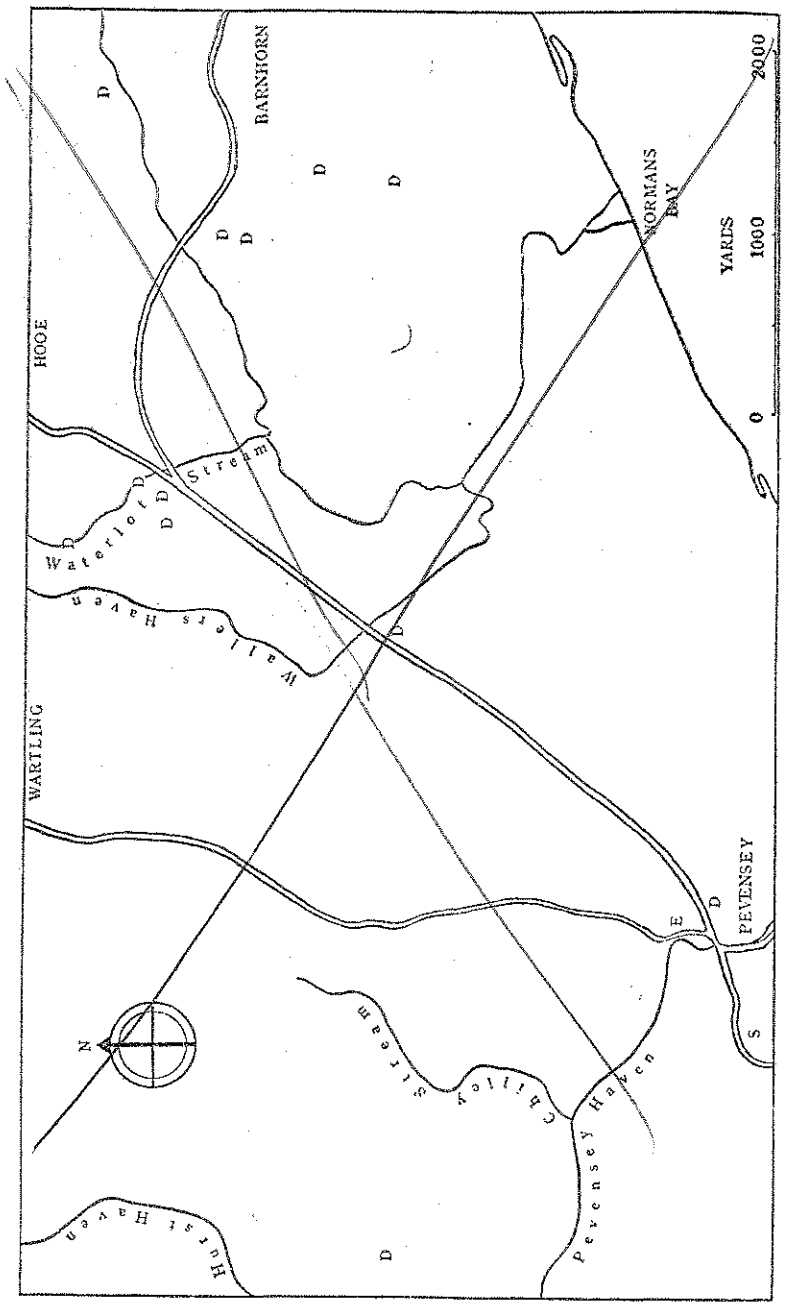


Distribution of *Pisidium pseudosphaerium* at Pevensey. S: Stelfox, 1911. E: Ellis, 1927. D: Dance, 1955.

