. In some cases chironomid larvae and small aquatic oligochaets were provided. The water in the dishes was renewed every two or three days but running water and special aeration were not required. The dishes containing the specimens were kept in a subdued light at ordinary room temperatures.

Eggs laid in the dishes were usually attached to the side or the bottom. Some, however, were not attached. These were placed on cotton wool submerged in water to prevent them from rolling about when the water was changed. Eggs taken from the hosts were removed together with the portion of integument to which they were attached. In this way handling of the eggs was facilitated and damage to them avoided.

Specimens of *Temnocephala* intended for sectioning were fixed in Apathy's alcoholic corrosive sublimate. The sections were stained in Ehrlich's haematoxylin and counterstained with eosin. Specimens for whole mounts were stained in alum carmine.

### DESCRIPTION OF SPECIES

#### Order TEMNOCEPHALIDEA

#### Family TEMNOCEPHALIDAE.

Genus **TEMNOCEPHALA** E. Blanchard, 1849.

Key to Australian species of *Temnocephala*.

1. Six tentacles present ..... 2  
With less than six tentacles ..... 3
2. Opaque, white and without pigment  
*T. comes* Haswell.  
Brown in colour ..... *T. simulator* Haswell.
3. With five tentacles ..... 4  
With four tentacles and a flat median lobe ..... 10
4. With a pair of posterior glandular organs  
*T. chaeropsis* Hett.  
Without such organs ..... 5
5. Eyes absent ..... *T. caeca* Haswell.  
Eyes present ..... 6
6. Pigmented with dark brown  
*T. fasciata* Haswell.  
Grey or white without pigment ..... 7
7. Cilia behind tentacles ..... *T. minor* Haswell.  
No cilia behind tentacles ..... 8
8. Testes lobed ..... *T. dendyi* Haswell.  
Testes not lobed ..... 9

9. Front testes smaller than hind testes  
*T. engaei* Haswell.  
Front testes larger than hind testes  
*T. cita* sp. n.
10. Eyes absent ..... *T. tasmanica* Haswell.  
Eyes present ..... 11
11. Dark brown ..... *T. quadricornis* Haswell.  
Not so coloured ..... 12
12. White without pigment ..... *T. pygmaea* sp. n.  
Yellow or brownish yellow ..... 13
13. Four pairs of intestinal septa  
*T. aurantiaca* Haswell.  
Seven pairs of intestinal septa ..... *T. fulva* sp. n.

*Temnocephala cita* sp. n.  
(Text-figs. 1-7, Pl. I, fig. 1.)

**General features.** The animal (Text-fig. 1) is somewhat elongate. The largest specimens when contracted are about 1.26 mm. long and 0.69 mm. wide. When fully extended they measure about 2.86 mm. long and 0.38 mm. wide. The dorsal surface is convex and the ventral surface flat or slightly convex. There are no marginal flanges and the fully extended animal is almost cylindrical. Apart from the eyes there is no pigmentation, the body being white and translucent, with the intestine clearly visible through the integument. Five sub-equal tentacles are present, the outer one on each side being slightly shorter than the others. The eyes are situated a short distance behind the base of the median tentacle. The excretory pores open one on each side in a plane slightly behind the eyes. The mouth is a slit-like aperture in the normal position on the ventral surface about 370 $\mu$  from the base of the tentacles. The sucker is 300 $\mu$  in diameter and extends slightly beyond the posterior end of the body. The genital aperture is slightly in front of the sucker.

**Body-wall and Integumentary Glands.** The cuticle is smooth and perforated by numerous small pores. In section the epidermis has the usual striated appearance. The nuclei are few and widely scattered. They are generally oval in shape and measure about 15 $\mu$  x 12 $\mu$ . Their form, however, depends on the degree of contraction or extension of the animal. In some cases they are very flat. A thin basement membrane is present below the epidermis. No cilia occur on any part of the integument.

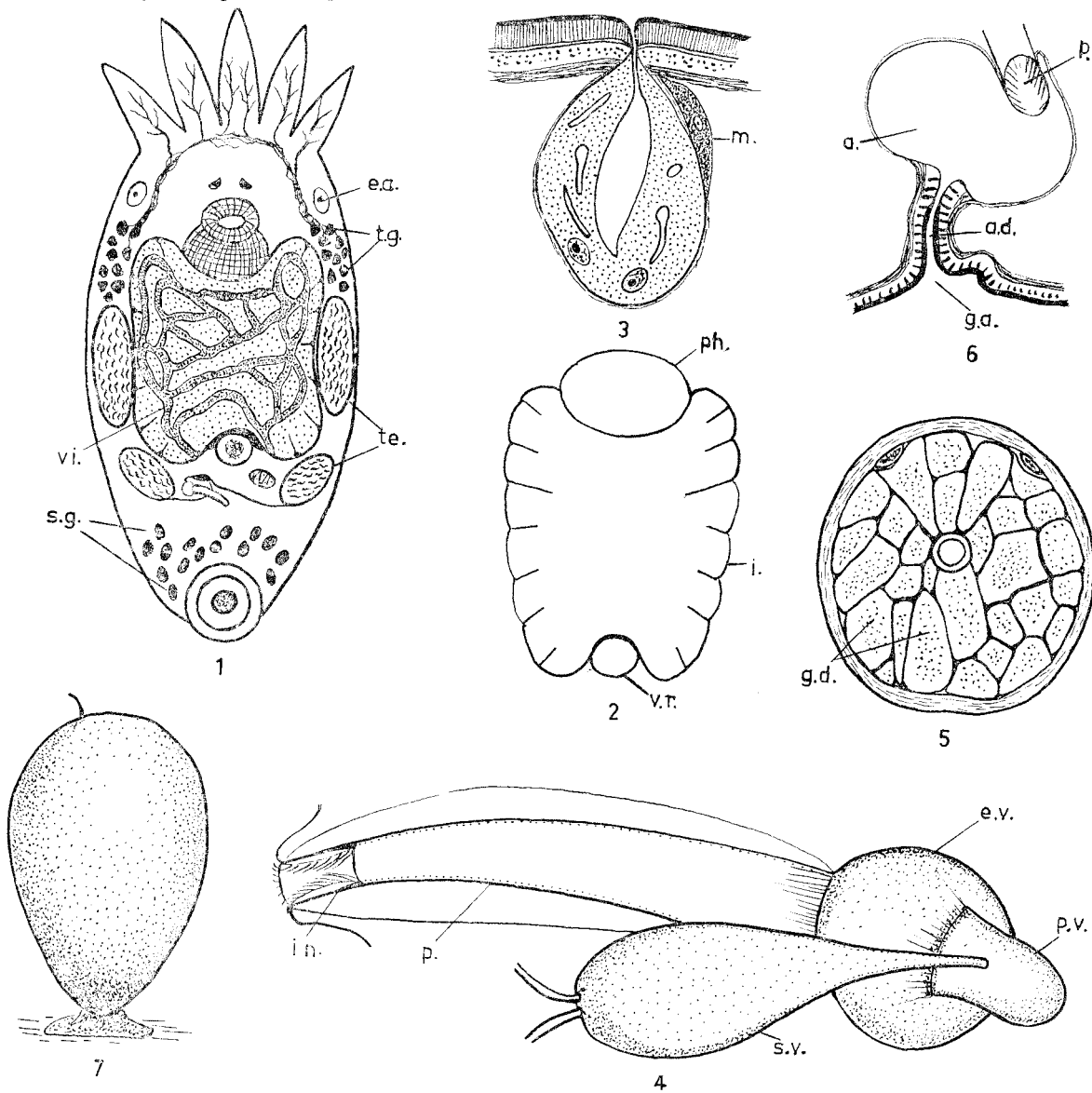
The dermal muscular sheath is composed of the usual transverse, diagonal and longitudinal fibres. On the ventral side the longitudinal fibres are more strongly developed than elsewhere. In front of the mouth are a number of transverse muscles, which lie internal to the layer of ventral longitudinal fibres. Numerous dorso-ventral muscles occur throughout the body.

The tentacular or rhabdite glands form a group lying between the excretory vesicle and the anterior testis on each side of the body. The glands are mainly pyriform in shape. They do not extend in front of the excretory vesicles but their fine thread-like ducts pass forward and give off branches to the tentacles. The median tentacle receives branches from the glands on each side of the body. Both the glands and their ducts stain deeply with haematoxylin. The rhabdites measure about 3 $\mu$  in length and the cell nucleus 10 $\mu$  in diameter. The

sucker glands are situated behind the posterior testes and also in front of the sucker. They are irregular in shape and their nuclei about  $12\mu$  in diameter.

**Digestive System.** The mouth leads into a short prepharynx or pharyngeal pouch. The pharynx has the form of a pharynx bulbosus and is about  $190\mu$  in diameter. It is provided with a large number of pharyngeal glands, which are situated among the radial muscles and are more numerous dorsally than ventrally. The posterior sphincter muscles are

more strongly developed than are the anterior ones. Between the pharynx and the intestine is a short oesophagus, but oesophageal glands appear to be absent. The intestine is a somewhat rectangular sac which, except in the contracted condition, is longer than wide. It has a number of slight constrictions. In front it projects on each side of the pharynx. Posteriorly it is concave round the vesicula resorbens. The lumen of the intestine is partly divided by seven pairs of lateral septa (Text-fig. 2).



*Temnocephala cita* sp.n.

Fig. 1.—General view of external and internal features.  
Fig. 2.—Outline of digestive canal.  
Fig. 3.—Section of excretory bladder.  
Fig. 4.—Male reproductive organs.

Fig. 5.—Transverse section of ejaculatory vesicle.  
Fig. 6.—Sagittal section of atrium and atrial duct.  
Fig. 7.—Egg viewed from the side.

**Excretory Bladder.** The excretory apertures are situated one on each side of the dorsal surface. They lie in a transverse plane slightly behind the eyes and are about  $45\mu$  from the margin. The excretory bladder is pyriform,  $75\mu$  long and  $45\mu$  wide. It has a very thick wall, which appears finely granular and contains a number of small canals and vacuoles (Text-fig. 3). At the base of the vesicle are two nuclei. A thin muscular investment surrounds the bladder, but the thick fibrous layer seen in some other species is absent. A long spindle-shaped myoblast is closely applied to the anterior surface of the bladder and extends up to the aperture.

**Nervous System.** The brain and main nerve cords are similar to those in other species of *Temnocephala*. The width of the brain is about  $150\mu$  and it has the form of a transverse band of fibrous material. At each side it is curved slightly downward and backward. Anteriorly it gives off a pair of stout nerves which pass forward forming branches which enter the tentacles. From the sides of the brain the usual three pairs of longitudinal cords arise and pass posteriorly. Associated with each side of the brain are numerous ganglion cells with nuclei about  $12\mu$  in diameter. Immediately above the front of the brain are the two eyes. Each has the form of a pigmented cup, which is poised obliquely. In the mouth of the cup is a clear refractive body. The eyes are about  $24\mu$  in diameter and  $30\mu$  apart.

In front of the brain are two pairs of large cells, one pair above the other. The upper pair are about  $33\mu$  in diameter. Their cytoplasm is vacuolated and their nuclei measure  $15\mu$  in diameter. The lower pair are of about the same size but their cytoplasm is finely granular and their nuclei  $18\mu$  in diameter. These cells do not seem to form part of the nervous system but are always closely associated with the brain and are therefore mentioned in this section. Haswell (1893) figures similar cells in *T. fasciata* and refers to them as "problematical cells". They may be paranephrocytes concerned with excretion, but as Fyfe (1942) points out paranephrocytes are wandering cells. The paired cells in front of the brain in *Temnocephala* appear constant in position and to occur in most species.

**Reproductive System.** In the male system there are two pairs of testes, an anterior pair and a posterior pair. The anterior testes are oval and elongate being about  $493\mu$  long and  $82\mu$  wide. They are situated one on each side of the intestine. The posterior testes are also oval but much shorter than the anterior pair. They measure  $301\mu$  long and  $164\mu$  wide. They are situated somewhat obliquely behind the lateral angles of the intestine. A short duct passes from the posterior end of each anterior testis to the ventral side of the neighbouring posterior testis. The vasa deferentia arise ventrally from the posterior testes and run transversely to enter the base of the seminal vesicle.

The seminal vesicle (Text-fig. 4) lies more or less obliquely in front of the penis. When distended with spermatozoa it is somewhat pyriform. It is about  $96\mu$ – $150\mu$  in length and  $42\mu$ – $45\mu$  in diameter at its widest part. Its narrow distal end (seminal

duct) enters the anterior side of the prostate vesicle.

The prostate vesicle is a bladder-like structure projecting from the anterior side of the ejaculatory vesicle. It has a muscular wall and a thick finely granular protoplasmic lining which contains few nuclei and no cell boundaries. Its lumen is continuous with that of the ejaculatory duct.

The ejaculatory vesicle is somewhat spherical and  $51\mu$ – $66\mu$  in diameter. The ducts of the granule glands enter the front of the vesicle below the junction with the prostate vesicle. They fill the lumen surrounding the ejaculatory duct and extend into the penis. In a transverse section of the vesicle the ducts appear polygonal in form, probably due to mutual pressure (Text-fig. 5). The seminal, prostate and ejaculatory vesicles have a continuous muscular investment consisting of an outer layer of circular fibres and an inner layer of longitudinal fibres.

The penis (Text-fig. 4), surrounded by the cirrus sac, lies to the left of the median plane in a more or less transverse position. It is slightly curved and slopes downward towards the atrium. It has the usual form of a chitinous tube surrounded by two muscular layers continuous with those surrounding the ejaculatory vesicle. Its length is  $144\mu$ – $180\mu$ , its diameter being  $36\mu$ – $42\mu$  at the base and  $15\mu$ – $18\mu$  at the apex. The introvert forms about one sixth of the total length of the penis. In the inverted state the inner wall of the introvert is lined with numerous spines, which vary in length from  $7\mu$ – $27\mu$ , the longer spines being towards the base and the shorter ones towards the apex.

Granule glands occur on each side of the intestine and also surround the greater part of the seminal vesicle, but their ducts could be found only where they entered the ejaculatory vesicle.

The female part of the reproductive system consists of the usual organs, namely, the germarium, vesicula resorbens, receptacula seminis, ootype, uterus and vitellarium.

The germarium is oval in shape and about  $90\mu$  long and  $69\mu$  wide. It is situated to the right of the median plane and slightly behind the vesicula resorbens. The ova have the characteristic wedge shape. The germiduct is very short and the germarium opens almost directly into the right side of the ootype.

When not compressed the vesicula resorbens is more or less spherical and  $45\mu$ – $75\mu$  in diameter. In some specimens the lining of the vesicle is thick and finely granular with a number of nuclei. In other specimens it may be thin and without nuclei. An open genito-intestinal canal was not present in any of the specimens examined. In one, however, the anterior wall of the vesicle formed a narrow extension into the epithelium of the intestine, as if a canal were in process of formation. Posteriorly a short duct from the vesicle becomes continuous with the ootype.

