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NEMATODES PARASITIC ON SEA WEEDS OF THE GENERA *ASCOPHYLLUM* AND *FUCUS*

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(Text-figs. 1–3)

In 1892 Barton described galls found on the sea weed *Ascophyllum nodosum* from the Isle of Cumbrae, west coast of Scotland, and from Stonehaven, east coast of Scotland. The affected areas on the thallus of the plant appeared as swellings covered with small rounded nodules, and were almost invariably confined to the parts of the thallus just above or below the air vesicles. A transverse section through the swellings showed each nodule as a more or less hollow space containing numerous nematodes, specimens of which were sent to J. G. de Man, who (1892) described the worm as a new species, *Tylenchus fucicola*, the first-known marine tylenchid.

On the basis of de Man's description Cobb (N. A. Cobb in M. V. Cobb, 1933) erected the genus *Halenchus* for this species. Since then, other species of *Halenchus* have been described, but only as free-living forms.

From time to time galls on other sea weeds have been reported, but attributed to other animal agents, bacteria and fungi.

During visits by the author to the Laboratory of the Marine Biological Association at various times during 1955–57 galls were found very commonly on *Ascophyllum nodosum* in the Plymouth area (Wembury Bay). They agree well with Barton's description and contain numerous specimens of a nematode, which appears to be identical with de Man's form. Similar galls were also found at Croyde Bay on the north Devon coast in August 1955 (Fig. 1A).

Galls were also found on the sea weed *Fucus vesiculosus* (Fig. 1B) from Wembury Bay, Devon, and at Hannafore, Looe, Cornwall. They were found only on the older growths of the plant and occurred mainly on the stipes, and less frequently on the base of the fronds. The galls are quite noticeable and are usually a little lighter in colour than the rest of the stipes, but are not so large as some of those seen on *Ascophyllum*. The surface of the swellings is rugose and not so papillate as the galls on the other plant. When the galls were opened nematodes were found, but there were only a few in each in contrast with the galls on *Ascophyllum* which contain large numbers. At first the worms were thought to be identical with *Halenchus fucicola*, except that the anterior end appeared rather larger. On closer examination, however,

several small differences have been noted and are considered to be of sufficient significance to warrant the recognition of a distinct species.

Frequently non-tylenchid nematodes are found in the galls as well as the marine mite *Rhombognathus* (*Rhombognathopsis*) *seahami* (Hodge), kindly identified by Dr G. O. Evans. The nematodes appear to represent a variety of species no one of which appears to be consistently present; thus leading one to conclude that they are not the causal agents.

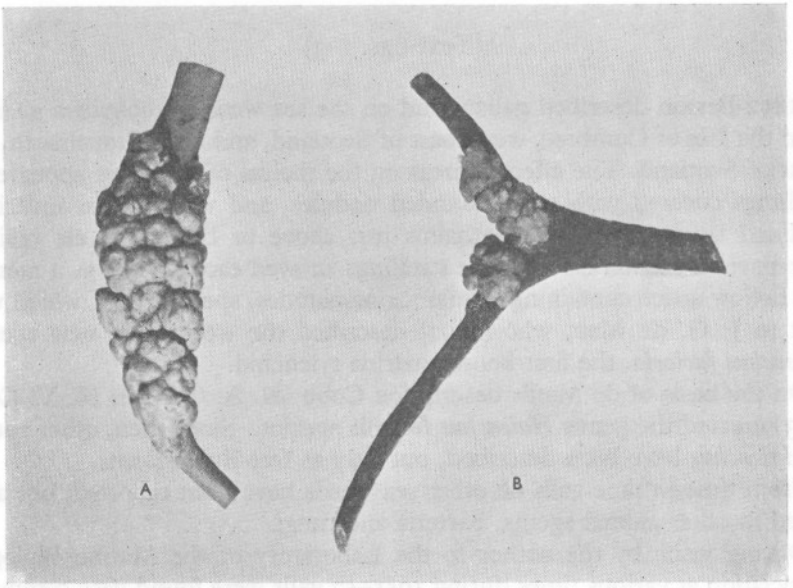

Fig. 1. Galls on (A) *Ascophyllum nodosum*, and (B) *Fucus vesiculosus*. (Approx. natural size.)

