

THE LAW OF OSTRACOD GROWTH

by F. W. ANDERSON

ABSTRACT. A method of calculating the dimensions of ostracod growth stages is described and applied to the analysis of already published data referring to 26 species ranging in age from Ordovician to Recent.

THE first attempt to formulate a law of growth for the Arthropoda was made by Brooks (1886). Working on *Coronis* larvae he found that the successive instar sizes could be approximately calculated by multiplying the length of the previous instar by 1.25. Fowler (1909) applied this rule to living ostracods from the Bay of Biscay and claimed that each stage increased by a fixed percentage of its length approximately constant for its species and sex. He named this rule 'Brooks's Law' and found that for species of Halocypridae the growth factors ranged from 1.26 to 1.78. In 1931 Przibram assumed a growth factor of 1.26 for all arthropods. This was based on the assumption that the mass is doubled at each moult, 1.26 being the cube root of 2.0. It is extremely unlikely that this is true and in fact the principle has been largely abandoned for arthropods in general. Animals which add to the number of appendages at each moult are not likely to obey this law even approximately, and certainly the method does not give satisfactory results for the ostracods.

Brooks's Law stated as a formula reads: $L_{n+1} = kL_n$, where L_n is the length of carapace at n th instar, and k is the growth factor. As has been demonstrated for *T. fittoni* (see preceding paper by Sohn and Anderson) the growth factor is not necessarily constant even for one species and, as will be shown subsequently, for ostracods generally there is a wide range of growth rates. Many ostracods, however, in the adult stage have lengths near to 1.0 mm. and should therefore, according to the method of calculation suggested below, have an incremental factor of 0.100, which is the logarithm of 1.259, i.e. approximately 1.26, so that the fact that Przibram's growth rate is not applicable generally is not always readily apparent.

In the search for a more satisfactory method of calculating instar sizes the dimensions of the individuals of *T. fittoni* were recorded as logarithms to the base 10. It was then apparent that the logarithms of the mean dimension of each instar were approximately equidistant. Thus the law which is immediately suggested is that which might have been deduced on purely theoretical grounds, i.e. some form of the compound interest formula $y = y_0 e^{kx}$, since growth is incremental and logarithmic. In this formula x is the time at which the size y is obtained, y_0 is a constant depending on the size at time 0, and k is a constant (the efficiency index). On taking logarithms, $\log y = \log y_0 + kx$, which simplifies subsequent operations. This is, of course, an expression of the general form $y = a + bx$, the equation for a straight line. The distribution of the measurements for length and height of *T. fittoni* suggests that the growth formula for this species at least is an equation of this kind. In the case of fossil ostracods, however, x cannot be expressed in units of time which are not determinable, but since the logarithms of the means of each instar size are equidistant, x can be legitimately replaced not by the instar number,

[Palaeontology, Vol. 7, Part 1, 1964, pp. 85-104]

which again is not necessarily determinable, but by a growth-stage number. If it can be assumed that the first growth stage in all ostracods in which the adult is of the same order of size, has the same dimensions, and for all practical purposes this may well be true, then the incremental factors of growth in length (K_L) and in height (K_H) can be determined as follows:

$$K_L = \log L_n - \log L_{n-1}$$

$$\text{and } K_H = \log H_n - \log H_{n-1},$$

where n is the number of any growth stage. If K_L is taken as the length of the first growth stage then growth stage 10 will have the length $10K_L$. In *T. fittoni* and a number of other species growth stage 10 is the mature adult, i.e. the instar numbered 8 or 9 according to the author concerned.

In the calculation of height another factor, the length/height ratio, must be taken into account. Let r equal the fundamental L/H ratio, that of growth-stage 0, which will be constant for the species if the shape is to remain the same. During growth, however, there is a change of shape with each instar, usually in the form of an increase in the L/H ratio so that the shell becomes proportionately more elongate as growth proceeds. Thus another factor, p , again a constant for the species, must be introduced, which alters the value of r with each moult and must operate uniformly if the change in shape is to be gradual and incremental. This factor is simply the difference between the two growth rates K_L and K_H . The relationship between length and height in any growth stage is therefore expressed by:

$$\log L_n - r - pn = \log H_n.$$

Thus for the Berwick (1) individuals of *T. fittoni* the difference between $\log L_n$ and $\log L_{n-1}$ is 0.096 (K_L), and between H_n and H_{n-1} is 0.083, so that $p = K_L - K_H = 0.072$ and $r = \log L_o - \log H_o = 0.013$.

The L/H ratio in the female appears to be constant only in the pre-maturation moults, presumably because much of the increase in size at the maturation moult is in the *width* of the posterior half of the carapace. Thus in any assemblage which includes a large number of females the average length and height will be smaller than calculated. This is very evident in some of the data reproduced below.