There are four receptacula seminis. They surround the ootype and enter into it slightly anterior to the entrance of the germiduct. Each is finger-like in shape and about  $39\mu$  long and  $12\mu$  in diameter.

The ootype has very thick muscular walls and small lumen. Behind the entrance of the germiduct it bends ventrally and expands to form the uterus. The latter is a much larger chamber, which in the non-gravid condition has folded walls. Opening into it and also into the ootype are a number of unicellular glands. A narrow vagina surrounded by strong circular and radial muscles leads from the lower part of the uterus to the right side of the atrium, into which it opens.

The vitellarium consists of a number of glands situated above and below the intestine. They form a somewhat reticulate pattern (Text-fig. 1). Posteriorly they give rise to two vitelline ducts, which open, one on each side, into the ootype.

The atrium varies considerably in appearance in different specimens. In the gravid condition or immediately after egg-laying it is a large oval chamber with smooth walls. At other times it is much smaller and has folded walls. A number of pyriform unicellular glands open into it. The atrial duct arises from the middle of the ventral surface of the atrium and leads to the genital aperture. It is about  $27\mu$  long, curved slightly forward and surrounded by strong sphincter muscles (Text-fig. 6).

**Host and Locality.** *Temnocephala cita* was taken from specimens of the burrowing land-crayfish, *Parastacoides tasmanicus* (Erichson), found living in tunnels in damp soil near Lake Pedder, Western Tasmania, 25th February, 1966. The species occurred mainly on the pleopods and under surface of the abdomen. A few were found in the gill chambers.

**Eggs and Incubation.** The eggs are pale yellow in colour and pyriform in shape (Text-fig. 7). They measure  $0.343\text{--}0.457$  mm. long and  $0.228\text{--}0.286$  mm. wide. They are generally attached by the narrow end to the anterior surface of the pleopods. (Plate I, fig. 1). At the wider distal end the chorion is produced into a short slender projection. A few eggs were found in the gill chambers of the crayfish. Unlike the eggs on the pleopods they were attached along one side and not by the narrow end. This difference in the mode of attachment suggested that the eggs might belong to another species. However, when the eggs were hatched in the laboratory, the young were found to be no different from those hatched from eggs on the pleopods. No doubt the narrow space in the gill-chamber compelled the animal to attach the eggs in the manner described.

An egg laid in the laboratory on 2nd March, 1966, was attached by its narrow end to the side of a glass dish containing water in which a number of adults were being kept. It hatched on 8th May, 1966, after a period of 67 days, the average temperature of the water during the period being  $16^{\circ}\text{C}$ . Fifteen eggs were removed from specimens of the crayfish and hatched in the laboratory. The longest time required for any one of the eggs to hatch was 53 days.

The newly hatched young are white and translucent. When contracted they are about  $0.514$  mm. long and  $0.343$  mm. wide, but they are able to extend to a length of about  $1.37$  mm.

**Survival apart from the host.** *T. cita* proved more difficult to maintain under laboratory conditions than any other of the Tasmanian species. Newly

hatched young ones did not survive longer than 13 days and the rate of growth was therefore not studied. Most of the adults removed from their host lived for less than a month. The crayfish, *Parastacoides tasmanicus*, was found to carry numerous Rotifers, Vorticellids and Macrostromids. It is probable that some or all of these formed the natural food of *T. cita* and that such food was necessary for survival.

#### *Temnocephala tasmanica* Haswell

(Text-figs. 8-13, Pl. I, fig. 2)

**General Features.** In the contracted condition the largest specimens are about  $2.85$  mm. long and  $1.30$  mm. wide. When fully extended they measure about  $5.1$  mm. in length and  $0.86$  mm. in width. There are four long tentacles and a short median truncate lobe (Text-fig. 8). No eyes are present. Haswell (1900) gives a drawing of the anterior end of the body, which shows a pair of eyes. This is apparently an error and in contradiction to the text, in which he states "there are no eyes". The colour of the body is usually pale cream or white. In some specimens, however, the dorsal surface is tinged with orange in front of and behind the region of the intestine. Haswell (1900) states "the integument is devoid of pigment". The body is convex above and flat below. The excretory apertures are situated, one on each side of the dorsal surface, in a transverse plane slightly behind the front of the pharynx, and about  $240\mu$  from the lateral margins. The mouth is an oval aperture in the usual position on the ventral surface and about  $490\mu$  from the front. The genital aperture lies about  $330\mu$  in front of the ventral sucker. The diameter of the sucker is  $590\mu$ . The posterior end of the body extends slightly beyond the sucker.

**Body-wall and Integumentary Glands.** The integument consists of the usual layers, namely cuticle epidermis and basement membrane. The cuticle is about  $3\mu$  in thickness and is perforated by a large number of small pores. Its surface especially on the dorsal side, has a rough appearance due to the presence of numerous minute papillae. The epidermis is about  $6\mu$  in thickness and has the usual striated structure with widely scattered nuclei. The basement membrane varies in thickness, in some places being extremely thin, in others almost as thick as the cuticle.

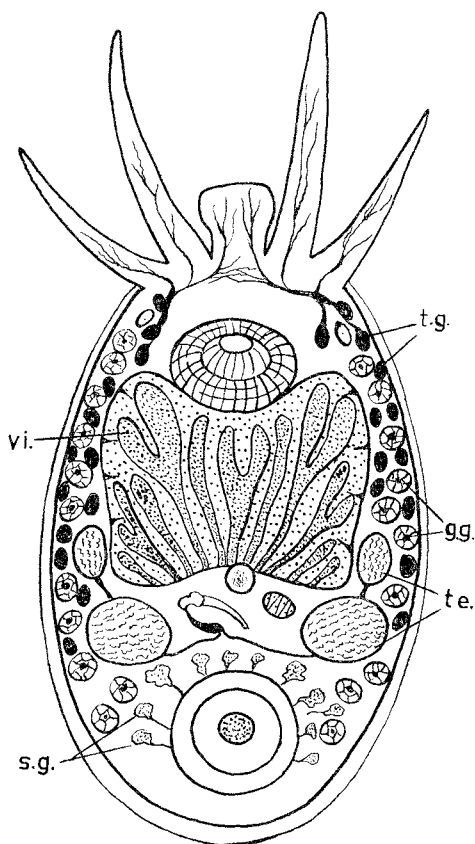
The dermal muscular sheath consists of an outer layer of circular or transverse muscles, an inner layer of longitudinal muscles and an intermediate layer of diagonal fibres. The layer of circular muscles is about  $6\mu$  in thickness, that of the longitudinal muscles  $15\mu$  in thickness. In front of the mouth and immediately internal to the ventral longitudinal muscles is a layer of transverse fibres, which extends round the lateral angle on each side and for a short distance below the layer of dorsal longitudinal muscles. Numerous dorso-ventral fibres pass through the parenchyma in all parts of the body.

The tentacular or rhabdite glands form a lateral series situated on each side of the intestine. They extend forward to slightly in front of the excretory bladder and backward to the posterior testes. Most of them are dorsal to the granule glands (described under the reproductive system). The sucker glands

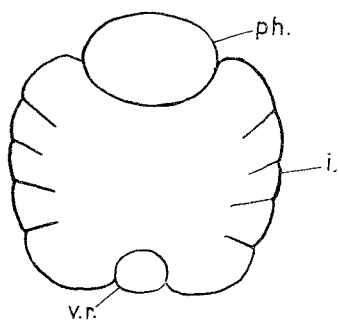
are in the posterior part of the body in front of and on each side of the sucker. Their ducts converge towards the stalk.

**Digestive System.** The mouth leads into a short prepharynx or pharyngeal pouch. The pharynx has the form of a pharynx bulbosus. It is relatively

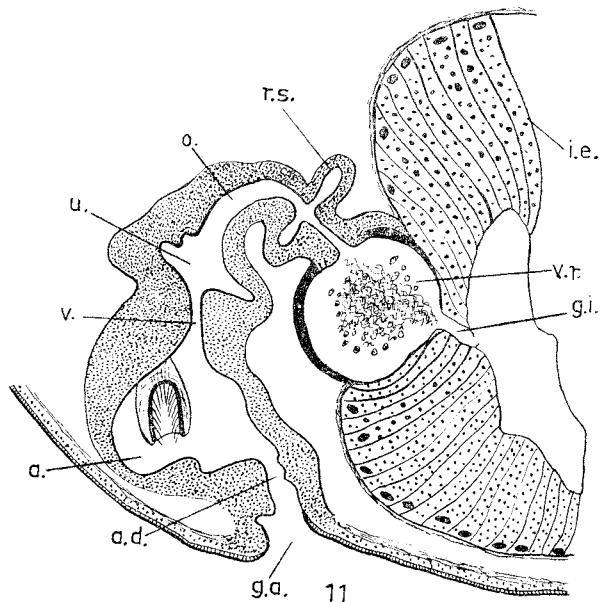
large measuring  $500\mu$  long and  $570\mu$  wide. The posterior sphincter muscles are very strongly developed. A number of unicellular pharyngeal glands lie in the spaces between the radial muscles. Between the pharynx and the intestine is a short oesophagus with a folded inner wall. It is sur-



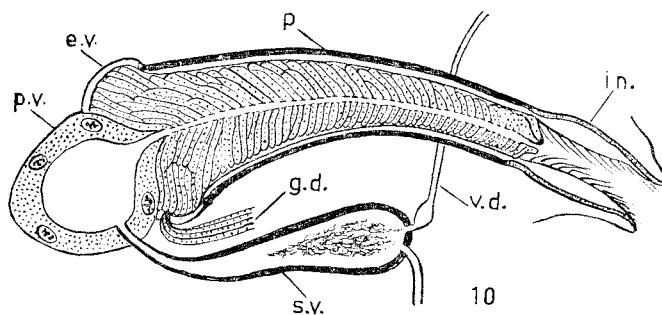
8



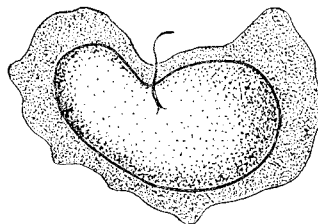
9



11



10



12

*Temnocephala tasmanica* Haswell.

Fig. 8.—General view of external and internal features.

Fig. 9.—Outline of digestive canal.

Fig. 10.—Longitudinal section of male reproductive organs.

Fig. 11.—Longitudinal section of female reproductive organs.

Fig. 12.—Egg viewed from above.

rounded by strong sphincter muscles and numerous unicellular pyriform glands. The intestine has the usual form of a more or less rectangular sac, which is shorter than wide. The anterior wall projects forward slightly on each side of and below the pharynx. The posterior wall forms a concavity round the vesicula resorbens. The lumen of the intestine is partially divided by four septa on each side (Text-fig. 9). Haswell states that the intestine is devoid of constrictions and septa. In all the specimens I have examined septa are present, but external constrictions slight or not evident.

**Excretory Bladder.** As mentioned above the excretory apertures are in the usual position and about  $140\mu$  from the margin. The excretory bladder is somewhat pyriform,  $610\mu$  long and  $410\mu$  wide. On the postero-lateral side it is coiled on itself. The loop narrows distally and becomes continuous with the excretory duct. Near the base of the bladder the duct divides to form two branches, one of which curves dorsally and follows the course of the longitudinal dorso-lateral nerve, the other passes ventrally and follows the ventral longitudinal nerve. Smaller branches pass anteriorly from near the junction of the two main ducts.

**Nervous System.** The brain and nervous system conform to the usual arrangement in *Temnocephala*. The brain is situated in front of the pharynx and is about  $150\mu$  in width. It curves slightly downward on each side. Two stout nerves are given off from the front of the brain, pass forward and divide to form branches which enter the tentacles and median lobe. The usual dorsal, dorso-lateral and ventral longitudinal nerves arise from each side of the brain.

As in the previous species there are two pairs of large cells in front of the brain. They lie between the two anterior nerves. The lower pair of cells are fused together, their cytoplasm forming a finely granular syncytium. The total diameter is about  $180\mu$ . The two nuclei are oval and measure  $30\mu \times 27\mu$ . The upper pair of cells are separate and slightly smaller, each being  $81\mu$  in diameter. The cytoplasm appears somewhat fibrous forming radial strands round the nucleus, which measures  $21\mu \times 18\mu$ .

**Reproductive System.** In the male system there are two pairs of testes, an anterior and a posterior pair. The anterior pair lie one on each side of the posterior quarter of the intestine. They are ovoid in shape and measure about  $360\mu$  long and  $290\mu$  wide. The posterior testes are situated one on each side behind the lateral angles of the intestine. They are also ovoid, but larger than the anterior pair, being  $490\mu$  long and  $360\mu$  wide. A short duct passes from the posterior end of the anterior testis to the anterior side of the neighbouring posterior testis.

The vasa deferentia arise from the inner ends of the posterior testes. That from the right testis passes in front of the atrium to the base of the seminal vesicle, which is situated to the left of the median plane. The vas deferens from the left testis is shorter and wider than that from the right testis and passes directly to the base of the seminal vesicle. The two vasa deferentia enter the seminal vesicle independently.

The seminal vesicle is elongate and pyriform.

When filled with spermatozoa it is about  $210\mu$  long and  $70\mu$  wide. It lies more or less transversely below the penis. Its wall has an outer layer of circular muscles surrounding a layer of longitudinal muscles. The lumen is lined with a thin layer of protoplasm. The seminal duct formed by the narrow distal end of the vesicle enters the prostate vesicle ventrally.

The prostate vesicle is a rounded or oval sac, about  $81\mu$  long and  $90\mu$  wide. It has muscular walls and a thick finely granular protoplasmic lining containing a few nuclei but no cell boundaries. It forms a wide junction with the ejaculatory vesicle. Its lumen is continuous with that of the ejaculatory duct. Haswell (1900) gives a figure of the male reproductive system but omits the prostate vesicle and does not mention it in his very brief description.

The ejaculatory vesicle is about  $110\mu$  in diameter, but shorter than the prostate vesicle. Near its junction with the latter on the postero-ventral side it is entered by the fine ducts of the granule glands. On passing through the wall of the vesicle the ducts form numerous branches, which surround the ejaculatory duct. They extend into the penis almost as far as the introvert and open into the ejaculatory duct for most of its length (Text-fig. 10).

The penis is situated transversely on the left of the median plane and curves downward towards the atrium. It has the usual form and is about  $300\mu$  long. At the base it is  $100\mu$  wide, but tapers to  $45\mu$  wide at the apex. The introvert forms about three tenths of the length of the penis. In the inverted state the wall of the introvert is lined with sharp spines, which vary in length from  $12\mu$  to  $60\mu$  the longer spines being near the base and the shorter ones near the apex.