During a one-day visit to Lyme Regis, Dorset, in July 1957, galls were seen on the stipes of *Fucus vesiculosus*, and in some plants there were also galls on the fronds. In this locality galls were also seen on the stipes of *F. serratus*. On examination, these were found to be very similar to those on *F. vesiculosus*, and contained the same species of nematode.

The examination of the nematodes in the above material has been based on living specimens, as well as on others killed by heat, fixed in formalin and subsequently cleared in lactophenol and glycerine.

A redescription is given below of *Halenchus fucicola*, together with a description of the new species, *H. dumnonicus*.[1]

[1] From the Dumnonii, the British tribe that inhabited the south-west.

Halenchus fucicola (de Man, 1892) Cobb, 1933

Tylenchus fucicola de Man, 1892. *Festschr. zum Siebenzigsten Geburtstag Rudolf Leuckart*, pp. 121–5.
Anguillulina fucicola, Goodey, 1932. *J. Helminth.* Vol. 10, p. 27.
Halenchus fucicola, Cobb, 1933. *J. Parasit.* Vol. 20, p. 94.

Type host. In galls on the sea weed *Ascophyllum nodosum* Le Jol.

Material studied. From galls on *A. nodosum*, Wembury Bay, Devon, August 1955, June 1956, and May 1957.

Dimensions. Given in Table 1.

Long slender worms, gradually tapering at the extremities, with a characteristic hook-like tail, bent ventrally in both sexes. The cuticle is faintly transversely striated. The striations, which appear to be absent on the head-region, being about 1 μ apart. Lateral fields are present, which are about one-eighth of the body thickness; they appear to start at about half-way between the anterior end of the body and the excretory pore and can be traced to the tail region.

The head is marked off by a slight constriction, this latter being about 6 μ in diameter. There appear to be no distinct lips, the head-framework being divided into six sectors defined by faint ridges. Papillae are present on the two subdorsal and two subventral sectors, and the openings of the amphids are on the lateral ones. The amphidial pouches are situated laterally on either side of the stylet (Fig. 2C). The stylet is fairly well developed (15–16 μ long in the males and 15–18 μ long in the females) and is divided into two portions, a cylindrical posterior portion, with three well-pronounced basal knobs, and a conical anterior portion (Fig. 2C, D).

The excretory pore and its duct are well defined and characteristic, being heavily cuticularized. The pore is situated ventrally about one-eighth of the body length from the anterior end and the duct runs spirally in a posterior direction. The oesophagus is poorly developed. About mid-way along its length there is a slight swelling of the oesophageal wall associated with which is a somewhat ellipsoid widening of the lumen, probably representing a middle bulb. The lumen of the oesophagus can be seen in living specimens to have a wavy outline. The junction of the oesophagus and intestine is not clear, and was only seen in living specimens, where it occurred at about 20–25 μ anterior to the excretory pore. The granulated material of the intestine was seen to commence at this region and sometimes could be seen to run anteriorly into the oesophagus. Close behind the nerve ring, which is situated at the posterior end of the oesophagus, a dorsal oesophageal gland emerges from the wall of the oesophagus as a glandular diverticulum running alongside the intestine. This gland has a fairly well-defined nucleus and opens into the lumen of the oesophagus about 2–3 μ behind the base of the stylet. The distance of the extremity of the gland from the anterior

