Suture and location of the coiling axis in gastropod shells

Christian Van Osselaer and Philippe Grosjean

Abstract.—The general allometric equations for the logarithmic helicospiral can fit many extraconical shapes, but the isometric conditions traditionally used limit study only to conical growth. We present evidence to show that in real gastropod shells, the logarithmic helicospiral equations fit the suture. Poor location of the coiling axis and/or an inappropriate pole for the logarithmic helicospiral has often led to the rejection of this model. The differences between the errors associated with measurement or previously available models are discussed. Two methods, based on suture trace measurements, are proposed to locate the coiling axis both in apical and lateral views. The first is a graphical method based on an elementary property of the logarithmic spiral. The second is a computational method based on iterative reprojections of the suture. It is shown that the protoconch and the teleoconch must be treated separately. The precision of the new methods (especially the computing method) enables deviations from logarithmic helicospiral trajectory to be identified and differentiated from irregularities of the shell and sequential growth phases. Application of these methods may be useful not only for other gastropod morphological features, but also for other taxa such as brachiopods and other mollusks.

Christian Van Osselaer. Laboratory of Bio-Ecology, Université Libre de Bruxelles, 50 avenue F. Roosevelt C.P. 160/14, B-1050 Brussels, Belgium. E-mail: cvanosse@ulb.ac.be
Philippe Grosjean. Marine Biology Laboratory, Université Libre de Bruxelles, 50 avenue F. Roosevelt C.P. 160/15, B-1050 Brussels, Belgium. E-mail: phgrosje@ulb.ac.be

Introduction

The shapes of shells have long been of interest (for examples see Lison 1949; D'Arcy Thompson 1961; Raup 1961, 1962, 1966; Raup and Michelson 1965), and the accretionary process of shell growth has often been described by a logarithmic helicospiral. Many models have been proposed to characterize coiled shells in terms of a few parameters (independent or not), and these can generate a high diversity of shapes. Such models have mostly been used in theoretical morphology to mimic existent forms or to explore the possible range of morphological variability (e.g., computer simulation of shells [Raup 1961, 1962, 1966; Raup and Michelson 1965; McGhee 1978, 1980; Harasewych 1981; Ekaratne and Crisp 1983; Løvtrup and Løvtrup 1988; Ackerly 1989a,b; Cortie 1989; Illert 1989; Savazzi 1990; Prusinkiewicz and Fowler 1995; Stone 1995, 1996a, 1997]) or to study theoretical morphospaces (Raup 1966; Raup and Michelson 1965; McGhee 1980, 1991; Schindel 1990; Sheldon 1993; Dawkins 1996; Tursch 1997).

The suture is the line of external contact points between successive whorls formed by the accretionary process. It therefore traces the ontogeny of the outermost point of adherence between whorls and contains ''information'' on whorl overlapping. It is of prime importance in fabricational or functional constraints (mechanical resistance of the shell, economy of shell material, etc. [Heath 1985]). Constraint is fundamental to understanding morphological variation, as it has substantial bearing on differentiation at all levels (Gould 1992).

It is thus important to find a way to study the suture. The consensus is that deriving equations from the intersections of consecutive generating curves is an almost impossible task (Tursch 1998). However, the suture of real shells can be studied by nondestructive methods, and it has already been used to estimate some elementary parameters of growth models and to investigate discriminant characters in systematics (Kohn and Riggs 1975; Harasewych 1981; Nemeschkal and Kothbauer 1989). One aim of this paper is to show that the suture of real shells, contrary to expectation, can be fitted by a simple logarithmic hel-

icospiral without reference to the intersections of consecutive curves.

Empirical morphometric studies are sometimes based on measurements of homologous points (landmarks). Some are based on reference systems that are not always easily defined (Bookstein 1982, 1993; Rohlf 1990). In the many studies on shell morphometry, most authors use their own reference systems or sets of measurements (Galler and Gould 1979; Verduin 1982; Goodfriend 1983; Janson and Sundberg 1983; Løvtrup and Løvtrup 1988; Grahame and Mill 1989; Kristensen and Christensen 1989; Johannesson and Johannesson 1990; Nemeschkal 1990; Boulding and Hay 1993; Chiba 1993). Many measurements are applicable only to restricted groups of taxa, limiting their use for broader comparisons.

The coiling axis cannot be easily located because it is not physically discernible on real shells. Even its existence remains controversial (Okamoto 1988; Ackerly 1989a,b; Illert 1989; Savazzi 1990). Despite this, it is *the* implicit reference of ''fixed axis'' models. At present there is no single method to locate the coiling axis. It can be roughly estimated, in some cases, by the columella direction, which is only visible either by radiography or by destructive methods (cross-sections). Some authors do not describe their methodology to locate the coiling axis (Vermeij 1971; Murray 1982; Ekaratne and Crisp 1983; Grahame and Mill 1989; Johannesson and Johannesson 1990). Others use various conventions to define a reference axis but it is not necessarily the coiling axis (Kohn and Riggs 1975; Harasewych 1981; Coppois and Glowacki 1982; Stepczak 1988; Schindel 1990; Boulding and Hay 1993; Stone 1995, 1996a, 1997; Wagner 1996 [detailed in personal communication 1998]). Reliably defining it on real shells is essential for deriving a standardized reference system in morphometrical studies (Raup 1966).