In *T. fittoni* growth stage 10 is the mature adult and eight pre-maturation instars have been recognized. It does not follow that there are ten instars in the development of this species, and in the following discussion the growth stages which are arbitrarily taken to equal nK_L are not necessarily numerically equated with the instars.

The determination of ostracod instars has been thoroughly discussed by Kesling (1951, 1952, 1953), who has devised a circular slide rule (1953, fig. 2) to assist in the recognition of growth stages. The method, however, is based on Prizibram's concept and is somewhat complex. In fact, the various methods of calculation so far suggested do not give results which differ greatly in the median range of ostracod sizes. The method adopted here, however, is simpler to operate than that advocated by Kesling and will give more satisfactory results for ostracods much smaller or larger than the average.

1. *Pterygocythereis jonesi* (Baird). Recent, marine, from bottom samples in the Irish Sea south of the Isle of Man. Measurements carried out by the writer. $K_L = 0.0882$, $K_H = 0.0680$, $r = 0.040$, $p = 0.0202$.

The method of calculating instar sizes suggested here can best be illustrated by taking

as an example measurements taken on the carapaces of a living species of ostracod, *Pterygocythereis jonesi*. In this species the adult is easily recognized by its development of a large clear hemispherical eye tubercle which is not present in earlier moults. The valves of 175 individuals were measured, right and left valves being recorded separately, but as the difference in length between the two was only 0.025 mm. in the adult it became apparent that this would have no significant effect on the scatter of the measurements.

Most valves (73) ranged from 0.713 to 0.813 mm. in length (mean 0.763) and from 0.400 to 0.488 mm. in height (mean 0.438). The next smallest instar (39 individuals) had lengths ranging from 0.588 to 0.675 mm. (mean 0.621) and heights ranging from 0.325 to 0.400 mm. (mean 0.363). The constant for growth in length (K_L) is therefore assumed to be close to 0.883 (log of 0.763) minus 0.793 (log of 0.621), that is about 0.090. Thus the instar with a length of 0.763 mm. would, according to the method described, be growth stage 10 and a closer approximation to K_L would be 0.088. In fact a value of 0.0882 for K_L gives the best fit between calculated and measured means.

The average difference between the logarithms of the heights in adjacent instars is 0.068. Thus the value for the constant p is 0.0202. The hypothetical growth stage 0 would therefore have the dimensions: length 0.100, height 0.091 mm., and the L/H ratio at growth stage 0 (r) = 0.040.

In Table 1 calculated means have been determined for each growth stage and compared with the means of those measured. It will be seen that the maximum difference between calculated and measured lengths is 0.006 mm., which is well within the standard deviation ($\sigma = 0.016$) of the measured lengths. Similarly the maximum difference between calculated and measured heights is 0.011 ($\sigma = 0.016$).