TABLE 1. DIMENSIONS OF *HALENCHUS FUCICOLA* (DE MAN, 1892) FROM WEMBURY BAY

Sample		Body length (μ)	Body length / Body thickness	Body length / Excretory pore	Body length / Length of tail (anus to tip)	Body length / Length of stylet	Body length / Length of spicules	V (%)
August 1955, ♂♂	Range	800–970	34·58–48·50	7·17–8·18	10·90–12·93	51·90–64·67	36·36–43·00	—
	Mean	891	38·10	7·78	11·73	58·67	40·70	—
	Standard deviation	±55·26	±7·08	±0·28	±0·63	±4·16	±2·18	—
	No. of specimens	10	10	10	10	10	10	—
August 1955, ♀♀	Range	970–1120	32·50–46·67	7·30–9·55	10·18–13·75	60·62–70·00	—	60·00–68·04
	Mean	1052·70	40·52	8·51	12·95	65·45	—	62·17
	Standard deviation	±54·50	±5·45	±0·56	±1·49	±3·31	—	±2·44
	No. of specimens	11	11	11	8	11	—	9
June 1956, ♂♂	Range	820–970	35·38–51·11	7·39–8·94	10·90–13·14	45·55–64·67	37·27–45·00	—
	Mean	883	42·06	8·11	11·63	56·50	41·68	—
	Standard deviation	±48·31	±4·69	±0·44	±0·75	±5·45	±2·12	—
	No. of specimens	10	10	10	9	10	10	—
June 1956, ♀♀	Range	980–1100	33·44–49·52	8·00–9·48	12·22–15·00	61·25–73·33	—	59·09–64·00
	Mean	1056	41·69	8·85	13·48	66·46	—	61·37
	Standard deviation	±41·35	±4·96	±0·48	±1·06	±3·55	—	±1·55
	No. of specimens	10	10	10	6	10	—	10
May 1957, ♂♂	Range	920–1060	35·92–45·91	7·36–7·92	11·05–12·80	57·50–67·33	40·00–55·71	—
	Mean	963	42·20	7·67	11·87	62·18	44·08	—
	Standard deviation	±43·72	±3·57	±0·17	±0·57	±3·19	±5·07	—
	No. of specimens	10	10	9	8	10	9	—
May 1957, ♀♀	Range	1040–1430	33·94–49·26	7·47–8·22	12·18–14·05	61·17–79·44	—	59·61–65·76
	Mean	1159	42·51	7·84	12·99	68·43	—	63·76
	Standard deviation	±46·80	±4·98	±0·28	±0·71	±6·17	—	±1·99
	No. of specimens	10	9	8	8	10	—	8

The ratio body length/excretory pore has been used instead of the usual '*b*' (body length/oesophagus) because of the difficulty of determining the posterior limit of the oesophagus. *V* is the distance of the vulva from the anterior end of the body expressed as a percentage of the body length.

TABLE 2. DIMENSIONS OF *HALENCHUS DUMNONICUS* SP.NOV. FROM WEMBURY BAY, 1955, 1956, 1957, AND HANNAFORE, LOOE, 1956

Sample		Body length (μ)	Body length / Body thickness	Body length / Excretory pore	Body length / Length of tail (anus to tip)	Body length / Length of stylet	Body length / Length of spicules	V (%)
♂♂	Range	850–1200	33·85–46·15	6·44–7·84	9·56–13·33	39·54–57·14	35·42–50·00	—
	Mean	989·10	40·09	7·20	11·12	47·57	40·45	—
	Standard deviation	±38·15	±3·27	±0·52	±1·23	±6·12	±4·26	—
	No. of specimens	11	11	10	10	11	11	—
♀♀	Range	900–1480	30·86–47·62	6·43–9·31	9·69–11·95	42·86–61·36	—	64·76–88·89
	Mean	1091·20	39·41	7·52	10·96	50·76	—	69·94
	Standard deviation	±166·55	±4·79	±0·76	±0·75	±5·08	—	±6·20
	No. of specimens	16	16	12	10	16	—	12

end of the body varies from 155 to 253 μ. The intestine terminates in a short rectum.

Deirids were not seen, while phasmids are present on the tail in the posterior region of the lateral caudal alae in the males, and occur in the region about half-way between the anus and the tip of the tail in the females.