AGE DETERMINATION IN *ANODONTA*

By T. E. Crowley

(*Read before the Society*, 15 *December* 1956)

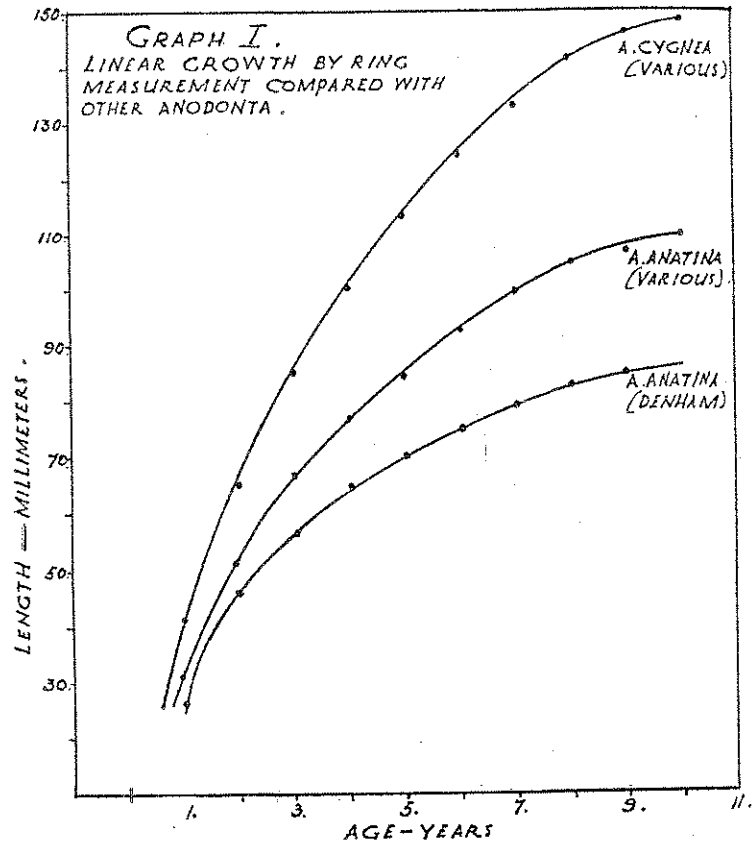
Most bivalves grow in size throughout life, and many possess a series of dark lines extending circumferentially from the umbones and following the shape of the shell in a fashion which suggests that they represent stages in the growth of the mollusc; they have in fact been termed "winter rings". They appear to be caused by the thickening of the periostracum and when this is removed they can still usually be traced by slight puckerings in the surface of the shell. Their relationship with growth is further suggested by the fact that any comparative measurements taken on the two valves of a shell invariably show identical or almost identical results, and moreover, the segment of shell added between rings is always a gnomon to the rest, that is to say, it increases the size of the mollusc without altering the shape. It would appear that the dark lines are laid down at regular stages of growth.

The notes that follow attempt to analyse this pattern of growth in the case of one species, but the conclusions might be regarded as of more general application. *Andonta anatina* (L.) was the species chosen for two reasons: first that it is known to be variable in its size and shape, and second that a good quantity of material was available for study purposes.

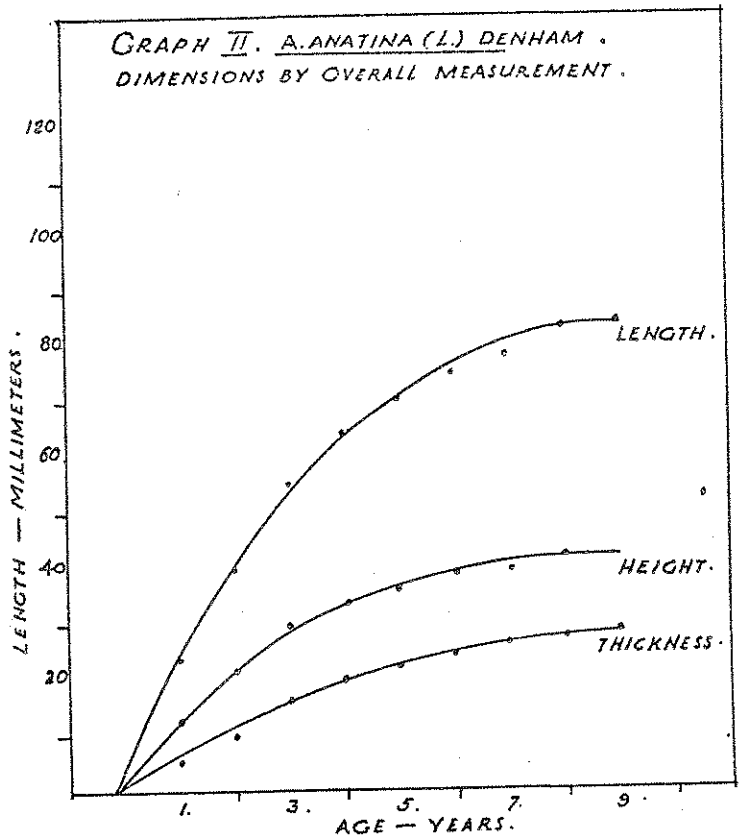
Anodonta anatina was for many years confused with its related species *A. cygnea* (L.) and *A. minima* Millet, and it appears that it was not without trouble that the three species were differentiated. Forbes and Hanley were emphatic about the existence of only a single British species; Montagu, Turton and Gray all agreed with this finding. This may perhaps be taken as good evidence of individual variability, and an examination of a good number of specimens demonstrates that this variability is not solely a response to locality in the broad sense, since widely differing shapes may be taken in a few square yards of river bed, but seems to be a sensitive response to the microhabitat in the immediate vicinity of the shell (exact depth, type of bottom, light values, currents, surrounding vegetation, commensals, etc.) and is, partly at least, a basic characteristic of the species. The fact reduces the possibility of an investigator being misled by statistical information, since irregularity of growth tends to eliminate coincidental results.