The granule glands are large and conspicuous. Most of them lie at the sides of the body below the rhabdite glands. They are unicellular, more or less rounded and lobed. They measure up to  $90\mu$  in diameter. Their cytoplasm has the appearance of a reticulation formed by minute granules. The nucleus is central and about  $24\mu$  in diameter. The glands stain faintly with haematoxylin. Some granule glands lie near the testes, vasa deferentia and seminal vesicle. Their ducts enter the ejaculatory vesicle in the position already described.

The female reproductive system (Text-fig. 11) consists of the germarium, vesicula resorbens, receptacula seminis, ootype, uterus, vitellarium and associated glands.

The germarium lies on the right side of the median plane close behind the intestine. It is ovoid in shape and measures  $165\mu$  long and  $105\mu$  wide. From its inner end arises a very short germiduct, which opens into the ootype. The advanced ova in the germarium have the characteristic wedge shape. The more immature ova at the end remote from the germiduct are small and rounded.

The vesicula resorbens is a rounded bladder incorporated in the posterior wall of the intestine. It may be spherical, ovoid or pyriform in shape and may vary in diameter from  $90\mu$  to  $126\mu$ . Its outer wall has a thin muscular investment. Its lumen usually has a thick lining of granular protoplasm with a few nuclei but no cell boundaries. In some cases no nuclei are present. In sections of three

specimens the anterior end of the vesicle had formed a temporary genito-intestinal canal leading into the lumen of the intestine. Haswell (1924) records a similar feature in specimens of *T. tasmanica*, which he examined. Posteriorly the vesicula resorbens gives rise to a short duct, which becomes continuous with the ootype.

There are four receptacula seminis. They have the form of narrow diverticula about  $45\mu$  long and  $18\mu$  wide. They are arranged more or less symmetrically round the ootype and open into it a short distance behind the vesicula resorbens and anterior to the entrance of the germiduct.

The ootype passes posteriorly for a short distance and then curves downward enlarging to form the uterus. In the non-gravid condition the uterus has strongly folded walls. Ventrally it forms a narrow vagina opening into the right side of the atrium. The ootype and uterus have thick muscular walls and are surrounded by a number of pyriform unicellular glands, which stain darkly with haematoxylin.

The vitellarium lies above and below the intestine. It has the form of a number of thick elongate lobes which are slightly branched and lie more or less longitudinally. Posteriorly the vitellarium forms a pair of vitelline ducts, which open, one on each side, into the ootype near the openings of the receptacula seminis.

The atrium is a large transverse chamber with strongly folded muscular walls. It lies slightly behind the genital aperture and the atrial duct slopes downwards and forwards. A number of unicellular cement glands surround the atrium and also the atrial duct. The genital aperture is a short transverse slit-like opening situated close in front of the anterior margin of the sucker.

*Hosts and Localities.* This species occurs on the small freshwater crayfish, *Astacopsis franklinii* (Gray), found in creeks flowing down the slopes

*Temnocephala tasmanica* usually occurs on the great chelae and mouthparts of the host, but if large numbers are present they may also occur on the carapace, legs and abdomen. A crayfish taken at the Cascades on 9th March, 1966, carried 150 specimens of the temnocephalid distributed over most of the body.

The species was also found on specimens of the large fresh-water crayfish, *Astacopsis gouldi*, (Clark), taken in the river Don at Sheffield in northern Tasmania, 23rd December, 1964.

*Eggs and Incubation.* The eggs (Text-fig. 12 and Pl. I, fig. 2) are distinctly reniform and narrower at one end than at the other. They measure about  $510\mu$  long and  $290\mu$  wide, the capsule is brownish and transparent. On the upper side, and nearer to one end than the other, the capsule is produced into a short narrow projection with a curved or twisted tip. The eggs are always deposited in the gill chamber of the crayfish. They may be fastened to the thoracic wall, the gills or the inner wall of the branchiostegite. The eggs are not massed together but attached singly. The whole under-surface of the capsule is firmly cemented to the place of attachment. The cementing material is often voluminous and in some cases almost envelops the capsule.

Specimens of *T. tasmanica* removed from the host and kept in water in glass dishes sometimes deposited eggs in the dishes. The eggs were either attached to the side or free on the bottom of the dish. Five eggs (A-E) were kept until they hatched. The period of incubation (Table 2) varied considerably, being partly dependent on temperature conditions. On hatching the upper surface of the egg-capsule fractures allowing the young one to escape.

*Rate of growth.* An egg removed from the gill chamber of *Astacopsis franklinii* hatched on 12 February, 1964. The newly hatched young one in the contracted state measured 0.57 mm. long and 0.40 mm. wide. At the end of 233 days it measured, when contracted, 2.85 mm. long and 1.30 mm. wide.

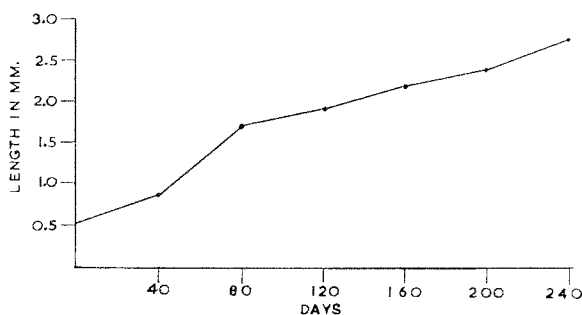
TABLE 2.

Egg	Date laid.	Date hatched.	Period of incubation in days.	Average temperature of the water in degrees C.
A	24 September, 1964	3 December, 1964	70	16.4
B	24 December, 1964	28 January, 1965	35	18.0
C	24 December, 1964	6 February, 1965	44	18.0
D	30 January, 1965	22 March, 1965	51	18.7
E	27 March, 1965	27 May, 1965	61	16.0

of Mount Wellington, especially at the Cascades and Lenah Valley. Haswell (1900) states that the specimens examined by him were "found in the branchial cavities of *Astacopsis tasmanicus* in small streams near Hobart". There is little doubt that the two crayfishes belong to the one species.

The average temperature of the water during the period was  $14.9^{\circ}\text{C}$ . The rate of growth is shown in the graph (Text-fig. 13).

*Survival apart from the host.* *T. tasmanica* is readily maintained under laboratory conditions. Two specimens removed from the crayfish, *Asta-*



13

*Temnocephala tasmanica* Haswell.

Fig. 13.—Graph showing growth of a specimen reared apart from its host from date of hatching, 12th February, 1964, to 2nd October, 1964, that is for 233 days.

*copsis franklinii*, were placed in water in a glass dish on 23rd October, 1964. The water in the dish was changed occasionally, but no special aeration was provided. The specimens were fed mainly with small particles from the internal organs of flies, especially from the intestine, fat body and Malpighian tubules. The two specimens are still alive at the present time, 30th September, 1966, after being maintained apart from the host for a period of 707 days.

*T. tasmanica* is able to survive for considerable periods without food and with very little air. An adult specimen was placed in 3.0 ml. of water in a specimen tube measuring 5.0 cm. x 1.2 cm, and the tube then firmly corked. No food was given and the cork was not removed. The specimen lived from 30th November, 1964, until 10th April, 1965, a period of 100 days. During this time it decreased in length from about 2.5 mm. to 0.46 mm.

*Temnocephala quadricornis* Haswell.

(Text-figs. 14-19)

**General Features.** In the contracted state the largest specimens measure about 9.0 mm. long and 6.0 mm. wide. The species is the largest member of the genus occurring in Tasmania. The colour of the dorsal surface is dark brown mottled with yellowish brown. A pair of yellowish spots marks the position of the excretory apertures and there is usually a transverse patch of yellow above the region of the intestine. The ventral surface is light brown and the lateral flange almost colourless. There are four tentacles and a short flat median lobe. In the resting state the inner pair of tentacles measure 3.7 mm. long, the outer pair 2.9 mm. and the median lobe 1.4 mm. Two eyes, situated about 2.0 mm. from the base of the median lobe, are present. The mouth is in the usual position on the ventral surface and about 2.0 mm. from the front. The sucker is large measuring about 2.6 mm. in diameter. Its posterior margin is overlapped by the end of the body. The genital aperture is slightly in front of the sucker.

**Body-wall and Integumentary Glands.** The usual integumentary layers are present. The cuticle is about 3 $\mu$  in thickness. Its surface is raised into numerous small conical papillae and perforated by

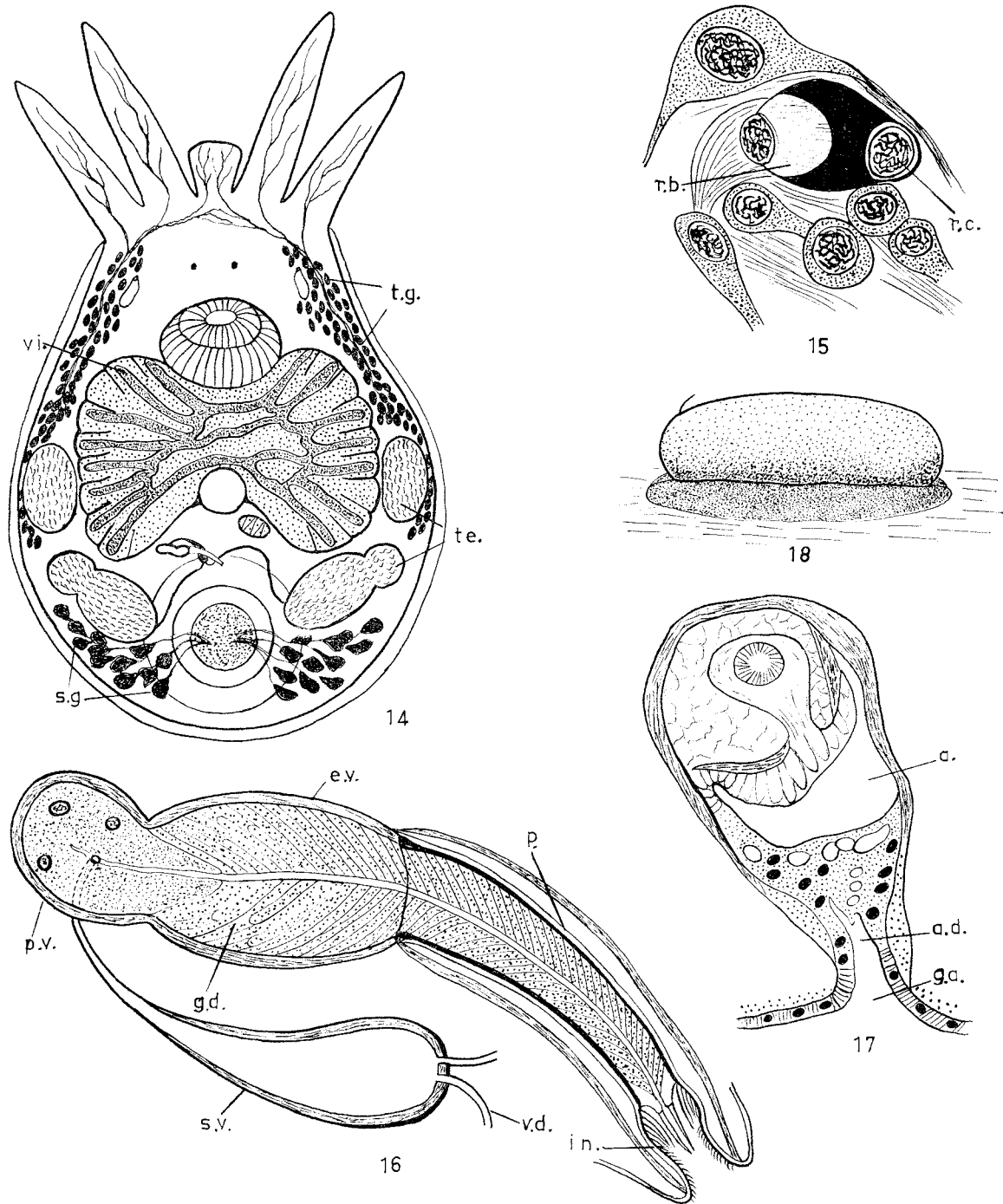
minute pores. The epidermis is about 15 $\mu$  thick. In section it is striated and appears to consist of vertical fibrillae. The nuclei of the epidermis are oval and measure about 21 $\mu$  x 15 $\mu$ . They are widely scattered. The basement membrane is about 7 $\mu$  in thickness. No cilia were found on the integument.

The dermal muscular sheath consists of a layer of transverse or circular muscles immediately internal to the basement membrane. Internal to the circular muscles is a much thicker layer of longitudinal muscles and between the two a thin layer of diagonal fibres. Numerous pigment granules lie in the parenchyma internal to the longitudinal muscles. The largest granules are about 6 $\mu$  in diameter. In the region between the front of the pharynx and the anterior end of the body is a second layer of circular muscles. This layer is dorsal to the layer of ventral longitudinal muscles. Numerous dorso-ventral fibres occur throughout the body. Most of the muscles appear tubular in section with a deeply staining cortex surrounding a non-staining core. Brandes (1892) observed a similar condition in the muscles of *Temnocephala brevicornis* Monticelli. However, Haswell (1893) considers the tubular appearance of the muscles to be due to unsatisfactory fixation and says it "is rarely seen in specimens that have been fixed by means of a corrosive sublimate or osmic acid solution". The specimens of *T. quadricornis* on which the present description is based were fixed in Apathy's fluid, which contains corrosive sublimate.

The tentacular or rhabdite glands extend along each side of the body from in front of the excretory vesicles to the posterior testes. The nuclei of the cells are about 36 $\mu$  in diameter and the rhabdites 6 $\mu$  in length. The sucker glands lie on each side of the posterior part of the body. They are larger than the tentacular glands and somewhat irregular in shape. Their ducts converge on the stalk of the sucker.

**Digestive System.** The mouth leads into a short pharyngeal pouch with strongly folded walls. The pharynx has the usual form of a pharynx bulbosus. It is about 1.10 mm. long and 1.52 mm. wide. The posterior sphincter is more strongly developed than the anterior one. A number of ganglion cells and a few gland cells occur among the radial muscles. Posteriorly the pharynx leads into a short oesophagus, which is surrounded by a large number of unicellular oesophageal glands. As in other species the intestine has the form of a somewhat rectangular sac. The anterior wall forms a pouch-like projection on each side of the pharynx. The posterior wall forms a concavity round the vesicula resorbens. The lumen of the intestine has nine septa on each side (Text-fig. 14). The outer surface exhibits corresponding constrictions. When fully formed the cells of the intestinal epithelium are elongate and club-shaped. The cell nuclei are basal in position. However, in some cases cell walls are absent and the epithelial lining forms a syncytium.

**Excretory Bladder.** The two apertures of the excretory system open on the dorsal surface, one on each side, in a transverse plane slightly behind the eyes. They are about 1.10 mm. from the margin. The bladders are long and pyriform, measuring



*Temnocephala quadricornis* Haswell.

