THE OCCURRENCE IN TASMANIA OF THE LAND NEMERTINE, GEONEMERTES AUSTRALIENSIS DENDY, WITH SOME ACCOUNT OF ITS DISTRIBUTION, HABITS, VARIATIONS AND DEVELOPMENT.

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(With two plates and 20 figures in the text)

ABSTRACT

The terrestrial nemertine, *Geonemertes australiensis* Dendy, is widely distributed in Tasmania, but is never found in large numbers. It occurs in cool and moist situations from near sea-level to the summit of mountains 4000 ft. in height. The sexes are separate. Males reach a maximum length of about 60 mm. and females about 84 mm. The colour varies from pale cream to reddish brown. Some specimens are blotched with brown, others are marked with longitudinal dark brownish stripes. The nemertine feeds on young myriapods and small insects, particularly Collembola, which it captures with its proboscis and kills with its stylet. The eyes vary in number from four in recently hatched specimens to over 170 in some adults. The number of proboscidial nerves is established before hatching. An examination of 187 adults and 374 young shows the number to vary from 11 to 21, the most frequent number being 14. Two reserve stylet pouches are present in young specimens that have just emerged from the egg-capsule but as many as 11 may be present in adults.

The gelatinous egg-capsules are deposited under logs, stones, moss, fallen leaves, &c. They vary in size from 8.0 mm. x 4.0 mm. to 48.0 mm. x 10.0 mm. Small capsules may contain only four eggs, whereas large ones may contain several hundred. One female may deposit as many as seven capsules in a period of two months. Egg laying occurs throughout the year but appears to be most active in April and May. At a temperature of 13° C. the eggs hatch in the gelatinous matrix in about 15 days, but the newly hatched young are in a very immature condition and remain in the capsule for another 24 days.

In the early stages of development cleavage is holoblastic, equal and of the spiral type. A typical hollow blastula is formed. Gastrulation is brought about by the ingression of blastomeres into the blastocoel at the vegetative pole. At the same time cells separate off from the inner ends of the blastomeres forming the wall of the blastula and fall into the blastocoel. These cells constitute mesectoderm. The blastocoel becomes filled with a mass of cells and its lumen obliterated. The outer ends of the blastomeres remain as large yolky cells surrounding the embryo and supply nourishment to the proliferating mesectoderm.

INTRODUCTION

The terrestrial nemertine, *Geonemertes australiensis* Dendy, was first recorded from Gippsland, Victoria, by Dendy in 1889 and described by him in 1892. Fletcher mentioned the occurrence of land nemertines in Tasmania and New South Wales in 1891. He sent two specimens from these localities to Dendy, who remarked (1892) in reference to them: "it is somewhat doubtful whether they belong to the same species as the Victorian specimens, though from the examination of the external characters, which I have been permitted to make, I am inclined to believe that they do ".

Spencer (1892) stated that he found four specimens in Tasmania, which he regarded as identical with the Victorian species. Three years later in recording the occurrence of *Peripatus insignis* in Tasmania he also remarked that at St. Clair, Dee Bridge and Parattah he found " considerable numbers of the land nemertine, *Geonemertes australiensis* ".

Haswell (1914) and Steele (1926) have also mentioned the occurrence of the nemertine in this State but have given no further details.

Flynn (1928) remarked that a terrestrial nemertine, probably of another species, was by no means rare in gulleys of the lower slopes of Mount Wellington.

In view of the zoological interest in terrestrial nemertines and the little that has been recorded concerning their occurrence in Tasmania, it seems desirable to place on record some observations which I have made during the past 30 years as opportunity occurred.

In spite of its marked variations there appears to be only one species in Tasmania and there is no doubt that it is identical with *Geonemertes australiensis* Dendy. I have been able to compare Victorian and Tasmanian specimens and can find no justification for regarding them as different species. In the course of the present study over 200 specimens of the nemertine and many egg-capsules have been collected from different parts of the State.

On account of the work carried out by Dendy (1892) a detailed anatomical study is not required. However, special attention is given to variations in colour, number of eyes, and proboscidial nerves, &c. The main features of the embryonic development are also described.

METHODS AND MATERIALS

Observations on colour and length were usually made on the living animal. For anatomical study the nemertine was narcotised in the vapour of chloroform and immediately placed in a fixative (Gilson's mixture, sublimate acetic or Bouin's picro-formol). Sections were cut at 10μ and stained with Ehrlich's haematoxylin, eosin being sometimes used as a counter stain.

In order to obtain the eggs live specimens of the nemertine were kept in the laboratory. No difficulty was experienced in keeping them for six months or longer provided the temperature of the vivarium did not rise above 23° C. A temperature of 27° C. usually proved fatal. Hence during the summer, when there was any danger of high temperatures being reached, the specimens were transferred to a cool chamber. Each female was kept in a separate tin measuring about 10.0 cm. in diameter and 6.0 cm. in height. The tins contained moss, decaying leaves and rotten wood. The material was kept slightly moist and the tin closed with a lid. Collembolids were sometimes provided as food but usually sufficient small organisms were present amongst the moss and decaying leaves.

Gravid females collected in the field sometimes deposited their egg-capsules in two to four weeks after being placed in the tins. To ensure fertility male specimens were usually placed with the females. During summer many of the egg-capsules were destroyed by moulds. A similar destruction was also observed sometimes to occur in the field. However, in autumn and winter the eggs developed satisfactorily. The capsules were examined under the dissecting microscope each day during the course of incubation, hatching in the gelatinous matrix, and the emergence of the young from the capsules.

From time to time portions of the matrix containing eggs at different stages of development were taken, fixed in Bouin's fluid and sectioned. On other occasions the eggs were removed from the fixed material and sectioned separately. To avoid rendering the yolk of the eggs brittle the time in the embedding oven was made as short as possible, about 20 minutes.

In addition to the eggs laid by specimens in the laboratory others were obtained from capsules found in the field.

Young ones newly emerged from the capsules were placed on decaying leaves and rotten wood in small petri dishes, which were kept in the dark. The small nemertines readily caught collembolids offered as food.

OCCURRENCE AND DISTRIBUTION

In Tasmania *Geonemertes australiensis* usually occurs in cool and moist situations in shady gullies or on the margin of forest clearings. It is found under decaying logs, moss-covered stones, fallen leaves and the loose bark of dead trees. During the warm and dry periods of the year the nemertine often retreats into crevices of decaying logs or under deeply embedded stones. Large cream coloured specimens are generally found only in rain forest areas, whilst the darker reddish brown forms may be found in both rain forest areas and more open regions, such as the Trevallyn hills. Adult specimens may bo collected throughout the year.

As may be seen from Table 1 the nemertine is widely distributed in the State. In addition to the localities mentioned in the Table, it also occurs near the Great Lake and Lake St. Clair on the Central Plateau, at Anson's Bay on the East Coast and at Catamaran in the South. At Anson's Bay and Eaglehawk Neck it may be found almost at sea-level and sometimes within a short distance of the shore. However, it never occurs in the splash zone. If placed in sea water it reacts violently, everting its broboscis and failing to survive longer than about 30 minutes.

On some of the mountains it is found at considerable altitudes. Thus on Quamby Bluff, which has a height of 4200 ft., it occurs at the summit.

At no locality have I seen the nemertine in large numbers and it is a common experience to search areas, where it is known to occur, and yet not find a single specimen.