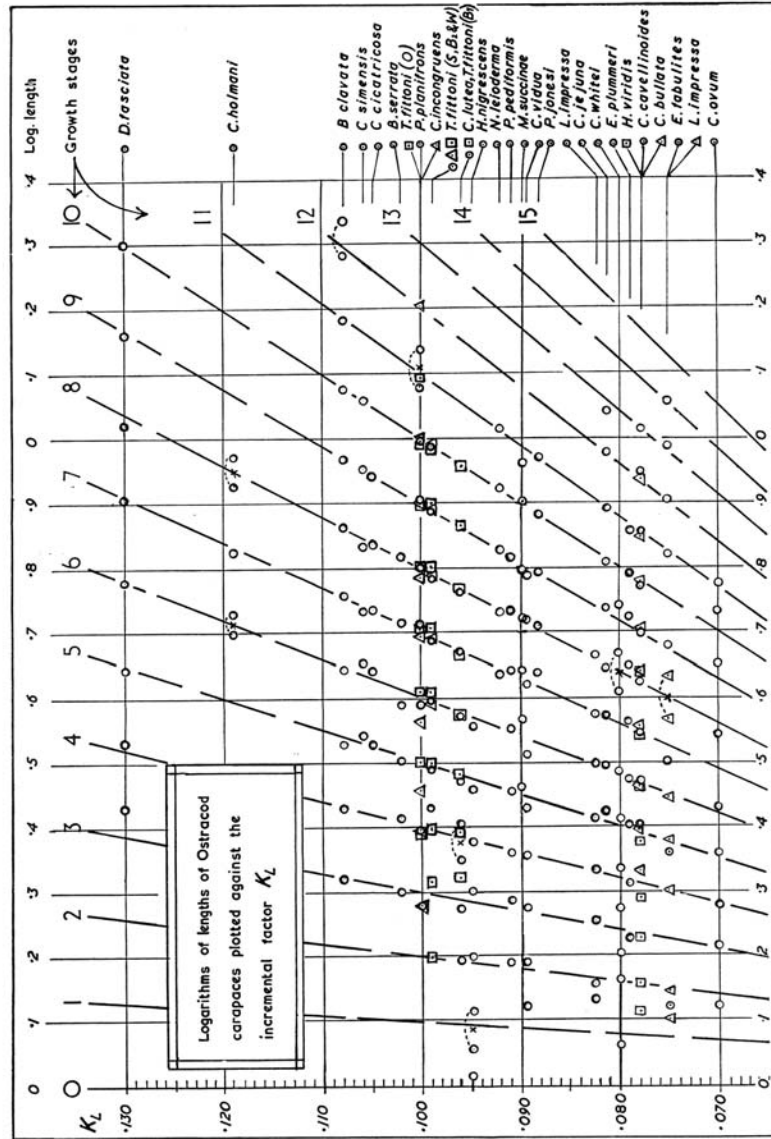
TABLE 1

Growth stage	Measured means (mm.)		Calculated means (mm.)		Number measured
	Length	Height	Length	Height	
7	0.438	0.275	0.414	0.273	1
8	0.513	0.313	0.508	0.319	8
9	0.621	0.363	0.622	0.373	39
10	0.763	0.438	0.762	0.437	73
*11	0.938	0.500	0.933	0.511	54

* Adult with eye tubercle

Much labour can be avoided by using the chart set out in text-fig. 1. All that is necessary is to mark off the logarithms of the means of the measured lengths of a species on the scale at the top of the chart and move down the vertical scale until the best fit for all growth stages is obtained, at which point the reading on the left hand scale will give the incremental factor K_L . It can be seen at a glance if any growth stages have been missed, or if two values have been obtained for the same instar. The method can be used to find both K_L and K_H , from which the other factors r and p can be calculated. Logarithms of means should fall on or near the broken lines.

Measurements of ostracod instars so far published indicate values for K_L ranging from a minimum of 0.070 (1.175) to a maximum of 0.128 (1.343). There appears to be no



TEXT-FIG. 1

obvious relationship between the number of possible growth stages and the dimensions of the ultimate instar (Table 28).

This method is here utilized to calculate dimensions for instars of those species for which measurements are available. Where differences between calculated and measured dimensions are greater than the standard deviation in any one growth stage further investigation is needed. It is suggested that errors are most frequently due to:

- (a) the number of individuals measured in any one growth stage being too small;
- (b) failure to collect representatives of some of the growth stages;
- (c) failure to recognize the growth stage to which individuals belong;
- (d) failure to recognize as the same species juveniles and adults which change markedly at the maturation moult, or to recognize sexual heteromorphs as the same species.

Most recent workers have recognized the importance of measuring a large number of individuals and it is usually only in older publications that the effect of measuring too few individuals becomes serious. More common is the omission of a growth stage, usually an early instar. Individuals belonging to the earlier growth stages are not easily found or abundant and are easily damaged, so that reliable means are difficult to obtain. Consequently individuals at extreme and opposite limits of the range for the instar may be thought to belong to different instars. Examples of this are illustrated below. It is suspected, but difficult to prove, that in some cases the juveniles have not been recognized as the same species as the adult. For example, if the eye tubercle in *Pterygocythereis jonesi* were taken to be a diagnostic feature of the species, then the pre-maturation moults would be excluded. Similarly in *Macrodentina retirugata* (Jones) the hingement changes sufficiently during development to place adult and early moults in distinct genera if a too rigid system of classification is adopted.

2. *Normanocythere leioderma* (Norman). Recent. From various localities, but mainly Spitzbergen. Data by Neale 1959. $K_L = 0.092$, $K_H = 0.072$, $r = 0.048$, $p = 0.020$.

TABLE 2

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
7	0.435	0.280	0.441	0.286
8	0.540	0.330	0.545	0.337
9	0.675	0.400	0.673	0.398
10	0.840	0.470	0.832	0.470
11	1.030	0.550	1.028	0.555

Neale estimated the incremental factor to be 1.2445 (i.e. $K_L = 0.095$) and compared it with the generalized value of 1.256 given by Kesling (1953) (i.e. $K_L = 0.099$). He apparently assumed that the growth increment is the same for both length and height, but it is obvious that in this species this is not the case. Mean values are not given by Neale and the figures quoted above have been taken from the published graph (text-fig. 4). The maximum difference between measured and calculated means is 0.008 mm. Growth stage 11 is the mature adult. Neale assumes nine instars, thus his first instar

would be growth stage 3, for which the calculated dimensions are: length 0.189, height 0.147, compared with Neale's estimate of length 0.18 mm. It is not stated why earlier growth stages are not possible. Growth stage 2 is estimated to be length 0.153, height 0.125, a much closer approximation to the figures for *Cythere lutea* (length 0.156 mm.) and *Cyprideis littoralis* (length 0.150 mm.) given by Elofson (1941).

