

AGE AND GROWTH OF *CALLIONYMUS LYRA* L.

By Hsiao-Wei Chang

British Council Scholar and Ray Lankester Investigator
(Academia Sinica, Shanghai)

(Plate I and Text-figs. 1-4)

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The Common Dragonet, *Callionymus lyra* L., is one of the commonest fishes in the Plymouth area, and is widely distributed in European seas. Recent reports indicate that it occurs also off the coast of West Africa (Fowler, 1936; Poll, 1949). This fish, like others of the genus, attracts attention because, although it has very little economic importance, it is strikingly coloured and the sexes are markedly different. Work has been done on the breeding by Holt (1897, 1898), and by Holt & Scott (1898); on ova and larvae by M'Intosh (1885), M'Intosh & Prince (1889), Cunningham (1891), Holt (1897), Ehrenbaum (1905-9), Fage (1918), Mielck (1925), Duncker, Ehrenbaum, Kyle, Mohr & Schnakenbeck (1929); on seasonal abundance and distribution of post-larvae off Plymouth by Russell (1930-47) and Corbin (1948); and on the skeleton by Günther (1861) and Ford (1937). The mature males are provided with remarkable secondary sexual characters both in coloration and in relative lengths of snout and of median fins, which render them so different from the females that they were originally regarded as different species and known as the Gemmeous Dragonet (male *C. lyra* L.) and the Sordid Dragonet (female *C. lyra* L. = *C. dracunculus* L.) respectively (Donovan, 1808; Yarrell, 1859; Couch, 1863). The sexual dimorphism and seasonal variation of this species has been much studied by Holt (1898), Smitt (1892-95), Gallien (1934), Letaconnoux (1949) and Desbrosses (1949). Very little information has so far been provided about its age and growth, with which the present paper deals.

I am greatly indebted to Mr F. S. Russell, F.R.S., for suggesting this investigation to me; and to Mr G. A. Steven for advice and assistance while

it was being carried out and for much help in the preparation of the manuscript; to Mr G. M. Spooner for statistical advice and assistance; to Dr T. J. Hart and Mr M. D. Menon for help in the use of the radial bone for age determination; and to Dr J. S. Alexandrowicz who took the photographs. I have also the greatest pleasure in recording my indebtedness to the British Council and to the Trustees of the Ray Lankester fund for financial assistance without which this work could not have been done.

COLLECTION OF THE MATERIAL

All the specimens for this study were trawled off Plymouth by the research vessels *Sula* and *Sabella* and the research launch *Gammarus* during a period of 18 months, from December 1948 till May 1950. Some young fish were obtained also in the autumn and winter of 1950. During the first few months of the investigation the specimens were caught mainly by ordinary otter-trawl and partly by small beam-trawl (shrimp-netting), and very few fish below 50 mm. in length were collected. In order to obtain more young fish an Agassiz trawl with fine mesh and an otter-trawl with small mesh cover to the cod-end were also used later on. Nevertheless, the difficulty of obtaining sufficient numbers of young fish had not been solved. The total number of fish thus collected for this work amounts to over 4000 specimens varying from 20 to 240 mm. in standard length, including both sexes.

Monthly samples were taken and treated separately. Each fish was labelled and measured to the nearest millimetre, from the tip of the snout to the tip of the distal end of the longest caudal ray (total length) and from the tip of the snout to the distal end of the caudal hypural (standard length or body length). Then they were weighed to the nearest gram in a Salter spring balance and sexed. The large males above 80 mm. can easily be sorted out by means of the male secondary sexual characters, but those below that length were all confirmed by examining the gonads. Before preservation in formalin for other purposes, an otolith or the complete right pectoral girdle, or both of them, were removed and kept in small numbered envelopes for later study.

DETERMINATION OF AGE AND RATE OF GROWTH

There are no published data on the age and growth of this fish. Dr P. Desbrosses told me, in October 1949, that he had successfully used the otoliths to determine the age of *C. lyra*, but his results have not yet been published.

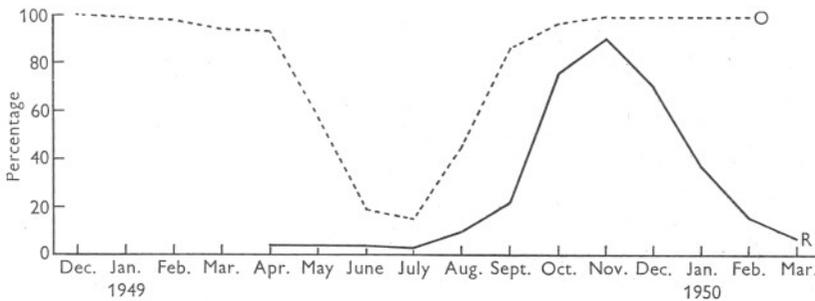
Age Reading from the Otolith

As *C. lyra* is devoid of scales, the otoliths were at first used for the age determination. The otolith belongs to the labrid type; its outer side is flat, inner side convex, dorsal rim domed and regular, and ventral rim curved (Frost, 1928). It is quite thin, and the number of rings on the fresh otoliths

can easily be read under a binocular dissecting microscope against a dark background. If the otolith has been dried it must be immersed in water before examination, otherwise the rings cannot be distinguished easily. The central area of the otolith is opaque, with alternating rings of transparent (slow growth zone) and opaque (rapid growth zone) material. Altogether, 2407 otoliths taken

TABLE I. PERCENTAGE OF FISH WITH SLOW OR RAPID GROWTH ZONES AT THE MARGIN OF THE OTOLITH AND OF THE SECOND RADIAL BONE

Month	No. examined	Percentage of otoliths with		No. examined	Percentage of radial bones with	
		slow growth zone at the margin	rapid growth zone at the margin		slow growth zone at the margin	rapid growth zone at the margin
Dec. 1948	72	100	0	—	—	—
Jan. 1949	200	99	1	—	—	—
Feb. 1949	119	98	2	—	—	—
Mar. 1949	64	94	6	—	—	—
Apr. 1949	88	93	7	45	4	96
May 1949	101	57	43	126	4	96
June 1949	206	19	81	134	4	96
July 1949	390	15	85	97	3	97
Aug. 1949	230	43	57	162	10	90
Sept. 1949	146	86	14	95	22	78
Oct. 1949	82	96	4	75	75	25
Nov. 1949	124	99	1	274	90	10
Dec. 1949	164	99	1	311	70	30
Jan. 1950	241	99	1	236	37	63
Feb. 1950	180	99	1	177	18	82
Mar. 1950	—	—	—	132	7	93



