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How complete are diagnoses of coiled shells of regular build? A mathematical approach

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INTRODUCTION

Because little or no attention seems to have been given to the completeness of diagnoses of coiled shells, many existing diagnoses, even of very recent origin, are more or less incomplete. Only a few years ago, for instance, the dimensions of the top whorl were found to be of paramount importance in the taxonomy of the European marine gastropod genus *Rissoa*. Because neither the diagnoses nor the available pictures contain information with regard to this character, the nomenclature of many species of the genus is in a chaotic state, and the information about their distribution therefore unreliable. The number of whorls is another character which has often been neglected, as is the sculpture of the protoconch. Thus, there seems to be ample reason for discussing the completeness of diagnoses.

The results of this paper are to be used in a conchometrical analysis (Verduin, 1982), and therefore a few experiments have been added with regard to the accuracy with which some of the characters discussed can be measured.

ANALYSIS

In this paper, shells which meet the requirement that the form of the cross-section of the whorls is constant all over the shell, will be called conical. In Appendix 2 it is demonstrated that whorl expansion rate A, i.e. the ratio of the linear dimensions of two successive whorls, must necessarily also be constant in such shells. Shells which only meet the much wider requirement that the form of the generating curve of the whorls, plus its position with regard to the vertical (see fig. 3), is constant throughout the shell, will be called regular.

In fig. 1 the longitudinal section of a conical shell is shown. In Appendix 3 it is demonstrated that, among others, the following set of characters completely defines such shells:

- The full outline of the cross-section of the whorl, as shown in fig. 3, inclusive of the thickness of the wall, and inclusive of its position with regard to the vertical. This is the generating curve of the shell. (1a)
- Length l_N of the shell. (1b)
- Slenderness l_N/D_{N-1} of the shell. (1c)
- Relative height of the mouth M_N/l_N. (1d)

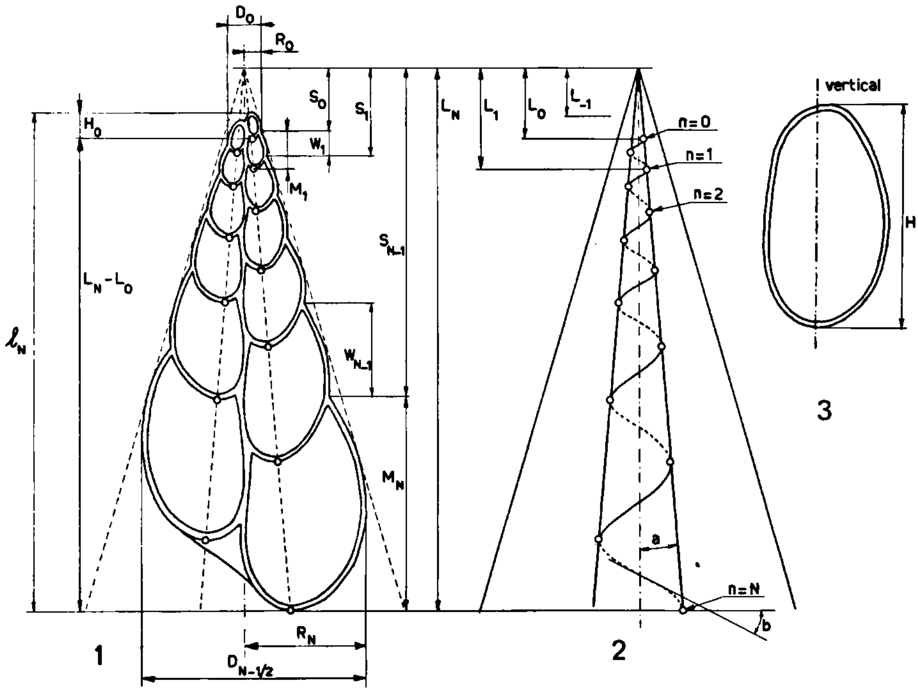


Fig. 1-3. 1. Longitudinal section of a conical shell; 2. Model derived from fig. 1; 3. Complete outline of a cross-section of a whorl, i.e. the generating curve of the shell plus its position with regard to the vertical.

- Whorl expansion rate A, i.e. the ratio of the linear dimensions of two successive whorls. (1e)
- Diameter D_0 of the apex, see fig. 4. (1f)
- The coiling direction of the spire, dextral or sinistral. (1g)
- Features of the ornamentation; on the protoconch, the inside of the aperture and the remainder of the shell. Other particulars. (1h)
- The colour of the shell. (1i)

Of course, this is not the only set of characters suited for defining a conical shell. Ratio A, for example, may be replaced by height over width ratio W_n/D_n of the whorls; diameter D_0 of the apex may be replaced by number of whorls N, counted as shown in fig. 4. Generally, characters 1b-1f may be replaced by any other set of five independent[1] numerical characters. Usually, however, one will prefer characters which prove to be about constant in a species. In addition, the characters should be easily and accurately measurable, and visualize the shell as well as possible. In this connection it should be mentioned that in set of characters 1 ratio l_N/D_{N-1} has been preferred over its inverse,

[1] Independent means that the value of any one of the five characters may theoretically vary independently of the values of the four remaining characters.

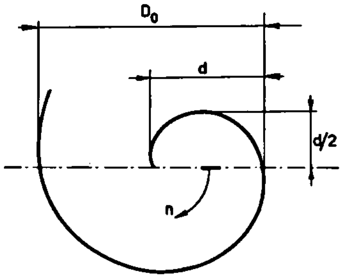


Fig. 4. Definition of n = 0; definition of the dimensions of the apex.

because it is larger the more slender a shell is. In addition, D_{N-1} has been preferred over $D_{N-1/2}$ because the possible presence of a labial rib might impair the accuracy with which $D_{N-1/2}$ can be measured. D_0 has been preferred over N because it proved to be rather constant in most species and does not depend on the length of the individual shells.