This study mainly concerns approximately two hundred specimens of *A. anatina* dredged from the River Colne at Denham, April 1955, which were therefore almost all alive. Results, however, have been checked with a number of shells obtained in June 1956 from the same locality, which had died naturally, and with shells from other places. Brief studies were also made with *A. cygnea*.

It may be supposed that the dark lines on the shells indicate for the most part recurring cycles of growth, in much the same way as annular rings on tree trunks which are known usually to occur at yearly intervals. The season of the year is obviously the predominating factor in the

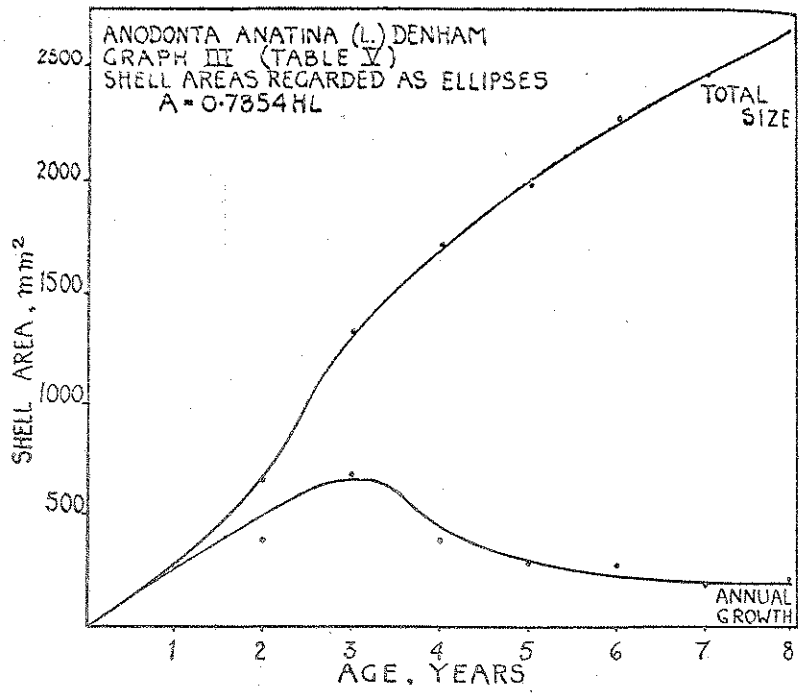


study of growth of all kinds and the possibility that lines on shells indicate years of age is strong. At the same time it can be observed that growth lines are of two types—those occurring at regular intervals and a fainter interposed kind, observable on only a few shells and often incomplete, which may be termed "disturbance lines" and appear attributable to a change in conditions of living which causes a check of growth. Such a change does not appear to occur very frequently in the case of *Anodonta*, but may be due to such factors as transport by floods or pollution. In some cases, also, it appears that two rings may be laid down in a winter, one ring being much the fainter. In the analysis of ring measurements the fact that some of these markings may occur strongly enough to be confused with winter rings must be considered, but if this were so to any appreciable extent in the present analysis the statistical results would be likely to show anomalies which are not in fact observed. This statement does not hold true with every genus; Winckworth in the case of *Paphia undulata* (Born) concluded after plotting that winter rings were



masked by disturbance rings, and quotes other instances. *Paphia*, however, is thought to live less than two years.