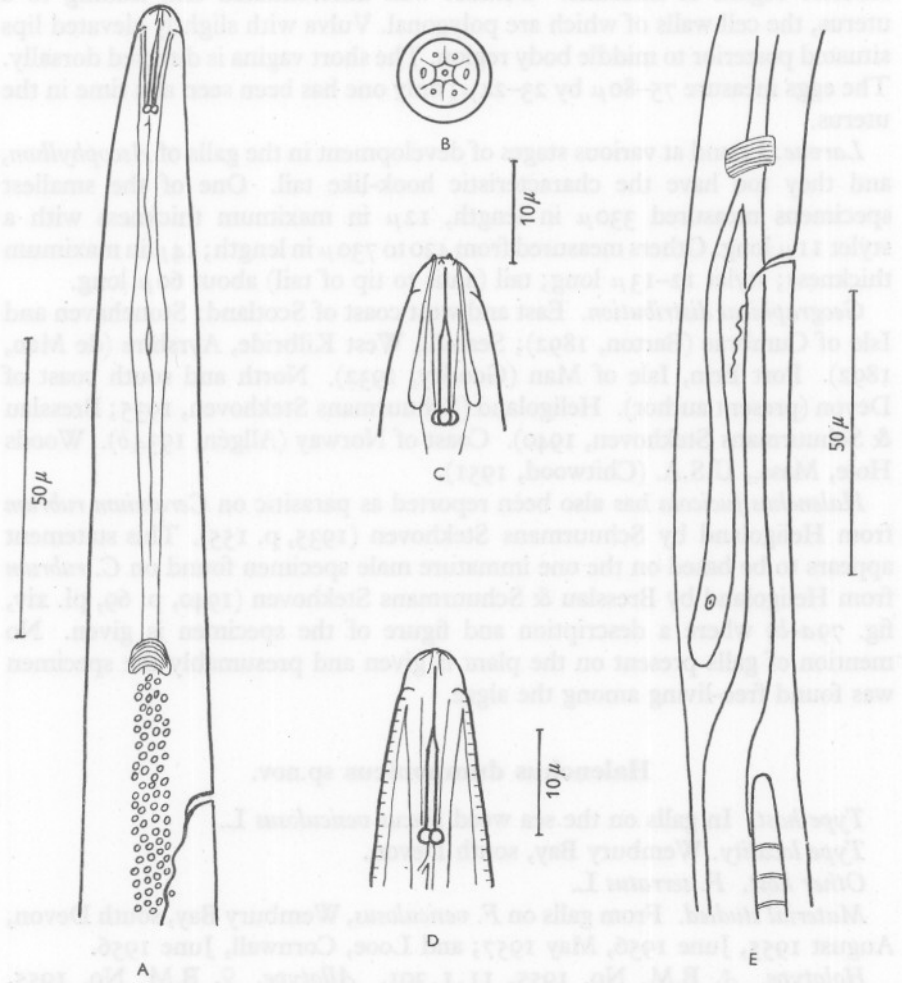

Fig. 2. A, *Halenchus fucicola*, anterior end; B, *H. fucicola*, head (*en face*); C, *H. fucicola*, head (ventral view showing papillae and amphids) (B and C to same scale); D, *H. fucicola*, head (lateral view); E, *H. dumnonicus*, posterior oesophageal region (lateral view).

Male. Testis single and straight, commencing at the anterior region of the intestine, opening without any apparent constriction into a vas deferens, which ends in a short ejaculatory duct. Spicules paired and equal, arched,

with slight variations, 20–24 μ in length (Fig. 3C, F and G). Gubernaculum trough-like, about 6–7 μ in length in a lateral view. Lateral alae present, commencing just anterior to proximal end of spicules and extending to about mid-way between cloaca and tip of tail.

Female. Ovary single and straight, anterior to vulva, and commencing at anterior region of intestine. Oviduct well differentiated and leading to a uterus, the cell walls of which are polygonal. Vulva with slightly elevated lips situated posterior to middle body region. The short vagina is directed dorsally. The eggs measure 75–80 μ by 23–24 μ; only one has been seen at a time in the uterus.

Larvae: Found at various stages of development in the galls of *Ascophyllum*, and they too have the characteristic hook-like tail. One of the smallest specimens measured 330 μ in length, 12 μ in maximum thickness with a stylet 11 μ long. Others measured from 420 to 730 μ in length; 14 μ in maximum thickness; stylet 12–13 μ long; tail (anus to tip of tail) about 60 μ long.

Geographical distribution. East and west coast of Scotland: Stonehaven and Isle of Cumbrae (Barton, 1892); Seamill, West Kilbride, Ayrshire (de Man, 1892). Port Erin, Isle of Man (Goodey, 1932). North and south coast of Devon (present author). Heligoland (Schuurmans Stekhoven, 1935; Bresslau & Schuurmans Stekhoven, 1940). Coast of Norway (Allgén, 1934*b*). Woods Hole, Mass., U.S.A. (Chitwood, 1951).

Halenchus fucicola has also been reported as parasitic on *Ceramium rubrum* from Heligoland by Schuurmans Stekhoven (1935, p. 155). This statement appears to be based on the one immature male specimen found on *C. rubrum* from Heligoland by Bresslau & Schuurmans Stekhoven (1940, p. 69, pl. xiv, fig. 79*a–b*) where a description and figure of the specimen is given. No mention of galls present on the plant is given and presumably the specimen was found free-living among the algae.