Generally, no shell will be completely conical in the mathematical sense. It will depend on circumstances whether or not one wants to add information about aberrations to the diagnosis. In this connection it should be noted that in shells with a deep umbilicus, at least the top half whorl must depart from a strictly conical form, because otherwise the umbilicus should also pierce the apex, so as to be visible from the outside.

If a shell departs considerably from a conical form, things are somewhat more complicated, though not fundamentally different. Such shells are discussed in Appendices 1 and 3.

Usually, a good, coloured picture with known magnification factor will contain most of the information necessary for the complete definition of a shell. Only if the upper part of the shell had been pictured with extreme care, however, one may be able to make a rough guess with regard to values D_0 and/or N. For this reason it is important that these values are mentioned separately in the diagnosis[2]. The same is true as regards other characters of the protoconch, such as ornamentation, number of whorls, etc. If available, information about the variability of the species should also be mentioned in the diagnosis.

EXPERIMENTAL PART

Things are different, however, if one wants to use histograms, e.g. when closely related species of considerable local and geographical variability are to be investigated conchometrically. It then may be desirable to consider all numerical characters required for defining a shell. As to this, we will restrict ourselves to conical shells, i.e. to characters 1b-1f. Generally, characters l_N, D_{N-1}, M_N and D_0 can be easily measured with reasonable accuracy. The same is true for number of whorls N. With regard to A and/or W_n/D_n the

[2]It should be noted that for this reason a lectotype designated by means of a picture may prove to be an essentially defective definition if the shell has been lost!

situation is more complicated, because these characters may be rather susceptible to irregularities of the shell, and because they can be measured in more than one way, which might easily result in slightly different values. Therefore, the numerical determination of A and W_n/D_n has been investigated below. In order not to be compelled to begin the measurements exactly at n = 0, as required by formulae A18-A20, the following formulae were derived from these:

$$D_n = D_x A^{n-x} \qquad (2)$$
$$S_n = S_x A^{n-x} \qquad (3)$$
$$W_n = W_x A^{n-x} \quad (x \geqslant 1) \qquad (4)$$

In these formulae, quantity x represents the number of whorls n from where the measurements begin. It may be arbitrarily chosen, and differ in D, W and S measurements.

Seven shells of *Rissoa labiosa* (Montagu, 1803), from three localities, have been used for this investigation. In order to prevent complications introduced by the presence of strong longitudinal ribs, smooth and nearly smooth shells were selected for the purpose. Five of the shells are shown in figs. 7a-11a. Another one appears in fig. 13. Of these shells, quantities D_n, W_n and S_n-S_x were measured in relation to n. These quantities can best be plotted as shown in figs. 5 and 6. If the shell is strictly conical and if the measurements are accurate, the results will be arranged on a straight line, the slope of which is a measure for A. In order to plot quantities S_n, quantity S_x should be known. Quantity S_x, however, cannot be measured directly. By trial and error it must be determined so that quantities S_n arrange themselves as closely as possible to a straight line, if plotted as shown in fig. 6.

The results of the measurements are presented in figs. 7b-12b, figs. 7c-12c and table 1. The measurements are micrometer readings. $D_{N-\frac{1}{2}}$ has not been measured because of the labial rib at the aperture of the shells. In measuring S_{N-1}-S_x and W_{N-1}, the suture had to be slightly extrapolated upon the labial rib at the aperture, as shown in fig. 12b. From figs. 7b-12b it can be seen that there are no indications that, among the shells analysed, quantities S and W behave essentially different from the mathematical model of a conical

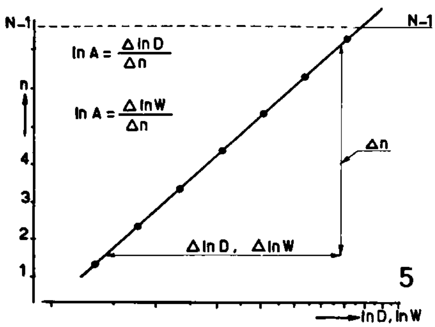


Fig. 5. Numerical determination of value A from D or W measurements.

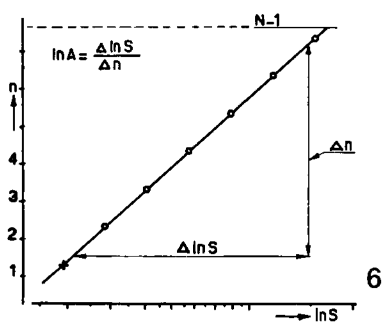


Fig. 6. Numerical determination of value A from S measurements. Only values S_n-S_x can be measured. Value S_x, indicated by +, cannot be measured itself. It must be determined by trial and error so that values S_n arrange themselves as closely as possible to a straight line.

Figs. 7a-11a and 13. Part of the shells measured. The numbers of figs. 7a-11a correspond to those of figs. 7b-11b and 7c-11c. For the labels, see Verduin, 1982, table 1, samples 19, 22 and 27. Magnification x 7.5.

shell. The impossibility to arrange the results of these measurements exactly on a straight line may therefore be ascribed to individual irregularities of the shells and/or inaccuracy of the measurements. From comparison of figs. 11b and 12b, and of figs. 11c and 12c, it may be concluded, however, that inaccuracy of the measurements plays a minor part, except as regards very small measurements. These figures represent a shell which has been measured twice, each time in a different position.

In contrast to quantities S and W, discussed above, quantity D usually departs essentially from the conical model at the first and the last whorl. Because of the large number of measurements of intermediate whorls, this aberration is of restricted consequence for the usefulness of the data.

In each of the figs. 7b-12b, values A have been derived completely independently from W, S and D measurements, though the W measurements have been taken from the S measurements. In figs. 7c-12c, values A have been determined from combined W and D measurements. These values A therefore are independent of those of figs. 7b-12b, except that the same measurements have been used. Thus, the accuracy of the procedure can be judged by comparing values A derived in different ways, see table 1. With regard to this table, it should be remarked that the best value S_x could often not be determined very precisely, with the consequence that values A could not be determined with great accuracy from the S measurements. For this reason, the three values S_x in each of the figs. 7b-12b have been selected in such a way that the true value A would probably be within the extremes derived. The middle value S_x was considered to be the best choice.