Text-fig. 1. *Callionymus lyra*, O (broken line), percentages of otoliths with transparent (slow growth) zone at margin, from December 1948 till February 1950. R (continuous line), percentages of radial bones with slow growth zone at margins, from April 1949 till March 1950.

from specimens of various ages of both sexes have been examined, over a period of 15 months, from December 1948 to February 1950 inclusive. The results confirm that the rings on the otoliths are formed annually, as there is a complete turning over of one sort of margin to the other during a certain period of the year (Table I; Text-fig. 1). The opaque rings are laid down cover-

ing the outer margin of the transparent zone during the summer months. It is a gradual increase in intensity of calcification rather than an increase in width during a short period. The transparent zone begins to appear after July, and the percentage of otoliths with the transparent margin reaches its peak (99–100%) during the winter and early spring. By reading the rings on the otoliths the age and the particular year group to which a fish belongs can be determined without difficulty. Nevertheless, the margins of the rings are very diffuse and the size of the otoliths is subject to great variation. It is very difficult to fix the centre and the line of growth. Although the otolith has been used successfully in reading the age of the fish, it is not practicable to measure it for back-calculation of growth rate. Soon my attention turned towards the other skeletal structures of the fish, since many bones in other fishes have been widely used for age determination (see Menon, 1950).

Age and Rate of Growth from the Second Radial Bone

On the vertebrae, coracoid, hypural and radials of *C. lyra*, there are very obvious alternating transparent and opaque zones, as found also in some bones of other fishes. After careful study, the zones on the second radial were found to be very constant, and the number of zones had a definite relationship with that on the otoliths of the same specimen. This bone was therefore selected for further study.

As a result of the great expansion of the pectoral girdle in *C. lyra*, the second radial bone becomes very flat and greatly enlarged. Its upper and lower surfaces are ossified, and in between the surface layers is the cartilage. During the autumn and winter the margin of the bone becomes almost completely ossified. Thus the narrow, ossified zone (i.e. the slow growth zone or winter ring) is formed.

Method of Preparation

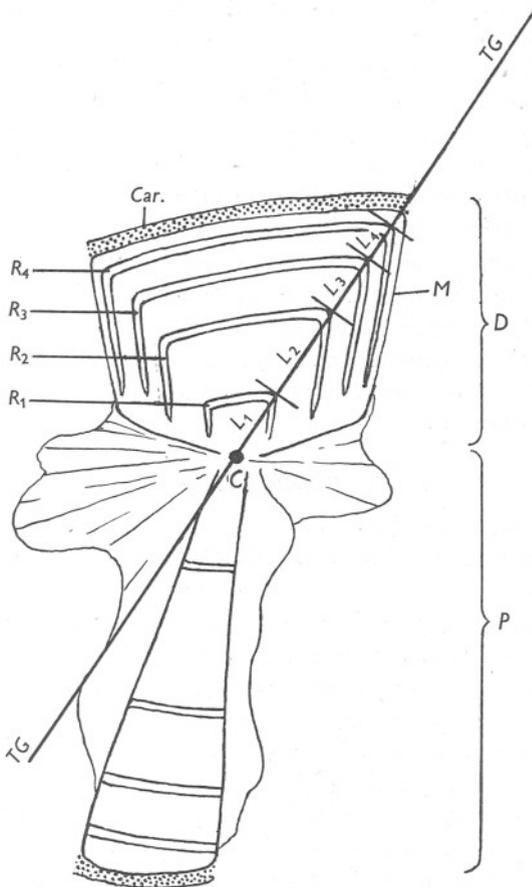
The method of preparing the bone is very easy. After the specimens are measured and numbered, the complete right pectoral girdles are removed one by one with a pair of dissecting scissors, and put into numbered glass dishes. Then they are dipped into a hot bath of water at 70–80° C. for 2–3 min. After this simple treatment, the complete girdle can readily be cleaned with a cloth between the fingers or in a pair of curved forceps. The pectoral girdles of small specimens less than about 80 mm. long are rather delicate, and must be carefully cleaned with forceps under the dissecting microscope, after which they are placed in labelled envelopes and left to dry.

Line of Growth and Method of Measurement

The distal half of the radial bone grows in three directions, as shown in Text-fig. 2. The centre of growth of the bone is very clear. If a straight line is drawn from the centre towards the angle of the bone, it crosses all the angles

of the ossified rings. The measurements taken were along this line, the intervals L_1 , L_2 , L_3 , etc., representing successive annual increments.

Since the radial is a cartilage bone, it shrinks a great deal after drying. The surface is no longer flat and the zones have lost their original shape. Therefore the radial bone of this fish has to be soaked for one to several days before



Text-fig. 2. The second radial bone of *Callionymus lyra* L. Diagram showing the theoretical growth line, and the way of measuring the length of the bone and the annual increments at different ages. TG , the hypothetical line of growth; R_1 to R_4 , the annual rings; C , the centre of growth; L_1 , L_2 , L_3 and L_4 , the first, second, third and fourth years' growth of the second radial bone; $Car.$, cartilage layer; M , margin of the bone.

measuring. After this treatment the bone recovers its former size and shape, and the rings become as clear as if the bone were fresh. As the radial bone is not thin enough for projecting, it was measured under a low-power microscope with an eye-piece micrometer.

Validity of the Zones for Age Determination

The main evidence supporting the validity of age determination from the second radial in this fish is that the rings on the bone are formed annually.

Monthly observations on the nature of the margins of the second radial were carried out over one complete year. Altogether 1860 radials were examined specially for this test. The results obtained, together with those of the otoliths, are given in Table 1 and Text-fig. 1. The data reveal two important points: (i) that there is a nearly complete turning over in a certain period of the year from one kind of margin to the other, and (ii) that there is also a definite agreement between the number of rings on the radial and that on the otoliths. In the second radial bone the narrow ossified zone (the slow-growth zone or winter ring) begins to appear in September. Its percentage occurrence is highest in November and falls rapidly after December. Usually, in young fish, the formation of the first ring takes place comparatively early, whereas in some of the mature fish the completion of the rings is much delayed. Therefore, there is no complete turning over from one kind of margin to the other throughout the entire population at any period.