3. *Cypridopsis vidua* (O. F. Müller). Recent, marine, parthenogenetic. Material: culture from a single ostracod from Crystal Lake, Champaign County, Illinois. Data from Kesling 1952, p. 235, Table 2. $K_L = 0.0895$, $K_H = 0.080$, $r = 0.160$, $p = 0.0095$.

TABLE 3

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
1	0.1322	0.0920	0.1229	0.0830
2	0.1555	0.1060	0.1510	0.1000
3	0.1882	0.1238	0.1856	0.1200
4	0.2268	0.1456	0.2281	0.1450
5	0.2698	0.1697	0.2802	0.1740
6	0.3334	0.2038	0.3444	0.2090
7	0.4180	0.2505	0.4232	0.2510
8	0.5280	0.3162	0.5200	0.3020
9	0.6170	0.3726	0.6390	0.3630

The correspondence between measured and calculated means is reasonably good, with a maximum difference of 0.022 mm., and this in the adult, which since the individuals were all females could have been anticipated. The effect of captivity on growth rate has not yet been demonstrated so that the figures given above may not be applicable to the species in its natural environment. Nine growth stages were recognized, of which the last is the adult moult.

4. *Hirshmannia nigrescens* (Baird). Recent, marine. Data from Elofson 1941, p. 400, lengths only. $K_L = 0.095$.

TABLE 4

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
0	0.103	0.100
1	0.114 0.122	0.125
	0.130	
2	0.158	0.155
3	0.200	0.193
4	0.236	0.240
5	0.287	0.299
6	0.361	0.372

Analysis suggests that the two mean lengths 0.114 mm. and 0.130 mm. refer to one instar; the mean 0.122 is close to the calculated length for growth stage 1. Apart from this the correspondence between measured and calculated lengths is close, with a maximum difference of 0.012 mm. The relatively large growth increment suggests the possibility of later instars as yet unidentified.

5. *Hirschmannia viridis* (O. F. Müller). Recent, marine. Data from Elofson 1941, lengths only. $K_L = 0.078$.

TABLE 5

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
1	0.130	0.120
2	0.144	0.143
3	0.170	0.171
4	0.195	0.205
5	0.238	0.246
6	0.295	0.294
7	0.350	0.352
8	0.434	0.421

Eight growth stages are recognized, the lengths of which correspond closely to those calculated, the maximum difference being 0.013 mm.

6. *Heterocypris incongruens* (Ramdohr). Recent, marine. Data from Schrieber 1922, lengths only. $K_L = 0.100$.

TABLE 6

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
3	0.190	0.200
4	0.250	0.251
5	0.288	0.316
6	0.368	0.398
7	0.496	0.501
8	0.608	0.631
9	0.800	0.794
10	1.008	1.000
11	—	1.260
12	1.600	1.590

The maximum difference between measured and calculated lengths is 0.030 mm. in growth stage 6. It is apparent that the pre-maturation moult, i.e. growth stage 11, has not been recorded.

7. *Macrocypris succinae* (G. W. Müller). Recent, marine. Data from G. W. Müller 1893, lengths only. $K_L = 0.090$.

TABLE 7

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
5	0.290	0.282
6	0.370	0.347
7	0.440	0.427
8	0.530	0.525
9	0.630	0.646
10	0.800	0.794
11	0.920	0.977

The correspondence between measured and calculated lengths is reasonably good, except in the last instar, where the difference is 0.057 mm. It is not known, however, how many individuals were measured and therefore how close the figure of 0.977 mm. is to the mean length of this instar.

8a. *Loxococoncha impressa* (Baird). Recent, marine. Data from G. W. Müller 1893, lengths only. $K_L = 0.075$.

TABLE 8

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
1	0.100	0.119
2	0.140	0.141
3	—	0.168
4	0.200	0.200
5	0.240	0.237
6	0.280	0.282
7	—	0.335
8	0.370 } 0.430 } 0.400	0.398

As the figures given below (8b, after Elofson) show, the growth in this species is quite normal, so that the irregularities in Müller's record must be due to the fact that some growth stages have been missed, namely stages 3 and 7. Furthermore, it is evident that the lengths 0.370 and 0.430 mm. must refer to the same instar. If this interpretation is correct then the maximum difference between measured and calculated lengths is 0.019 mm.