HABITS

In captivity *Geonemertes australiensis* does not move about very much. Specimens will remain in the one position for three or four days in succession apparently waiting for their prey. When at rest the nemertine is usually encased in a tough covering of mucus with only the front of its head exposed. The mucus coat extends forward for a short distance below and in front of the head forming a small area, which is covered with viscid slime secreted by the cephalic gland. If a small insect comes into contact with this area of sticky slime or if it merely touches against the body of the nemertine, the resting animal suddenly everts its proboscis in an attempt to capture the insect. Sometimes the prey is merely held by the adhesive papillae of the proboscis, but at other times the organ is coiled partly round the victim. The proboscis is extremely mobile and flexible. A small specimen of the nemertine was observed to evert its proboscis and bend it round in order to capture a collembolid, which was walking across the middle of its body. The captured insect was then drawn into the viscid slime in front of the head and the proboscis retracted. As the collembolid continued to struggle the proboscis was again fully everted and the insect pierced with the stylet. When the prey had ceased to move the rhynchostome was applied to it and the soft parts of its body sucked out, the skin and other hard parts being discarded.

Dendy (1892) has described the use of the proboscis as a means of locomotion but said that he was inclined to regard it as accidental and thought that the proboscis was normally used only as a weapon of offence or defence, probably for catching insects, but this he had not observed. From my own observations I am convinced that the proboscis is not only used in the capture of prey but is also normally employed as a means of sudden locomotion, when the nemertine endeavours to

TABLE 1

Localities at which specimens of *Geonemertes australiensis* were found and the numbers of males and females collected.

Date	Locality	Males	Females	Total
23 Dec. 1927	Wilmot	—	1	1
14 Apr. 1928	Trevallyn	—	1	1
20 Apr. 1929	Trevallyn	3	—	3
18 Apr. 1931	Trevallyn	2	2	4
28 May 1931	Trevallyn	—	3	3
27 Jun. 1931	Trevallyn	2	2	4
4 Jul. 1931	Trevallyn	2	1	3
11 May 1929	Glen Dhu	2	—	2
13 Nov. 1929	Glen Dhu	—	1	1
28 May 1930	Glen Dhu	1	1	2
12 Jul. 1930	Glen Dhu	4	8	12
19 May 1931	Glen Dhu	3	3	6
18 Jul. 1931	Glen Dhu	—	2	2
1 Aug. 1931	Glen Dhu	4	6	10
28 Aug. 1931	Exeter	1	2	3
8 Jul. 1957	Mt. Barrow	—	1	1
23 Feb. 1929	Liffey Falls	3	5	8
30 Mar. 1929	Liffey Falls	7	12	19
20 Sep. 1930	Quamby Bluff	1	3	4
22 Jan. 1931	Western Creek	4	3	7
23 May 1954	Surprise Valley	—	1	1
25 May 1954	Tarraleah	—	1	1
24 Dec. 1954	Tarraleah	4	2	6
29 Dec. 1954	Tarraleah	4	7	11
28 Mar. 1932	National Park	—	8	8
13 May 1928	Mt. Hobbs	1	5	6
29 Apr. 1939	Mt. Hobbs	—	1	1
4 Jan. 1929	Levendale	—	1	1
30 Nov. 1940	Eaglehawk Neck	1	—	1
22 Aug. 1951	Eaglehawk Neck	—	1	1
8 Mar. 1960	Eaglehawk Neck	—	3	3
12 Nov. 1957	Mt. Dromedary	1	—	1
4 Jan. 1934	Lenah Valley	—	1	1
1 Jun. 1948	Lenah Valley	2	2	4
16 Jul. 1948	Lenah Valley	—	2	2
6 Nov. 1956	Lenah Valley	2	1	3
15 Nov. 1956	Lenah Valley	—	4	4
27 Nov. 1956	Lenah Valley	4	3	7
12 Dec. 1956	Lenah Valley	2	1	3
22 Jan. 1957	Lenah Valley	1	4	5
28 Jan. 1957	Lenah Valley	—	1	1
28 May 1929	Cascades	1	1	2
29 Aug. 1930	Cascades	—	3	3
3 Sep. 1930	Cascades	2	4	6
1 Sep. 1931	Cascades	3	13	16
18 Nov. 1933	Cascades	1	1	2
18 Apr. 1961	Cascades	—	1	1
26 Oct. 1933	Fern Tree	—	1	1
18 Jan. 1962	Fern Tree	2	3	5
12 Apr. 1962	Fern Tree	1	1	2
4 May 1962	Fern Tree	1	1	2
7 May 1962	Fern Tree	1	—	1
5 Dec. 1955	Organ Pipes	1	—	1
22 Nov. 1955	Arve Forest	1	—	1
22 Nov. 1939	Hastings	—	1	1
Totals		75	136	211

escape from its enemies. Very small specimens, just emerged from the egg-capsule, will if irritated evert the proboscis, attach it to the substrate and quickly draw the body on to it. By repeating the process two or three times in succession a rapid forward movement is attained. Sometimes the proboscis is thrust into a crevice and the nemertine drawn in after it.

VARIATIONS

Length: Seventy-five sexually mature males varied in length from 12 mm. to 60 mm., and 136 sexually mature females varied from 12 mm. to 84 mm. In describing Victorian specimens Dendy (1892) stated that large ones when crawling reached a length of about 40 mm.

Colour and markings (Pl. 1, figs. 1-3): In both sexes the colour varies from pale cream, almost white, to dark reddish brown. The head region is generally darker and the ventral surface lighter than the rest of the body. In many cases the dark colour of the head is continued posteriorly as a median dorsal stripe, extending partly or entirely the full length of the animal. In reddish brown forms the colour is sometimes of a uniform shade; at other times it is dispersed in irregular blotches on a ground colour varying from cream to pale brown. Some specimens have the blotches arranged in longitudinal rows forming an incipient striped pattern, whilst others are marked with well-formed brown stripes. In the latter there is usually a median dorsal stripe with a single lateral stripe on each side. In other examples the median stripe is double, the animal thus having four longitudinal stripes. Striped and non-striped examples are sometimes found in the one habitat, and it is not unusual for egg-capsules to contain young ones with brown blotches and also young ones with little or no pigmentation.

Fletcher (1895) has recorded that some specimens found in Tasmania by Spencer were longitudinally striped with red. Dendy (1892) described the colour of Victorian specimens as being chiefly yellow, sometimes orange and at other times brownish. He also stated that some specimens had a brown median dorsal band and two narrow stripes of a darker brownish tint down each side.

Eyes: In young specimens that have recently hatched four eyes are usually visible (text-fig. 1). Two are situated one on each side of the front of the head, and the other two, which are slightly smaller, a short distance behind them. Before or shortly after the young have left the egg-capsule further small eyes appear in proximity to the primary four (text-fig. 2). It thus happens that the eyes tend to be arranged in four groups, right and left anterior and right and left posterior. In Table 2 these groups are indicated by the letters RA, LA, RP and LP respectively. By the time the nemertine has grown to a length of 5 mm. it usually has about 16 eyes, four in each group (text-fig. 3). In adult specimens the total number of eyes varies from about 39 to 176. Usually the number is greater in large than in small specimens, but this is not always the case (Table 2). However, the great powers of extension and contraction of the nemertine and the fact that the length of a female decreases considerably after the eggs are laid make it difficult to obtain measurements of length that are strictly comparable.

In some specimens the anterior and posterior groups on each side merge so that the animal appears to have only one large group on each side.

Dendy (1892) stated in reference to Victorian specimens that the eyes, of which there might be as many as thirty or forty, were arranged in two groups, one on either side of the opening of the rhynchodaeum at the anterior extremity of the body. Each group, containing about twenty eyes of various sizes, might show indications of a division into an anterior and posterior portion.