From the above evidence there can be no doubt that the zones on the second radial are annual, and it is therefore concluded that the second radial is valid for age determination in this fish.

RESULTS OF GROWTH MEASUREMENTS

Altogether 1059 second radials from male fish and 627 from females were measured. Among the 1059 male radials 876 were from immature and 183 from mature fish.

The mean lengths of both body and radial at each 5 mm. group in the immature males and females are given in Table II. When the mean radial lengths are plotted against the mean body lengths all the points lie practically along a straight line, as shown in Text-fig. 3.

The snout in mature males is greatly prolonged and subjected to great variation. As its length is correlated with the state of sexual maturity and is not in direct proportion to the body length, correction must be made in total length measurements for the excess of snout length (see p. 289). After this correction has been made and the mature males regrouped, the proportion of the mean lengths of the radials and the corrected body length in different length groups came into agreement with those of the immature males and the females (Table VI; Text-fig. 3).

By graphic method the formula for the correlation curve of the radial length and the body length in this fish is as follows

$$R = 0.04 + 0.0199 B,$$

where R is the length of the radial and B is the body length; both measured in mm. By using this formula the theoretical lengths of either radial bone or

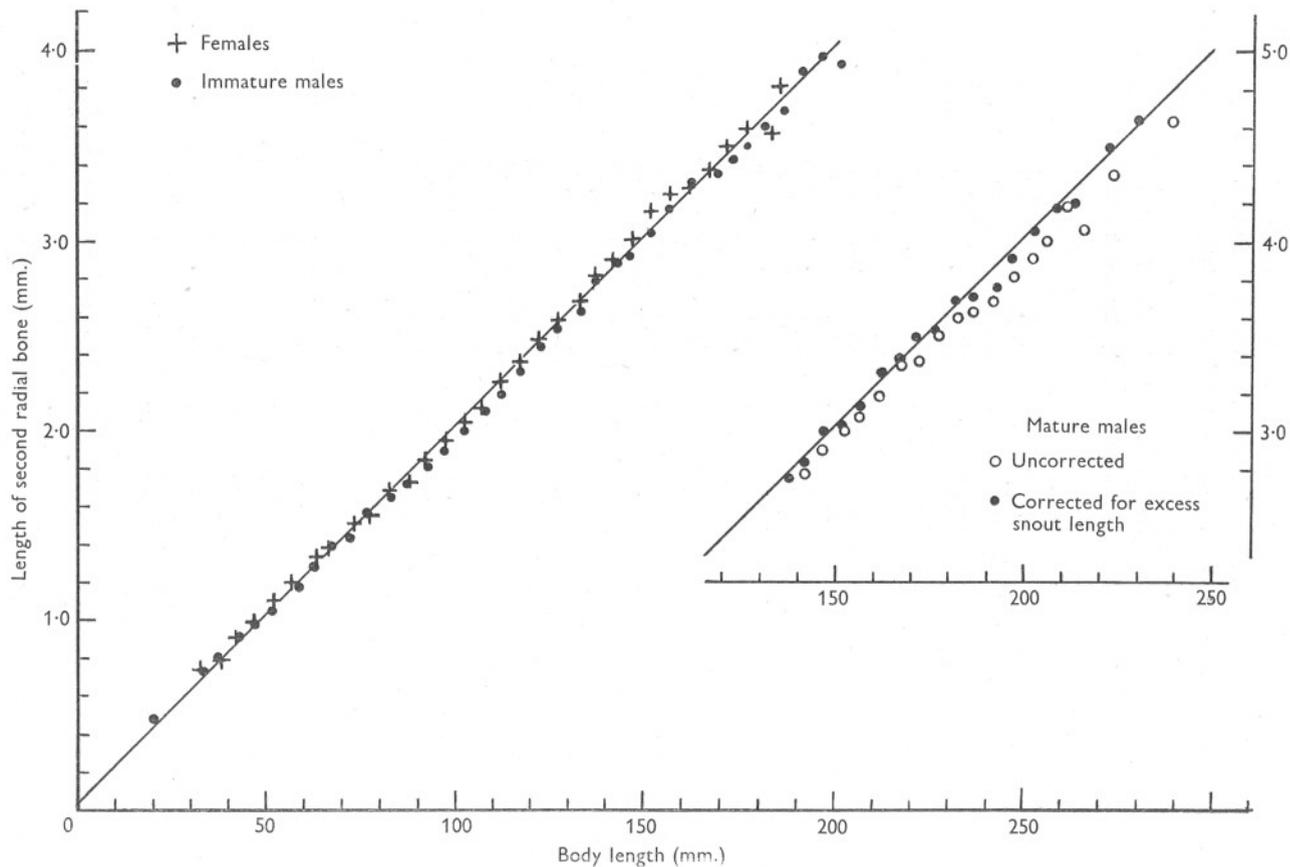
the body length of each 5 mm. group above 35 mm. can be worked out, given one or the other. In Table II the calculated body lengths (given the observed radial bone lengths) are listed for immature males and females, and in Table VI for mature males. The differences between the empirical lengths and