8b. *Loxococoncha impressa* (Baird). Recent, marine. Data from Elofson 1941, lengths only. $K_L = 0.0825$.

TABLE 9

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
1	0.136	0.121
2	0.144	0.146
3	0.180	0.177
4	0.216	0.214
5	0.260	0.259
6	0.316	0.313
7	0.375	0.378
8	0.463	0.457

Except for the first growth stage the correspondence between measured and calculated lengths is very close. These figures show that, as in *Theriosynoecum fittoni*, the growth rate in *L. impressa* is variable so that, for example, growth stage 7 in the individuals measured by Elofson is intermediate in size between growth stages 7 and 8 in the individuals measured by Müller.

9. *Bairdia serrata* Müller. Recent, marine. Data from G. W. Müller 1893, lengths only. $K_L = 0.102$.

TABLE 10

Growth stages	Measured means (mm.)	Calculated means (mm.)
	Length	Length
3	0.200	0.202
4	0.260	0.256
5	0.320	0.324
6	0.390	0.409
7	0.520	0.518
8	0.660	0.655

Correspondence between measured and calculated lengths is good except for growth stage 6, where the difference is 0.019 mm. This appears to be a rather high growth rate for a species with an adult only 0.660 mm. long. It is possible that later moults have been recorded as a distinct species.

10. *Cythere lutea* (O. F. Müller). Recent, marine. Data from Elofson 1941, lengths only. $K_L = 0.096$.

TABLE 11

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
2	0.156	0.156
3	0.188	0.194
4	0.224 0.255	0.240
5	0.296	0.302
6	0.375	0.377
7	0.470	0.470
8	0.578	0.586

Correspondence between measured and calculated lengths is good if, as is suspected, the lengths 0.224 and 0.255 mm. belong to the same instar. As in *B. serrata* the growth increment is large for a species with a maximum recorded length of less than 0.600 mm.

11. *Cyclocypris ovum* (Jurine). Recent, fresh-water. Data from Claus 1872, lengths only. $K_L = 0.070$.

TABLE 12

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
2	0.132	0.138
3	0.165	0.162
4	0.190	0.191
5	0.230	0.224
6	0.270	0.263
7	—	0.309
8	0.350	0.363
9	0.450	0.427
10	0.540	0.501
11	0.600	0.589

No length for growth stage 7 was recorded. The difference between measured and calculated lengths in growth stages 9 and 10, i.e. 0.023 and 0.039 mm. respectively, is rather large, otherwise the correspondence is reasonably good.

12. *Dolerocypris fasciata* (O. F. Müller). Recent, fresh-water. Data from Claus 1872, lengths only. $K_L = 0.130$.

TABLE 13

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
3	0.270	0.246
4	0.340	0.331
5	0.440	0.447
6	0.600	0.603
7	0.800	0.813
8	1.050	1.096
9	1.450	1.480
10	2.000	2.000

The difference between measured and calculated lengths is rather high in growth stage 8 (0.046 mm.), otherwise the correspondence is reasonably good.

13. *Cythereis simensis* (Le Roy) = *Archicythereis newportensis* Le Roy. 'Middle Pliocene', San Diego formation, California. Data from Spjeldnaes 1951, after Le Roy 1945. $K_L = 0.106$, $K_H = 0.100$, $p = 0.006$, $r = 0.194$.

TABLE 14

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
5 (A')	0.350	0.190	0.339	0.218
6 (A')	0.450	0.270	0.433	0.255
7 (A)	0.540	0.310	0.552	0.321
8 (B)	0.680	0.390	0.705	0.404
9 (C)	0.900	0.510	0.900	0.508
10 (E)	1.180	0.640	1.150	0.640

Le Roy believed that an instar (D) occurred between C and E but this is clearly not the case. The length of growth stage A' was misquoted by Spjeldnaes as 0.380 mm.

14. *Cythereis holmani* Le Roy. Miocene, marine, east coastal area of Sumatra. Data from Spjeldnaes 1951, after Le Roy 1945. $K_L = 0.119$, $K_H = 0.105$, $r = 0.140$, $p = 0.014$.

TABLE 15

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
6 (A B)	0.500 0.540	0.520	0.300 0.310	0.305
7 C	0.670		0.400	0.681
8 (D♀ D♂)	0.850 0.940	0.895	0.510 0.470	0.490
			0.895	0.501

These figures are difficult to interpret. Presumably the dimensions given for growth stages A and B appertain to one instar. Only the average dimensions of the adult male and female are closely related to those calculated for growth stage 8.