In the case of *Anodonta*, as with many other molluscs, the border of the mantle incorporates a groove consisting of secretory epithelium which is responsible for producing the periostracum. A narrow strip of mantle behind this groove secretes shell material, depositing it in a layer below the periostracum. Protection of the edge of the shell is thus ensured, as there is no gap between the periostracum and the mantle edge when the shell gapes, or between the periostracum and the meeting point of the valves when the shell is closed. Secretion of the periostracum occurs at a rate which appears very little affected by the season, while the shell itself grows rapidly at certain times and practically not at all at others. Hence, during periods of rapid shell growth the periostracum is laid down as a comparatively thin covering and when growth is slow the surplus secretion of periostracum causes overlapping and puckering on a small scale and, particularly near the beaks, a certain amount of incorporation occurs and a line of growth is the result.



The statistical survey was conducted as follows: the *A. anatina* were collected during the course of dredging operations which were being carried out on the River Colne by means of a dragline at grid reference 042889, O/S Map 160. The fact that the whole bottom surface of the river was removed over about 200 yards length assisted the possibility of obtaining a completely random sample and collecting was done with this in mind, although such samples are almost impossible to procure in practice. *Unio pictorum* and *Anodonta minima* were also collected but are here comparatively rare.

Specimens were then measured with dividers. Measurements taken in each case included overall length, height over umbones and thickness, and past lengths as indicated by each growth line. All measurements were taken to the nearest millimetre.

The habits of growth revealed by analysing these figures, considering the variability of the species, showed very consistent results. The linear measurements between successive rings showed a steady and consistent decrease, and although this was not observable in the case of every individual specimen, there was no trace of any regular fluctuation such as would be present if rings were added at the rate of two or more per year, an arrangement which would certainly produce two or more distinguishable rates of growth per year. The *Anodonta* almost all died within a few days and thus provided the data which would have tended

to show up fluctuations of this kind, had they been present. In the case of the oyster and other molluscs, it has been established that growth takes place for a few weeks during the spring and again in the autumn when spawning is complete, being negligible at other times. No trace of this habit is observable with the river mussel; it is more likely, as with many marine lamellibranchs, that growth occurs when the water is above a given temperature and stops completely below this limit.

TABLE I

Anodonta anatina, Denham

Age in years by ring count	Lengths by Ring Count		Dimensions by Overall Measurement			
	No. of measurements	Average length in mm.	No. of measurements	Average length in mm.	Average height in mm.	Average thickness in mm.
1	202	25·9	1	24	13	5
2	201	46·0	4	39·3	21·2	11·5
3	197	56·7	15	55·4	29·8	16·5
4	181	64·5	85	64·0	33·7	19·5
5	96	70·0	57	70·0	36·2	22·0
6	39	75·2	15	75·8	38·4	24·0
7	25	78·9	15	77·5	39·7	26·0
8	9	82·9	8	83·6	42·5	27·0
9	1	84·0	1	84	39	28·0

INCREMENTS IN SIZE BETWEEN SUCCESSIVE RINGS

TABLE II

Anodonta anatina, Denham

(Number in Sample: 197)		(Number in Sample: 25)	
1st to 2nd	20·1 mm.	Last to last but one	6·0 mm.
2nd to 3rd	10·7 mm.	Last but one to last but 2	6·5 mm.
3rd to 4th	6·8 mm.	Last but 2 to last but 3	8·8 mm.
4th to 5th	5·5 mm.	Last but 3 to last but 4	8·4 mm.
5th to 6th	5·2 mm.	Last but 4 to last but 5	10·4 mm.
6th to 7th	3·7 mm.	Last but 5 to last but 6	12·0 mm.
7th to 8th	4·0 mm.		