TABLE II. MEAN LENGTHS OF THE SECOND RADIAL IN RELATION TO THE MEAN LENGTH OF FISH AT THE DIFFERENT LENGTH GROUPS

Length group (mm.)	No. of fish	Immature males				Females				
		Mean body length (mm.)	Length of 2nd radial (mm.)		Theoretical body length (mm.)	No. of fish	Mean body length (mm.)	Length of 2nd radial (mm.)		Theoretical body length (mm.)
			mean	σ				mean	σ	
20	1	20.0	0.48	—	22.1	0	—	—	—	—
25	0	—	—	—	—	0	—	—	—	—
30	4	33.2	0.73	0.03	34.7	4	32.8	0.74	0.02	35.2
35	5	37.2	0.80	0.06	38.2	12	36.8	0.79	0.07	37.7
40	15	42.8	0.91	0.05	43.7	19	42.1	0.91	0.05	43.7
45	11	47.1	0.98	0.02	47.2	9	46.8	0.99	0.05	47.7
50	7	57.4	1.04	0.05	50.3	6	52.0	1.10	0.05	53.3
55	7	58.6	1.17	0.07	56.8	6	56.7	1.20	0.05	58.3
60	4	62.7	1.28	0.08	62.3	7	63.1	1.33	0.04	64.8
65	6	67.2	1.39	0.06	67.8	10	66.6	1.38	0.06	67.3
70	7	72.0	1.43	0.05	69.8	6	73.0	1.51	0.11	73.9
75	9	76.7	1.56	0.07	76.4	17	76.6	1.56	0.10	76.4
80	9	82.6	1.65	0.07	80.9	14	82.0	1.68	0.08	82.4
85	15	87.0	1.72	0.06	84.4	24	87.2	1.73	0.07	84.9
90	32	92.4	1.81	0.09	88.9	46	91.8	1.84	0.08	90.5
95	43	97.0	1.89	0.07	93.0	46	97.2	1.95	0.09	96.0
100	45	102.0	2.00	0.08	98.5	40	102.0	2.04	0.09	100.5
105	55	107.4	2.10	0.08	103.5	43	106.8	2.12	0.09	104.5
110	50	111.9	2.19	0.10	108.0	32	111.9	2.26	0.10	111.6
115	43	117.0	2.31	0.08	114.1	35	117.0	2.36	0.11	116.6
120	37	122.1	2.44	0.10	120.6	44	121.8	2.48	0.10	122.6
125	25	127.0	2.54	0.10	125.6	38	127.0	2.58	0.11	127.6
130	40	131.6	2.62	0.11	129.6	20	132.3	2.68	0.09	132.7
135	30	137.1	2.79	0.12	138.2	29	136.6	2.81	0.11	139.2
140	23	142.9	2.88	0.09	142.7	25	141.6	2.90	0.14	143.7
145	36	146.8	2.92	0.13	144.7	21	146.8	3.01	0.18	149.2
150	35	151.7	3.04	0.13	150.8	18	151.5	3.16	0.11	156.8
155	30	156.3	3.17	0.10	157.3	13	156.7	3.25	0.13	161.3
160	36	162.0	3.31	0.14	164.3	19	161.5	3.29	0.14	163.3
165	42	166.9	3.36	0.15	166.8	7	167.0	3.38	0.10	167.8
170	49	172.6	3.43	0.14	170.4	10	171.1	3.50	0.18	173.9
175	39	176.4	3.50	0.13	173.9	2	176.5	3.59	0.24	178.4
180	37	181.5	3.60	0.13	178.9	3	183.0	3.57	0.08	177.4
185	25	186.4	3.68	0.15	182.9	2	185.0	3.81	0.04	189.4
190	12	191.6	3.89	0.16	193.5	—	—	—	—	—
195	4	196.5	3.97	0.19	197.5	—	—	—	—	—
200	7	201.2	3.92	0.16	195.0	—	—	—	—	—

the calculated lengths of the body are less than 5 mm. except at a few points.

An analysis of the length frequency in relation to the number of rings on the 2nd radial bone shows that the male may attain an age of 5 years (with four complete ossified winter rings), while the females may live 2 years longer



Text-fig. 3. Relation between body length and length of the second radial bone.

The graph line in the inset is identical with that in the main diagram, showing that the 'corrected' males conform with the females and immatures.

(with six complete ossified winter rings). However, the males grow much more quickly and to a larger size than the females (Table III).

It is also shown that among the 1059 radials from male fish, 1024 have one or more ossified winter rings; 680 radials have two or more; 164 radials have three or more; and only six radials have four complete ossified winter rings. If the mean lengths of the 1st, 2nd, 3rd and 4th rings are worked by back-calculation derived from the radial, the annual increment of the body length can be obtained irrespective of the actual length of the fish. Similarly, the annual increment of the body length in females at different ages can be calculated (Tables IV and V; Text-fig. 4).

The mean lengths of both the body and the radial of the mature males are entered in Table VI. When mean lengths of radials are plotted against the mean fish lengths, nearly all the points are far below the correlation curve for the immature males and the females (Text-fig. 3). If the snout length in the mature males be corrected according to the following averages derived from the immature males, all the points lie very close to the correlation curve of mean radial length and body length of both immature males and females:

$$\text{snout length (mm.)} = -0.3625 + 0.1275 \times \text{body length.}$$

NATURAL DEATH OF THE SPENT MALES

During the spring and summer of 1949, some interesting phenomena were observed. First, sexual maturity in the males was not directly related to the length of the body, since the spawning males varied from about 130 mm. to nearly as long as 240 mm., and at the same time many large immature males were found in the catches (Table VII). Secondly, the majority of the spawning males lost weight very quickly after the breeding season started, generally in the latter part of January off Plymouth, and their secondary sexual characters became extremely prominent. Thirdly, the majority of spent males suddenly disappeared after June and July. This sudden disappearance could be explained in three ways: (i) by degeneration or reabsorption of all the secondary sexual characters, (ii) by migration of the spent males to deeper waters after the breeding season, and (iii) by natural death of the spent males after the breeding season. However, there was no evidence to support the first two possibilities.

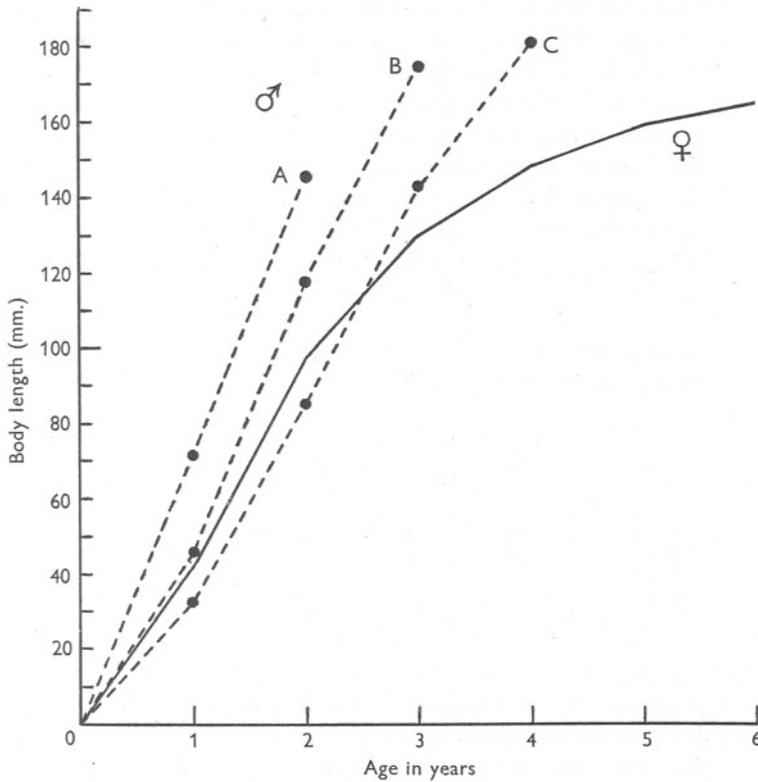
An analysis of the age of all the males collected from April 1949 to March 1950 inclusive, shows that the spawning males clearly fall into three age groups and that all the year round there are mature males; but the percentages of such fish exceeding 120 mm. in length (the size of the smallest mature males) showed a tremendous seasonal change. It was as low as 4.4% in October and as high as 78.1% in March (Table VI). Throughout the 20 months of direct observations on the catches, the gradual changes in the development of the secondary sexual characters in the males could easily be followed, and there was no indication of any recovery of the body condition