We propose using real sutures to verify the adequacy of the coiling axis and accurately locate it. This will facilitate a broad range of investigations in ontogeny, morphology, and morphometry.

However, there are practical limitations when measuring sutures. We have found that oscillations consistently appear in the plot of the logarithm of the radii vs. the number of volutions. We present evidence to show that they are due to experimental errors, specifically incorrectly projecting the suture (not perfectly perpendicular to the coiling axis) and/or taking the origin of measurement not exactly at the pole of the spiral. These errors have been large enough for some authors to propose rejecting the logarithmic helicospiral for describing shells (Raup 1966; Vermeij 1993). We demonstrate that the residuals of the logarithm of the radii vs. the number of volutions can be used to locate accurately the coiling axis of most gastropod shells. We also show that the suture can reveal subtle growth features after thorough elimination of the sinusoidal components that otherwise hide such phenomena. This could extend the understanding of gastropod growth beyond what can be seen by an experienced eye. An example where this new approach will be particularly useful is for studying the protoconch and teleoconch, as each grow and respond differently at different stages of life. The use of a same-continuous-growth equation for both parts of the shell is problematic and we show that there is considerable difference in the growth of the protoconch compared with the teleoconch. We also show for an *Oliva* shell that there are two separate growth phases in the teleoconch.

Methodology

To describe our methodology, we first introduce the general logarithmic helicospiral. We have adapted the terms for the suture and have kept the radial expansion rate independent of the longitudinal (i.e., unconstrained). Such a general model allows the description of many extraconical shapes and takes into account allometric relationships. We verify that sutures of real shells can be fitted by the general equations of the logarithmic helicospiral. A graphical and a computing method are described to locate the coiling axis of the teleoconch in both lateral and apical projection. We developed a program that implements the computing method (ShellAxis) and is available on the SciViews web site (http://

www.sciviews.org). A complementary image analysis module (Pixmeter), which facilitates morphometric measurements, is also available. It allows accurate determination of points or segments parallel or perpendicular to the calculated coiling axis (the length, the width, etc.) on the picture. The examples discussed herein, and some additional ones, are also provided.

Logarithmic Helicospiral Model for the Teleoconch Suture

In a cylindrical coordinates system, a three-dimensional logarithmic helicospiral, which is usually used to describe shell growth process, can be expressed by the following equations with four parameters, in which the coiling axis coincides with the z-axis:

$$\begin{cases} r = r_0 \cdot S_r^{\theta} \\ z = z_0 \cdot S_z^{\theta} \end{cases} \tag{1}$$

where r is the distance from the coiling axis to the suture (although the suture is not necessarily constituted by homologous points, these equations can be applied to any set of ''homologous'' points on a shell); z is the longitudinal coordinate from the origin of the logarithmic helicospiral; θ is the number of volutions; S_r is the radial expansion rate of the suture, S_z is its longitudinal expansion rate along the coiling axis; and S_r and S_z are dimensionless and are independent from each other. These symbols have been chosen to avoid confusion with shell model growth parameters (for instance, S_r is mathematically similar to Raup's W). Parameters r_0 and z_0 correspond to the radial and the longitudinal distances of the suture from the pole of the spiral when θ equals zero. Their selective amplification by S_r^{θ} and S_z^{θ} will influence the size and the shape of the helicospiral for a given θ. Both r_0 and z_0 are expressed in linear units (mm or μm). They will be discussed later in this paper, but they do not interfere with the evaluation of the equations adequacy, with the location of the coiling axis, or with the determination of S_r and S_z.

It must be noted that longitudinal and radial measurements can be related by an allometric relationship ($y = \alpha \cdot x^{\beta}$ [Huxley and Teissier 1936]).

$$z = \alpha \cdot r^{\beta} \tag{2}$$

Solving equation (2) with equations (1) gives the following relationship between allometric parameters and logarithmic helicospiral parameters:

$$z_0 = \alpha \cdot r_0^{\beta} \quad \text{and} \quad S_z = S_r^{\beta} \tag{3}$$

The equality of both expansion parameters ($S_z = S_r$, $\beta = 1$) is only a particular case. Coefficients α and β of the allometry between radial and longitudinal expansions of the suture are easily calculated from the helicospiral parameters:

$$\alpha = \frac{z_0}{r_0^{\beta}} \quad \text{and} \quad \beta = \frac{\ln S_z}{\ln S_r} \tag{4}$$

Is the Logarithmic Spiral Adequate?

The orthogonal projection of the helicospiral in a plane perpendicular to the coiling axis (apical projection) is given by the first of equations (1) and can be linearized ($y = a \cdot x + b$) as follows:

$$\ln r = \ln S_r \cdot \theta + \ln r_0 \tag{5}$$

To verify the adequacy of this equation to fit the apical projection of the suture, one could plot the logarithm of suture radii r vs. the number of volutions θ. These radii must be measured from the pole of this two-dimensional spiral. In an apical view, this pole is the intersection of the coiling axis and the projection plane. It has often been called the ''center'' of the spiral.