TABLE III

Anodonta cygnea, various localities

(Number in Sample: 18)

1st to 2nd	23·5 mm.	6th to 7th	9·0 mm.
2nd to 3rd	20·5 mm.	7th to 8th	8·0 mm.
3rd to 4th	15·5 mm.	8th to 9th	5·0 mm.
4th to 5th	12·0 mm.	9th to 10th	2·0 mm.
5th to 6th	11·0 mm.		

TABLE IV

Anodonta anatina, Denham

Ratios of the three main dimensions

Ratio	Year 1	2	3	4	5	6	7	8
$\frac{\text{Height}}{\text{Length}}$.	·54	·54	·54	·53	·52	·51	·51	·51
$\frac{\text{Thickness}}{\text{Length}}$.	·21	·29	·30	·30	·31	·32	·33	·32
$\frac{\text{Thickness}}{\text{Height}}$.	·39	·54	·55	·58	·61	·63	·66	·64

It will be seen from the tables that successive increments show a progressive decrease which could only be the case if these increments were annual, since they cannot accrue at a rate of less than one per year. The conclusion is that the rings denote the winter boundaries of successive annual amounts of growth.

In addition to ring measurements, total dimensions in all three planes were recorded. Analysis confirms that linear growth takes place at a continually declining rate throughout life in all three dimensions. The mean variations decrease with advancing age, which indicates a decreasing response to environment; further, as seen in Table IV, there is a marked tendency for the thickness of the mollusc to increase relatively throughout life, although most of this relative increase occurs during the first two years. The same tendencies are observable in the case of *Anodonta cygnea*, but growth is more rapid at all stages.

An attempt was then made to translate the data obtained on linear growth to provide an indication of the area of shell added year by year. This was done by considering the shell as a regular ellipse of axis measurements equal to the length and height of the shell. This must necessarily be a rather rough approximation, and takes no account of the increase in thickness, and hence of the shell weight added yearly. However, by using the formula for elliptical areas ·7854 LH we get a set of results as follows:—

TABLE V

Anodonta anatina (L), Denham

Annual increase in shell area (mm².)

	Year 1	2	3	4	5	6	7	8
Elliptical area of one shell . . .	264	649	1,327	1,707	1,990	2,268	2,460	2,671
Increase in area .	264	385	678	380	283	278	192	210

This table shows a rate of growth which rises to a maximum in the third year, by far the most vigorous period in the life of the mollusc. When this table is plotted (Graph III) it is seen to produce the well-known S-curve typical of nearly all forms of growth from that of yeasts to that of the human species (D'Arcy Thompson).

The average life of *Anodonta anatina* in the Denham district is about five years and the oldest specimen found indicated nine seasons. This seems typical of the Thames valley, where no specimen older than nine years or longer than 95 mm. has been examined. In Nottinghamshire, where specimens of 130 mm. are common, the average age is slightly higher, 10–11-year mussels being found. Growth here is, however, greater at all stages and the dimension ratios are quite normal. *A. cygnea* on brief analysis provided analogous results and a similar maximum age.

Attention may be drawn to a cognate study on a marine bivalve recently published by Green (1957).

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***Edouardia herbigrada* (Pilsbry) in Uganda.**—Early in 1955 Mr. W. Wilkinson, of the Colonial Termite Research Unit, made a small collection of Mollusca during his search for termites in Uganda and the Sudan. All the specimens were found æstivating in dead wood or hollow twigs, and comprise species of *Trochonanina*, *Vitrina*, *Helicarion* and Pachnodidae. I have not named much of this collection yet, since comparison is needed with types in European museums. One record, however, is of interest. A single specimen of *Edouardia herbigrada* (Pilsbry, 1919, *Bull. Amer. Mus. Nat. Hist.* **40**, 308, fig. 157) was found in a dead branch 33 miles from Masindi on the Atura road, Uganda, at an altitude of 1,200 metres, on 19 February. The species was originally ascribed to *Pachnodus* and described from specimens collected at Faradje, Belgian Congo, in hollow twigs; I have traced no other record. In the collection from a different locality are two other species of *Edouardia* (juvenile) which, although easily confused with *E. herbigrada*, have a much more elongate form and less reflected columella. The specimen is in the Coryndon Memorial Museum, where the writer is building up collections of East African Mollusca.

B. VERDCOURT.

(*Read before the Society*, 15 *December* 1956)