In a Victorian specimen which I examined there were 79 eyes arranged in four irregular groups corresponding in position to the four primary eyes of the newly hatched young (text-fig. 4). This is the arrangement found in most Tasmanian specimens (text-fig. 5). Some of the eyes in young specimens appear to be formed by division of the primary eyes. Others seem to arise independently.

Vascular system: Anteriorly the median blood vessel ends in two cellular plugs, which project into the rhyncocoelom immediately above the ventral commissure of the brain. In reference to these structures in a Victorian specimen Dendy (1892) remarked that the median vessel seemed to be connected with both these cellular plugs and that it appeared to be directly continuous with the stalk of the one and to send off a branch to the other. Whether there was any constant distinction between the right and the left in this respect he was not able to say.

In Tasmanian specimens the median blood vessel divides dichotomously at its anterior end forming two symmetrical short branches, one on each side leading to the corresponding vascular plug. There is no indication of the median vessel being directly continuous with the stalk of one of the plugs rather than the other.

Proboscidial nerves (Pl. 2, figs. 7-12): The proboscidial nerve sheath is thickened at regular intervals to form a number of longitudinal nerves. Dendy (1892) did not state the number in the Victorian specimen which he described, but the figure he gave shows eighteen. Darbishire (1909), who examined twelve specimens given to him by Dendy, stated that two of the specimens had 16 nerves, two 17, seven 18 and one 19. He therefore concluded that the specimen, whose proboscis was figured by Dendy, represented the commonest type.

In order to determine the range of variability in the number of proboscidial nerves in Tasmanian examples of the nemertine, 187 adult specimens collected in the field and 374 young ones bred from three egg-capsules were examined. The results are shown in Tables 3 and 4.

The specimens obtained from the three egg-capsules were ones that had recently emerged from the gelatinous matrix. Their gonads had not developed and it was not possible to determine their sex.

From the data given in Tables 3 and 4 it is apparent that the number of longitudinal proboscidial nerves may vary from 11 to 21 and that 14 represents the number most frequently met with. It is also clear that both males and females show much the same range of variability.

TABLE 2

Number of eyes in 10 males and 10 females of *Geonemertes australiensis.*

Length of specimen in mm.	Sex	RA group	Number of eyes LA group	RP group	LP group	Total
12	♂	15	15	9	9	48
15	♂	16	20	11	11	58
20	♂	11	11	9	8	39
25	♂	16	14	11	9	50
35	♂	18	15	15	14	62
35	♂	18	21	19	17	75
35	♂	41	41	35	37	154
35	♂	18	23	22	26	89
40	♂	23	23	21	23	90
47	♂	14	18	13	11	56
10	♀	15	13	9	9	46
15	♀	15	16	8	6	45
20	♀	43	42	37	36	158
30	♀	24	23	19	16	82
36	♀	38	24	22	22	106
42	♀	28	24	26	23	101
51	♀	36	36	55	49	176
59	♀	32	32	49	51	164
70	♀	22	19	20	14	75
81	♀	28	33	27	32	120

TABLE 3

Number of longitudinal proboscidial nerves in 187 adult specimens of *Geonemertes australiensis.*

Number of proboscidial nerves	Number of specimens Males	Females	Total
11	—	1	1
12	1	4	5
13	4	11	15
14	43	65	108
15	8	20	28
16	8	17	25
17	2	1	3
18	1	—	1
21	1	—	1
TOTALS	68	119	187

Reserve stylet-sacs: In young specimens newly emerged from the egg-capsule there are two reserve stylet-sacs, one on each side of the proboscis. Each sac contains two or sometimes three stylets. In adult specimens the number of sacs varies from two to eleven (Table 5). The most usual number is five, three on one side and two on the other. The number of stylets contained in a sac varies from one to five (Pl. 1, fig. 6).

Dendy (1892) remarked that in one of his specimens he counted as many as five stylet-sacs. In a Victorian specimen which I examined there were definitely eight sacs and perhaps ten, two being indistinct. Dendy did not succeed in finding any communication between the reserve sacs and the lumen of the eversible part of the proboscis, but assumed that some communication existed. In many of my specimens the communication is quite distinct.

TABLE 4

Number of longitudinal proboscidial nerves in 374 young specimens of *Geonemertes australiensis* bred from three egg-capsules.

Number of proboscidial nerves	Number of specimens Capsule 1	Capsule 2	Capsule 3	Total
12	1	1	1	3
13	—	2	2	4
14	73	44	45	162
15	3	68	34	105
16	4	52	26	82
17	—	7	5	12
18	—	2	3	5
19	—	—	1	1
TOTALS	81	176	117	374

TABLE 5

Number of reserve stylet-sacs in 66 specimens of *Geonemertes australiensis*.

Number of stylet sacs	Number of specimens		
	Males	Females	Total
2	2	3	5
3	4	2	6
4	3	14	17
5	8	12	20
6	6	4	10
7	3	—	3
8	2	—	2
9	—	2	2
11	—	1	1
TOTALS	28	38	66

EGG-LAYING AND INCUBATION

A brief description of the gelatinous egg-capsule of *Geonemertes australiensis* has been given by Dendy (1893). However, his assumption that the animal discharged its eggs and poured out the jelly, while slowly crawling along, is not correct. The nemertine remains stationary while depositing its eggs. A specimen collected at Trevallyn on 14th April, 1928, and kept in the laboratory was observed in the act of egg-laying on 18th May, 1928. With the exception of the head the body of the worm was encased in a smooth elastic coat of tough mucus, which did not appear to differ from that normally surrounding the body of the resting animal. When first noticed at 3.30 p.m. a number of eggs on each side of the body had already been discharged and were lying in gelatinous material between the mucus coat and the surface of the body. As the eggs were discharged from the ovigerous sacs movements of the musculature occurred forcing the eggs through the narrow ducts leading to the surface. At the place where each egg had been expelled a small lesion appeared, no doubt due to the rupture of the narrow opening through which the egg had passed. The laying of the eggs was observed under a dissecting microscope until 4.10 p.m., when the nemertine was photographed while further eggs were being discharged (Pl. 1, fig. 4). By 6 p.m. the worm had crawled out of the surrounding mucus coat leaving the eggs suspended in the gelatinous matrix. The elastic nature of the mucus coat causes it to close at the ends, when the body of the nemertine has been withdrawn.

The egg-capsules thus made are generally spindle-shaped or sausage-shaped (Pl. 1, fig. 5) and vary in size from 8 mm. x 4 mm. to 48 mm. x 10 mm. The small egg-capsules may contain only four eggs, whereas the largest may hold several hundred. One measuring 15 mm. x 4 mm. contained 87 eggs, while one 23 mm. x 7 mm. contained 290.

It is not unusual for the nemertine to make several egg-capsules at short intervals. Dendy (1893) has recorded one of his specimens as depositing three lots of eggs between 7th July and 1st August. A large specimen, which I collected at the Fern Tree on 19th January, 1962, and kept in the laboratory, deposited seven egg-capsules between 6th April and 23rd May. When found the nemertine measured 84 mm. long and 5 mm. wide, but after depositing the seventh lot of eggs it measured only 50 mm. long and 2 mm. wide.

A specimen which was disturbed when about to lay its eggs made a complete egg-capsule (20 mm. x 7 mm.) filled with the usual gelatinous material but without eggs.

In the field egg-capsules are deposited under logs, stones, fallen leaves, moss, &c., in cool and moist situations. In rain forest areas they may be found throughout the year, but in more open localities, such as the Trevallyn hills, they are deposited only during the autumn and winter. The transparency of the egg-capsule makes it possible to examine the eggs and embryos in the living condition and to recognise some of the stages of development in capsules found in the field (Table 6).