From table 1, and from the above considerations, it is concluded that values A derived

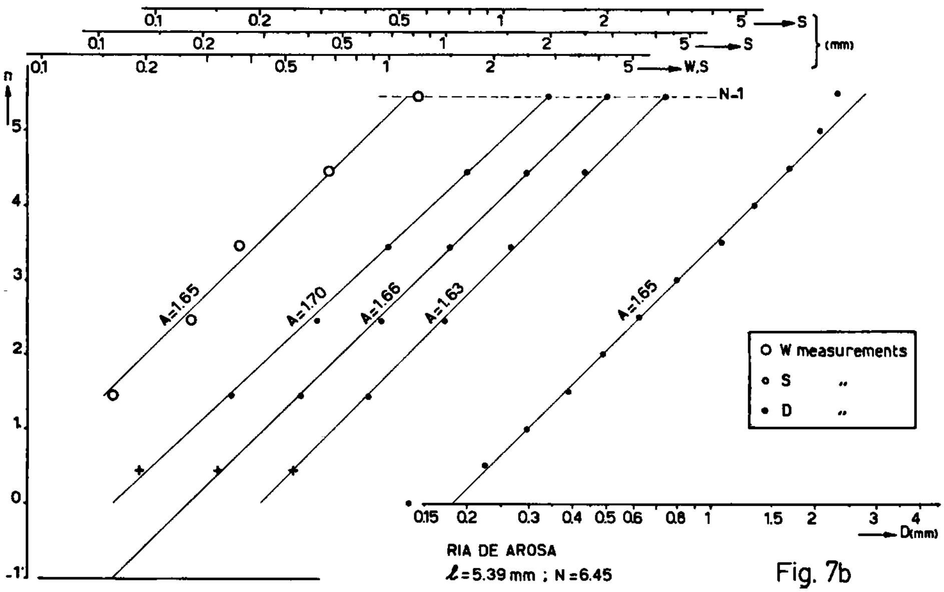


Fig. 7b

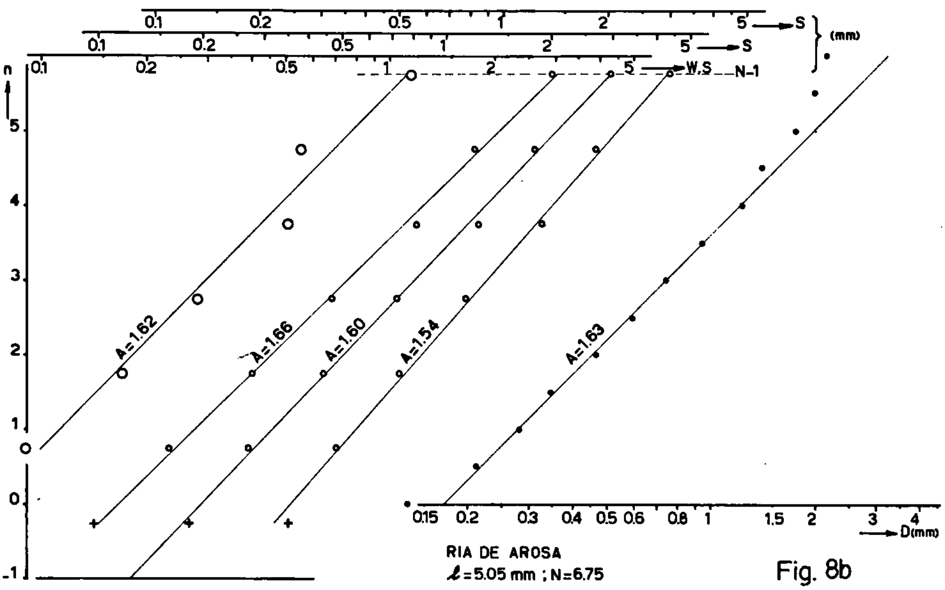
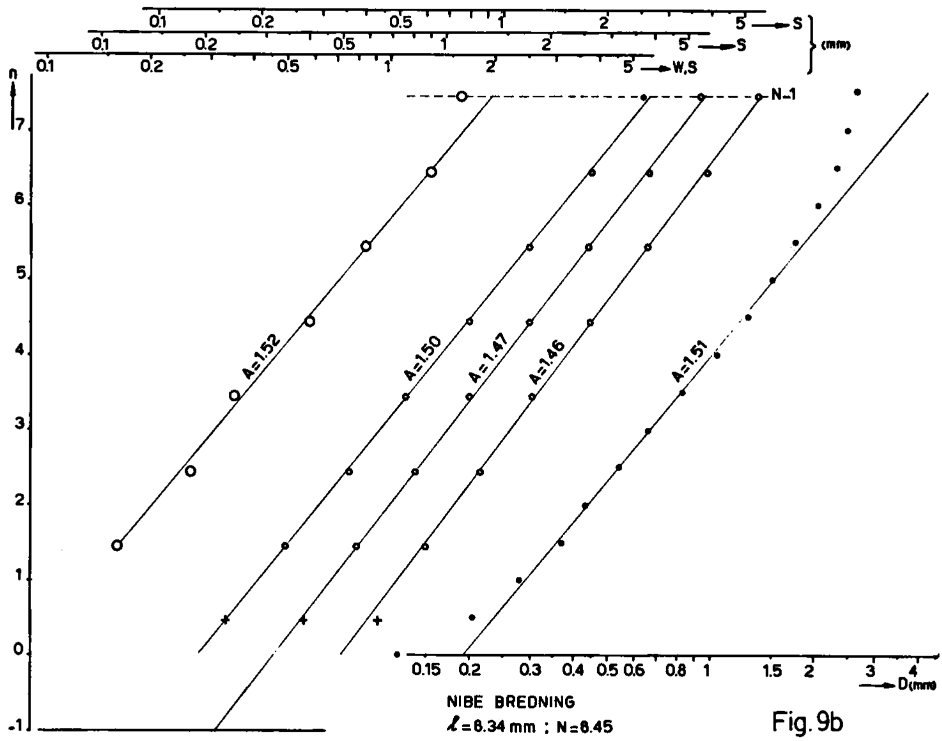