Halenchus dumnonicus sp.nov.

Type host. In galls on the sea weed *Fucus vesiculosus* L.

Type locality. Wembury Bay, south Devon.

Other host. F. serratus L.

Material studied. From galls on *F. vesiculosus*, Wembury Bay, south Devon, August 1955, June 1956, May 1957; and Looe, Cornwall, June 1956.

Holotype. ♂, B.M. No. 1955, 11.1.301. *Allotype.* ♀, B.M. No. 1955, 11.1.302. *Paratypes:* B.M. No. 1955, 11.1.303–311 (5 ♂♂, 4 ♀♀); 1957, 8.1.1–12 (6 ♂♂, 6 ♀♀). Host material registered under B.M. No. 1955, 11.1.312–325. 1957, 8.1.13–16.

Dimensions. Given in Table 2.

The shape of the body is very similar to that of *Halenchus fucicola* except that the anterior end is much more strongly developed in proportion to the

total length of the worm, and the stylet, although of similar shape to the other form, is much longer (20–22 μ long in the males and 20–25 μ long in the females). The tip of the tail is again hook-like, bent ventrally in both sexes.

The transverse striations of the cuticle, lateral fields, structure of the head and papillae are the same as in *H. fucicola*.

The excretory pore and its duct bear a considerable resemblance to those seen in *H. fucicola*, although the duct does not appear to be quite so heavily cuticularized and is situated ventrally about one-eighth of the body length from the anterior end. The structure of the oesophagus is also similar to that of the other species and the nerve ring is situated at the posterior end of it. The connexion of the oesophagus with the intestine is not clear in this species also and occurs just posterior to the nerve ring, about 20–25 μ anterior to the excretory pore. The dorsal oesophageal gland usually appears more slender than it does in the previous species, but this structure is somewhat variable in size. In some of the preserved and cleared specimens the connexion of the gland and the wall of the oesophagus is more easily seen (Fig. 2E). The opening of the gland into the lumen of the oesophagus occurs at about 2–3 μ from the base of the stylet. The distance of the extremity of the gland from the anterior end of the body is about 200 μ. The intestine is as in *H. fucicola*.

Deirids have not been seen. The phasmids have not been seen in this form.

Male. Testis and vas deferens as in *H. fucicola*. Spicules are longer, stouter and differ in shape from those in the other form (21–27 μ in length). In lateral view a well-pronounced protuberance can be seen raised in the form of a hump on the ventral side in mid-region; towards the proximal end there is also a greater curvature (Fig. 3D, H). Gubernaculum is trough-like, about 7 μ in length in a lateral view. Lateral alae are present as in *H. fucicola*.

Female. Ovary, oviduct and uterus similar to that in *H. fucicola*. Two specimens were found each bearing an egg; in one case the egg measured 66 by 22 μ and in the other 108 by 27 μ. Vulva with slightly elevated lips, situated posterior to the middle body region. Seen in a lateral position the vagina appears to have a greater cuticular development than in *H. fucicola* (Fig. 3E). A short post-vulvar uterine sac is present.

Larvae. Not seen.

Geographical distribution. South Devon and south Cornwall; Lyme Regis, Dorset.

The new species is a slightly larger form and differs from *H. fucicola* principally in the greater development of the stylet and in the shape of the spicules. In *H. fucicola* the males average about 900 μ in length and the females, including those bearing an egg, average just over 1000 μ. Only one specimen was found as long as 1430 μ and specimens over 1100 μ are not common. The maximum body thickness varies from 18 to 28 μ in the males and 20–33 μ in the females. In *H. dumnonicus* the males average about 1000 μ in length and the females about 1100 μ. Only two gravid specimens were