15. *Candona whitei* Scott and Smith. Eocene, fresh-water. Data from Scott and Smith 1951. $K_L = 0.080$, $K_H = 0.074$, $r = 0.180$, $p = 0.006$.

TABLE 16

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
1	0.120	0.092	0.120	0.078
2	—	—	0.145	0.093
3	—	—	0.174	0.110
4	0.204	0.146	0.209	0.131
5	0.258	0.159	0.251	0.155
6	0.304	0.187	0.302	0.184
7	0.367	0.218	0.363	0.218
8	0.434	0.258	0.437	0.258
9	0.532	0.306	0.525	0.306
10	—	—	0.631	0.363
11	0.718 0.824	0.771	0.407 0.468	0.438
12	0.974	0.554	0.912	0.511

The correspondence between measured and calculated dimensions is so close in the earlier growth stages that the figures given for the last three instars need to be critically examined. A possible interpretation is that growth stage 10 has not been recorded, and that for the next growth stage both high and low variants have been given. The graph in Scott and Smith's paper, however, shows no obvious grouping of the length/height ratios. The dimensions given under growth stage 1 are those of the supposed egg.

16. *Cytherella bullata* Alexander. Cretaceous, marine. Prairie Bluff, Pontotoc County, Mississippi. Data from Shaver 1953. $K_L = 0.078$, $K_H = 0.076$, $r = 0.144$, $p = 0.002$.

TABLE 17

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
4	0.216	0.139	0.205	0.145
5	0.250	0.163	0.246	0.172
6	0.294	0.192	0.294	0.205
7	0.364	0.243	0.352	0.244
8	0.439	0.291	0.421	0.291
9	0.508	0.337	0.504	0.347
10	0.597	0.400	0.603	0.413
11	0.707	0.473	0.721	0.492
12	0.867	0.588	0.863	0.586

Measured and calculated values correspond very well throughout, the maximum difference in length being 0.018 mm. in growth stage 8, and in height 0.019 mm. in growth stage 11.

17. *Aurikirkbya wardensis* (Hamilton). Permian, Glass Mountains, Texas. Data from Sohn 1950a. $K_{L\text{hinge}} = 0.083$, $K_H = 0.079$.

TABLE 18

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Hinge length	Height	Hinge length	Height
n	0.828	0.414	0.826	0.430
n1	0.999	0.519	1.000	0.515
n2	1.219	0.631	1.211	0.618
n3	1.426	0.730	1.466	0.741
n4	1.768	0.882	1.774	0.889

The data relating to this species have proved most difficult to analyse. Sohn's figures suggest a periodicity which could be mistaken for instar intervals. The author says (p. 36) that it is not possible by examining these figures to recognize growth stages by measurement alone. The obvious periodicity is, however, due to some extraneous factor, most probably the micrometer unit interval. If, for example, the micrometer unit used was 0.049 mm. and the half unit estimated as either 0.02 or 0.03 such a periodicity could be expected. A detailed analysis of Sohn's figures suggests that five growth stages were represented in the material and that their dimensions are approximately as given in the table above.

18. *Pseudobythocypris pediformis* Knight. Pennsylvanian, marine. Exline Shale, Peoria County, Illinois. Data from Shaver 1958. $K_L = 0.091$, $K_H = 0.078$, $r = 0.148$, $p = 0.013$.

TABLE 19

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
2	0.155	0.103	0.152	0.102
3	0.193	0.123	0.188	0.122
4	0.230	0.138	0.231	0.146
5	0.286	0.167	0.285	0.175
6	0.358	0.208	0.352	0.209
7	0.440	0.250	0.434	0.250
8	0.542	0.300	0.535	0.299
*9	0.656	0.354	0.659	0.359

* Includes both males and females

Correspondence between measured and calculated values is very close, with a maximum difference of only 0.008 mm.

19. *Cavellina cavellinoides* (Bradfield). Marine, Pennsylvanian, Lonsdale Zone, Vermillion County, Illinois. Data from Shaver 1951, lengths only. $K_L = 0.078$.

TABLE 20

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
5	0.254	0.246
6	0.297	0.294
7	0.352	0.352
8	0.422	0.421
9	0.500	0.504
10	0.592	0.603
11	0.720	0.721
12	0.892	0.863
13	1.038	1.033

The greatest discrepancy between measured and calculated values (0.029 mm.) is in growth stage 12.

20. *Cavellina jejuna* Coryell and Sample. Marine, Pennsylvanian, Exline Shale, Peoria County, Illinois. Data from Shaver 1951, lengths only. $K_L = 0.0815$.