FIG. 14.—General view of external and internal features.  
FIG. 15.—Section of eye with surrounding nerve cells.  
FIG. 16.—Longitudinal section of male reproductive organs.

FIG. 17.—Sagittal section of atrium and atrial duct showing syncytial plug.  
FIG. 18.—Egg viewed from the side.

about  $520\mu$  in length and  $190\mu$  in width. At the base each vesicle is bent on itself, and gradually narrows to form a tubular portion, which curves posteriorly and branches to form two main excretory vessels. One of the vessels bends upward and runs longitudinally above the intestine, the other bends downwards and runs longitudinally below the intestine. Closely applied to the posterior surface of the bladder is a large myoblast. At the base of the vesicle, where it is bent on itself are two nuclei. The wall of the bladder is thick and densely fibrous. It is furnished with few canals. The whole vesicle has a thin muscular investment. A number of large excretory cells occur in the parenchyma, especially near the dorsal surface above the reproductive system. The cytoplasm of the cells is traversed by numerous minute canals and in some cases definite cell-walls are absent. The nuclei are oval and large measuring  $57\mu \times 42\mu$ .

**Nervous System.** The structure of the brain and the distribution of the main nerve cords are much the same as in other species. The brain consists of a transverse mass of nerve fibres and is situated in front of the pharynx. On each side it curves slightly backward and downward. Arising from the front of the brain are two stout nerves which pass forward, one on each side of the eyes, and give off branches to the tentacles and median lobe. The usual dorsal, dorsolateral and ventral longitudinal nerves are given off from each side of the brain and pass backward. The dorsal longitudinal nerves extend upward, one on each side of the front of the pharynx, and run posteriorly above the intestine, uniting near the end of the body. The dorsolateral longitudinal nerves pass upwards and backwards behind the excretory bladder. They lie external to the anterior testes in the angle between the testes and the dorsal body wall. The ventral longitudinal nerves pass downwards at the sides of the pharynx and continue posteriorly at the sides of the intestine. They lie in the angle between the lower surface of the anterior testes and the intestine.

The two eyes are  $430\mu$  apart and situated above the front of the brain. Each consists of a pigmented cup about  $90\mu$  in diameter. The mouth of the cup is filled with a spherical refractive body (Text-fig. 15). The base of the cup is occupied by a single retinula cell. The refractive body has a somewhat fibrillar structure and is capped by a ganglion cell. The eye lies somewhat transversely with the refractive body directed outwards. Above and slightly in front of the eye is a large bipolar nerve cell.

In front of the brain are the usual two pairs of large cells, one pair more or less above the other. Their cytoplasm has a fibrillar structure and is traversed by numerous muscle strands. A distinct cell wall appears to be absent. The nuclei are oval and measure about  $75\mu \times 60\mu$ .

**Reproductive System.** In the male system there are two pairs of testes, an anterior pair and a posterior pair. The anterior testes lie one on each side of the intestine. They are oval in shape and measure 1.12 mm. long and 0.822 mm. wide. The posterior pair are situated, one on each side, behind the intestine (Text-fig. 14). They are bilobed and measure 1.46 mm. long and 0.85 mm. wide. The two testes on each side are united by a short

seminal duct.

The vasa deferentia arise ventrally from the inner lobe of the posterior testes. The vas deferens from the left testis passes directly to the base of the seminal vesicle, that from the right testis bends round in front of the atrium before reaching the vesicle. They enter the vesicle separately.

The seminal vesicle is situated more or less obliquely below the penis. It is elongate and pyriform in shape, measuring about 1.01 mm. long and 0.27 mm. in diameter at its widest part. Its wall is very stout being about  $45\mu$  in thickness and is formed mainly of circular muscles surrounding a thin layer of longitudinal muscles. The lumen has a thin protoplasmic lining with a few scattered nuclei. The distal end of the vesicle narrows to form a short seminal duct, which enters the anterior surface of the prostate vesicle.

The prostate vesicle is a rounded sac-like structure about 0.24 mm. in diameter (Text-fig. 16). It has thick muscular walls and its lumen is almost obliterated by a dense mass of finely fibrous protoplasm containing a few nuclei but no cell boundaries.

The ejaculatory vesicle is about 0.26 mm. in diameter and 0.58 mm. long. It is separated from the prostate vesicle by a slight constriction, but both vesicles have a similar and continuous muscular wall. The ducts of the granule glands enter on the anterior side below the junction with the prostate vesicle. On entering they surround the ejaculatory duct and extend into the penis.

The penis lies on the left side of the median plane. It slopes obliquely downward to open into the left side of the atrium. It is supported by the usual chitinous tube and is about 0.97 mm. long. At the base it is 0.21 mm. wide but tapers to 0.13 mm. at the apex. The introvert is about 0.30 mm. long and somewhat swollen in the proximal half. In the inverted state it is thickly lined with spines. Those lining the apical half are very short being only  $9\mu$  long. Those lining the basal half increase in length proximally from  $30\mu$  to  $120\mu$ . Several very long curved spines are attached to the end of the ejaculatory duct at the base of the introvert. These spines are about  $210\mu$  in length. When the introvert is half everted, they project into the atrium.

The granule glands are situated on each side of the intestine and extend from the excretory vesicle to the posterior testes. Some also lie along the courses of the vasa deferentia and at the sides of the seminal vesicle. Their ducts enter the ejaculatory vesicle through numerous small apertures on the anterior side near the junction with the prostate vesicle.

In the female reproductive system the germarium lies on the right of the median plane close behind the intestine. It is more or less ovoid in shape and measures  $390\mu$  long and  $260\mu$  wide. The germiduct is very short and the germarium opens almost directly into the right side of the ootype. The ova have the characteristic wedge shape.

The vasicula resorbens is a pyriform or almost spherical sac incorporated in the posterior wall of the intestine. It measures about  $312\mu$  in diameter. Haswell (1924) has described and figured a tempor-

any genito-intestinal canal leading from the front of the vesicle into the intestine. In the sections of one of the specimens examined in the present study part of the anterior wall of the vesicle is broken down, but the epithelium of the intestine is intact. Since the vesicle is almost empty it may be assumed that the canal is in process of closing. Posteriorly the vesicula resorbens gives rise to a short duct, about  $130\mu$  in diameter, which becomes continuous with the ootype.

Four receptacula seminis are arranged more or less symmetrically round the ootype slightly anterior to the opening of the germiduct. Each receptaculum is a finger-like diverticulum measuring  $150\mu$  long and  $48\mu$  wide, and possessing strong muscular walls.

Behind the entrance of the germiduct the ootype bends downwards and expands to form the uterus, which is almost vertical in position. Ventrally the uterus narrows giving rise to a short vagina which runs horizontally to enter the right side of the atrium. The uterus, ootype and vagina all have thick muscular walls. Numerous shell glands open into the uterus. The glands tend to fuse with one another forming a composite gland with several ducts.

The vitellarium consists of a number of slender lobes above and below the intestine. The lobes are more numerous dorsally than ventrally and tend to lie transversely. Some of them branch and form anastomoses. On each side of the posterior wall of the intestine the vitellarium gives rise to a vitelline duct. The two ducts converge on the ootype, which they enter near the openings of the receptacula seminis.

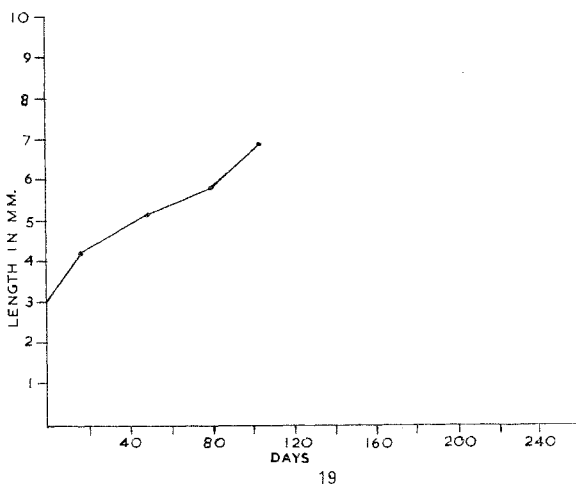
The atrium is a large sac-like structure disposed transversely. It is 0.78 mm. wide, 0.52 mm. high and 0.43 mm. from front to back. Its walls are strong and muscular with fibres running in all directions. When not distended by the presence of an egg, the walls are strongly folded. A number of atrial glands open into the atrium. They probably supply the cementing material by which the egg is attached. From the ventral side of the atrium a short atrial duct, surrounded by strong sphincter muscles, leads to the genital aperture. Between periods of reproductive activity the duct is closed by a plug, which seems to be derived from the epidermis (Text-fig. 17). It has the form of a syncytium containing a number of nuclei and vacuoles. It seems probable that the long curved spines, present in the introvert of the penis, are used to pierce the plug during copulation.

**Host and Localities.** *T. quadricornis* has been found only on the large fresh-water crayfish, *Astacopsis gouldi* (Clerk). Specimens of the crayfish taken in the Forth Falls rivulet (December, 1926), the Don River near Devonport (9th September, 1943) and Deep Creek near Smithton (30th January, 1966) were all found to be carrying the temnocephalid, which occurred mainly on the large chelae and the carapace.

**Eggs and Incubation.** The eggs are long, oval and very slightly reniform in shape. They measure about 2.91 mm. in length and 1.37 mm. in width. The capsule is dark brown and has a short slender projection from the upper surface near one end (Text-fig. 18). The eggs are usually deposited on the carapace, less frequently on the abdominal terga.

They are often placed in grooves or depressions of the surface and may occur singly or in groups. The whole under surface of the capsule is cemented to the place of attachment. When hatching takes place, the upper surface of the capsule is torn open longitudinally.

Specimens of *T. quadricornis* kept under laboratory conditions failed to deposit eggs and hence the exact period of incubation could not be determined. However, it appears to be prolonged. Three eggs removed from the host on the 30th January, 1966, were successfully hatched in the laboratory. One required 136 days, another 166 days and the third 196 days. In the last case the average temperature of the water during the period was  $13.9^{\circ}\text{C}$ . It may therefore be assumed that the incubation period at that temperature is not less than 28 weeks.



*Temnocephala quadricornis* Haswell.

Fig. 19.—Graph showing growth of a specimen reared apart from its host from date of hatching, 15th June, 1966, to 30th September, 1966, that is for 107 days.

**Rate of Growth.** The newly hatched young are dark brown like the adult. When contracted they measure about 3.03 mm. long and 2.63 mm. wide, but are able to extend to a length of 5.7 mm. A specimen which hatched on 15th June, 1966, from an egg removed from the host was maintained under laboratory conditions and its rate of growth recorded (Text-fig. 19). In the 107 days from the date of hatching to 30th September, 1966, it increased in length from 3.03 mm. to 6.74 mm., both measurements being made on the contracted animal. The average temperature of the water during the period was  $11.5^{\circ}\text{C}$ . If the rate of growth is maintained, adult size should be reached in about 190 days from hatching.

**Survival apart from the host.** Specimens of *T. quadricornis* removed from the host and kept under laboratory conditions did not feed very readily and failed to survive for more than 76 days. However, specimens hatched in the laboratory were much easier to maintain. They fed readily on particles of the internal organs of flies and have survived for at least 107 days.

A small specimen about 4.0 mm. long was placed in 3.0 ml. of water in a small specimen tube and the tube firmly corked, as was done in the case of *T. tasmanica*. The specimen survived for 56 days without food, change of water, or admission of fresh air.

*Temnocephala pygmaea* sp. n.

(Text-figs. 20-26, Pl. I, fig. 3)

**General Features.** When alive and in a contracted state the largest specimens measure about 1.60 mm. long and 1.03 mm. wide. When fully extended they measure 2.57 mm. long. The body is colourless and more or less translucent. It is convex above and flat or slightly concave below. The margin is surrounded by a narrow transparent flange. There are four tentacles and a short flat median lobe (Text-fig. 20). The outer tentacles are about three quarters as long as the inner tentacles. Two eyes, situated about  $342\mu$  from the front, are present. The mouth is a rounded aperture in the normal position on the ventral surface and about  $613\mu$  from the front. The sucker is large being about  $630\mu$  in diameter. It is overlapped by the posterior end of the body. The genital aperture is very slightly in front of the sucker.

**Body-wall and Integumentary Glands.** The cuticle is smooth and about  $1\mu$  in thickness. The epidermis is about  $6\mu$  thick and in sections exhibits the usual vertical striations. The nuclei are oval and measure  $5\mu \times 7\mu$ . They are few and widely scattered. The basement membrane is slightly thicker than the cuticle. Numerous fine pore-canal pass through the integument. No cilia could be found on any part of the surface.

The dermal muscular sheath consists of a thin layer of circular fibres immediately below the basement membrane, an inner thicker layer of longitudinal muscles and an intermediate layer composed of a few diagonal fibres. Below the intestine the layer of ventral longitudinal muscles is more than twice the thickness of the dorsal layer, but becomes thinner laterally. Between the mouth and the front of the body there is a well developed layer of transverse muscles immediately internal to the layer of ventral longitudinal muscles. Numerous dorso-ventral fibres pass through the parenchyma in all parts of the body.

The tentacular glands are numerous and are distributed in a broad band along the sides of the body. They extend from immediately in front of the excretory bladders to the posterior testes. Fine strands of ducts from the glands pass forward and give off a number of branches, which enter the tentacles and median lobe. The rhabdites formed by the glands are about  $6\mu$  in length. The sucker glands occur on each side of the posterior end of the body and also in a transverse band in front of the sucker. Their ducts pass through the stalk and spread out radially to all parts of the sucker.

**Digestive System.** The mouth leads into a short prepharynx or pharyngeal pouch, which has strongly folded walls. The bulbous pharynx is relatively large and has a transverse diameter of  $640\mu$  and a length of  $470\mu$ . The posterior sphincter is much more strongly developed than the anterior sphincter. Some pharyngeal glands are present among the radial muscles, but are not numerous.

The pharynx leads into a short oesophagus, which is surrounded by pyriform salivary glands. The opening into the intestine is encircled by a sphincter. The intestine has the usual form of a flat somewhat rectangular sac. In front it projects slightly on each side of the pharynx. Its posterior wall is concave round the vesicula resorbens. The lumen is partly divided by four pairs of septa which extend inwards from the lateral walls (Text-fig. 21). Corresponding constrictions of the intestine are very slight. The epithelium lining the lumen consists of elongate club-shaped cells filled with numerous rounded granules. The nuclei of the cells are basal in position. Externally the intestine is invested by a thin muscular layer.