TABLE III. LENGTH FREQUENCIES OF FISH AND RELATION TO NUMBER OF OSSIFIED RINGS ON THE SECOND RADIAL BONES

Mature males enumerated separately in heavy type

Length group (mm.)	Males. Ossified rings on second radials						Females. Ossified rings on second radials								
	0	1+	2+	3+	4+	Total	0	1+	2+	3+	4+	5+	6+	Total	
20	I	—	—	—	—	I	0	—	—	—	—	—	—	—	
25	0	—	—	—	—	0	0	—	—	—	—	—	—	—	
30	4	—	—	—	—	4	3	I	—	—	—	—	—	4	
35	5	—	—	—	—	5	4	8	—	—	—	—	—	12	
40	II	4	—	—	—	15	5	5	—	—	—	—	—	19	
45	7	4	—	—	—	11	4	4	—	—	—	—	—	9	
50	2	5	—	—	—	7	2	4	—	—	—	—	—	6	
55	3	5	—	—	—	8	0	6	—	—	—	—	—	6	
60	I	5	—	—	—	4	0	6	I	0	—	—	—	7	
65	I	5	—	—	—	6	I	6	0	0	—	—	—	10	
70	—	7	—	—	—	7	0	9	6	0	—	—	—	6	
75	—	7	2	—	—	9	I	14	6	0	—	—	—	17	
80	—	7	2	—	—	9	—	8	6	—	—	—	—	14	
85	—	12	3	—	—	15	—	14	10	—	—	—	—	24	
90	—	10	13	—	—	32	—	30	16	—	—	—	—	46	
95	—	37	6	—	—	43	—	26	20	—	—	—	—	46	
100	—	32	13	—	—	45	—	23	17	—	—	—	—	40	
105	—	36	14	—	—	50	—	26	17	—	—	—	—	43	
110	—	32	11	—	—	43	—	17	15	—	—	—	—	32	
115	—	26	11	—	—	37	—	14	15	6	—	—	—	35	
120	—	15	10	—	—	25	—	6	30	8	—	—	—	44	
125	—	20	20	—	—	40	—	8	24	6	—	—	—	38	
130	—	10	17	—	—	30	—	2	14	3	—	—	—	20	
135	—	7+I	15+6	3	—	30	—	I	18	9	I	—	—	29	
140	—	8+I	26+6	I	—	44	—	I	10	7	—	—	—	25	
145	—	2+0	32+8	I+3	—	46	—	I	7	12	I	—	—	21	
150	—	0+0	30+8	0+5	—	46	—	—	2	15	—	—	—	18	
155	—	I+I	30+3	5+6	—	46	—	—	4	6	—	—	—	13	
160	—	I	40+3	I+II	—	56	—	—	I	11	—	—	—	19	
165	—	—	41+6	8+9	—	64	—	—	—	2	—	—	I	7	
170	—	—	35+8	4+17	—	64	—	—	—	3	—	—	—	10	
175	—	—	31+0	6+7	I	45	—	—	—	5	I	—	—	2	
180	—	—	21+I	4+II	—	37	—	—	—	I	2	—	—	3	
185	—	—	10+2	2+10	—	24	—	—	—	—	—	—	—	2	
190	—	—	2+3	2+10	—	17	—	—	—	—	—	—	—	—	
195	—	—	7+I	9	—	19	—	—	—	—	—	—	—	—	
200	—	—	—	7	2	8	—	—	—	—	—	—	—	—	
205	—	—	—	3	I	6	—	—	—	—	—	—	—	—	
210	—	—	—	5	I	6	—	—	—	—	—	—	—	—	
215	—	—	—	4	I	5	—	—	—	—	—	—	—	—	
220	—	—	—	—	—	0	—	—	—	—	—	—	—	—	
225	—	—	—	—	—	0	—	—	—	—	—	—	—	—	
230	—	—	—	—	—	0	—	—	—	—	—	—	—	—	
235	—	—	—	I	—	I	—	—	—	—	—	—	—	—	
Totals	35	34I	46I	39	119	6	1059	30	240	229	95	29	3	I	627

of the spent males or reabsorption of the secondary sexual characters. The most distinct feature of the secondary sexual characters other than coloration is the great prolongation of the snout and of all the median fins, including the



Text-fig. 4. Growth of *Callionymus lyra*. ♂ (broken line), A, third-year breeder; B, fourth-year breeder; C, fifth-year breeder. ♀ (continuous line), mixed.

TABLE IV. MEAN LENGTH OF SUCCESSIVE ANNUAL RINGS

	Male				Female			
	No.	Range	Mean length (mm.)	S.D.	No.	Range	Mean length (mm.)	S.D.
1st ring	1024	0.39-1.90	1.04	0.28	597	0.40-1.90	0.88	0.27
2nd ring	680	0.68-2.08	1.37	0.27	357	0.58-1.98	1.14	0.26
3rd ring	159	0.30-1.88	1.10	0.31	128	0.22-1.40	0.69	0.28
4th ring	6	0.46-1.04	0.81	0.23	33	0.10-0.80	0.41	0.19
5th ring	—	—	—	—	4	0.20-0.36	0.25	0.36
6th ring	—	—	—	—	1	—	0.16	0.00

dorsal, anal and caudal fins. The prolongation of the snout is mainly effected by the elongation of the process of the premaxillary (Günther, 1861, pp. 140-2). For example, the premaxillary of a spent male, 166 mm. long,

collected in May 1949, reached 28 mm., while an immature one 168 mm. long, collected in the same month, was only 22 mm. long. The length of the first dorsal fin-ray of the former was 125 mm. and of the latter 51 mm. In two other specimens, one a mature male, 204 mm. long (May 1949), and the other an immature male, 201 mm. long (November 1949), the lengths of the premaxillary were 40 and 29 mm., and of the first dorsal fin-rays 145 and 95 mm. respectively. Since the fin-ray and the ossified premaxillary are not epidermal structures, they are very different from the nuptial organ (or pearl organs) found in many fresh-water fishes, which can be dropped off after the breeding season (Kimura & Tao, 1937) and the fleshy hump on the forehead of the cichlids (Cichlidae), which is absorbed after the breeding season (Norman, 1947, p. 301). The possibility of sudden absorption of the skeletal structure or of the greatly elongated fin-rays in this fish would seem impossible.