TABLE 6

Stages of development of eggs or young in capsules of *Geonemertes australiensis* found in the field.

Date	Locality	Number of capsules	Stage of development of eggs or young.
9 Jun., 1928	Trevallyn	1	Early cleavage
18 Aug., 1928	Trevallyn	5	Young moving in matrix
23 Feb., 1929	Liffey Falls	2	Young with four eyes
21 Mar., 1933	Cascades	1	Near hatching
29 Dec., 1954	Tarraleah	3	Young moving in matrix
11 Nov., 1955	Arve Forest	2	Late segmentation
10 Jan., 1962	Fern Tree	1	Hatching in matrix
12 Apr., 1962	Fern Tree	1	Late segmentation
7 May, 1962	Fern Tree	1	Near hatching
18 Jul., 1962	Fern Tree	1	Near hatching

The period of incubation is relatively short and varies even amongst the eggs in the one capsule. On 6th May, 1962, a capsule measuring 12 mm. x 5 mm. and containing about 120 eggs was deposited by a specimen kept in the laboratory. The eggs were examined under the dissecting microscope each day until they hatched in the gelatinous matrix. The daily observations were then continued until the young left the capsule. During the period the ambient temperature fluctuated betwen 10° C and 16° C with an average daily temperature of 13° C. Most of the eggs hatched in the gelatinous matrix in 15 to 16 days, but some took 19 days. The newly hatched young remained in the capsule for another 24 days. The period of incubation and rate of development within the egg-capsule are shown in Table 7.

TABLE 7

Rate of development of the eggs of *Geonemertes australiensis* in a capsule deposited in the vivarium.

Date	Stage of development
6 May, 1962	Eggs laid
7 May, 1962	Most embryos at four cell stage
8 May, 1962	Morula
12 May, 1962	Embryos at late segmentation stage
21 May, 1962	Some embryos hatching in gelatinous matrix
23 May, 1962	Young measure 0.63 mm. long
25 May, 1962	Young moving about in gelatinous matrix
27 May, 1962	Two anterior eyes visible in some young
29 May, 1962	Young measure 1.08 mm. long
1 Jun., 1962	Young more active. Some with four eyes
2 Jun., 1962	Head region darkening
5 Jun., 1962	Young measure 1.26 mm. long
8 Jun., 1962	Faint brownish blotching on body of some young
10 Jun., 1962	Young congregating at upper end of capsule
14 Jun., 1962	Young measure 1.83 mm. long. Leaving capsule

Dendy (1893) has recorded that he examined on the 26th August embryos in a mass of eggs, which had been deposited on 1st August and found that some of the embryos were still enclosed in the delicate egg-membrane, whilst others had hatched and were moving about in the gelatinous matrix.

EMBRYONIC DEVELOPMENT

(Text-figs. 6-20)

The newly laid egg is spherical and has a diameter of 0.63 mm. to 0.74 mm. It is white or pale yellow, opaque, laden with yolk granules and surrounded by a delicate investment. The nucleus is slightly excentric in position and without a well defined nuclear membrane.

In the early stages of development segmentation is holoblastic and equal (text-figs. 6-9). The first cleavage usually occurs about 12 hours after the egg is laid. The two blastomeres so formed are loosely held together and readily fall apart, when the egg is removed from the gelatinous matrix. At the end of 24 hours most of the eggs in a capsule have undergone the second cleavage and reached the four cell stage.

Further cleavages are of the spiral type and give rise to a typical morula followed by a hollow blastula. The wall of the blastula consists of a single layer of wedge-shaped cells (text-fig. 10). As segmentation proceeds the blastomeres become long and narrow (text-fig. 11).

On or shortly after the fourth day of incubation gastrulation occurs. Cells at the vegetative pole enter the blastocoel by a process of ingression and constitute the endoderm. A small temporary depression appears on the surface of the embryo at the place where the cells are moving inward but there is no marked invagination (text-fig. 12.)

While gastrulation is taking place other cells are separating off from the inner portions of the elongate blastomeres forming the wall of the blastula. These cells surround the endoderm and appear to constitute mesectoderm. The outer ends of the elongate blastomeres remain unchanged until a late stage. They have the form of large cells, which are full of yolk and bulge on the surface making the embryo appear as if it were still in the stage of an advanced morula. These outer cells, which surround the embryo, will be referred to as *ectoembryonic* cells.

By the end of th seventh day the blastocoel is completely filled with a mass of cells and its lumen obliterated (text-fig. 13). The large ectoembryonic cells have nuclei, which measure about 18 μ in long diameter, whereas those forming the inner mass have nuclei measuring only 6 μ in diameter.

The next stage in development is marked by a proliferation of the mesectoderm cells, which form the outer zone of the inner cell mass and lie immediately below the ectoembryonic cells. A dense group of cells formed in the mesectoderm at the anterior end of the inner cell mass gives rise to the rhynchodaeum, proboscis and brain. The rhynchodaeum and proboscis develop as an invagination of the cells immediately below the anterior ectoembryonic cells (text-figs. 14 and 15). The ectoembryonic cells are still laden with much yolk and do not take part in the invagination. Their large nuclei seem to disintegrate and the main function of these cells appears to be the supplying of nourishment in the form of yolk to the actively dividing cells below them. At this stage they also close the entrance to the rhynchodaeum.

The right and left lobes of the brain first appear as groups of ganglion cells on either side of the invagination forming the proboscis (text-figs 15 and 16). At the same time the lateral nerves are formed as two longitudinal ridges in the mesectoderm on each side and immediately below the large ectoembryonic cells (text-figs. 17). The two ridges extend from the brain to the posterior end of the inner cell mass, where they unite.

Some cells of the proliferating mesectoderm now become differentiated to form the dermal muscular sheath, whilst other cells grow out and invade ths large yolky ectoembryonic cells using up the yolk and forming here and there patches of ciliated epithelium (epidermis). The embryo now rotates within the delicate egg-membrane.

By this time the endodermal part of the inner cell mass consisting mainly of large blocks of yolk granules with a few scattered nuclei, has become delimited to form the primitive gut. In some cases a small cavity appears in the centre of the mass.

The embryo is now about eleven days old and shows signs of muscular movement. The proboscis has grown back for about half the length of the body and is surrounded by the wall of the rhynchocoelom, which has been formed by delamination from the developing proboscis. Below the proboscis and growing inwards from the rhynchodaeum the oesophagus is being differentiated (text-figs. 14 and 16).

During the next few days the embryo elongates. The posterior half of the rhynchocoelom together with the rudiments of the retractor muscle of the proboscis develop. The ectoembryonic cells become replaced entirely by the ciliated epidermis, which has formed in patches but now covers the whole embryo.

On or about the fifteenth day of incubation the young nemertine escapes from the delicate investing egg-membrane and moves into the gelatinous material of the egg-capsule. In some cases hatching occupies several hours. The membranous investment does not appear to be torn or burst open but to have a narrow rounded hole formed in it. Through this hole the nemertine slowly squeezes its body and when about half-way through it appears constricted in the middle or dumb-bell shaped. When moving in the gelatinous matrix and fully extended it measures about 1.0 mm. in length, but is still in a very immature condition (text-fig. 18). The rhynchostome is closed and the stylet region of the proboscis not fully developed. The gut is full of yolk and its endothelium not formed. The blood vascular system is not apparent and numerous yolk granules are present in various regions of the body. In most cases the eyes are not evident, but in some the two main anterior eyes may be seen.

As mentioned previously the young nemertine remains in the egg-capsule for a further 24 days or longer. During this period it grows to a length of from 2.0 to 3.0 mm., and on leaving the egg-capsule its main organs, excepting the gonads, are formed.