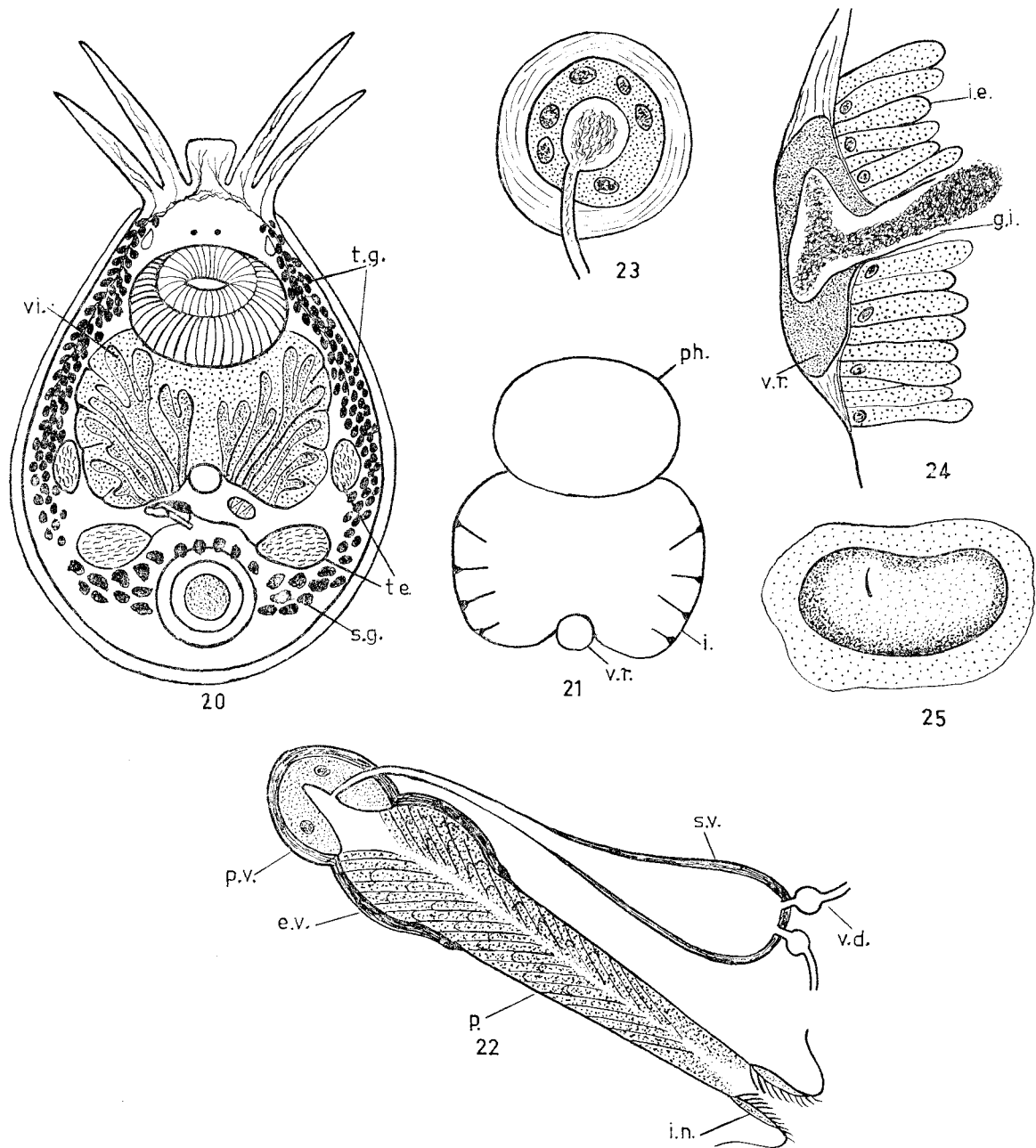
**Excretory Bladders.** The two excretory apertures are situated one on each side of the dorsal surface and in a transverse plane immediately behind the eyes. They are about  $264\mu$  from the margin. The bladder is somewhat pyriform, measuring  $178\mu$  long and  $96\mu$  wide. Its wall is thick and dense, with a number of small canals and vacuoles. Externally it is invested by a loose fibrous layer surrounded by a thin muscular sheath. The narrow inner end of the bladder is bent on itself. It gives rise to a short duct which divides to form two branches one of which passes forward and the other backward. Two nuclei are situated in the wall of the bladder near the inner end. A large spindle-shaped myoblast, which stains deeply with haematoxylin, is closely applied to the posterior surface of the bladder and extends from the external aperture almost to the inner end.

**Nervous System.** The brain consists of a transverse bar of fibrous nervous tissue surrounded by numerous ganglion cells. In front it gives off a pair of stout nerves, which pass forward and form branches which supply the tentacles and median lobe. The latter structure receives branches from both nerves. As in other species a pair of dorsal, a pair of dorso-lateral and a pair of ventral longitudinal nerves are given off from the sides of the brain. The dorsal longitudinal nerves are more slender than the others. They pass backward above the intestine and nearer to the median line than to the lateral margins. They are connected by a number of transverse commissures. The dorso-lateral nerves extend outwards from the brain and curve posteriorly behind the excretory bladders. They lie along the sides of the intestine and pass above the anterior testes and dorso-laterally to the posterior testes. The ventral longitudinal nerves extend downwards at the sides of the pharynx and continue towards the posterior below the sides of the intestine and ventral to the testes.

The eyes are situated above the front of the brain. They are separated by a distance of  $99\mu$ . Each has the form of a pigmented cup,  $30\mu$  in diameter, and poised obliquely. In the base of the cup is a single retinula cell, and in the mouth a more or less spherical refractive body.

In front of the brain are two large nuclei, about  $21\mu$  in diameter. They are situated in a common cytoplasm without a dividing cell wall.

**Reproductive System.** The male system consists of a pair of anterior testes, a pair of posterior testes, vasa deferentia, seminal vesicle, prostate vesicle, ejaculatory vesicle, penis and granule glands.



*Temnocephala pygmaea* sp. n.

Fig. 20.—General view of external and internal features.  
Fig. 21.—Outline of digestive canal.  
Fig. 22.—Longitudinal section of male reproductive organs.  
Fig. 23.—Transverse section of prostate vesicle.  
Fig. 24.—Parasagittal section of vesicula resorbens discharging contents through genito-intestinal canal.  
Fig. 25.—Egg viewed from above.

The anterior testes are oval in shape and lie one on each side of the posterior half of the intestine. In mature specimens they measure 340 $\mu$  long and 210 $\mu$  wide. The posterior testes are also oval and lie one on each side in a transverse position behind the intestine. They are larger than the anterior pair and measure 410 $\mu$  long and 270 $\mu$  wide. From the posterior end of each anterior testis a

short duct passes to the outer end of the neighbouring posterior testis. The vas deferens from the right posterior testis arises ventrally from the inner end of the testis, passes transversely in front of the atrium, and enters the base of the seminal vesicle. The vas deferens from the left posterior testis is much shorter. It likewise arises ventrally from the inner end of the testis, passes in front of the penis and enters the base of the seminal vesicle. The two vasa deferentia enter close together but independently. Each is swollen into a small bulb before entry (Text-fig. 22).

The seminal vesicle is elongate and pyriform in shape, about  $260\mu$  long and  $40\mu$  in diameter at its widest part. It lies above or on the right side of the penis and is almost parallel with it. At its distal end it narrows forming a seminal duct which enters the prostate vesicle on the right side. The wall of the seminal vesicle has an outer layer of circular muscles surrounding an inner layer of longitudinal muscles. The lumen is lined by a thin layer of protoplasm.

The prostate vesicle (Text-fig. 22) is a rounded sac-like structure about  $60\mu$  in diameter. It is situated on the left side of the body, behind the intestine and close below the dorsal muscles. Its wall is strongly muscular and its lumen is lined with a thick layer of finely granular protoplasm containing a few nuclei, but no cell boundaries (Text-fig. 23).

The ejaculatory vesicle is a bulbous structure continuous with the prostate vesicle and penis. It has a stout muscular wall and is lined with a layer of protoplasm. On the right side, below the junction with the prostate vesicle, it is entered by the ducts of the granule glands. These ducts surround the central ejaculatory duct and extend into the penis (Text-fig. 22).

The penis is almost straight and is directed obliquely downwards from the ejaculatory vesicle to the left side of the atrium. The wall of the penis is supported by the usual chitinous tube, which is about  $60\mu$  in diameter at the base tapering to  $30\mu$  at the apex. The introvert is  $78\mu$  long and forms about one quarter of the length of the penis, which measures about  $288\mu$  long. The lumen of the introvert is lined with rows of sharp spines varying in length from  $12\mu$  to  $60\mu$ . The longer spines are nearer the base of the introvert and the shorter ones near the apex.

The granule glands are numerous. They form a lateral band lying below the rhabdite or tentacular glands. They also occur along the courses of the vasa deferentia and partly surround the seminal vesicle. Their ducts enter the ejaculatory vesicle as described above.

The female reproductive system includes the germarium, vesicula resorbens, receptacula seminis, ootype, uterus, vitellarium and various glands.

The germarium is oval measuring  $102\mu$  long and  $81\mu$  wide. It is situated behind the intestine and to the right of the median plane. The ova at the base of the germarium are small and rounded, those near the middle wedge-shaped and those near the entrance to the germiduct large and rounded. The germiduct is very short and leads directly from the inner end of the germarium into the dorsal side of the ootype.

The vesicula resorbens is normally a large rounded sac about  $150\mu$  in diameter. Its shape, however, depends to some degree on the contraction and extension of the animal. In some cases it is laterally compressed, in others compressed from front to back. It is incorporated in the middle of the posterior wall of the intestine. In some specimens the lining of the vesicle is thick and finely granular, in others it is vacuolated or very thin. The whole sac has a thin muscular investment. In one series of sections the genito-intestinal canal was open and the vesicle discharging its contents into the intestine (Text-fig. 24). Posteriorly a short duct from the vesicle becomes continuous with the ootype.

There are four receptacula seminis arranged round the ootype and opening into it slightly in front of the entrance of the germiduct. Each receptaculum is short and finger like, about  $33\mu$  long and  $12\mu$  wide. Its wall is thick and muscular being continuous with that of the ootype.

The ootype has thick muscular walls and small lumen. It runs posteriorly from the vesicula resorbens and after being entered by the receptacula seminis, the vetelloducts and the germiduct, it curves downwards and forwards enlarging to form the uterus. The latter has strongly folded muscular walls and is surrounded by a number of pyriform shell-glands. At its lower end the uterus forms a narrow vagina, which enters the right side of the atrium.

The vitellarium, when fully developed, has the form of slightly branched finger-like lobes situated above and below the intestine. The lobes are directed more or less longitudinally (Text-fig. 20). Those of each side unite posteriorly to form a vitelloduct. The two vitelloducts thus formed enter the ootype laterally near the entrance of the germiduct.

The atrium is an oval chamber lying slightly behind the genital aperture. When not distended by the presence of an egg it is about  $75\mu$  wide. However, it is capable of great expansion and when containing an egg it may occupy almost the whole space between the posterior testes, other organs being pushed out of place. Numerous large unicellular fusiform glands open into the atrium. The atrial duct slopes downward and forward. It is surrounded by strong sphincter muscles.

*Locality and Host.* This species was found on the large fresh-water crayfish, *Astacopsis gouldi* (Clark), taken at Britton's Swamp, near Smithton, Tasmania, 30th January, 1966. The temnocephalid occurred mainly on the third maxillipeds.

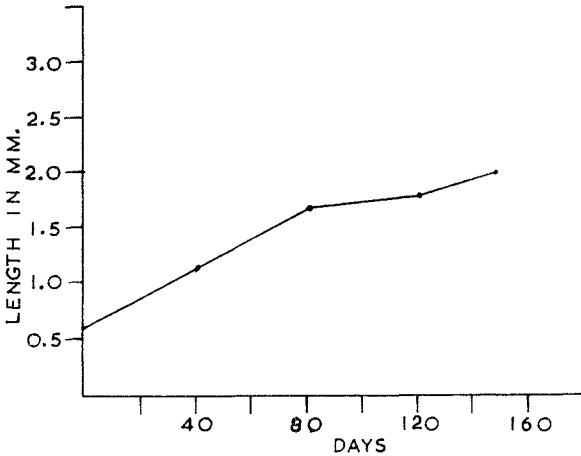
*Eggs and Incubation.* The egg is slightly reniform and measures about 0.57 mm. long and 0.30 mm. wide. It is enclosed in a pale yellowish-brown transparent capsule, which has a short slender projection on the upper surface about a third of the length from one end (Text-fig. 25). The whole of the under surface of the capsule is cemented to the place of attachment. The eggs are deposited on the sides of the carapace of the crayfish, especially in the marginal groove. Three eggs were laid by specimens of *T. pygmaea* kept in water in glass dishes in the laboratory. They hatched in 31 or 32 days, the average temperature of the water being between  $19^{\circ}\text{C}$ . and  $20^{\circ}\text{C}$ . (Table 3).

TABLE 3.

Egg	Date laid	Date hatched.	Period of incubation in days.	Average Temperature of the water in degrees C.
A	8 February, 1966	12 March, 1966	32	19.7
B	14 February, 1966	17 March, 1966	31	19.8
C	23 February, 1966	27 March, 1966	32	19.4

*Rate of Growth.* In the contracted condition newly hatched young are about 0.63 mm. long and 0.34 mm. wide. They are colourless and translucent. A specimen, which hatched from an egg removed from the carapace of the crayfish, was reared to full size in the laboratory in 152 days (Text-fig. 26). As in the case of preceding species it was fed on small particles of the internal organs of flies.

*Survival apart from the host.* Adult specimens removed from the crayfish and kept under laboratory conditions did not live longer than 59 days. However, specimens hatched and reared in the laboratory have survived for 222 days. An adult specimen, placed in 3.0 ml. of water in a small specimen tube and the tube then firmly corked, survived for 48 days without food, change of water or admission of air. During the period it decreased in size to that of a newly hatched specimen.



26

*Temnocephala pygmaea* sp. n.

Fig. 26.—Graph showing growth of a specimen reared apart from its host from date of hatching, 31st January, 1966, to 24th July, 1966, that is for 152 days.

*Temnocephala aurantiaca* Haswell

(Text-figs. 27-32, Pl. I, fig. 4)

*General Features.* In the contracted state the largest specimens measure 2.57 mm. long and 1.31

mm. wide. However, they are able to extend to about 3.43 mm. in length. The body is convex above and flat below. The animal is more or less white with a yellow tinge on the dorsal surface. The extent of the colouration varies considerably in different specimens, but is generally well marked behind the intestine. Four tentacles and a short median lobe are present (Text-fig. 27). Two eyes are situated about 0.29 mm. from the base of the median lobe. The excretory apertures occur one on each side of the dorsal surface in a transverse plane slightly behind the brain. They are about 180 $\mu$  from the margin. The mouth is in the usual position on the ventral surface and about 0.60 mm. from the front of the body. The sucker is 350 $\mu$  in diameter. It is overlapped by the posterior end of the body. The genital aperture is usually about 75 $\mu$  in front of the sucker, but in contracted specimens may be overlapped by the front margin of the sucker.