In practice, when measurements are taken from an origin, oscillating components usually appear in the plot of $\ln r = f(\theta)$. Such components have been already observed as ''an oscillating error term'' by Schindel (1990) but have not been discussed. This is illustrated in Fig. 1A for a specimen of *Anctus angiostomus* (J. A. Wagner, 1827). Plotting the residuals (the variation of $\ln r$ that is not explained by the function; that is, $\ln r$ observed $-$ $\ln r$ predicted) vs. θ better evidences this effect (Fig. 1B).

If the equations were adequate to fit the data and if the projection orientation and the pole chosen as the origin of measurements were correct, the plot should have been linear and
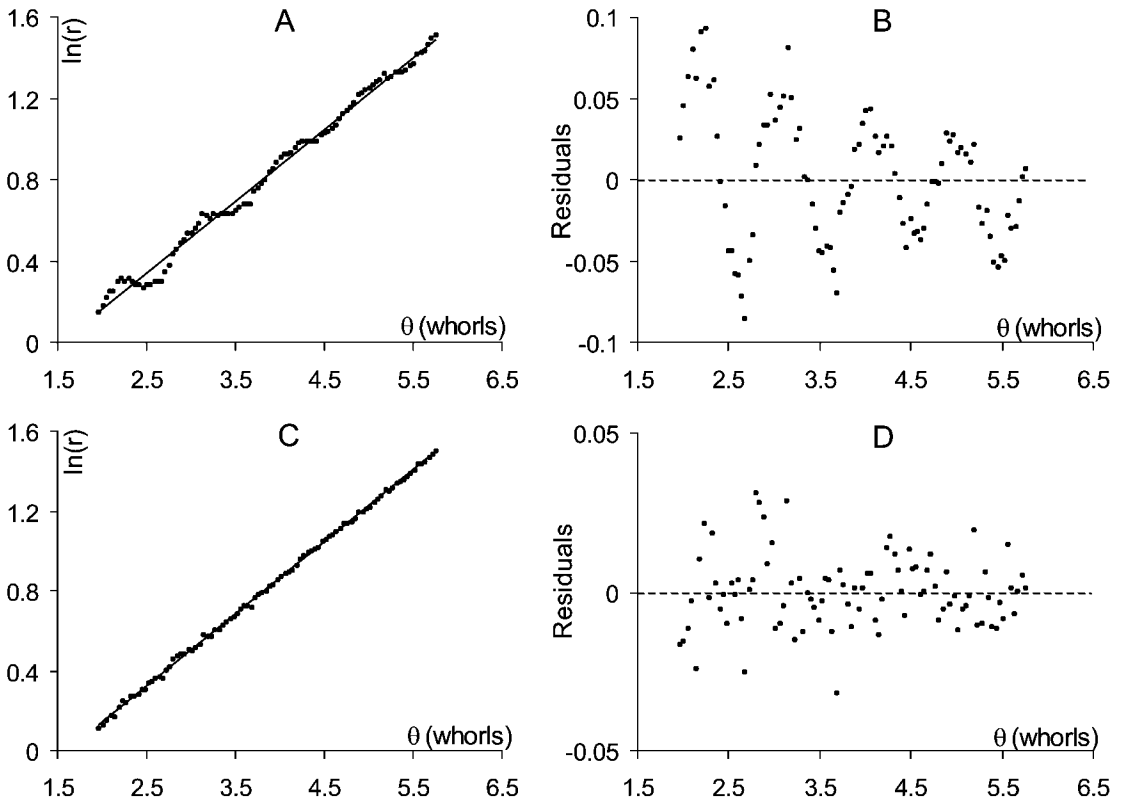
FIGURE 1. Teleoconch suture of a specimen of *Anctus angiostomus* (specimen also depicted in Fig. 5). A, ln $r = f(\theta)$ (taken every 15°). The radii are measured from a visually estimated origin in apical projection (coefficient of determination of the linear regression $r^2 = 98.8\%$. B, Residuals of the linear regression (oscillating component). C, Same data as A, recalculated by the computing method ($r^2 = 99.92\%$). The weak corrections for the relocation of the pole and the correction of the projection are as follows: $a = -1.14°$; $b = 0.51°$; $x_p = 0.05$ mm; $y_p = 0.12$ mm (see Fig. 6 for the meaning of these parameters). D, Residuals from the linear regression on the recalculated data (random distribution, weaker amplitude—note the change of scale).

vice versa. The residuals should have also been randomly distributed.

In practice, there is little chance of projecting the suture perfectly perpendicular to the coiling axis because of errors in visual orientation of the shell. There is also, a priori, little chance of taking the origin of measurements at the exact pole of the spiral whose accurate location is unknown. If the same specimen of *Anctus angiostomus* is now differently oriented and with radii taken from another origin, the plot of ln $r = f(\theta)$ is perfectly linear and the residuals are randomly distributed (Fig. 1C, D). The difference between the projections of Fig. 1A and Fig. 1C is about 1°, and the distance between both origins is about 0.1 mm. This means that the apical projection of the teleoconch suture of this specimen is well fitted by a simple logarithmic spiral and that the

previously observed oscillating components of the residuals were only due to experimental errors. The distribution of residuals appears highly sensitive to very small bias.