The head is dark and the dorsal surface and sides of the body faintly blotched with brown. In many cases the blotching tends to form stripes. However, some specimens show very little pigmentation. Four eyes are usually present and sometimes eight or nine. The rhynchostome is open to the exterior. The longitudinal nerves of the proboscis are already established in number (text-fig. 19), and the stylet region well developed. The main stylet is about 36 μ in length, while the pyriform base on which it is mounted measures about 50 μ in length and 30 μ in greatest width. Two reserve stylet sacs are present, one on each side (text-fig. 20). They contain two and sometimes three stylets. The proboscis can be everted and withdrawn as in the adult.

The lobes of the brain, dorsal and ventral commissures, the lateral nerves and accessory lateral nerves are all well formed. The ciliated ducts or cephalic pits leading to the ganglia of the lateral organs are open to the exterior. The head gland, dorsal and epidermal glands are established.

The blood vascular system resembles that of the adult. The median vessel bifurcates at its anterior end to form two short branches, which lead to the vascular plugs in the wall of the rhynchocoelom. Here and there in the parenchyma tubules of the nephridial system may be seen.

In the alimentary canal the wall of the oesophagus is now folded and its endothelial lining ciliated. The intestine, however, still contains much yolk, and the large yolky endoderm cells have not yet formed the endothelium of the gut.

DISCUSSION

The egg-capsules of *Geonemertes australiensis* resemble those of *Geonemertes dendyi* Dakin as illustrated by Pantin (1961), but in mose cases are of larger size.

Coe (1939) has suggested that occasional viviparity may possibly occur in some species thought to be exclusively oviparous. No cases of viviparity, protandry or hermaphroditism were observed among the specimens of *G. australiensis* examined during the present investigation.

Little appears to have been recorded concerning the embryology of terrestrial nemertines. Coe (1904) has given a brief account of the development of the viviparous species, *Geonemertes agricola* (Willimoes-Suhm), which occurs in Bermuda. Dendy (1893) states that he had little success in investigating the development of *G. australiensis*, since the large quantity of food yolk made the living embryos opaque and moreover the cutting of sections did not yield satisfactory results. It is true that the yolk is an obstacle to the examination of the living embryos. It also tends to become brittle after fixation and embedding, thus making the cutting of sections difficult. However, the difficulty may be overcome to some extent by reducing the times of fixation and embedding to a minimum.

From my own observations the development of *G. australiensis* bears some resemblance to that of *Prostoma graecense* (Böhmig) as recorded by Reinhard (1941). In both nemertines gastrulation takes place by a process of ingression of cells at the vegetal pole. However, the formation of the mesoderm differs in the two species.

The large ectoembryonic cells of *G. australiensis* are not unlike the large outer cells of the newly hatched larva of *Oerstedia dorsalis* (Abildgaard) as figured by Coe (1943). In the latter case, however, they appear to give rise directly to the epidermis of the adult, whereas in *G. australiensis* they seem to degenerate and merely provide yolk for the proliferating cells below them. In describing the development of *G. agricola* Coe (1904) has stated that "it is not quite certain that the ciliated covering of the young embryo is actually converted into the ciliated integument of the adult worm". He thought that it might be sloughed off. The ectoembryonic cells of the embryo of *G. australiensis* are not ciliated and are not cast off. However they do not appear to give rise to the integument of the adult.

Development of *G. australiensis* is direct and the mode of formation of the various organs resembles that found in other Metanemertini.

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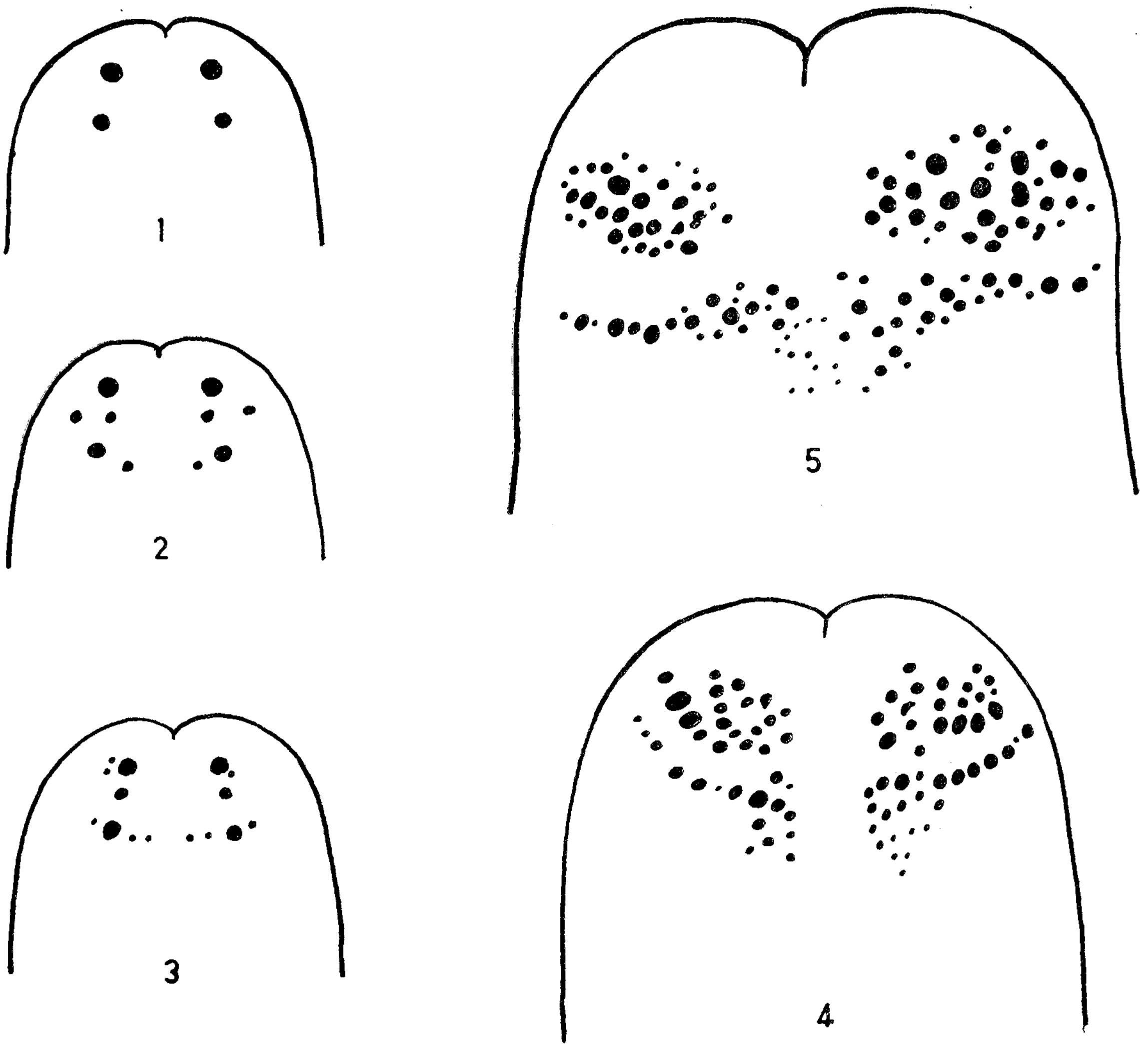
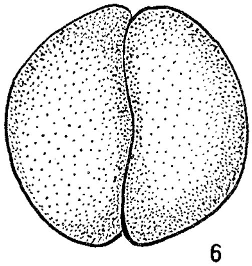