TABLE 21

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
5	0.267	0.256
6	0.314	0.308
7	0.375	0.372
8	0.443	0.449
9	0.548	0.541
10	0.646	0.653
11	0.779	0.788
12	0.953	0.951
13	1.098	1.147

Correspondence between measured and calculated lengths is good except for the ultimate stage. This species and *C. cavellinoidea* have more than the average number of growth stages.

21. *Ectodemites plummeri* Cooper. Marine, Pennsylvanian, lower Marble Falls formation, Texas. Data from Cooper 1945. $K_L = 0.079$, $K_H = 0.079$, $r = 0.185$, $p = 0$.

TABLE 22

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
3	0.169	0.113	0.173	0.113
4	0.206	0.138	0.207	0.135
5	0.253	0.163	0.248	0.162
6	0.300	0.193	0.298	0.195
7	0.369	0.244	0.357	0.233
8	0.447	0.281	0.429	0.280
9	0.531	0.338	0.514	0.336
10	0.619	0.400	0.617	0.403
11	0.725	0.466	0.740	0.481

Correspondence between measured and calculated dimensions is close, the maximum difference being 0.018 mm. in growth stage 8. This is one of those rare cases where $p = 0$, i.e. where the growth rate in length and height is the same, so that the adult is proportionately higher than the juvenile.

Cooper used a method of calculation based on Huxley's (1932) differential growth formula $y = bx^k$, and found that $H = 0.765 L^{0.969}$. This, however, assumes a uniform growth rate ratio, which is not the case in most other species.

22. *Ctenoloculina cicatricosa* (Warthin). Middle Devonian, marine, Norway Point formation, Traverse Group, Michigan. Data from Kesling 1951. $K_L = 0.105$, $K_H = 0.100$, $r = 0.233$, $p = 0.005$.

TABLE 23

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
5	0.338	0.187	0.335	0.185
6	0.441	0.235	0.427	0.233
7	0.541	0.288	0.543	0.293
8	0.686	0.369	0.692	0.369
9	0.874	0.474	0.881	0.474

Correspondence between measured and calculated dimensions is good with a maximum difference of 0.014 mm. If in fact growth stage 9 is the ultimate one it is apparent that the size attained by the adult is not directly related to the factor K_L . It may be that when K is large the number of moults is fewer, and when K is small more moults are needed to reach maturity. Thus it is possible that neither growth rate, number of instars, nor adult size are constant for the species, but that within certain limits all may vary according to ecological conditions.

23. *Beyrichia* (*Mitrobeyrichia*) *clavata* Kolmodin = *Beyrichia jonesi* Boll. Marine, Silurian, Mülde Marl (Wenlock), Gotland.

(a) Data from Spjeldnaes 1951, lengths only. $K_L = 0.108$.

TABLE 24

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
3	0.214	0.211
4	0.269	0.270
5	0.343	0.347
6	0.443	0.445
7	0.571	0.570
8	0.728	0.731
9	0.927	0.938
10	1.185	1.200
11	1.515	1.540
12	1.914 2.171	1.980

The last two lengths, though recorded as separate instars, are more probably sexual dimorphs. If a further growth stage were present it could be expected to have a length of 2.540 mm. Correspondence between measured and calculated lengths is reasonably good for all growth stages except the last.

(b) Data from Martinsson 1957. $K_{L\text{hinge}} = 0.094$, $K_{L\text{anterior}} = 0.100$.

TABLE 25

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Hinge length	Anterior length	Hinge length	Anterior length
n	0.360	0.250	0.359	0.250
n+1	0.440	0.305	0.446	0.315
n+2	0.540	0.380	0.553	0.396
n+3	0.670	0.480	0.687	0.499
n+4	0.830	0.620	0.853	0.628
n+5	1.060	0.790	1.060	0.791
n+6	1.320	0.990	1.320	0.996
n+7	1.630	1.240	1.630	1.254
n+8	1.950 $\frac{\delta}{\sigma}$	1.375 $\frac{\delta}{\sigma}$ 1.240 $\frac{\sigma}{\delta}$	2.030	1.578

The correspondence between measured and calculated dimensions is so close in all but the last instar that this remarkable departure from the normal growth rate at the maturation moult is difficult to explain, unless virtually all the growth in length has taken place in the posterior half of the carapace (see *T. fittoni*, where the posterior growth rate is greater than the anterior).

24. *Primitopsis planifrons* Jones. Marine, Silurian, Mülde Marl (Wenlock), Gotland. Data from Martinsson 1956, means taken from the graph, *not* from the table. $K_L = 0.100$, $K_H = 0.100$, $r = 0.140$, $p = 0$.