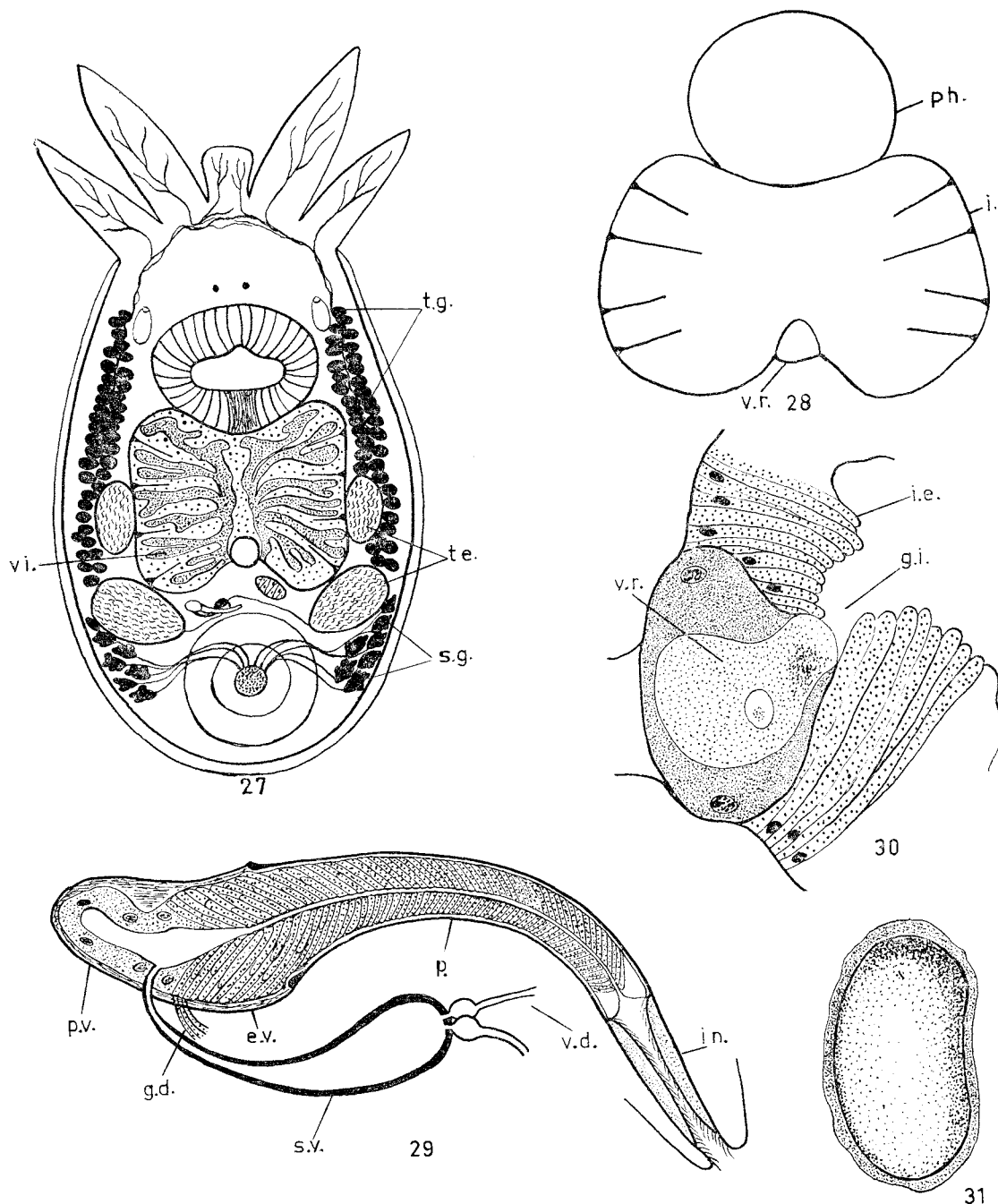
*Body-wall and Integumentary Glands.* The cuticle is about 3 $\mu$  in thickness. It is smooth and perforated by numerous minute pores. In section the epidermis, which is about 6 $\mu$  in thickness, has the usual striated appearance. The nuclei are widely scattered. They are about 7 $\mu$  in diameter. The basement membrane is slightly thinner than the cuticle. No cilia were found on any part of the integument.

The dermal muscular sheath has the usual form. Immediately below the basement membrane is a thin layer of transverse or circular muscles. These surround a much thicker layer of longitudinal muscles. Between the two layers are a few diagonal fibres. On the ventral side the layer of longitudinal muscles is much more strongly developed than on the dorsal side. In front of the mouth there is a second layer of transverse muscles. This layer is internal to the ventral longitudinal muscles.

The tentacular or rhabdite glands form a longitudinal band on each side of the body and extend from the excretory vesicles to the posterior testes. Each band is made up of a large number of oval follicles, which measure about 45 $\mu$  x 36 $\mu$ . They are closely arranged and lie transversely. Fine thread-like ducts pass forward from the glands to the tentacles and median lobe, the latter receiving ducts from the glands on both sides of the body. The sucker glands are situated at the posterior end of the body and lie on each side behind the posterior testes. They are larger than the tentacular glands and somewhat lobed.

**Digestive System.** The mouth leads into a short pharyngeal pouch. The pharynx has the usual form of a pharynx bulbosus. It is about  $440\mu$  in

diameter and  $340\mu$  long. The posterior sphincter is more strongly developed than the anterior sphincter. A few pharyngeal glands and ganglion



*Temnocephala aurantiaca* Haswell.

Fig. 27.—General view of external and internal features.

Fig. 28.—Outline of digestive canal.

Fig. 29.—Longitudinal section of male reproductive organs.

Fig. 30.—Parasagittal section of vesicula resorbens with the genito-intestinal canal in course of formation.

Fig. 31.—Egg viewed from above.

cells are scattered among the radial muscles. Between the pharynx and intestine is a short oesophagus into which open a few pyriform salivary glands. The entrance of the oesophagus into the intestine is surrounded by a weak sphincter. The intestine is a more or less rectangular sac. Its anterior wall projects slightly on each side of the pharynx. The posterior wall is concave round the vesicula resorbens. Projecting into the lumen of the intestine on each side are four septa, thus giving rise to five pairs of lateral caeca (Text-fig. 28). The length of the intestine measured in the median plane is shorter than its width.

**Excretory Bladders.** The vesicles are situated one on each side of the front of the pharynx. Each is about  $135\mu$  long and  $84\mu$  in diameter and has the usual form. The thick wall surrounding the central lumen is strongly vacuolated or traversed by large canals. As in other species two nuclei are situated at the base of the vesicle.

**Nervous System.** The brain is a transverse fibrous mass of nervous tissue lying in front of the pharynx. It is about  $210\mu$  in width and is curved slightly downward and backward on each side. Anteriorly it gives off a pair of stout nerves, which pass outwards and forwards, dividing into branches, which enter the tentacles and median lobe. Arising from each side of the brain are the usual dorsal, dorso-lateral and ventral longitudinal nerves. In live lightly pigmented specimens the arrangement of the dorsal and dorso-lateral nerves may be readily observed through the integument. The dorsal nerves lie above the pharynx and intestine. They pass posteriorly, one on each side of the median plane, and unite behind the stalk of the sucker. The dorso-lateral nerves lie one on each side of the intestine. They extend posteriorly passing on the outer side of the dorsal half of the anterior testes. Numerous transverse commissures connect the dorsal nerves to each other and to the dorso-lateral nerves. The ventral longitudinal cords, which are much stouter than the others, pass downwards from the brain and extend posteriorly. They lie one on each side of the intestine and close to the ventral muscles. They continue posteriorly below the testes.

The eyes are situated immediately above the front of the brain. They are about  $60\mu$  apart and each has the form of a pigmented cup about  $27\mu$  in diameter. They are poised obliquely.

Immediately in front of the brain are two pairs of very large cells, one pair above the other. The upper pair are about  $90\mu$  in width and appear fused. Their cytoplasm is dense and fibrous. The nuclei are about  $30\mu$  in diameter and have a large nucleolus. The lower pair of cells are about  $105\mu$  in width and quite separate. Their cytoplasm is fibrous but not as dense as that of the upper pair and the fibres have a radial arrangement. Their nuclei are  $24\mu$  in diameter and have a somewhat smaller nucleolus.

**Reproductive System.** In the male system there are two pairs of testes, an anterior pair situated one on each side of the posterior half of the intestine, and a posterior pair situated obliquely behind the posterior lateral angles of the intestine. The anterior pair are oval in shape,  $230\mu$  long and  $130\mu$  wide. The posterior pair are somewhat broadly pyriform and larger than the anterior pair. They

measure  $310\mu$  long and  $180\mu$  wide. A short duct leads from the ventral side of the hinder end of the anterior testis to the ventral side of the posterior testis, which it enters.

The vasa deferentia arise ventrally from the inner ends of the posterior testes. That from the left testis leads directly to the base of the seminal vesicle, whilst that from the right testis passes round the front of the atrium, before reaching the vesicle. The two vasa deferentia enter separately, and each forms a small bulbous expansion before entering (Text-fig. 29).

The seminal vesicle lies somewhat obliquely below the penis. It is elongate and pyriform, being about  $180\mu$  in length and  $54\mu$  in diameter at its widest part. Its distal narrow part forms a seminal duct, which opens into the under side of the prostate vesicle (Text-fig. 29).

The prostate vesicle is helmet-shaped, about  $69\mu$  long and  $84\mu$  wide. It has stout muscular walls and a thick lining of finely granular protoplasm with a few nuclei. In most specimens the vesicle is slightly bent to one side.

The ejaculatory vesicle is about  $60\mu$  long and  $91\mu$  in diameter. It is entered ventrally near its junction with the prostate vesicle by the ducts of the granule glands. The ducts surround the central ejaculatory canal and extend into the penis (Text-fig. 29). The figure given by Haswell (1900) does not differentiate between the prostate vesicle and the ejaculatory vesicle.

The penis (Text-fig. 29) has the usual structure. It is about  $410\mu$  long. The diameter is  $90\mu$  at the base and tapers to  $18\mu$  at the apex. The introvert is  $120\mu$  long and lined with needle-like spines, which vary in length from  $11\mu$  to  $21\mu$ . The longest spines are near the base and the shorter ones near the apex, when the introvert is inverted. The penis curves downwards and opens into the atrium dorsally almost above the genital aperture.

The granule glands lie on each side of the body below and sometimes between the tentacular glands. They extend from the excretory bladders to the posterior testes. Some are also situated along the vasa deferentia and at the sides of the seminal vesicle. Their ducts enter the ventral side of the ejaculatory vesicle as described above.

In the female reproductive system the germarium lies on the right side of the median plane close behind the intestine. It is ovoid in shape, about  $90\mu$  long and  $60\mu$  wide. The germiduct is very short and opens into the right side of the ootype.

There are four receptacula seminis. They are arranged more or less symmetrically round the ootype slightly anterior to the entrance of the germiduct. They are very short being but small pouches in the wall of the ootype.

Anteriorly the ootype leads by a very short duct into the vesicula resorbens, which is incorporated in the middle of the posterior wall of the intestine. The shape of the vesicle varies considerably. In some cases it is spherical and about  $84\mu$  in diameter, in others laterally compressed. It generally has a thick lining of finely granular protoplasm containing a few nuclei but no cell boundaries. Sometimes the lumen is divided into

an anterior and posterior compartment by a transverse septum. This partition may be developed prior to the formation of the genito-intestinal canal. The duration of the latter structure appears to be extremely short, since, although twenty-five specimens were examined in serial sections, not one was found to have the canal open. Several, however, showed it in process of formation (Text-fig. 30).

Behind the entrance of the germiduct the ootype bends ventrally and expands to form the uterus. At the lower end the uterus narrows forming a short vagina, which enters the right side of the genital atrium. The ootype, uterus and vagina have thick muscular walls and are surrounded by numerous fusiform unicellular glands.

The vitellarium consists of a number of branched lobes situated above and below the intestine. The lobes are mainly transverse in direction. They lead into a pair of vitelloglands, which open, one on each side, into the ootype near the receptacula seminis.

The genital atrium is a large transverse chamber with strong muscular walls. It is about  $178\mu$  in width and slopes upward on each side, its dorsal wall being depressed by the apex of the penis. Opening into the atrium are a number of atrial glands. The exit duct leading to the genital aperture is almost vertical and about  $69\mu$  in length.

**Host and Locality.** The specimens of *T. aurantiaca* were found on the burrowing land-crayfish, *Engaeus cunicularius* Erichson, at Wayatinah, Tasmania, during October, 1960 and December, 1964. The crayfish had made their burrows in damp soil at the side of a small runnel flowing down a hillside in an area of rain forest. As many as 84 specimens of the temnocephalid were collected from a single crayfish. They occurred mainly on the carapace and thoracic appendages.

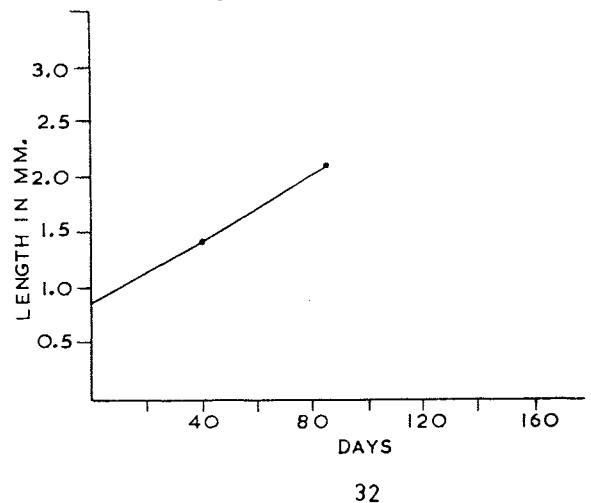
The specimens on which Haswell (1900) based his brief description are recorded as having been taken from an undetermined species of *Astacopsis* "found in burrows in damp ground in the neighbourhood of the Dee River towards the centre of Tasmania". As a rule species of *Astacopsis* found in Tasmania do not make burrows in the soil. The Dee River is only about 12 miles from Wayatinah and *Engaeus cunicularius* is the most common burrowing crayfish in the locality. As Haswell's so-called *Astacopsis* was not determined and was found in a burrow, one may doubt the accuracy of the record.

**Eggs and Incubation.** The eggs of *T. aurantiaca* are pale cream in colour and enclosed in a pale yellow capsule. They are very slightly reniform in shape and about  $620\mu$  long and  $370\mu$  wide (Text-fig. 31, Pl. I, fig. 4). A minute projection occurs on the upper surface of the capsule near one end. The projection is so small that it is easily overlooked. The eggs are deposited on the inner surface of the gill-cover of the crayfish. In one specimen of *Engaeus cunicularius* there were 100 eggs in the right and 90 in the left gill-chamber. The eggs are cemented by the whole under surface of the capsule. The upper surface splits open longitudinally when the young one hatches.