GEONEMERTES AUSTRALIENSIS DENDY

FIG. 1.—Eyes in a recently hatched specimen about 2.0 mm. long.
FIG. 2.—Eyes in a specimen about 3.6 mm. long.
FIG. 3.—Eyes in a specimen about 5.0 mm. long.
FIG. 4.—Eyes in a specimen from Victoria.
FIG. 5.—Eyes in an adult specimen from Tasmania.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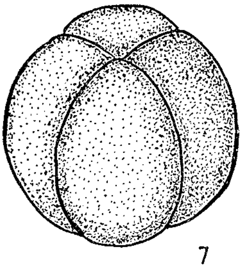
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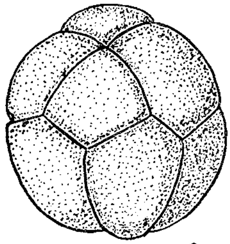
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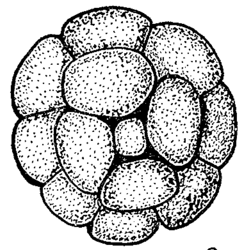
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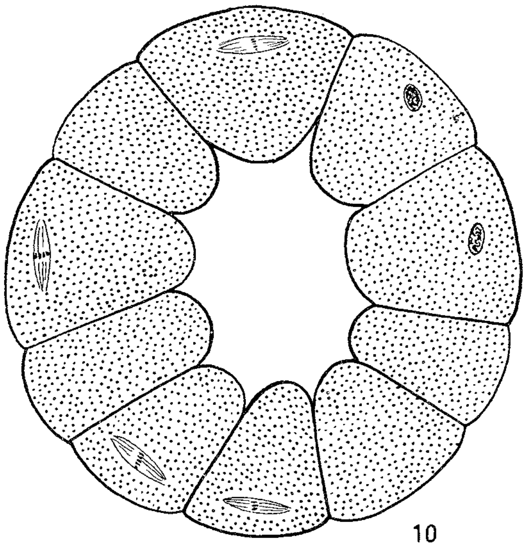
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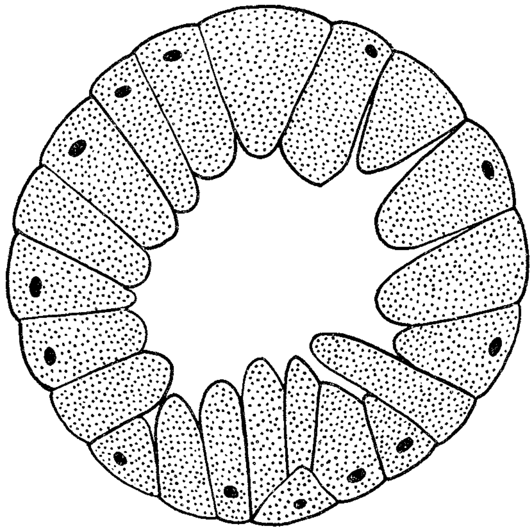
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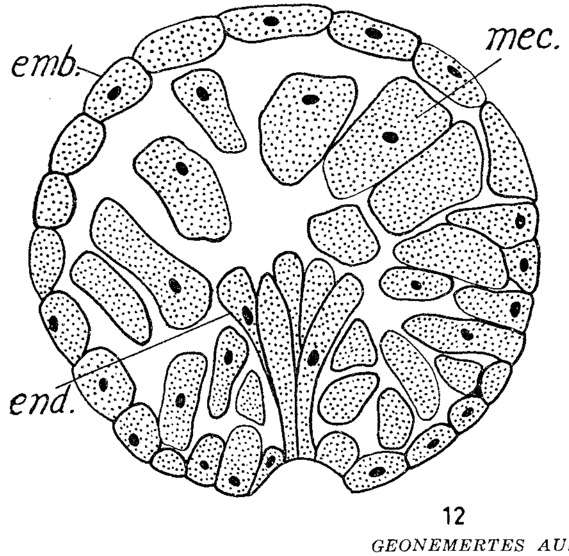

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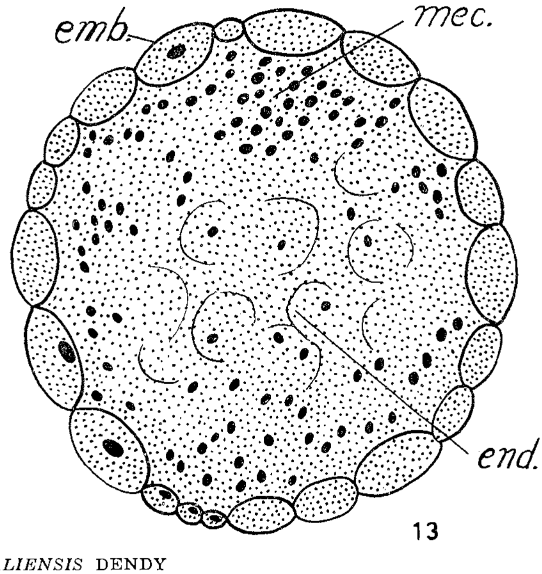

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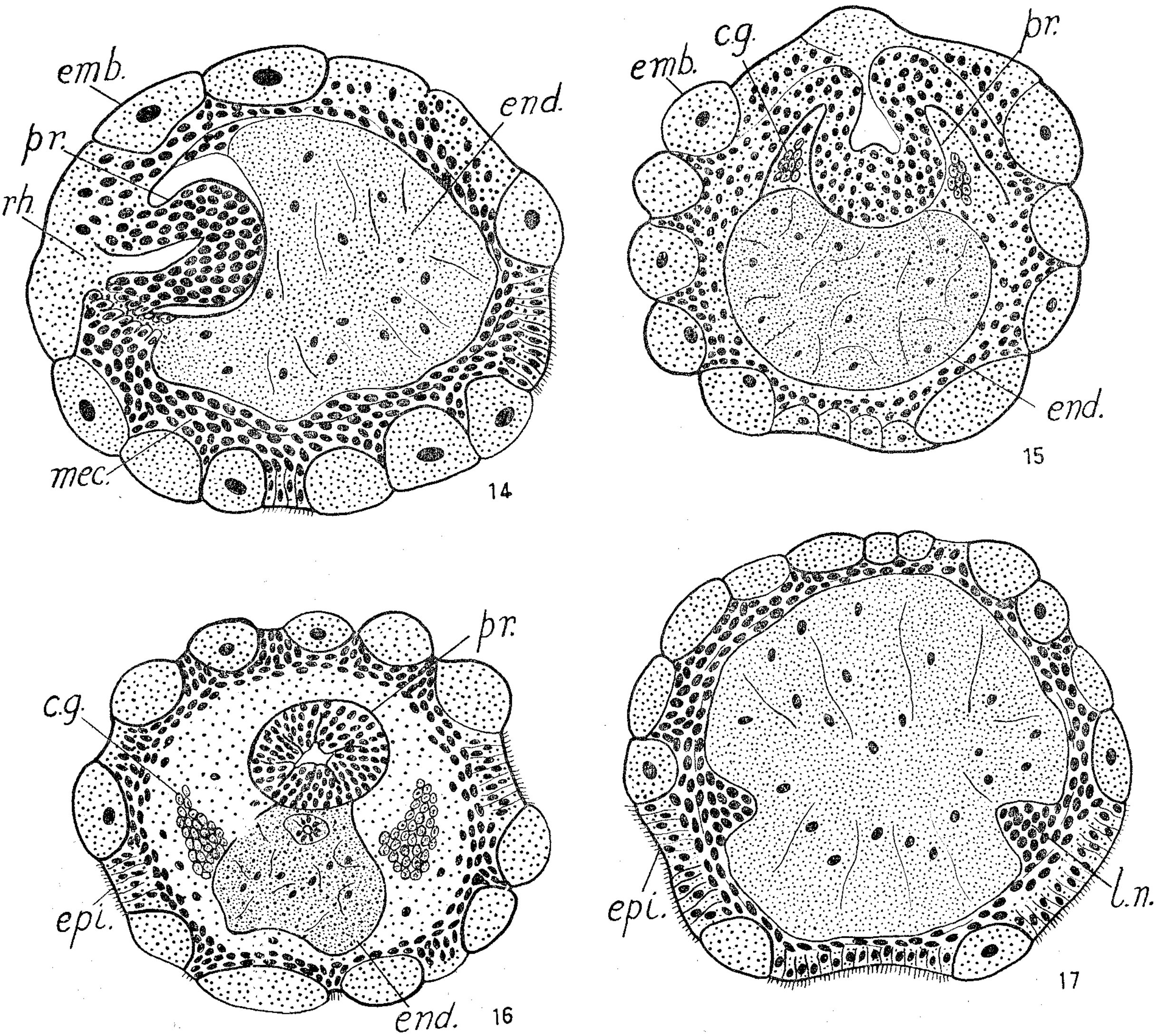
GEONEMERTES AUSTRALIENSIS DENDY