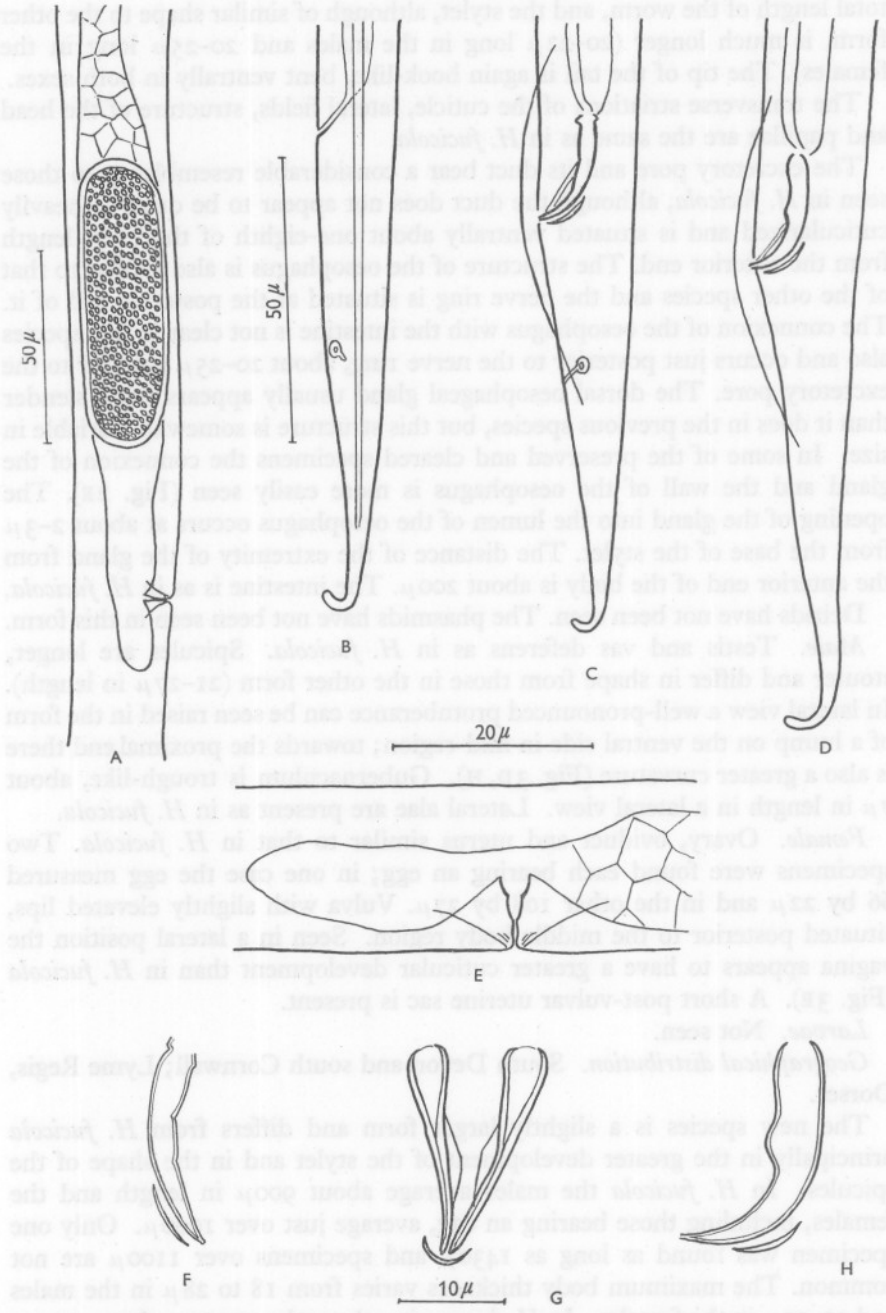

Fig. 3. A, *Halenchus fucicola*, posterior uterine region with egg; B, *H. fucicola*, female tail (showing lateral field and phasmid); C, *H. fucicola*, lateral view of male tail; D, *Halenchus dumnonicus*, lateral view of male tail (B, C and D to same scale); E, *H. dumnonicus*, posterior uterine region; F, *H. fucicola*, lateral view of spicule and gubernaculum; G, *H. fucicola*, ventral view of spicules and gubernaculum; H, *H. dumnonicus*, lateral view of spicule and gubernaculum (F, G and H to same scale).

found, each bearing one egg and measuring 1240 and 1270 μ in length respectively. The maximum body thickness varies from 20 to 31 μ in the males and 21–38 μ in the females.

The samples considered here are not random because the intention during sampling was to get some idea of the full range of size, so that the number of large and small specimens measured is probably biased in favour of such individuals. As a result of this it is valueless to compare the means of the absolute measurements. The difficulty, however, can be overcome by comparing ratios: while appreciating that ratios may also vary due to differential growth. For example, in *H. fucicola* the ratio body length/stylet length is 30 at a larval body length of 330 μ, 35 at 420 μ and 56 at 730 μ. In a sample of ten adults, mean body length 970 μ, the ratio is 59·60; and in another sample of 10 adults, mean body length 1159 μ, it is 68·43. These values were obtained by dividing a sample of twenty individuals into two halves on the basis of body length. From these figures it can be seen that the body grows at a greater rate than the stylet.