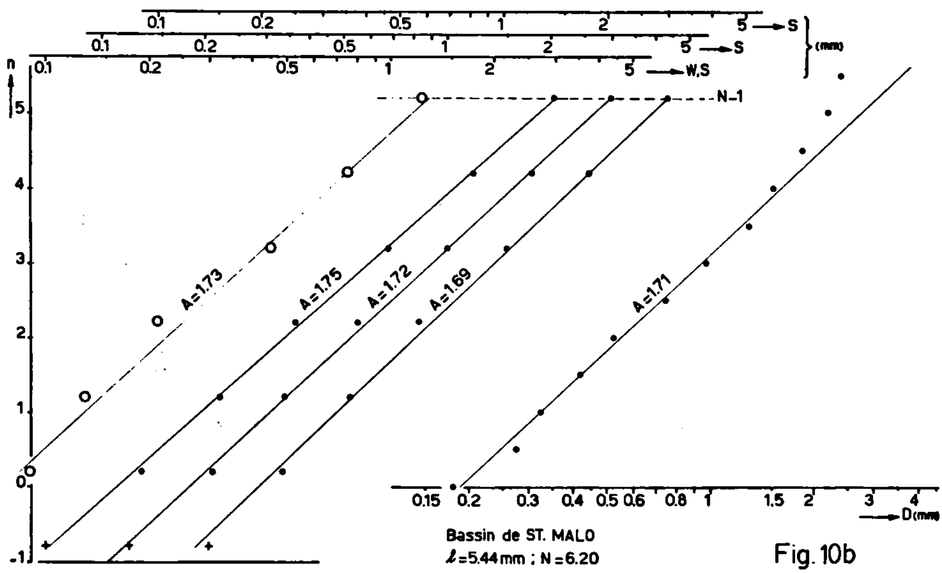
Fig. 8b

Figs. 7b-12b. Numerical determination of values A of the shells shown in figs. 7a-11a, from W, S and D measurements respectively. In order to demonstrate the influence of S_X, indicated by +, three different values S_X have been selected. The middle one is considered to be the best choice, the other ones about limit the range of proper values. See also fig. 6. Figs. 11b and 12b represent the same shell, which has been measured twice, each time in a different position.