Determination of the Logarithmic Helicospiral Starting Values

To fully quantify the logarithmic helicospiral equations of a suture, we must determine the origin of θ and parameters r_0 and z_0 (in eq. 1) (but this is not necessary to locate the coiling axis). The parameters r_0 and z_0 (corresponding to the values of r and z for $\theta = 0$) depend on the position of the whorls' origin. Their determination requires some additional constraints and conventions.

As noted by Gould (1989) and Stone (1995), the procedure for numbering shell whorls is not easily established. In the absence of a well-

defined origin, number of volutions are counted, shifted by an indeterminate amount θ_s (a problem similar to the translation of the longitudinal coordinates; see Discussion):

$$\theta' = \theta - \theta_s \tag{6}$$

The equations (derived from eq. 1) become

$$\begin{cases} r = r_0' \cdot S_r^{(\theta - \theta_s)} \\ z = z_0' \cdot S_z^{(\theta - \theta_s)} \end{cases} \tag{7}$$

which can be linearized:

$$\begin{cases} \ln r = \ln S_r \cdot \theta + [\ln r_0' - \ln S_r \cdot \theta_s] \\ \ln z = \ln S_z \cdot \theta + [\ln z_0' - \ln S_z \cdot \theta_s] \end{cases} \tag{8}$$

The independent terms (in brackets) of equations (8) contain different components and do not constitute operational scale parameters. These can be different for the same shell (with different arbitrary values of θ_s), and therefore cannot be compared between shells. Such problems can be circumvented by adopting a suitable convention for θ_s, for r_0, or for z_0 (the three are linked by the logarithmic helicospiral equations).

Constraining θ_s Amounts to Finding an Identifiable Landmark on the Suture.—θ has sometimes been chosen equal to zero at the aperture (McGhee 1980; Schindel 1990), and whorls are counted in negative values. In this case, the origin of the reference system moves when the shell grows. Both r_0 and z_0 are then varying and depending on θ.

θ could be chosen to equal zero at the beginning of the protoconch. ''Few non-malacologists realize that one cannot unambiguously define whorl numbers from the shell's apex; there is no clear zero point at the top of a shell where winding begins'' (Gould 1989: p. 519). Moreover, the origin of the protoconch cannot be postulated to be the origin of the teleoconch (see Discussion).

Some authors have fixed θ to equal zero at the transition between the protoconch and the teleoconch (namely θ_{trans}; Fig. 2) (Gould 1989; Johnston et al. 1991; Stone 1995, 1996a). This position corresponds to the actual beginning of the accretion of the teleoconch. In this reference system (the Transition Reference system or TR), equations (1) become:

$$\begin{cases} r = r_{0TR} \cdot S_r^{\theta_{TR}} \\ z = z_{0TR} \cdot S_z^{\theta_{TR}} \end{cases} \tag{9}$$

where r_{0TR} represents the radius and z_{0TR} the longitudinal coordinate of the transition point of the suture. These have the same values whatever the value of θ_{TR} at the aperture. Unless being counted down by negative values from θ_{trans} (as in Fig. 9), the angles of the protoconch suture need to be defined in the protoconch's own reference system, which has another origin. The use of r_{0TR} should be preferred to z_{0TR} for morphometrical comparison because it is actually measurable. In contrast, z_{0TR}, defined relative to the fictitious origin along the coiling axis (z_s or z_p), must be calculated.

Constraining r_0 or z_0.—The second approach to fully defining the logarithmic helicospiral equations is to assign a given value to r_0 or to z_0. This convention is particularly recommended when the transition from the protoconch to the teleoconch is not a precise mark (it is often gradual). Constraining r_0 instead of z_0 limits the number of parameters to be estimated in apical view. Arbitrarily choosing $r_0 = 1$ µm (similar to the approach in Løvtrup and Løvtrup 1988) yields positive values of θ along the teleoconch and seems appropriate also for micromollusks. In this system (the Micron Reference system or µR), equations (1) become

$$\begin{cases} r = S_r^{\theta_{\mu R}} \\ z = z_{0\mu R} \cdot S_z^{\theta_{\mu R}} \end{cases} \tag{10}$$

where r, z, and $z_{0\mu R}$ are in µm.

These equations represent infinite logarithmic helicospirals with $r = 1$ µm for $\theta_{\mu R} = 0$. All the parameters of equations (10) can be calculated independently of the transition from protoconch to teleoconch. The parameter $z_{0\mu R}$ contains information both about scale and shape. The consequences are that (1) sutures having different sizes and different shapes could belong to the same µR helicospiral, and (2) sutures having the same shape but different sizes do not belong to the same µR helicospiral unless S_r equals S_z (isometry) (see Fig. 2).