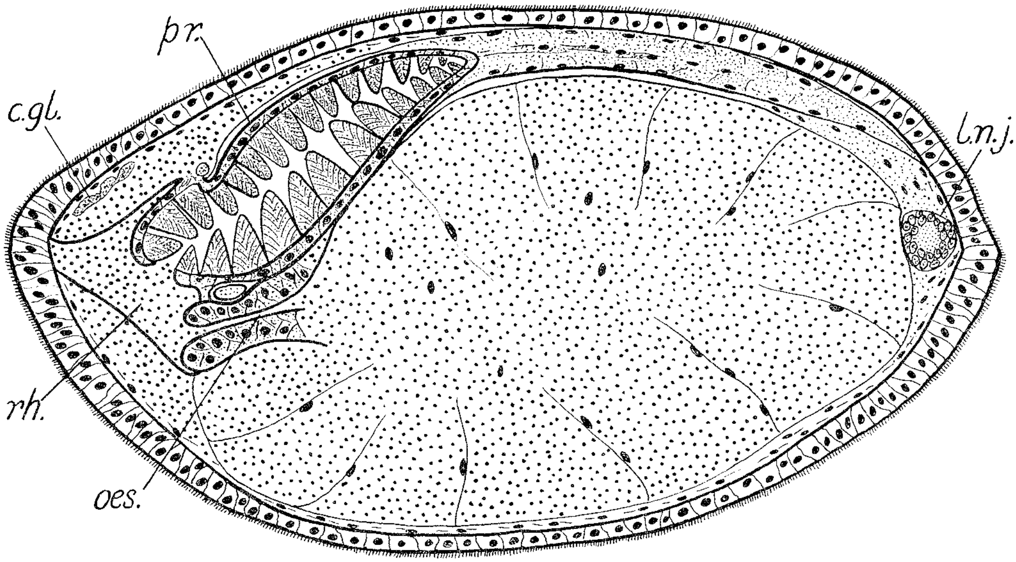
FIG. 6.—Two cell stage.
FIG. 7.—Four cell stage.
FIG. 8.—Eight cell stage.
FIG. 9.—Morula.
FIG. 10.—Section through early blastula.
FIG. 11.—Section through a more advanced blastula.

FIG. 12.—Section through gastrula showing ingression of cells at vegetal pole. *end.* endoderm, *emb.* ectoembryonic cells, *mec,* mesectoderm.
FIG. 13.—Section through a later stage showing inner mass of cells filling the blastocoel. Lettering as in Fig. 12.



GEONEMERTES AUSTRALIENSIS DENDY

FIG. 14.—Sagittal section through an embryo about 10 days old.
FIG. 15.—Frontal section through an embryo of about the same age.
FIG. 16.—Transverse section through an embryo about 10 days old and passing through the proboscis.
FIG. 17.—Transverse section through an embryo of about the same age but passing behind the proboscis. *c.g.* cerebral ganglion, *emb.* ectoembryonic cells, *end.*, *endoderm*, *epi*, epidermis, *l.n.*, lateral nerve, *mec.* mesectoderm, *pr.* proboscis, *rh.* rhynchodaeum.



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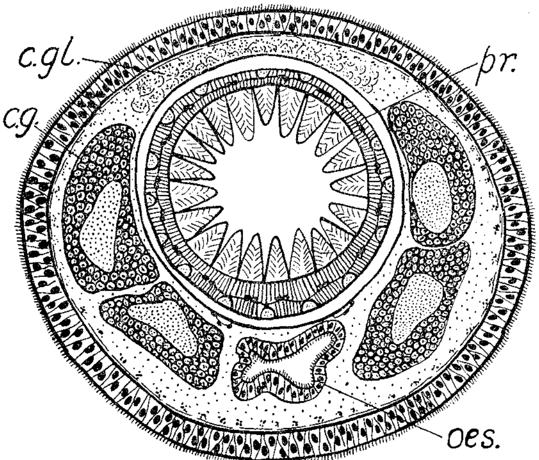

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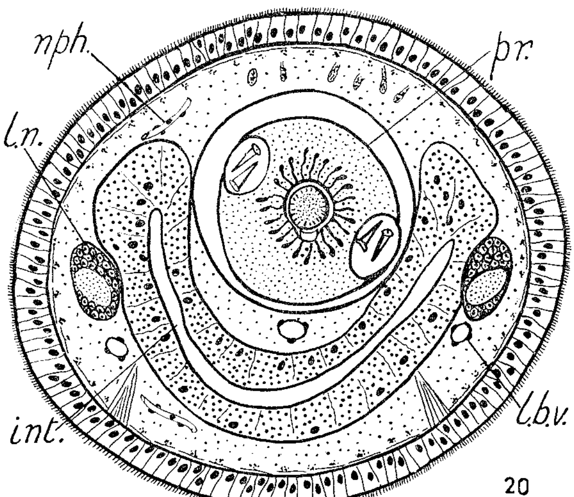

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GEONEMERTES AUSTRALIENSIS DENDY

FIG. 18. Sagittal section through a newly hatched specimen.
FIG. 19.—Transverse section at the level of the brain through a specimen recently emerged from the egg-capsule.
FIG. 20.—Transverse section through the middle of the body of a specimen recently emerged from the egg-capsule. The section passes through the stylet region of the proboscis.
c.g., cerebral ganglion (brain), *c.gl.* head gland, *int.* intestine, *l.b.v.* lateral blood vessel, *l.n.* lateral nerve, *l.n.j.* junction of lateral nerves, *nph.* nephridial tubule, *oes.* oesophagus, *pr.* proboscis.