Adults of *T. aurantiaca* kept under laboratory conditions in glass dishes sometimes deposited their eggs in the dishes. However, the eggs failed to

hatch and hence the exact period of incubation was not determined. Eggs removed from the gill-chamber of the host hatched readily. Fourteen eggs removed on 3rd December, 1964, were kept in water in the laboratory and the water renewed regularly. All the eggs hatched, the last one on 28th January, 1965. It would appear, therefore, that the incubation period during summer is not less than eight weeks.

**Rate of Growth.** A specimen of *T. aurantiaca*, which hatched on 4th December, 1964, from an egg removed from the host, was  $0.74\text{ mm.}$  long and  $0.40\text{ mm.}$  wide in the contracted state. It was kept in water in a small glass dish and fed on small particles of earth-worms and crushed flies. By the 31st March, 1965, that is after 117 days, it measured when contracted  $2.05\text{ mm.}$  long and  $0.97\text{ mm.}$  wide. Its rate of growth is shown in the graph (Text-fig. 32). Although maintained for another 207 days, it did not grow any larger.



*Temnocephala aurantiaca* Haswell.

Fig. 32.—Graph showing growth of a specimen reared apart from its host from date of hatching, 4th December, 1964, to 31st March, 1965, that is for 117 days.

**Survival apart from the host.** Adult specimens removed from their host on 3rd December, 1964, and kept under laboratory conditions survived until 5th August, 1965, that is for 245 days. A specimen placed in 3.0 ml. of water in a small specimen tube and the tube firmly corked survived for 70 days without admission of air, renewal of the water, or provision of food.

#### *Temnocephala fulva* sp. n.

(Text-figs. 33-38)

**General Features.** In a contracted state the largest specimens are about  $1.71\text{ mm.}$  long and  $1.31\text{ mm.}$  wide. The widest part of the body is in the anterior half. The dorsal surface is strongly convex; the ventral surface flat or concave. The colour is mainly golden brown and is well marked on the anterior and posterior thirds of the dorsal surface. There are four tentacles and a short median lobe. The mouth and genital aperture are in the usual positions on the ventral surface. The sucker is

large being  $560\mu$  in diameter. Posteriorly it is overlapped by the end of the body. Two eyes are present and situated about  $274\mu$  from the base of the median lobe.

**Body-wall and Integumentary Glands.** The cuticle is smooth and slightly less than  $3\mu$  in thickness. The epidermis has the usual striated appearance. It is about  $6\mu$  thick and has a few scattered nuclei, which are about  $7\mu$  in diameter. The basement membrane has about the same thickness as the cuticle. The layer of circular muscles lying immediately below the basement membrane is very poorly developed and is not as thick as the epidermis. The layer of longitudinal muscles is much stronger and is somewhat thicker ventrally than dorsally. The intermediate layer of diagonal fibres is also better developed on the ventral side.

The tentacular or rhabdite glands lie in a longitudinal band on each side of the body and extend from the excretory bladders to the posterior testes (Text-fig. 33). They are oval in shape and measure about  $48\mu \times 33\mu$ . The rhabdites are less than  $3\mu$  in length. Ducts from the glands extend forward on each side and enter the tentacles and median lobe.

The sucker glands form a group on each side of the body behind the posterior testes. They are larger than the tentacular glands and somewhat lobed. Their ducts enter the stalk of the sucker and then spread out in the disk.

**Digestive System.** The mouth is a more or less circular aperture,  $36\mu$  in diameter, and about  $160\mu$  from the base of the tentacles. It leads into a short prepharynx. The pharynx has the usual bulbous form. It is  $340\mu$  in diameter and  $310\mu$  in length. A number of ganglion cells and pharyngeal glands are distributed among the radial muscles. The posterior sphincter is more strongly developed than the anterior sphincter. The oesophagus is short and its entrance into the intestine is surrounded by sphincter muscles. The intestine has the form of a flat, more or less rectangular, sac. In front it extends forward on each side of the pharynx. Posteriorly it extends backward for a short distance on each side of the vesicula resorbens. The lumen of the intestine is partially divided on each side by seven septa (Text-fig. 34).

**Excretory Bladders.** The apertures of the excretory system are situated on each side of the dorsal surface in a transverse plane slightly in front of the pharynx. They are about  $260\mu$  from the lateral margin. The excretory vesicles lie one on each side midway between the pharynx and the side of the body. Each is somewhat rounded, measuring  $120\mu$  long and  $110\mu$  wide. Close to the anterior surface of the vesicle is a large fusiform myoblast, which stains deeply with haematoxylin.

**Nervous System.** The brain lies in the normal position in front of the pharynx. It has the form of a transverse bar of nerve fibres and is about  $270\mu$  wide. Anteriorly it gives rise to a pair of stout nerves, that pass forward and divide forming branches, which go to the tentacles and median lobe. Arising from each side of the brain are the dorsal, dorsolateral and ventral longitudinal nerves. The dorsal nerves pass backward above the intestine, one on each side of the median plane, and unite near the posterior end of the body. The dorso-

lateral pair are situated on each side of the intestine. They lie close below the dorsal musculature and on the inner side of the anterior testes. The ventral pair pass downward, one on each side of the pharynx, and extend posteriorly close to the ventral musculature and at the sides of the intestine.

The eyes have the usual form of pigmented cups about  $24\mu$  in diameter and  $78\mu$  apart. The base of the cup is occupied by a single retinula cell and the mouth of the cup by a spherical refractive body.

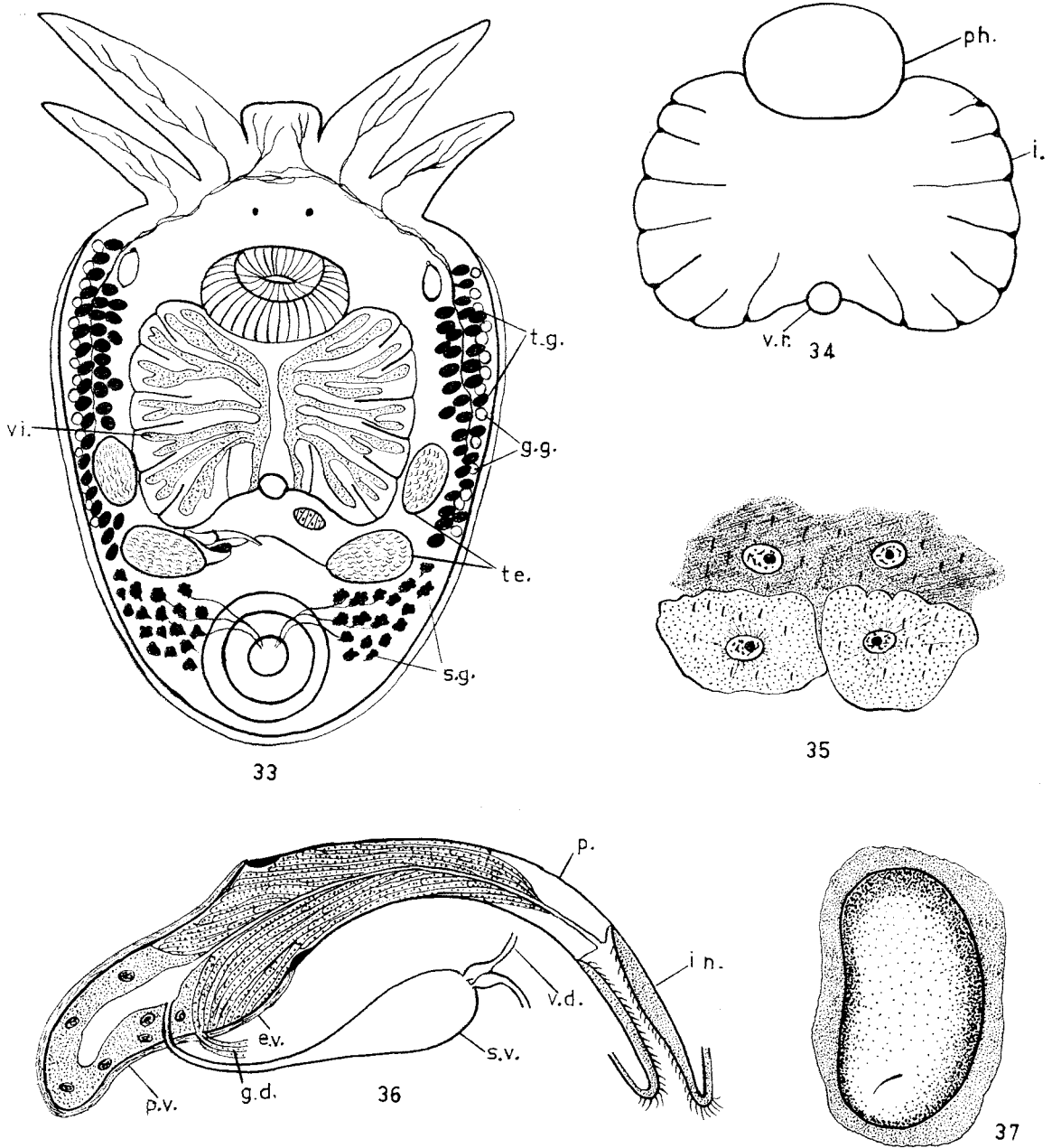
As in the other species two pairs of large cells, one pair above the other, occur close in front of the brain (Text-fig. 35). The upper pair are irregular in shape, without definite cell walls and appear fused. Their cytoplasm is very dense, finely fibrous and stains pink with eosin. Their nuclei are oval measuring  $27\mu \times 21\mu$ . The lower pair of cells are rounded and somewhat lobed. They are separate and have definite walls. Their cytoplasm is less dense and stains bluish with haematoxylin but does not stain with eosin. The nuclei measure  $24\mu \times 18\mu$ . Numerous muscle fibres pass through both pairs of cells. As mentioned under *T. cita* these cells do not appear to form part of the nervous system. They may be paranephrocytes and excretory in function but are always closely associated with the brain.

**Reproductive System.** In the male system there are four testes, an anterior pair and a posterior pair. The anterior pair are situated one on each side of the posterior half of the intestine. They are oval and up to  $340\mu$  in length and  $120\mu$  in width. The posterior pair are situated one on each side behind the intestine. They are somewhat pyriform in shape and have the narrow end directed inwards. They measure up to  $340\mu$  in length and  $160\mu$  in width. On each side a short duct passes from the anterior to the posterior testis. The vasa deferentia arise from the inner ends of the posterior testes. That from the left testis bends forward and passes directly to the base of the seminal vesicle, whilst that from the right testis curves round the front of the atrium before reaching the vesicle. The two vasa deferentia enter the vesicle separately, but close together. Each is slightly expanded before entry.

The seminal vesicle (Text-fig. 36) lies more or less transversely below the penis. It is elongate and pyriform in shape, about  $220\mu$  long and  $60\mu$  wide. Its distal end narrows to form a seminal duct, which enters the prostate vesicle ventrally.

The prostate vesicle lies on the left side close behind the intestine and immediately below the dorsal musculature. It is somewhat conical or helmet-shaped,  $116\mu$  long and  $72\mu$  wide at the base. It has a strong muscular wall and a thick protoplasmic lining, which is finely granular. A few nuclei are found in the lining but no cell boundaries. Externally the prostate vesicle merges into the ejaculatory vesicle without any distinct demarcation. It receives the duct from the seminal vesicle near its base.

The ejaculatory vesicle is about  $92\mu$  long and, when not distended,  $81\mu$  wide. It is entered ventrally near its junction with the prostate vesicle by the ducts of the granule glands. The ducts surround the ejaculatory canal and extend into the penis.



*Temnocephala fulva* sp. n.  
 Fig. 33.—General view of external and internal features.  
 Fig. 34.—Outline of digestive canal.  
 Fig. 35.—Transverse section through two pairs of large cells in front of brain.

Fig. 36.—Longitudinal section of male reproductive organs.  
 Fig. 37.—Egg viewed from above.

The penis lies more or less transversely on the left side of the body behind the intestine. It has the usual form and is about  $405\mu$  long. Its diameter at the base is  $81\mu$  and tapers to  $30\mu$  at the apex.

The introvert is  $135\mu$  long, thus forming one third of the length of the penis. The spines lining the introvert are very short being only about  $6\mu$  in length. They are uniform in size, except those

at the apex which are a little longer. The penis curves downward and projects into the left side of the atrium (Text-fig. 36).

The granule glands are distributed along the sides of the body and are mostly below the tentacular glands. They also occur along the vasa deferentia and at the sides of the seminal vesicle. Their ducts enter the ejaculatory vesicle as described above.

In the female system the germarium lies on the right side of the body close behind the intestine. It is about  $105\mu$  long and  $60\mu$  wide. It opens by a very short germiduct into the right side of the ootype.

There are four receptacula seminis. They are small and finger-like. The largest is  $24\mu$  long and  $9\mu$  wide. They are arranged round the ootype and open into it anterior to the entrance of the germiduct.

The anterior end of the ootype forms a short duct leading to the vesicula resorbens. The latter is a laterally compressed sac incorporated in the middle of the posterior wall of the intestine. Its transverse diameter is  $90\mu$  and its dorsoventral diameter  $165\mu$ . The lumen is small owing to the presence of a thick protoplasmic lining, which is finely granular and provided with a few nuclei. The opening into the vesicle is surrounded by the usual radial and sphincter muscles.

Behind the entrance of the germiduct the ootype bends ventrally and enlarges to form the uterus. At its lower end the uterus narrows giving rise to a short vagina, which enters the right side of the atrium. The ootype, uterus and atrium have strong muscular walls and are surrounded by a number of fusiform unicellular glands, which stain deeply with haematoxylin.

The vitellarium consists of a number of branched lobes situated above and below the intestine. Most of the lobes are directed transversely (Text-fig. 33). Posteriorly the vitellarium gives rise to a pair of viteloducts, which open, one on each side, into the ootype near the entrances of the receptacula seminis.

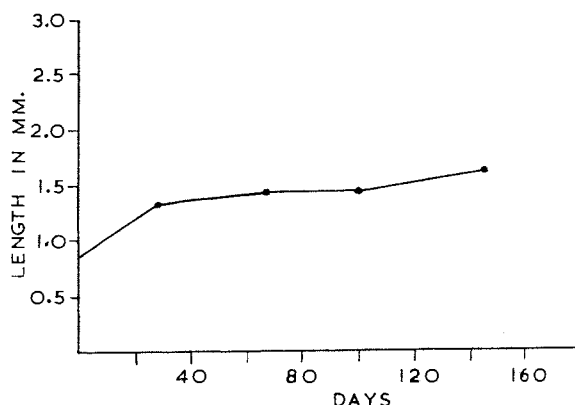
**Host and Locality.** Thirteen specimens of *T. fulva* were taken from the land-crayfish, *Parastacoides tasmanicus* (Erichson), found in burrows in damp soil near Lake Pedder, Tasmania, 25th February, 1966. The temnocephalid occurred mainly on the carapace and large chelae of the crayfish.