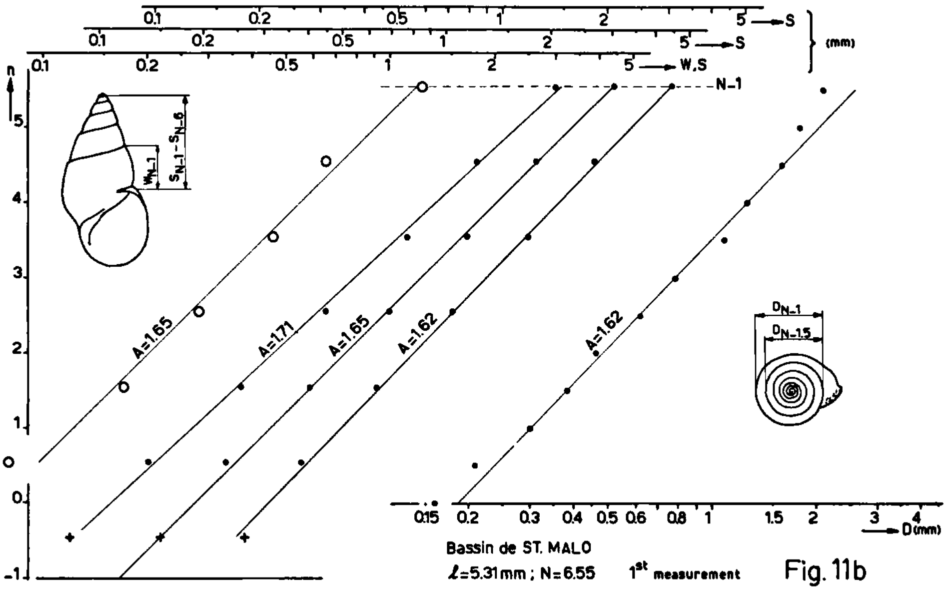
NIBE BREDNING
ℓ=8.34 mm ; N=8.45

Fig. 9b



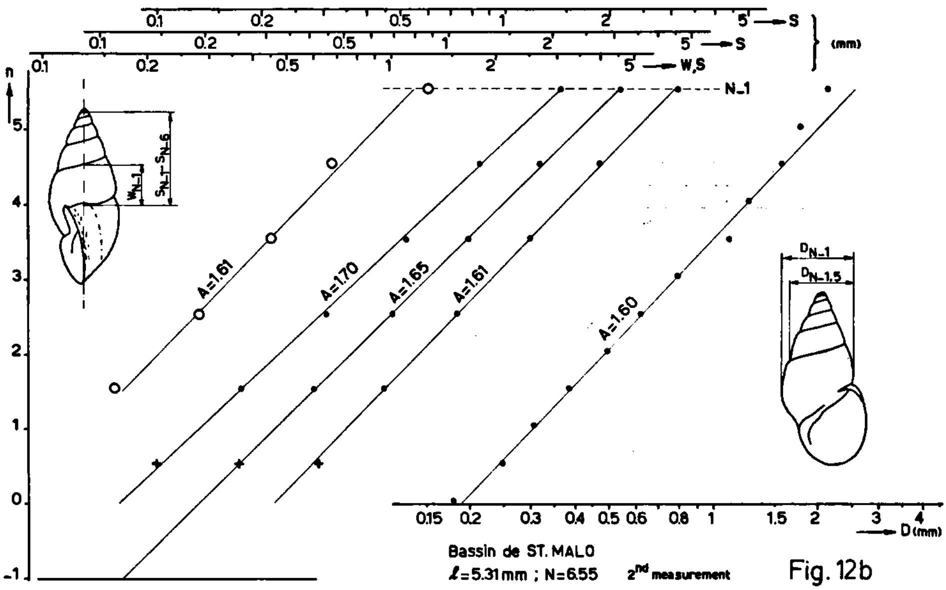
Bassin de ST. MALO
ℓ=5.44mm ; N=6.20

Fig. 10b



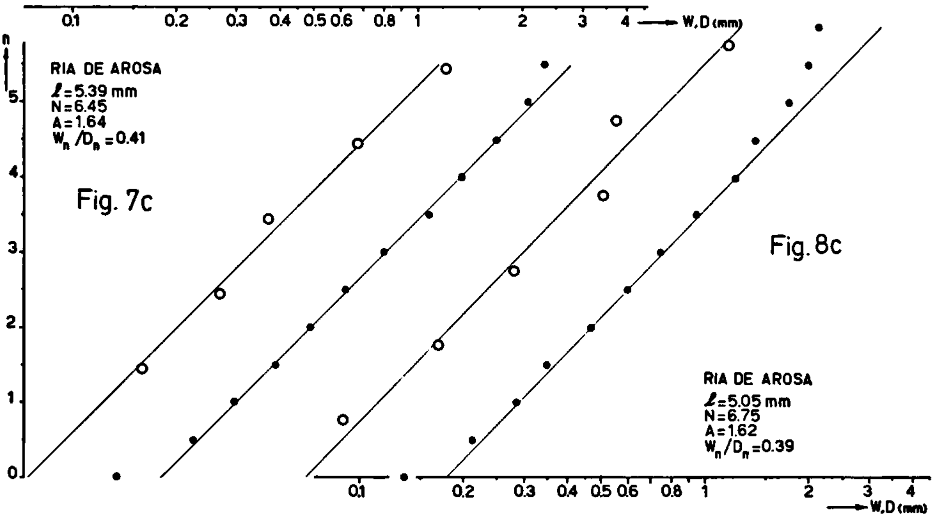
Bassin de ST. MALO
ℓ=5.31 mm ; N=6.55 1st measurement

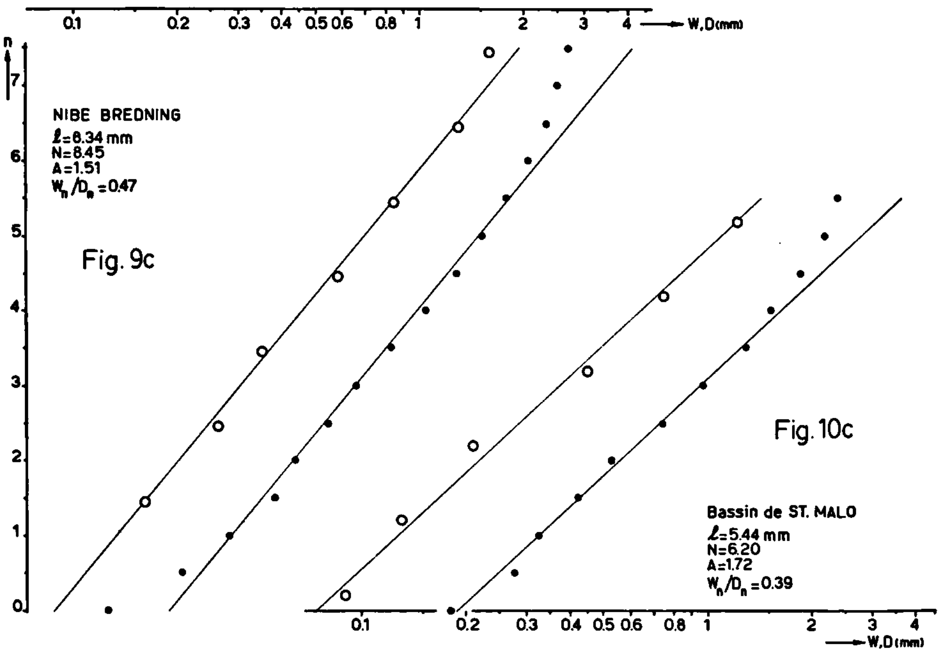
Fig. 11b



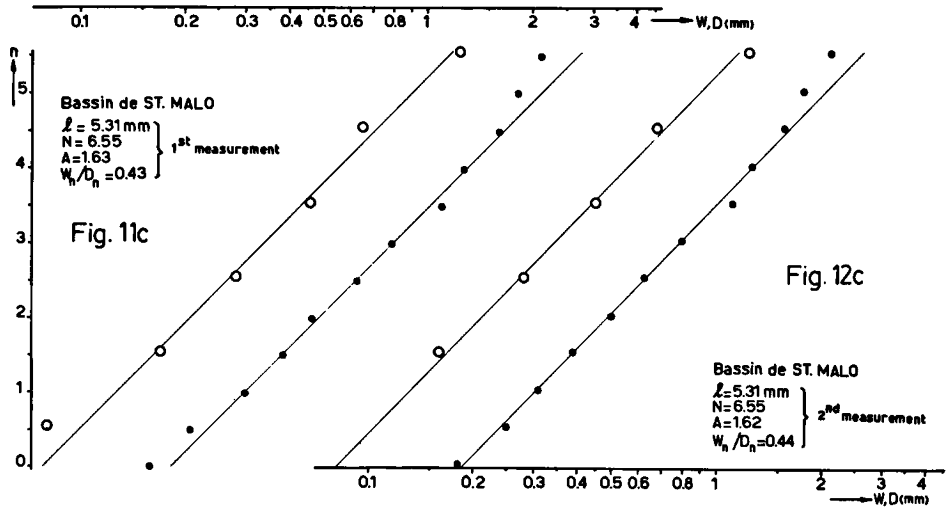
Bassin de ST. MALO
ℓ=5.31 mm ; N=6.55 2nd measurement

Fig. 12b





Figs. 7c-12c. Numerical determination of values A and W_n/D_n of the shells shown in figs. 7a-11a, from combined W and D measurements. Figs. 11c ~~and~~ 12c represent the same shell, which was measured twice, each time in a different position, see figs. 11b and 12b.