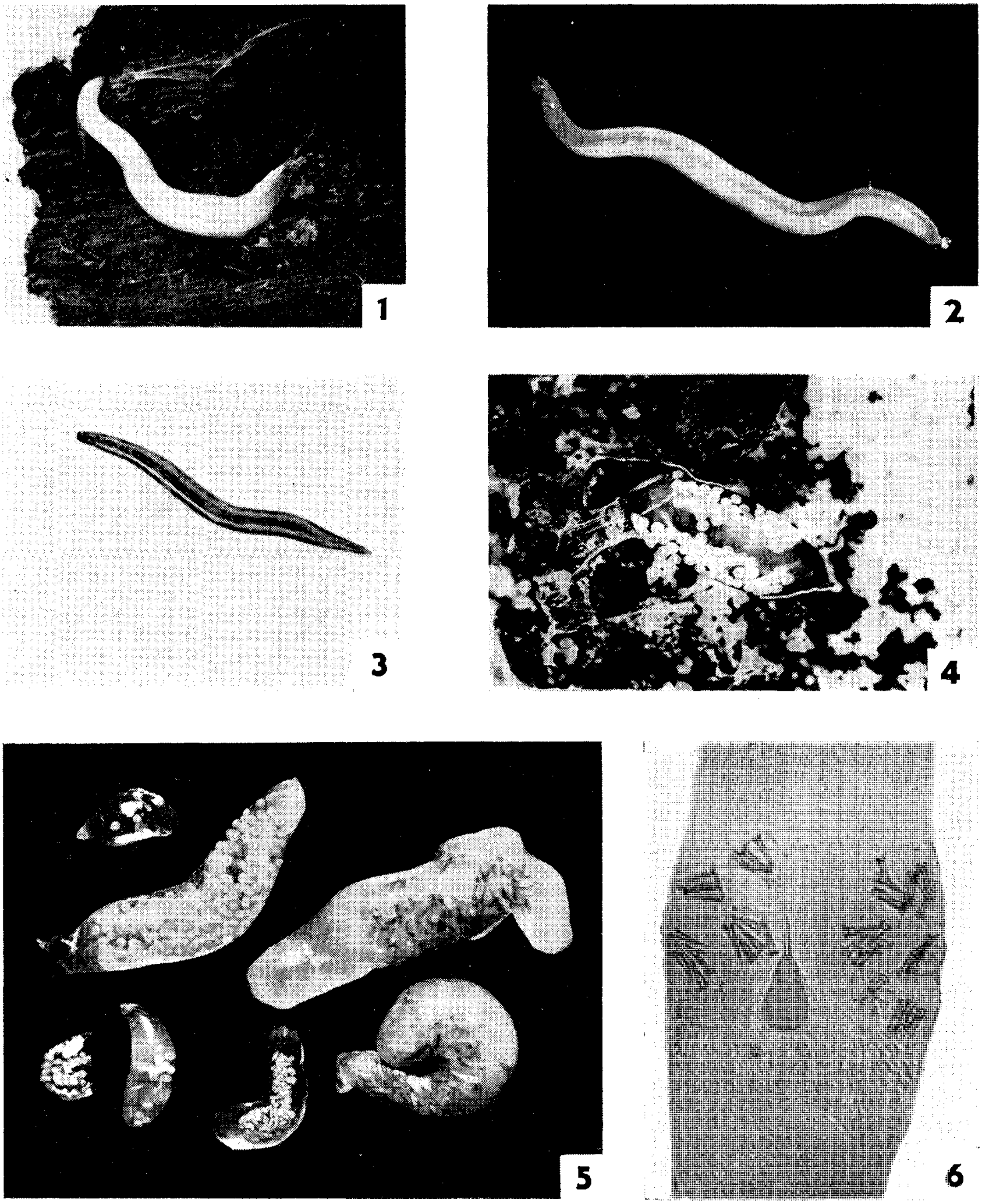

PLATE 1

Geonemertes australiensis Dendy

FIG. 1.—Pale cream specimen resting on piece of charred wood.
FIG. 2.—Cream specimen showing a median dorsal stripe.
FIG. 3.—Light brown specimen with dark brown stripes.
FIG. 4.—A brownish specimen laying eggs.
FIG. 5.—Egg-capsules.
FIG. 6.—Stylet region of proboscis compressed and showing ten groups of reserve stylets, each group being in a separate sac.

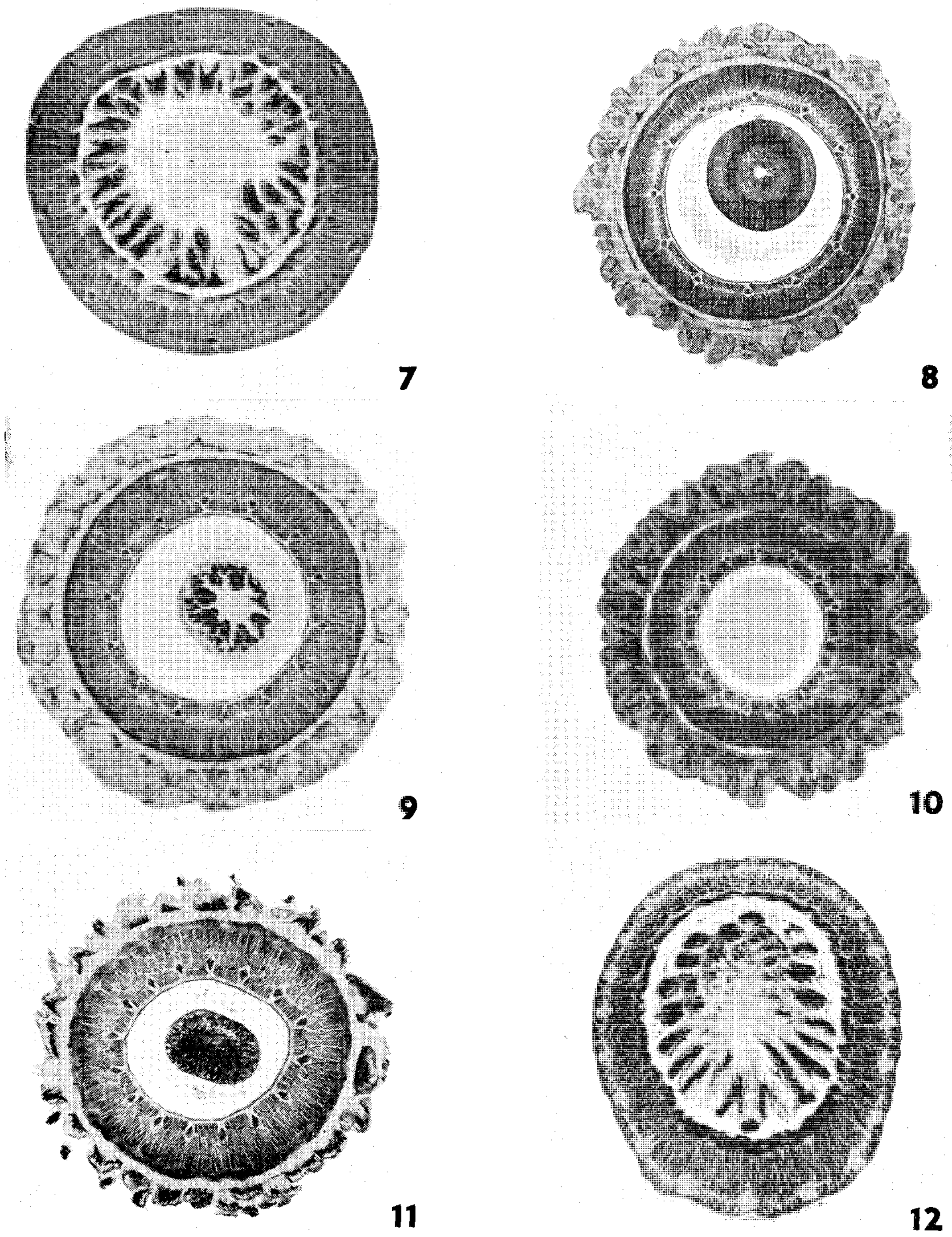

PLATE 2

Geonemertes australiensis Dendy

FIGS. 7-12.—Transverse sections of proboscides showing 11, 12, 14, 15, 16 and 21 nerves respectively. In Figs. 7 and 12 the proboscis is withdrawn; in the other figures it is everted.