TABLE V. THEORETICAL LENGTHS CALCULATED FROM MEASUREMENTS OF THE SECOND RADIAL BONES (MM.)

Towards the end of	Male		Female	
	Annual increment	Cumulative length	Annual increment	Cumulative length
1st ring	50.3	50.3	42.2	42.2
2nd ring	66.8	117.1	55.3	97.5
3rd ring	53.3	170.4	32.7	130.2
4th ring	38.7	209.1	18.6	148.8
5th ring	—	—	10.6	159.4
6th ring	—	—	6.0	165.4

No marking experiments have been done to elucidate whether or not the spent males migrate into the deeper water after the breeding season. But the age composition of the mature males in the spring of 1949 is similar to that in the spring of 1950. Here we may take the proportion of the spawning males in the month of April 1949 and those of March 1950 for comparison. The numbers of the third-year, fourth-year and fifth-year breeders in April are 10, 21 and 1; and in March 1950 are 24, 52 and 3 respectively. If the spent males did come back to breed again, the age distribution of the spawning males in the spring of 1950 should have included many more fifth-year breeders. Attempts have been made to study the histological structures of the testis at different stages, and to find out how they are correlated with the secondary sexual characters and seasonal changes, but the data so obtained have not yet been analysed.

Turning to the positive evidence that natural death takes place in the males after the breeding season, the age and rate of growth of 153 spent males were studied in detail. These comprised forty third-year breeders (with two complete winter rings), 107 fourth-year breeders (with three complete winter rings), and six fifth-year breeders (with four complete rings). It was found that the rates of growth of these groups were very different (Table VIII, Text-fig. 4). In those males breeding in the third year the rate of growth was

TABLE VI. *CALLIONYMUS LYRA*, MATURE MALES. LENGTHS OF BODY AND SECOND RADIAL BONE AS OBSERVED, AND AS CORRECTED FOR EXCESS SNOUT LENGTH

Length group (mm.)	Total specimens	Mean body length (mm.)	Mean length of 2nd radial (mm.)	Ossified rings on second radial (nos. of fish)			
				1+	2+	3+	4+
Empirical							
135	—	—	—	—	—	—	—
140	7	141.4	2.78	1	6	—	—
145	8	146.9	2.90	1	6	1	—
150	11	152.5	3.00	—	8	3	—
155	13	156.5	3.07	—	8	5	—
160	10	161.4	3.19	1	3	6	—
165	14	167.1	3.35	—	3	11	—
170	15	172.0	3.37	—	6	9	—
175	25	177.8	3.50	—	8	17	—
180	8	182.4	3.60	—	—	7	1
185	12	186.4	3.63	—	1	11	—
190	12	191.8	3.69	—	2	10	—
195	13	197.2	3.81	—	3	10	—
200	12	202.0	3.91	—	1	9	2
205	8	206.1	4.00	—	—	7	1
210	3	210.7	4.19	—	—	3	—
215	6	215.5	4.06	—	—	5	1
220	5	223.0	4.35	—	—	4	1
225	—	—	—	—	—	—	—
230	—	—	—	—	—	—	—
235	1	239.0	4.64	—	—	1	—
				3	55	119	6
Corrected							
135	3	138.0	2.75	1	2	—	—
140	9	142.0	2.83	—	9	—	—
145	7	147.4	2.99	1	5	1	—
150	15	151.9	3.03	—	8	7	—
155	11	156.8	3.11	—	5	6	—
160	13	161.9	3.30	1	4	8	—
165	16	167.2	3.37	—	5	11	—
170	9	171.2	3.49	—	3	6	—
175	27	176.9	3.53	—	7	19	1
180	15	181.9	3.69	—	1	14	—
185	7	186.9	3.71	—	1	6	—
190	19	192.4	3.76	—	3	15	1
195	8	196.6	3.91	—	1	6	1
200	15	202.6	4.05	—	1	12	2
205	3	208.2	4.17	—	—	3	—
210	2	213.0	4.20	—	—	1	1
215	—	—	—	—	—	—	—
220	3	220.0	4.49	—	—	3	—
225	—	—	—	—	—	—	—
230	1	230.0	4.64	—	—	1	—
235	—	—	—	—	—	—	—
				3	55	119	6

comparatively very high. Among the forty third-year specimens, the first year's growth of seventeen individuals was higher than the second year's growth, and the mean of the first year's growth is slightly lower than the second year's growth. In those males breeding in the fourth year the rate of twelve specimens was highest in the first year, of eighty highest in the second year, and in only fifteen highest in the third year. The mean of the first year's

TABLE VII. ACTUAL NUMBERS AND PERCENTAGES OF MATURE MALES ABOVE 120 MM., OBTAINED IN DIFFERENT MONTHS THROUGHOUT ONE COMPLETE YEAR

Month	No. of mature males	Percentage of mature males
Apr. 1949	42	62.7
May 1949	90	68.7
June 1949	55	25.3
July 1949	34	15.0
Aug. 1949	10	11.8
Sept. 1949	11	9.8
Oct. 1949	4	4.4
Nov. 1949	16	9.2
Dec. 1949	64	53.3
Jan. 1950	28	52.8
Feb. 1950	39	60.9
Mar. 1950	89	78.1
Total	482	—

TABLE VIII. COMPARISON OF THE RATE OF GROWTH IN THE MALES WHICH BREED AT THE THREE DIFFERENT AGES

Males breeding in	No.	Successive rings	Lengths of successive rings on radial (mm.)		Calculated annual increment of body length (mm.)	Calculated mean body length at the end of successive rings (mm.)
			mean	σ		
3rd year	43	1st ring	1.47	0.32	71.9	71.9
		2nd ring	1.50	0.27	73.4	145.3
4th year	107	1st ring	0.95	0.25	45.7	45.7
		2nd ring	1.48	0.25	72.4	118.1
		3rd ring	1.16	0.28	56.3	174.4
5th year	6	1st ring	0.69	0.17	32.7	32.7
		2nd ring	1.08	0.21	52.3	85.0
		3rd ring	1.19	0.25	57.8	142.8
		4th ring	0.81	0.20	38.7	181.5

growth was much smaller than in the other 2 years. Among the males breeding in the fifth year, two specimens showed their highest growth rate in the first year, three in the second year, and one has its third year's growth almost equal to that of the fourth year. As in their growth rates these three groups of breeding males are so different from each other, they must be very different from each other physiologically.