	A				l_N	Illust-ration:
	derived from					
	W&D	W	S	D		
Ria de Arosa	0	+½	+3½ +1 -½	0	5.39	Fig. 7
„ „ „	0	0	+2½ -1 -5	+½	5.05	Fig. 8
„ „ „	0	-½	+2 -½ -2½	0	5.43	---
Nibe Bredning	0	+½	-½ -2½ -3½	0	8.34	Fig. 9
„ „	0	0	+1½ -½ -2	+1½	8.05	Fig. 13
St. Malo	0	+½	+2 0 -2	-½	5.44	Fig. 10
„ „ 1st measurement	+½	+1½	+5½ +1½ -½	-½	5.31	Fig. 11
„ „ 2nd measurement	-½	-1	+4½ +½ -1	-1½	5.31	Fig. 12

Table 1. Main results of the experimental part, containing the procentual deviation of values A derived in figs. 7b-12b, with respect to the value derived from combined W and D measurements, as shown in figs. 7c-12c. The last shell has been measured twice, each time in another position; the deviations are related to the average of the two values A derived from combined W and D measurements. For the labels of the shells, see Verduin, 1982, table 1, samples 19, 22 and 27.

from parallel lines which fit satisfactorily to both W and D measurements, as shown in figs. 7c-12c, are the most accurate ones. Values W_n/D_n may be easily calculated from such combined W and D measurements, because the horizontal distance between the D line and the W line in figs. 7c-12c (with the negative sign if $D > W$) equals $\ln W_n/D_n$. If it is assumed that in figs. 7c-12c the accuracy of this horizontal distance equals about 1 mm, the accuracy of W_n/D_n is slightly over 5%. This is not very favourable in comparison with the accuracy of A, which probably only exceptionally exceeds 1½% among *Rissoa labiosa*, see table 1.

Quantities A and W_n/D_n are not the only characters which can be derived from D, W and S measurements. Other such characters are W_n/S_n and S_n/D_n. Equation 5 gives an interesting relation between the characters mentioned. From formula 3 follows:

$$1/A = \frac{S_{n-1}}{S_n}$$

From fig. 1 follows:

$$S_{n-1} = S_n - W_n$$

Consequently:

$$1/A = 1 - W_n/S_n = 1 - \frac{W_n/D_n}{S_n/D_n} \tag{5}$$

Obviously, W_n/S_n holds the same information as does A. Ratio S_n/D_n represents the slenderness of the spire of the shell and cannot be considered of special interest. It can be concluded from equation 5 that at least one of the characters A and W_n/D_n cannot be constant in a species if the slenderness of the spire is variable. This correlation between A and/or W_n/D_n on the one hand and the slenderness on the other hand may be different in different species. Some experience with regard to this is to be found in Verduin, 1982, fig. 16.

APPENDIX 1
A MATHEMATICAL MODEL OF A REGULAR SHELL

Measurement S_n-S_o varies with number of whorls n, see fig. 1. This is expressed by the formula:

$$S_n-S_o = f(n), \qquad f(0) = 0 \tag{A1}$$

Hence:

$$W_n = S_n-S_{n-1} = f(n)-f(n-1) \tag{A2}$$

Ratios R_n/W_n and M_n/W_n generally also vary somewhat with number of whorls n:

$$R_n/W_n = p(n) \tag{A3}$$

$$M_n/W_n = q(n) \tag{A4}$$

From fig. 1 follows:

$$L_n = S_{n-1} + M_n$$

and consequently:

$$L_n-S_o = f(n-1) + q(n)[f(n) - f(n-1)] \tag{A5}$$

From fig. 1 also follows:

$$D_n = R_n + R_{n+½}$$

and consequently:

$$D_n = p(n + ½)[f(n + ½) - f(n - ½)] + p(n)[f(n) - f(n-1)] \quad (A6)$$

Functions f(n), p(n) and q(n) of a shell can generally be approximated rather accurately by drawing a smooth curve through measured values S_n-S_o, R_n/W_n and M_n/W_n respectively. There, however, is a little problem because f(n) is not defined outside the range $0 \leqslant n \leqslant N\text{-}1$ (see fig. 1), so that W_n is not defined outside the range $1 \leqslant n \leqslant N\text{-}1$. As a consequence, functions p(n) and q(n) cannot be determined outside the latter range. This problem can be simply eliminated by extrapolating f(n) in a suitable way into the adjacent ranges $-1 \leqslant n < 0$ and $N\text{-}1 < n \leqslant N$. In the range $0 \leqslant n < 1$, function q(n) must be derived from measured values M_n-W_n, see fig. 1.

It will be demonstrated now that the longitudinal section of a regular shell is completely defined by:

- the generating curve, plus its position with regard to the vertical, as shown in fig. 3;
- functions f(n), p(n) and q(n), see equations A1 and A3-A4;
- number of whorls N, measured as shown in fig. 4; (A7)
- ratio H_n/H_o (see figs. 1 and 3) in the range $0 < n \leqslant 1$;
- the coiling direction of the spire.

From the above data, the longitudinal section of the shell can be drawn as follows. First, measurements R_o, R_1, M_o-W_o and M_1 are calculated from A7 and A2-A4. Next, measurement H_o is estimated and value H_1 which goes with it calculated from A7. Then fig. A1 is drawn. Obviously, the value for measurement H_o has been chosen too small in fig.