An additional parameter is needed to locate the suture on the infinite helicospiral. It can be
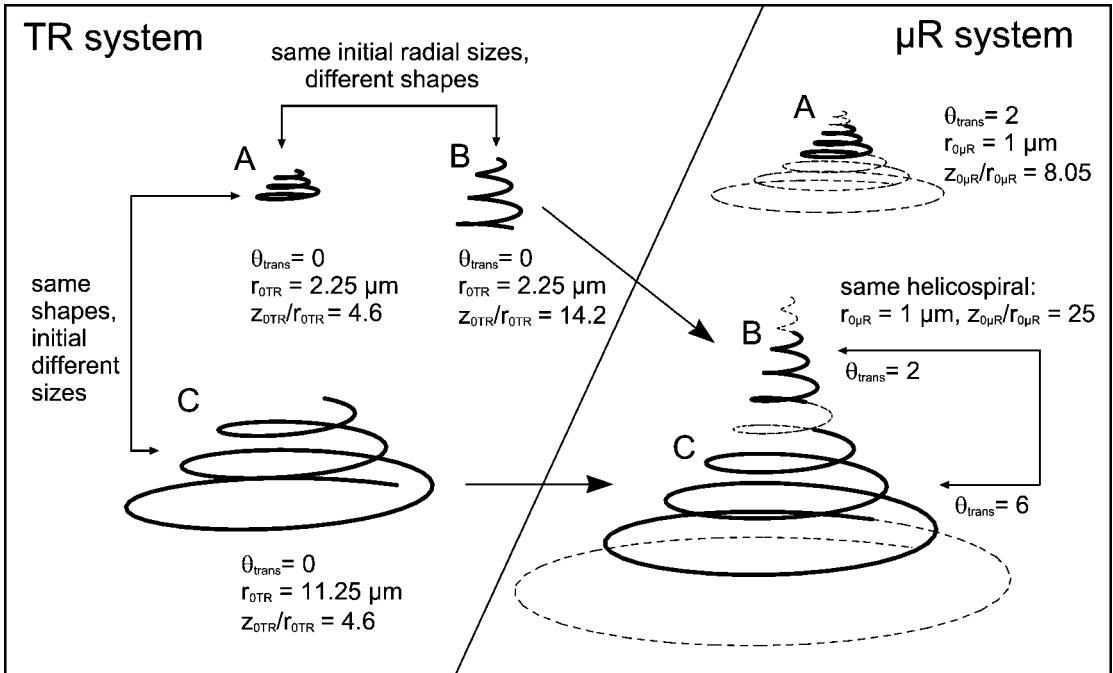
FIGURE 2.   Representation in the Transition and the Micron Reference systems (TR and μR) of three different fictitious extraconical ($S_r \neq S_z$) teleoconch sutures having identical values of S_r (1.5), S_z (1.13) and number of whorls (3). Sutures A and B have the same initial radial size, r_0, but different shapes. Sutures A and C have the same shape but different sizes, C being five time larger than A. In the TR system, r_0 is five times higher for C than for A, appearing to be a valid scale factor. The ratio z_{0TR}/r_{0TR} is a shape parameter as shown by comparing suture A with C (same shape, same values for z_{0TR}/r_{0TR}) and A with B (different shapes, different values for z_{0TR}/r_{0TR}). In the μR system, shells B and C belong to the same logarithmic helicospiral ($z_{0\mu R}$ are identical) but are located on different sections of it. The latter is indicated by their respective values for θ_{trans}, the value of $\theta_{\mu R}$ at the transition between the protoconch and the teleoconch of each shell. Sutures A and B do not originate from the same logarithmic helicospiral in the μR system, even though their initial radial sizes (r_0) are equal. Sutures A and C belong to distinct logarithmic helicospirals, despite their identical shapes.
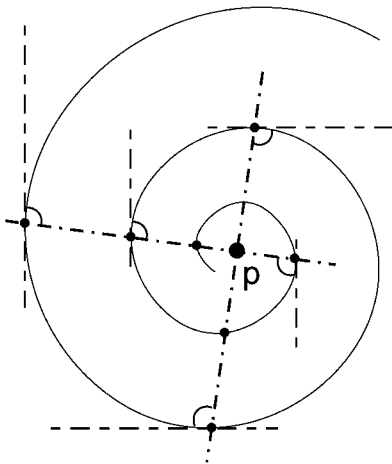

FIGURE 3.   Graphical determination of the intersection of the coiling axis and the projection plane in apical view, i.e., the pole of the logarithmic spiral (p). The pole is at the intersection of lines crossing contact points of opposite parallels tangent to the spiral.

the radial coordinate of any landmark on the suture. This could be, for example, the transition between the protoconch and the teleoconch (θ_{trans}). In this case, conversions between μR and TR systems are straightforward.

Determination of the Coiling Axis

Graphical Determination in Apical Projection.—The graphical method described herein is based on the equiangular property of the logarithmic spiral, i.e., that the logarithmic spiral crosses all the straight lines passing through its pole at a constant angle. It follows that the pole of a logarithmic spiral can be determined by the intersection of lines crossing contact points of opposite parallels tangent to the curve (Fig. 3). In theory, two lines are sufficient to determine the pole. In practice, three or four lines are recommended because in

some cases, all the lines do not intersect at one point but define instead a small polygon. This can be due to an inappropriate use of the logarithmic spiral, to irregularities of the suture, or to a projection not perfectly perpendicular to the coiling axis. The estimated center of gravity of the polygon is used as the pole of the spiral.