The presence of large immature males with three complete winter rings on

the radial, and of a considerable number of immature males, further proves that the fifth-year male breeders are neither the same third-year breeders of 2 years earlier nor the fourth-year breeders of 1 year earlier. Similarly, the fourth-year breeders are not the third-year breeders of 1 year before.

The length-weight relation and the secondary sexual characters also show that the males of *C. lyra* breed only once in their life. Besides the well-known example of *Anguilla*, which breeds only once during life, *Callionymus lyra* provides one of the most interesting illustrations of natural death among the large fishes.

SUMMARY

Both the otoliths and the second radials of the pectoral girdle can be used for age determination in *Callionymus lyra* L. Since the latter are far more satisfactory than the former, the second radial was selected for this work and the otolith was used only to check age reading. The radial is here used for the first time for age determination in fish.

The male may live up to 5 years (with four complete ossified winter rings), while the females may live 2 years longer (with six complete ossified winter rings). However, the males grow much quicker and to a larger size (239 mm. long) than the females (185 mm.).

The age of the spawning males falls into three age groups: (A) those that breed in the third year having two complete winter rings; (B) those that breed in the fourth year having three; (C) those that breed in the fifth year having four.

An analysis of the rates of growth of the spent males of three age groups shows that the rate of growth is highest in the third-year breeders, and is lowest in the fifth-year breeders.

Evidence has been given showing that the males of *C. lyra* breed only once and subsequently die. Breeding of the females has not been worked out.