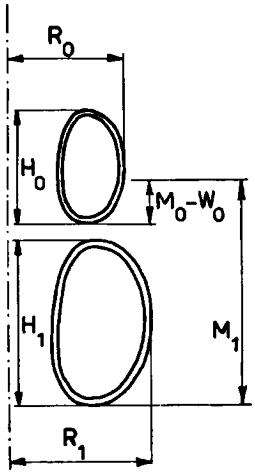


Fig. A1

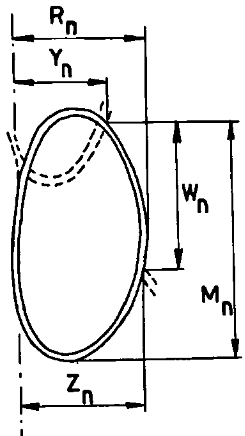


Fig. A2

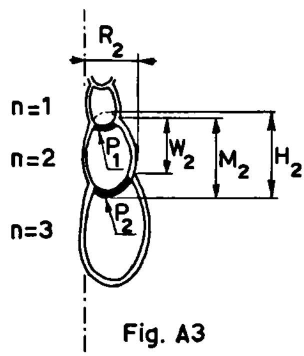


Fig. A3

Figs. A1-A3. Explanations see text of appendices 1 and 2.

A1, so that the suture is not in the correct place. By trial and error it is possible to arrive at the correct value of H_o, whereupon it is not difficult to reconstruct the whole shell.

The mathematical model represented by formulae A1-A4 and set of data A7 is of course not the only mathematical description possible. There even is no particular reason to prefer it to other such models. It is, however, a good representative of a mathematical model of a regular shell.[3]

APPENDIX 2
SPECIAL MODELS

If, for example, is assumed:

$$f(n) = S_oA^n + Cn - S_o \qquad C = \text{constant} \tag{A8}$$

equation A1 changes into:

$$S_n = S_oA^n + Cn \tag{A9}$$

and equation A2 changes into:

$$W_n = S_oA^{n-1}(A-1) + C$$

Therefore:

$$W_1 = S_o(A-1) + C$$

and:

$$W_n - C = (W_1 - C)A^{n-1} \tag{A10}$$

If moreover is assumed:

$$\left.\begin{aligned} p(n) &= \text{constant} \\ q(n) &= \text{constant} \end{aligned}\right\} \tag{A11}$$

the following formulae can be derived in a similar way:

$$R_n - pC = (R_o - pC)A^n \tag{A12}$$

$$M_n - qC = (M_1 - qC)A^{n-1} \tag{A13}$$

$$D_n - 2pC = (D_o - 2pC)A^n \tag{A14}$$

$$L_n - (n + q - 1)C = [L_o - (q-1)C]A^n \tag{A15}$$

At first sight, formulae A9-A15 represent the conchospiral model, mentioned by Ludwig (1932: 17). This, however, is only true as regards the measurements mentioned in these formulae, and certainly not for all measurements. In order to demonstrate this, measurement Y_n (see fig. A2) is written as:

$$Y_n = r(n)W_n \tag{A16}$$

Suppose now that r(n) varies with number of whorls n. Then follows:

$$Y_1 = r(1)[S_o(A-1) + C]$$

$$Y_n = r(n)[S_oA^{n-1}(A-1) + C]$$

and therefore:

$$Y_n/r(n) - C = [Y_1/r(1) - C]A^{n-1}$$

From the last equation follows that measurement Y_n can only comply with the conchospiral model, if quantity r(n) does not vary with n. Similarly, measurement Z_n (see fig. A2) can only comply with the conchospiral model if quantity t is constant in:

$$Z_n = t(n)W_n \tag{A17}$$

[3]If the requirement that the form and position of the generating curve must be constant throughout the shell is dropped, the flexibility of the model may be increased ad libitum by the application of n-dependent transformation techniques to the form and position of the generating curve.

As can be easily seen in fig. 1:

$Z_n = Y_{n+1}$

Hence from formulae A16-A17:

$W_{n+1}/W_n = t(n)/r(n+1)$

Because both t and r must be constant in the conchospiral model, it thus follows that W_{n+1}/W_n must be constant throughout the shell. This requirement, however, is incompatible with equation A10, unless C=0 or A=1. Obviously, it is not possible that all measurements of a shell simultaneously comply with the conchospiral model. Therefore, a consistent conchospiral model does not exist.

Next, conical shells will be discussed, i.e. shells of which the form of the cross-section of the whorls is constant throughout the shell. In fig. A3 three successive whorls of such a shell are shown. Obviously, whorl no. 2 is A times whorl no. 1. Therefore, part P_2 which the whorls nos. 2 and 3 have in common, is A times larger than part P_1. From this follows that whorl no. 3 must be A times larger than whorl no. 2 too, etc.

With C = 0, equations A8-A15 obviously comply with this requirement. This leads to the well-known logarithmic model:

$$S_n = S_o A^n \qquad (A18)$$
$$W_n = W_1 A^{n-1} \qquad (A19)$$
$$R_n = R_o A^n$$
$$M_n = M_1 A^{n-1}$$
$$D_n = D_o A^n \qquad (A20)$$
$$L_n = L_o A^n \qquad (A21)$$

From a strictly theoretical point of view, this is not the only mathematical model which applies to conical shells. According to set of data A7, information about ratio H_n/H_o in the range $0 < n \leqslant 1$ is required for a complete diagnosis of a shell. It can be demonstrated that the logarithmic model is based on the implicit assumption:

$$H_n = H_o A^n \qquad 0 < n \leqslant 1$$

Thus, the logarithmic model is essentially based on the assumption that conical shells grow conform to a regular spiral line on a cone, as shown in fig. 2. From a strictly theoretical point of view, it is not a priori excluded that conical shells depart more or less from such regularity. Actually, however, conical shells prove to grow conform to such regular spiral lines. Therefore, the logarithmic model is the only one which applies to conical shells.