TABLE 26

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
6	0.390	0.290	0.398	0.289
7	0.520	0.370	0.501	0.363
8	0.635	0.465	0.631	0.457
9	0.805	0.590	0.794	0.576
10	0.995	0.730	1.000	0.725
11	{ 1.200 1.300	0.865	1.291	0.912

Like *Ectodemites plummeri*, *P. planifrons* is unusual in that the length/height ratio does not change during development. Again, as has been noted in many cases, the mature individual is smaller than would have been expected if the growth rate were uniform throughout. Possibly at the maturation moult a part of the growth potential is diverted to the development of the reproductive organs.

25. *Eoleperditia fabulites* (Conrad). Marine, Middle Ordovician, northern Illinois. Data from Scott 1951. $K_L = 0.750$, $K_H = 0.701$, $r = 1.303$, $p = 0.049$.

TABLE 27

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
2	1.325	0.880	1.410	1.023
3	—	—	1.680	1.203
4	—	—	2.000	1.413
5	2.300	1.900	2.370	1.660
6	—	—	2.820	1.951
7	3.175	2.150	3.350	2.290
8	—	—	3.980	2.695
9	4.795	3.145	4.730	3.170
10	—	—	5.620	3.722
11	6.638	4.247	6.680	4.373
12	8.039	5.116	7.940	4.151
13	9.773	6.063	9.440	6.054
14	11.435	7.263	11.200	7.114

Unless this species differs from all other recorded species in its method of growth, then it is apparent that the dimensions of five growth stages have not been recorded. One of the useful applications of the method of analysing growth in ostracods described above is the ease with which missing growth stages can be detected and their approximate dimensions determined.

TABLE 28. Range of growth increments in Ostracods

Species	1	2	3	4	Age	5	6
<i>D. fasciata</i>	0.130	2.000	2.000	10	Recent	200	1.349
<i>C. holmani</i>	0.119	0.895	0.895	8	Tertiary	112	1.315
<i>B. clavata</i>	0.108	2.043	1.980	12	Silurian	165	1.282
<i>C. simensis</i>	0.106	1.180	1.150	10	Tertiary	115	1.276
<i>C. cicatricosa</i>	0.105	0.874	0.881	9	Devonian	98	1.274
<i>B. serrata</i>	0.102	0.660	0.655	8	Recent	82	1.265
<i>T. fittoni</i> (O)	0.100	1.080	1.000	10	Cretaceous	100	1.259
<i>P. planifrons</i>	0.100	1.300	1.291	11	Silurian	117	1.259
<i>H. incongruens</i>	0.100	1.600	1.590	12	Recent	133	1.259
<i>T. fittoni</i> (W, S, B ₂)	0.099	1.060	0.977	10	Cretaceous	98	1.256
<i>T. fittoni</i> (B ₁)	0.096	0.940	0.912	10	Cretaceous	91	1.247
<i>C. lutea</i>	0.096	0.578	0.586	8	Recent	73	1.247
<i>H. nigrescens</i>	0.095	0.361	0.372	6	Recent	62	1.245
<i>N. leioderma</i>	0.092	1.030	1.028	11	Recent	93	1.236
<i>P. pediformis</i>	0.091	0.656	0.659	9	Carboniferous	73	1.233
<i>M. succinae</i>	0.090	0.920	0.977	11	Recent	89	1.230
<i>C. vidua</i>	0.089	0.617	0.639	9	Recent	78	1.229
<i>P. jonesi</i>	0.088	0.938	0.933	11	Recent	85	1.225
<i>L. impressa</i>	0.083	0.463	0.457	8	Recent	57	1.209
<i>C. jejuna</i>	0.082	1.098	1.147	13	Carboniferous	88	1.206
<i>C. whitei</i>	0.080	0.974	0.912	12	Tertiary	76	1.202
<i>E. plummeri</i>	0.079	0.725	0.740	11	Carboniferous	67	1.200
<i>C. bullata</i>	0.078	0.867	0.863	12	Cretaceous	72	1.197
<i>C. cavellinoides</i>	0.078	1.038	1.033	13	Carboniferous	79	1.197
<i>H. viridis</i>	0.078	0.434	0.421	8	Recent	53	1.197
<i>E. fabulites</i>	0.750	11.44	11.20	14	Ordovician	80	1.189
<i>L. impressa</i>	0.075	0.400	0.398	8	Recent	50	1.189
<i>C. ovum</i>	0.070	0.600	0.589	11	Recent	54	1.175

Column 1, growth factor for length, K_L .

„ 2, mean of measured lengths, adult.

„ 3, calculated length of adult.

„ 4, number of theoretical growth stages.

„ 5, adult length divided by number of growth stages.

„ 6, incremental factor for growth in length.

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F. W. ANDERSON,
Geological Survey and Museum,
Exhibition Road,
London, S.W. 7