Graphical Determination in Lateral Projection.—In lateral view, the coiling axis is located between opposite suture points in identical proportions, as it is located between the same points in the apical view, which is a prerequisite. These points are located in a longitudinal plane (see Fig. 4A,B). A proportion determined in the apical projection (for example the ratio between the radius of point 1 and the sum of the radii of points 1 and 2: $r_1/(r_1 + r_2)$ in Fig. 4B) allows the determination of one point belonging to the coiling axis in the lateral projection (p′ in Fig. 4A). One should note that $r_1/(r_1 + r_2) = r_1'/(r_1' + r_2') = r_1''/(r_1'' + r_2'')$. Other proportions are calculated between as many opposite suture teleoconch points as possible in apical projection (for example between 2 and 3, 3 and 4, 1 and 4). These proportions allow the determination of several points belonging to the coiling axis. It is necessary to transpose proportions determined in apical view rather than using true values because the distances are not in parallel planes (r_1, r_2 vs. r_1', r_2' in Fig. 4). This method also has the advantage of being insensitive to a difference in the magnifications used in apical and lateral projections ($r_1'' \neq r_1$, $r_2'' \neq r_2$ in Fig. 4).

The constructed points that define the coiling axis in the lateral view (such as p′ in Fig. 4) are not always perfectly aligned. This is mostly the consequence of small errors introduced during the apical view analysis (small polygon, or elongated ellipsoid that defines the pole of the spiral). The coiling axis is therefore estimated by the best line passing by these points. This method provides corrections to the initial visual orientation, and its precision is about 1 to 2 degrees. Several coiling axis determinations are illustrated in Figure 5.

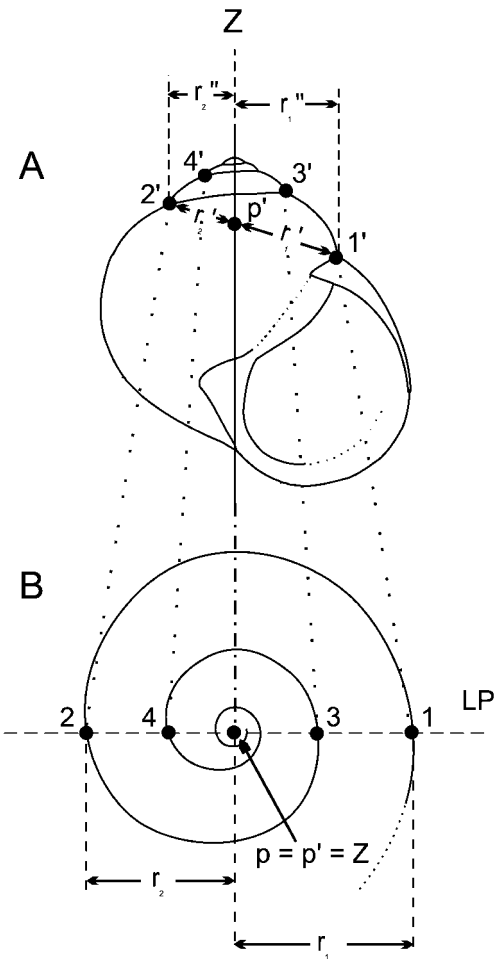Other features coiling around the axis could also be used for similar purposes, for example

FIGURE 4. Graphical determination of the coiling axis in lateral (apertural) view of a schematized shell. A, Lateral projection. B, Apical projection (different magnification) of its suture (not the shell) with its previously determined pole p. LP is the trace of the longitudinal plane passing trough the coiling axis and parallel to the optical axis in the apical view (equivalent to the plane of the sheet in the lateral projection). The $r_1/(r_1 + r_2)$ ratio measured in the apical view is transposed in the lateral view, allowing the determination of one point belonging to the coiling axis (p′). Several such points allow determining the coiling axis in lateral view. The Z-axis coincides with the coiling axis.

the filament channel sensu Van Osselaer and Tursch 1994, usually confused with the suture of the teleoconch in the genus *Oliva.*

For observation in a lateral position, we recommend marking the suture points of the outline of the shell. They will then be easily located in the apical projection. When not enough usable points are available in lateral view for a precise construction (e.g., presence
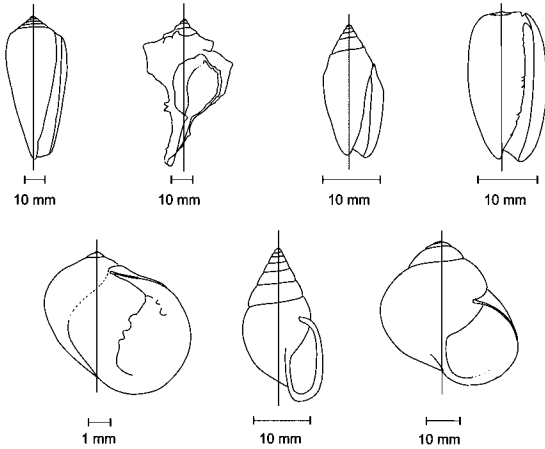
FIGURE 5. Different shells and their coiling axes, determined either by the graphical or the computing method (the axes found by the two methods are superimposed). From left to right: upper row: *Conus consors, Murex brandaris, Oliva parkinsoni, Oliva concavospira* (graphical method only); lower row: *Nerita peloronta* (graphical method only), *Anctus angiostomus, Helix pomatia.*

of a callus on the spire, or flat or concave spiral such as in *Oliva concavospira,* or varices such as in some Muricidae; see Fig. 5), one could also locate the pole in apical view relative to other particular points (outermost palatal point of the aperture, spines, etc.) on the shell and transpose these proportions in the lateral view. One could also approximate nonlinear axes (e.g., Eulimidae) by taking distinct poles of whorls one by one.