APPENDIX 3
THE DIAGNOSIS

We will now discuss the minimum information required for a complete diagnosis. In Appendix 1 it has been demonstrated that set of data A7 contains complete information about the longitudinal section of the shell, inclusive of the apical dimensions, and inclusive of the length of the shell. Also, none of the data A7 is superfluous. Thus, set of data A7 is representative of the minimum information required for a complete diagnosis. Additional information will be required as regards colour, ornamentation and other particulars.

Set of data A7, however, is not the only one which contains complete information about the longitudinal section of a shell. Number of whorls N may be replaced by length

l_N of the shell. Ratio H_n/H_o in the range $0<n\leqslant 1$ may be replaced by similar information from another range. Functions f(n), p(n) and/or q(n) may be replaced by other ones if another setup of the mathematical description is preferred, etc. Generally, set of data A7 may be replaced by any other equivalent set of data.

As long as no details are known with regard to the mathematical structure of functions f(n), p(n) and q(n), it is not very well possible to discuss the implications of the word 'equivalent' in this context. Therefore, these will be illustrated with regard to the most simple model possible, the logarithmic model of a conical shell, see Appendix 2. In such models, function f(n) is completely defined by values S_o and A. According to formula A11 functions p(n) and q(n) are constant. Information about H_n/H_o is superfluous because it has already been incorporated in the model, see Appendix 2. Thus, with regard to the logarithmic model of a conical shell, set of data A7 is reduced to:

- the generating curve;
- values S_o, A, p, q, and N;
- the coiling direction.

These, however, are not the only set of characters, and certainly not the most practical ones, for defining conical shells. Set of characters L_N-S_o, $D_{N-1}/(L_N$-$S_o)$, $M_N/(L_N$-$S_o)$, W_n/D_n and D_o for instance is equivalent to the set of characters S_o, A, p, q and N, because, with the help of fig. 1 and formulae A18 and A20, the latter set of characters may be calculated from the former one:

$$\left.\begin{array}{l} L_N - S_o - M_N = S_{N-1} - S_o = S_o(A^{N-1} - 1) \\ W_{N-1} = S_{N-1} - S_{N-2} = S_o A^{N-1}(1 - 1/A) \\ D_{N-1}/D_o = A^{N-1} \end{array}\right\} \text{from these equations } S_o\text{, A and N may be calculated}$$

From equations A1, A4 and A6 follows then:

$$\left.\begin{array}{l} M_N = qS_o A^{N-1}(A-1) \\ D_o = pS_o(A^{1/2} + 1 - A^{-1/2} - A^{-1}) \end{array}\right\} \text{from these equations p and q may be calculated}$$

Another set of characters which is equivalent to the set of characters S_o, A, p, q and N is the set of characters 1b-1f. In this case, characters S_o, p and q cannot be calculated from 1b-1f, but must be derived through graphical means. To this end, the longitudinal section of the shell must be drawn from the set of characters 1b-1f. After N has been calculated from D_{N-1}/D_o, this can be done with the help of the formula:

$$l_N = L_N - L_o + H_o = L_o(A^{N}-1) + H_o$$

which is derived from fig. 1 and formula A21. If a value for L_o has been chosen, the value for H_o correlated with it may be calculated from this formula. It is then possible to calculate all values L_n, D_n and H_n with the help of the formulae A20, A21 and:

$$H_n = H_o A^n$$

This means that the longitudinal section of the shell can be drawn. Generally, however, value M_N will prove to differ from that given by 1d. Consequently, by trial and error value L_o must be determined so that the longitudinal section meets the specification in this respect also.

From a mathematical point of view, drawing the longitudinal section of a conical shell from any five independent characters is equivalent to determining the set of characters S_o, A, p, q and N from five equations. If these equations were linear, which they are not, it might be concluded from this observation that any set of five independent characters would be necessary and sufficient to completely define the longitudinal section of a conical shell of which the generating curve (see fig. 3) and the direction of the coiling is known. As it is, however, there is no guarantee that any five independent characters will always produce only one longitudinal section. Strictly speaking, one should therefore conclude that at least five independent characters are required for defining the longitudinal section of a conical shell, in addition to the generating curve and the direction of the coiling.

ABSTRACT

The minimum information required for a complete diagnosis of coiled shells is discussed with the help of an advanced mathematical model of a shell. It is concluded that, in addition to a good, coloured, picture plus the main dimensions of the shell, information is required about either the number of whorls, or, preferably, the dimension of the apical whorl. In view of a planned conchometrical analysis, a few investigations have been performed with regard to the accuracy with which whorl expansion rate A and height over width ratio W_n/D_n of the whorls can be measured.

REFERENCES

CALOW, P., 1975. Length-dry weight relationships in snails: some explanatory models. - Proc. malac. soc. Lond. 41: 357-375.

FRANK, G.H. & A.H. MEYLING, 1966. A contribution to the conchometry of Biomphalaria pfeifferi (Basommatophora: Planorbidae). - Malacologia 3: 379-398.

HALLER-TJABBES, C. TEN, 1979. The shell of the whelk, Buccinum undatum L. Thesis: I-X, 1-132. Groningen.

LUDWIG, W., 1932. Das Rechts-Links-Problem im Tierreich und beim Menschen: I-XI, 1-496. Berlin.

MOSELEY, H., 1838. On the geometrical forms of turbinated and discoid shells. - Phil. Trans. Roy. Soc. Lond. 1: 351-370.

PIZZARY, P., 1975. The shape of shells. - La Conchiglia/The Shell 77/78: 3-5; 79/80: 3-6; 81/82: 3, 14-17.

RAUP, D.M., 1966. Geometric analysis of shell coiling: general problems. - J. Paleont. 40: 1178-1190.

THOMPSON, W. D'ARCY, 1942. On growth and form: I-VIII, 1-1116. London.

VERDUIN, A., 1982. On the taxonomy and variability of Recent European and North African species of the subgenus Rissostomia Sars, 1878, of the genus Rissoa Desmarest, 1814 (Mollusca, Gastropoda, Prosobranchia). - Basteria 45: 143-166.