Ratios have been calculated for body length/body thickness, body length/distance of excretory pore from anterior end, body length/tail length, body length/stylet length, body length/length of spicules, and the distance of the vulva from the anterior end expressed as a percentage of the body length, i.e. vulva × 100/body length. The mean body lengths, given in the tables, are in all cases not significantly different, so that the ratios calculated against them should be strictly comparable. The ratios were calculated for all specimens and means and standard deviations calculated for them. Of these only the ratios of body length/length of stylet are significantly different in the two forms.

Due to the low number of specimens, the measurements of *H. dumnonicus* have been lumped, and it is this total which has been compared to each sample of *H. fucicola*.

As mentioned earlier, the specimens in the galls of *Fucus vesiculosus* are much scarcer, and when living specimens are removed from the galls they are usually more active than those of *Halenchus fucicola* from *Ascophyllum*. Specimens are also scarce in the galls on *Fucus serratus*.

Of the remaining species of *Halenchus*,[1] *H. dumnonicus* differs from *H. mediterraneus* (Micoletzky, 1922) in the length of the stylet, the position of the caudal alae, which do not extend so far posteriorly, and in the size and shape of the gubernaculum, which is smaller and has a wavy outline.

Finally, the new species differs from *H. mexicanus* Chitwood, 1951, in the shape of the tail, which is not hook-like.

[1] *Tylenchus* (*Chitinotylenchus*) *zostericola* Allgén (1934*a*) found associated with *Zostera* in Holland was transferred to *Halenchus* by Chitwood (1951), but is now considered to belong to the genus *Radopholus* (see Allen, 1955).

These tylenchid nematodes occur on the fucoid algae which predominate in the middle zone of the shore, and at Wembury Bay much time has been spent by the writer looking for galls on *Fucus spiralis* and *F. serratus* without success, although on a later visit to Lyme Regis galls were seen on the latter species.

Ascophyllum nodosum and *Fucus vesiculosus* occur at approximately the same height on the shore, and at Wembury Bay galls were sometimes seen on both plant species where they were growing near to each other. It would therefore seem possible for both species of nematodes to infest either plant, since at some stage in the life cycle some of the worms presumably emerge from the galls to infest new host plants. An obstacle to the elucidation of the life history of the worms by experimental means, however, arises from the difficulty of maintaining the large brown sea weeds under laboratory conditions.

Sometimes *Halenchus fucicola* and *Halenchus* sp. are quoted as parasites of red sea weeds, *Furcellaria fastigiata*, *Chondrus crispus* and *Rhodymenia palmata*. It appears, however, that these statements are based on the reports in two other papers by Barton (1891, 1901). Barton's material of *Furcellaria* and *Chondrus*, which was found washed up at Lyme Regis in 1900, is in the algal collections of the British Museum (Natural History) and the writer has had the opportunity of examining it. Although the nematodes in the galls of these plants are in very poor condition they certainly do not appear to be tylenchids. According to Barton (1891), the nematodes from *Rhodymenia palmata* were found in galls attributed to a copepod, and in a recent paper by Harding (1954), in which a description is given of the life history of the copepod from galls on *Rhodymenia palmata*, nematodes were again reported in some of the galls.

Thanks are due to Dr H. W. Parker who suggested this line of research, to Mr W. G. Inglis and Mr S. Prudhoe for much help and advice during the course of the work, and to the staff of the Laboratory at Plymouth, especially to Dr M. W. Parke.

SUMMARY

The nematode *Halenchus fucicola* (de Man), causing galls on the thallus of the sea weed *Ascophyllum nodosum*, has been found in the Plymouth area (Wembury Bay) and at Croyde Bay on the north Devon coast, and a redescription of the worm is given. A new species of *Halenchus* (*H. dumnonicus*) causing similar growths on the sea weeds *Fucus vesiculosus* and *F. serratus* is described. This latter form is also found at Wembury Bay; at Looe, Cornwall, and at Lyme Regis, Dorset.

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