**Eggs and Incubation.** The eggs are pale yellow and enclosed in yellowish brown capsules. They are very slightly reniform and measure  $630\mu$  long and  $370\mu$  wide (Text-fig. 37). The upper surface of the capsule has a short curved projection about one fifth of the length of the egg from one end. The eggs are deposited singly in the gill-chamber. They are placed on the inner wall of the branchiostegite and cemented for the full length of the under surface of the capsule.

No eggs were laid by specimens of *T. fulva* kept apart from their host under laboratory conditions and hence the exact period of incubation could not be determined. However, twelve eggs removed from the gill-chamber of the crayfish were kept in water in small glass dishes, the water being changed every one or two days. Eleven of the eggs hatched. The

longest time required by any one of them was 63 days, the average temperature of the water being  $16.8^{\circ}\text{C}$ . It may be assumed, therefore, that at that temperature the incubation period is not less than nine weeks. In the process of hatching the capsule ruptures more or less longitudinally on the upper surface.

**Rate of Growth.** The newly hatched young are white and translucent. When contracted they usually measure about  $0.857\text{ mm.}$  long and  $0.571\text{ mm.}$  wide. A specimen which hatched on 25th April, 1966, was reared to maturity in the laboratory by feeding it with small particles of the internal organs of flies. It lived for 146 days and grew to a length of  $1.60\text{ mm.}$  and a width of  $0.97\text{ mm.}$  when contracted. The rate of growth is shown in the graph (Text fig. 38).



38

*Temnocephala fulva* sp. n.

Fig. 38.—Graph showing growth of a specimen reared apart from its host from date of hatching, 25th April, 1966, to 18th September, 1966, that is for 146 days.

**Survival apart from the host.** Adult specimens removed from their host and maintained under laboratory conditions did not thrive and failed to survive longer than a month. However, as indicated above, young ones hatched in the laboratory live much longer.

## DISCUSSION

The ability of various species of *Temnocephala* to survive for some time after removal from their hosts has been mentioned by a number of authorities, notably, Philippi (1870), Weber (1889), Chilton (1889), Haswell (1893), Goetsch (1935), Pereira & Cuocolo (1941) and Fyfe (1942). In most cases, however, no exact data on the duration of survival apart from the host are given. For example Haswell (1893) simply states that the forms with which he had the opportunity of experimenting were "able to live for a very long time, it might be almost said indefinitely after removal from the surface of their host". Chilton (1889) records specimens of *T. novaezealandiae* as living for months apart from their host. Pereira & Cuocolo (1941), on the other hand, provide more definite information on *T. brevicornis* Monticelli, which normally lives on the integument of certain freshwater turtles in Brazil. They removed a number of

the temnocephalids from their hosts and kept them in small aquaria, feeding them on particles of tubificid and naiddid worms. The temnocephalids survived for 71 days, and during this period deposited eggs in the aquaria. Some of the eggs hatched in 12 to 18 days. Most of the young did not survive longer than 15 days, but one lived for 93 days.

The Tasmanian species of *Temnocephala* described above varied in their ability to survive apart from their hosts. *T. cita* and *T. fulva*, both from the burrowing land-crayfish, *Parastacoides tasmanicus*, lived for about a month after removal from their host. However, *T. tasmanica* from *Astacopsis franklinii* has survived for 707 days and *T. aurantiaca* from *Engaeus cunicularius* for 245 days.

The nature of the relationship existing between temnocephalids and their hosts is obscure. Pereira & Cuocolo regard *T. brevicornis* as being an inquiline, obtaining from its chelonian hosts shelter needed for its existence and food in the form of naiddid worms, which occur on the integument of the turtles. An examination of the intestinal contents of *T. tasmanica* immediately after removal from its host showed that its normal food included chironomid larvae, nematodes, diatoms and *Stratioidrilus tasmanicus*. Of these, nematodes and *Stratioidrilus tasmanicus* are frequently found in the gill-chamber of the crayfish. Diatoms and chironomid larvae are probably stirred up from the bed of the creek during the movements of the crayfish in search of food. The normal food of *T. aurantiaca* includes Ostracods and Cyclopids, both of which occur in the mud in the burrows of *Engaeus cunicularius*. Under laboratory conditions and apart from their hosts both *T. tasmanica* and *T. aurantiaca* feed readily on particles of the internal organs of flies. The frequency with which many temnocephalids are found on or near the mouth-parts of their crustacean hosts suggests that they may share the food of their hosts by seizing small particles that float in the water, or which become caught on the setae of the oral appendages, while the crayfish is feeding. In the laboratory temnocephalids readily accept particles of food offered on the point of a needle, just as they might take it from the point of a seta.

Baer (1953) considers that the localization of the temnocephalid on its host ensures that it meets a continually renewed current of water needed to satisfy its oxygen requirement. He regards the association as a type of phoresy of an obligatory nature. Fyfe (1942) states that *T. novae-zealandiae* is able to live for several weeks in fresh-water without aeration. All the Tasmanian species were kept in water in small glass dishes. The water was changed occasionally, but no special aeration was provided and the dishes were covered. Furthermore as mentioned above a specimen of *T. tasmanica* lived in 3.0 ml. of water in a small corked tube for 100 days without food, change of water or admission of fresh air. Under similar conditions *T. aurantiaca* lived for 70 days, *T. quadricornis* for 56 days and *T. pygmaea* for 48 days. From these experiments it would seem that continuous aeration of the water is not such an important factor in considering the association of the temnocephalid with its host.

The opinion of Pereira & Cuocolo, that the obtaining of food and shelter are the main reasons underlying the association of the various species of *Temnocephala* with the animals that act as their hosts, is supported by the study of the Tasmanian species.

## ACKNOWLEDGMENTS

The author acknowledges with thanks the assistance given by D. P. Mahoney, J. Kay, H. L. Worthington and D. M. and J. L. Hickman, all of whom have helped in collecting live specimens of fresh-water and land-crayfishes in different parts of Tasmania.

## REFERENCES

- BAER, J. G., 1931.—Etude monographique du groupe des Temnocephales. *Bull. Biol. France & Belgique*, vol. 63, pp. 540-561.
- , 1953.—Zoological Results of the Dutch New Guinea Expedition 1939. No. 4. Temnocephales. *Zoologische Mededelingen*, XXXII, No. 13, pp. 118-140.
- BRANDES, G., 1892.—Zum feineren Bau der Trematoden. *Zeitschr. f. wiss. Zool.*, LIII, pp. 558-577.
- CHILTON, C., 1889.—Note on the parasite (*Temnocephala*) found on the fresh-water crayfish of New Zealand. *Trans. N.Z. Inst.* vol. 21, pp. 252-253.
- CLARK, E., 1939.—Tasmanian Parastacidae. *Pap. Roy. Soc. Tasm.* 1938, pp. 117-128, pls. XII-XIII.
- FYFE, M. L., 1942.—The anatomy and systematic position of *Temnocephala novae-zealandiae* Haswell. *Trans. R. Soc. New Zealand*, vol. 72, pp. 253-267, pl. XXI-XXII.
- GOETSCH, W., 1935.—Biologie und Regeneration von *Temnocephala chilensis*. *Zool.-Jahrb. Syst.*, vol. 67, pp. 195-212, 13 figs.
- HARRISON, R. A., 1947.—The embryology of *Temnocephala novae-zealandiae* Haswell. *Trans. R. Soc. New Zealand*, vol. 76, pp. 524-536.
- HASWELL, W. A., 1888.—On *Temnocephala*, an aberrant Monogenetic Trematode. *Q. J. Micro. Sci.*, N.S. vol. 28, pp. 279-302, pl. 20-22.
- , 1893.—A monograph of the Temnocephaleae. *Linn. Soc. N.S.W., Macleay Memorial Volume*, pp. 93-152, pl. X-XV.
- , 1900.—Supplement to a monograph of the Temnocephaleae. *Proc. Linn. Soc. N.S.W.*, vol. 25, pp. 430-434, pl. XXII.
- , 1901.—Note on the fauna of the gill-cavities of fresh-water crayfishes. *Report of the eighth meeting Aust. Assoc. Advance. Sci.*, 1900, pp. 235-236.
- , 1924.—Critical Notes on the *Temnocephaloidea*. *Proc. Linn. Soc. N.S.W.*, vol. 49, pp. 509-520, pl. 54-56.
- HETT, M. L., 1925.—On a new species of *Temnocephala* (*T. chaeropsis*) (Trematoda) from West Australia. *Proc. Zool. Soc. London*. pp. 569-575, 8 figs.
- MERTON, H., 1913.—Beiträge zur Anatomie und Histologie von *Temnocephala*. *Abh. Senckenberg. Naturf. Ges.*, vol. 35, pp. 1-28.
- , 1922.—Neue Beiträge zur Anatomie von *Temnocephala*. *Zool. Jahrb. Anat.*, vol. 43, pp. 539-556, pl. XXIII.
- PEREIRA, C. and CUOCOLO, R., 1940.—Contribuição para o conhecimento da morfologia, bionomia e ecologia de *Temnocephala brevicornis* Monticelli, 1889. *Arquiv. Inst. Biol. Sao Paulo*. vol. 11, pp. 367-398, pl. LVII-LXII.
- , 1941.—Estudos sobre Temnocephalidae Monticelli, 1899, com estabelecimento de dois novos gêneros australianos e descrição de duas novas espécies neotropicas. *Arquiv. Inst. Biol. Sao Paulo*. vol. 12, pp. 101-127, 22 figs.
- PHILIPPI, R. A., 1870.—Über *Temnocephala chilensis*. *Arch. Naturgesch.* vol. 35, pp. 35-40, 1 pl.
- WERER, M., 1889.—Über *Temnocephala* Blanchard. *Zool. Ergeb. einer Reise in Niederländisch-Ost-Indien*. pp. 1-29, pl. 1-3.

## ABBREVIATIONS USED IN TEXT-FIGURES.

a.—atrium	p.—penis
a.d.—atrial duct	ph.—pharynx
a.g.—atrial glands	p.v.—prostate vesicle
e.a.—excretory aperture	r.b.—refractive body
e.b.—excretory bladder	r.c.—retinula cell
e.v.—ejaculatory vesicle	r.m.—retractor muscle
g.—germarium	r.s.—receptaculum seminis.
g.a.—genital aperture	s.g.—sucker glands
g.c.—ganglion cell	sh.g.—shell glands
g.d.—ducts of granule glands	s.v.—seminal vesicle
g.g.—granule glands	t.g.—tentacular glands
g.i.—genito-intestinal canal	te.—testes
i.—intestine	u.—uterus
i.e.—intestinal epithelium	v.—vagina
i.l.—intestinal lumen	v.d.—vas deferens
in.—introvert	vi.—vitellarium
m.—myoblast	v.r.—vesicula resorbens
o.—ootype	

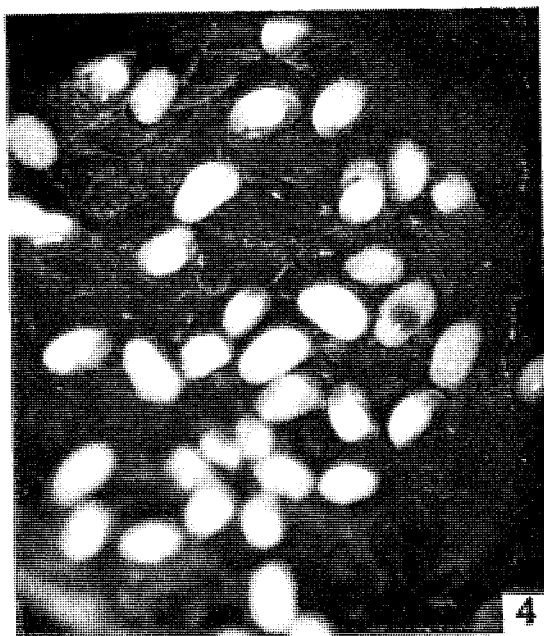
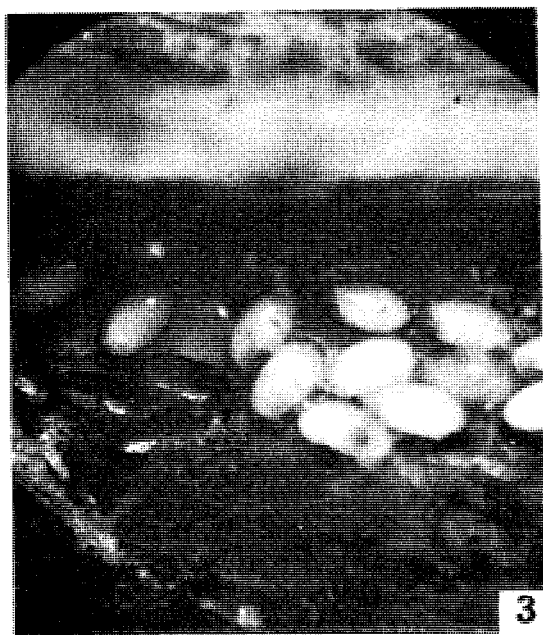
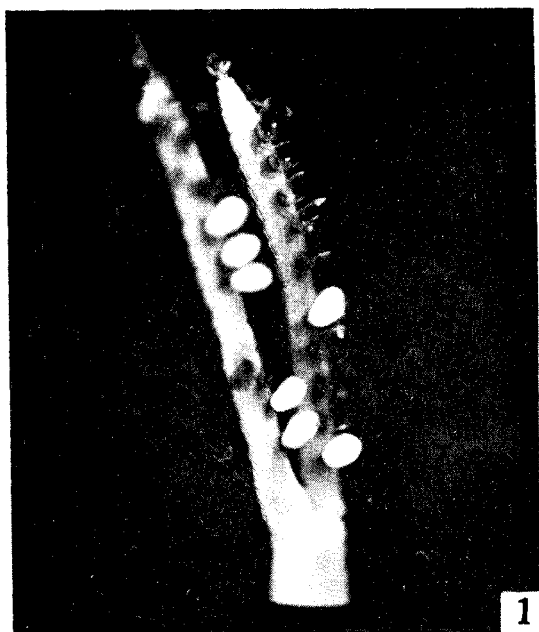


PLATE I.—

- Fig. 1.—Eggs and empty capsules of *Temnocephala cita* sp. n. on pleopod of *Parastacoides tasmanicus* (Erichson). x 15.  
 Fig. 2.—Eggs of *Temnocephala tasmanica* Haswell in gill-chamber of *Astacopsis franklinii* (Gray). x 20.  
 Fig. 3.—Eggs of *Temnocephala pygmaea* sp. n. on carapace of *Astacopsis gouldi* (Clark). x 20.  
 Fig. 4.—Eggs of *Temnocephala aurantiaca* Haswell on inner wall of branchiostegite of *Engaeus cunicularius* Erichson. x 15.