Computing Method in Apical Projection.—Accurate location of the axis necessarily entails the determination of a correct projection plane and a correct pole. Schindel (1990) proposed an empirical, approximate method to locate the position of the coiling axis in apical view. Ackerly (1989a,b) proposed a stereographic method that determines the orientation—but not the position—of the coiling axis in three dimensions. It is therefore inapplicable to locating the pole of the logarithmic spiral of the apical projection.

One could incorporate in the equations (1) correction terms accounting for the errors in the shell orientation and in the location of the pole of the spiral. Unfortunately, the general equations that describe a logarithmic helicospiral with any possible orientation of the reference system appear much too complicated for practical use. A more appropriate approach consists of finding the right pole and the right projection plane by trial and error.

This method consists of iteratively recalculating all coordinates in another projection plane (reprojection) and from another origin (relocation of the pole) until the plot of the logarithm of the newly obtained radii (r') vs. the recalculated angles (θ') is as linear as possible. For each trial, the goodness of fit is evaluated by the coefficient of determination r^2 (using the least-squares method) of $\ln(r') = f(\theta')$. This permits easy comparisons between different trials, the highest r^2 indicating the best fitting. The use of the r^2 as goodness-of-fit criterion is identical to that in a nonlinear least-squares regression method (Sen and Srivastava 1990). Differing from a usual regression, the estimated parameters are here spread across several equations that are not reducible to a simple function ($Y = f[X]$). Therefore the method presented here cannot be strictly called a regression but is clearly related to it (it is a more complex ''optimization procedure'').

One could adapt one of the various existing algorithms to obtain a rapid and efficient convergence through the best solution (Sedgewick 1988). This can be achieved with ShellAxis in ten seconds to a few minutes on an Intel Pentium 166 Mhz computer.

This approach is very similar to that of Aldridge (1998), published just prior to submission of our paper. But Aldridge's method (applied to the lateral outline of brachiopod valves' planar sections) deals only with the relocation of the pole and does not address the correction of projection, an important problem for three-dimensional objects.

To perform the reprojections, one must take into account the coordinates of the suture in the third dimension, which are not accessible in the apical view. Longitudinal coordinates of the few suture points of the shell outline are available in lateral projection. These points allow the determination of the parameters S_z and z_0 in equations (1), which will be used to calculate suture longitudinal coordinates in the apical view (see next section). These estimations are sufficient to allow the calculation of the change of plane.

Six parameters are necessary to describe a general change of coordinates system in a

three-dimensional space (three angles of rotations around x-, y-, and z-axes respectively, and three coordinates defining the new position of the translated origin). As we are not yet concerned with the position of the pole along the z-axis, the longitudinal translation of the origin (z_p) is neglected here. Similarly, as the coiling axis could be located without consideration of the origin of θ (rotation around the z-axis), the third angle (c) is also neglected. Four parameters then remain to be determined (Fig. 6): the angles defining the new direction of the projection relatively to the initial one (a, b), and the coordinates, in the rotated reference system, of the point chosen as new pole of the spiral (x_p, y_p). To facilitate the calculations, we converted the coordinates from cylindrical to Cartesian.

The initially obtained coordinates of the suture (i.e., with visual orientation of the shell and an approximate location of the pole) can be recalculated in another reference system as follows:

$$\begin{cases} x' = r \cdot \cos \theta \cdot \cos b + z \cdot \sin b - x_p \\ y' = r \cdot \sin \theta \cdot \cos a - r \cdot \cos \theta \cdot \sin a \cdot \sin b \\ \quad\quad + z \cdot \sin a \cdot \cos b - y_p \end{cases} \tag{11}$$

The corresponding cylindrical coordinates are deduced:

$$\begin{cases} r' = \sqrt{x'^2 + y'^2} \\ \theta' = \arctan \dfrac{x'}{y'} \end{cases} \tag{12}$$

The errors on estimated longitudinal coordinates z have little effect on recalculated r' and θ' because the terms containing z (in eq. 11) become close to zero (but cannot be completely eliminated) if the angles a and b are small. This should be always the case because one starts with a fairly well oriented projection.

The corrections from the first to the second data sets (specimen of *Anctus angiostomus*) illustrated in Figure 1 were calculated by this method. In the absence of physical verification on actual shells, we have also tested the proposed method on simulated data sets. We measured several simulated sutures in differ-

ent projection planes and from different origins. In all cases, we found coiling axes and parameters values very close to the actual ones (unpublished results).