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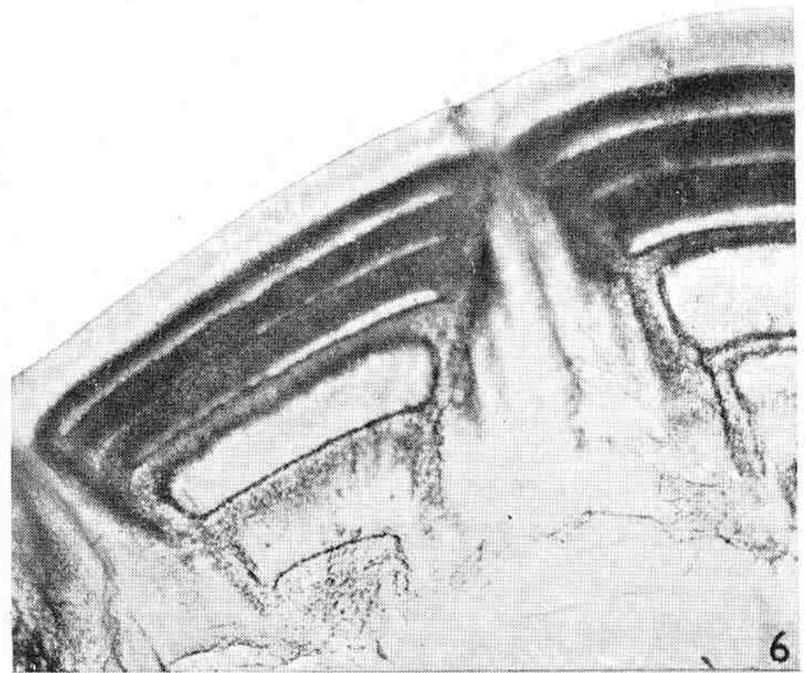
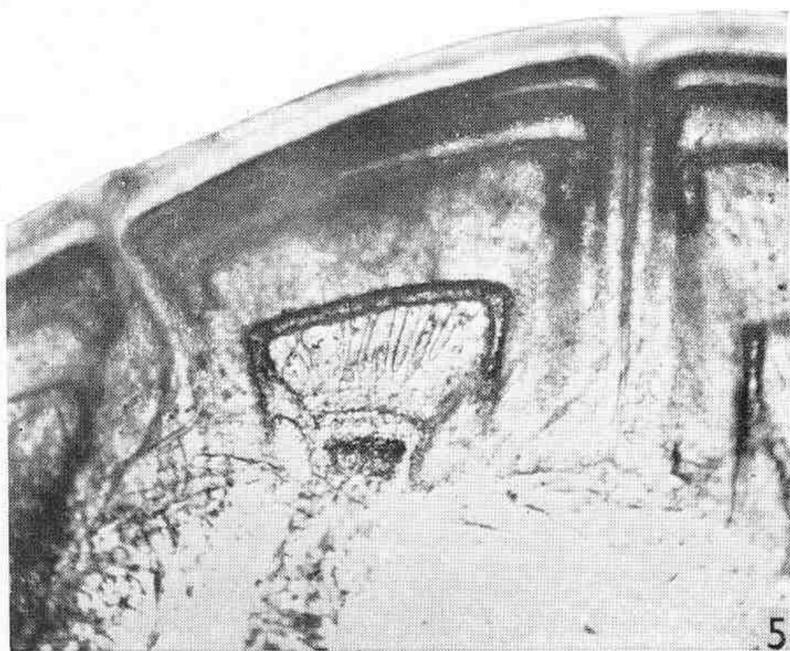
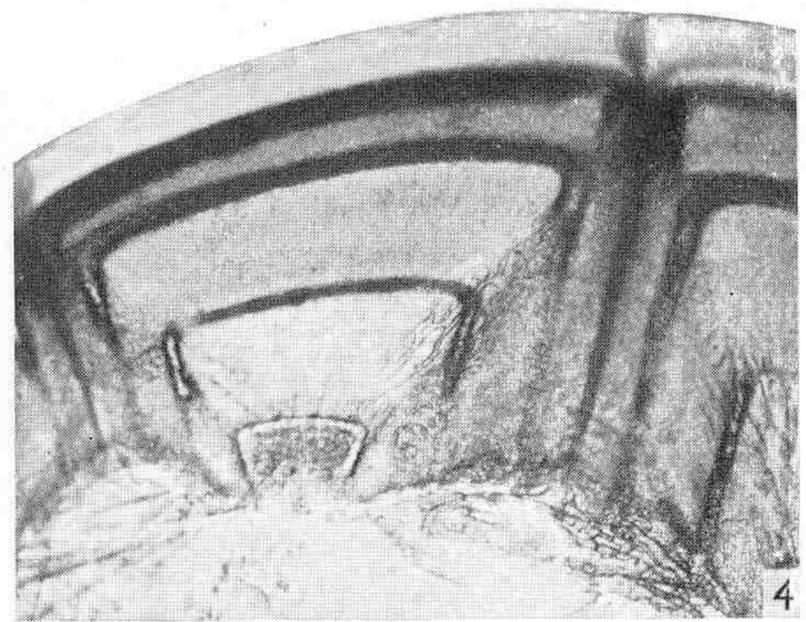
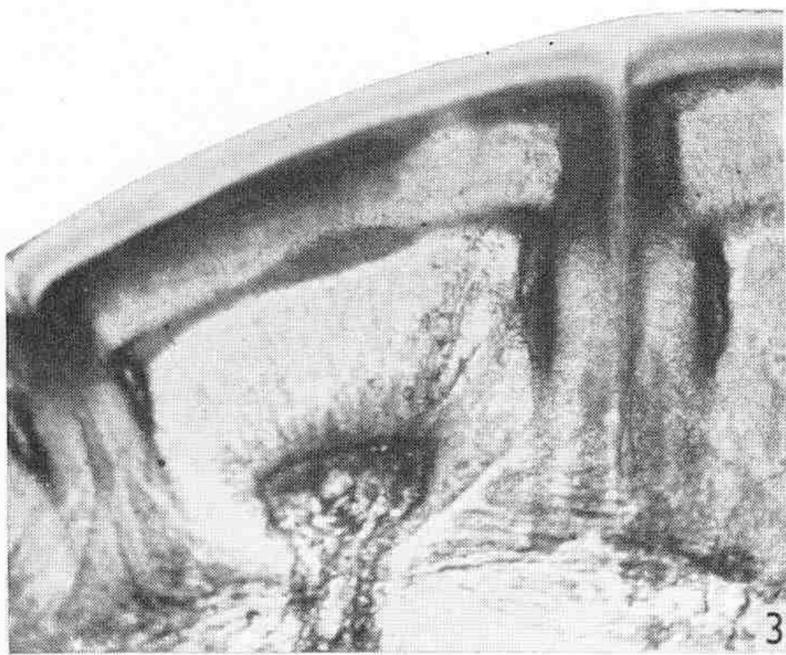
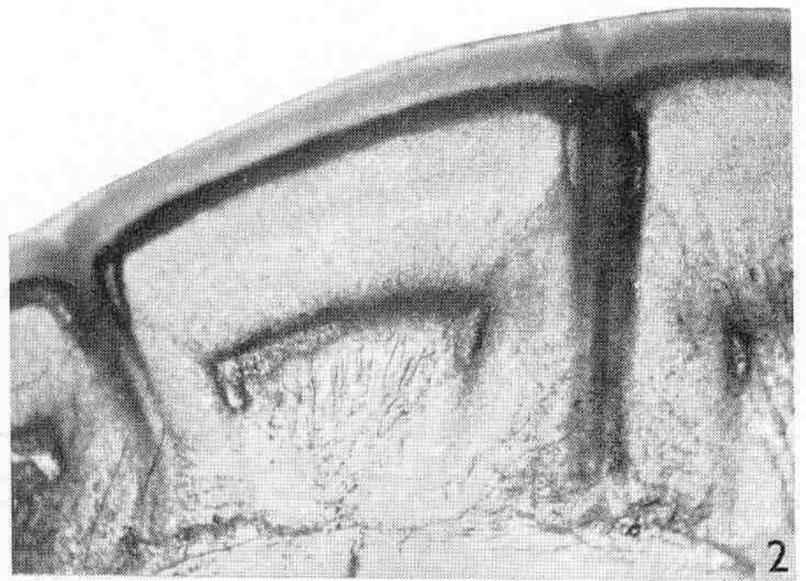
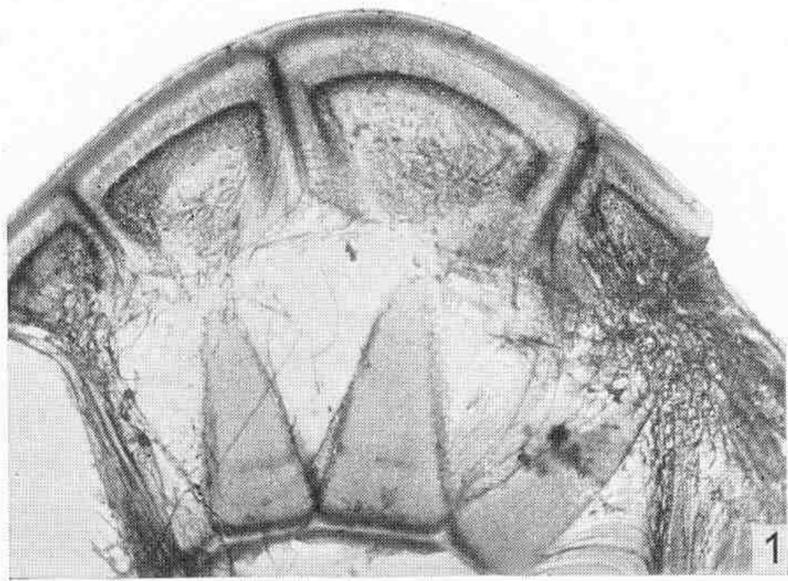
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EXPLANATION OF PLATE I

PLATE I. Second radials of *Callionymus lyra*

- Fig. 1. Female aged 1+, length 69 mm., April 1949.
- Fig. 2. Mature male aged 2+, length 168 mm., March 1949.
- Fig. 3. Mature male aged 3+, length 198 mm.
- Fig. 4. Female aged 4+, length 185 mm., May 1949.
- Fig. 5. Male aged 5+, length 172 mm., Oct. 1949.
- Fig. 6. Female aged 6+, length 179 mm., Nov. 1948.



Figs. 1-6.