Computing Method in Lateral Projection.—The computing method can be applied to any lateral projection, e.g., apertural. In a lateral projection, all the suture points of the outline of the shell lie every 180° in a single plane (corresponding to the xz-plane). With their coordinates, it is possible to determine the position of the coiling axis by iterative rotation and translation of the reference system until the data are best fitted by a logarithmic helicospiral. In a lateral projection, the relocation of the coiling axis is simply described by a rotation (around the y-axis, angle b) and a translation (x_p, z_p). The coordinates (x, z) of the suture points initially obtained from one approximate coiling axis will be recalculated in other reference systems (x', z') as follows:

$$\begin{cases} x' = x \cdot \cos b + z \cdot \sin b - x_p \\ z' = -x \cdot \sin b + z \cdot \cos b - z_p \end{cases} \tag{13}$$

Cylindrical coordinates are then easily calculated (z' being directly obtained in eq. 13):

$$\begin{cases} r' = |x'| \\ \theta' = \theta \end{cases} \tag{14}$$

Only negligible errors are introduced if the initial projection of the shell is not in a perfect sagittal view (i.e., with the coiling axis not exactly parallel to the projection plane). In contrast to the apical method, the reprojection of the points in three dimensions is not necessary. Simultaneously minimizing the coefficient of determination, r^2 (using the same iterative method used in apical view) of both linear regressions, $\ln r' = f(\theta')$ and $\ln z' = f(\theta')$, allows the determination of $\{x_p, z_p, b\}$ and leads to the best estimation of the coiling axis. This method requires the observation of at least two pairs of opposite suture points.

Coiling axes were also located by the computing method for the specimen displayed in Figure 7 and for the specimens drawn in Figure 5 (coiling axes identical to these found by the graphical method).
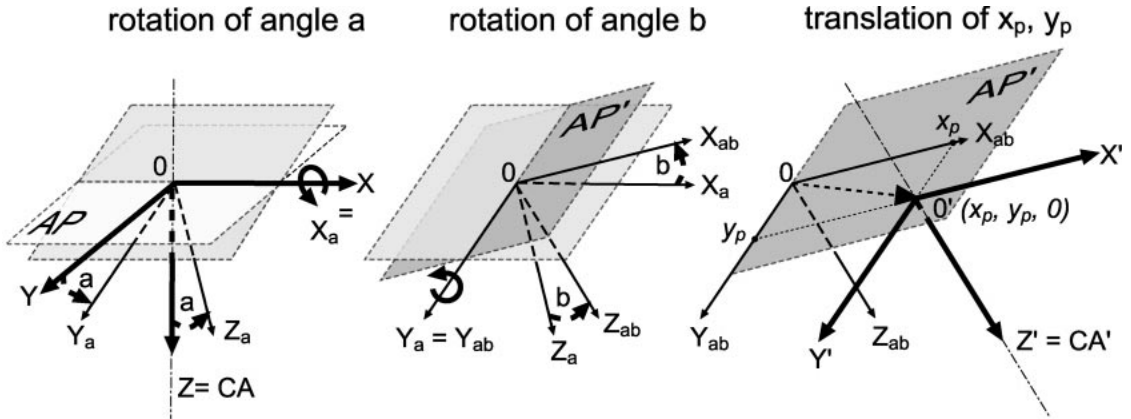
FIGURE 6.   Rotations and translation of the original coordinates system (X,Y,Z) related to the visual orientation of the shell along the presumptive coiling axis (CA) into the coordinates system (X′, Y′, Z′) oriented along the best-fitted coiling axis (CA′). The rotation is defined by two angles: a around X-axis and b around Y_a-axis, which is the Y-axis obtained after the first rotation (angle a). The origin (0) is translated to (0′) which has the coordinates $\{x_p, y_p, 0\}$ in the reference system (X_{ab}, Y_{ab}, Z_{ab}) after the two rotations (a, b). AP is the plane of the projection along the presumptive axis. AP′ is the plane of the projection after rotations.

Applications

The goodness of fit and the analyses of the residuals on numerous species suggest that the general logarithmic helicospiral equations are adequate to describe the suture of most gastropod teleoconchs. Subtle deviations from logarithmic helicospiral growth, different growth phases, modification in the coiling direction, etc. can be detected and quantified by the computing method. These approaches can be easily modified to test hypotheses about (dis)similarities among species in coiling parameter ontogenies.

FIGURE 7.   *Helix pomatia.* The shell has been cut to allow the visualization of the columella (shell length = 40.73 mm). The coiling axis was calculated by the computing method based on five points of the suture of the teleoconch outline (solid circles).

Identification of Teleoconch Growth Phases

Filament channel radii (see graphical determination in a lateral projection) of the whole teleoconch of a specimen of *Oliva porphyria* (L., 1758) were measured from a visually chosen origin. Except for the sinusoidal component, no change in expansion rate can be seen on the plot of $\ln r = f(\theta)$ (Fig. 8A,B). After recalculating the data by the computing method, the analysis of the residuals has revealed two growth phases (Fig. 8D; V-shape of the residuals). These phases are now also visible on the plot of $\ln r′ = f(\theta′)$ (Fig. 8C). The coiling axis is almost the same for the two growth phases, as nearly no sinusoidal components subsist in any side of the transition. The delimitation of the different phases was determined by first considering the points unambiguously belonging to them, i.e., excluding the points around the transition between them. The remaining points are posteriorly incorporated in one of the phases according to their influence (i.e., their membership) on the respective regressions. Fitting one phase at a time, the values of the respective expansion rate parameters can be calculated. These are very highly significantly different from each other (test for equality of slopes, $F_{1, 126} = 3930$, $p < 0.001$): S_r of phase 1 = 1.52 ($r^2 = 99.72\%$ and random residuals, $a = 9.19°$, $b = -2.99°$, $x_p = 0.35$ mm,
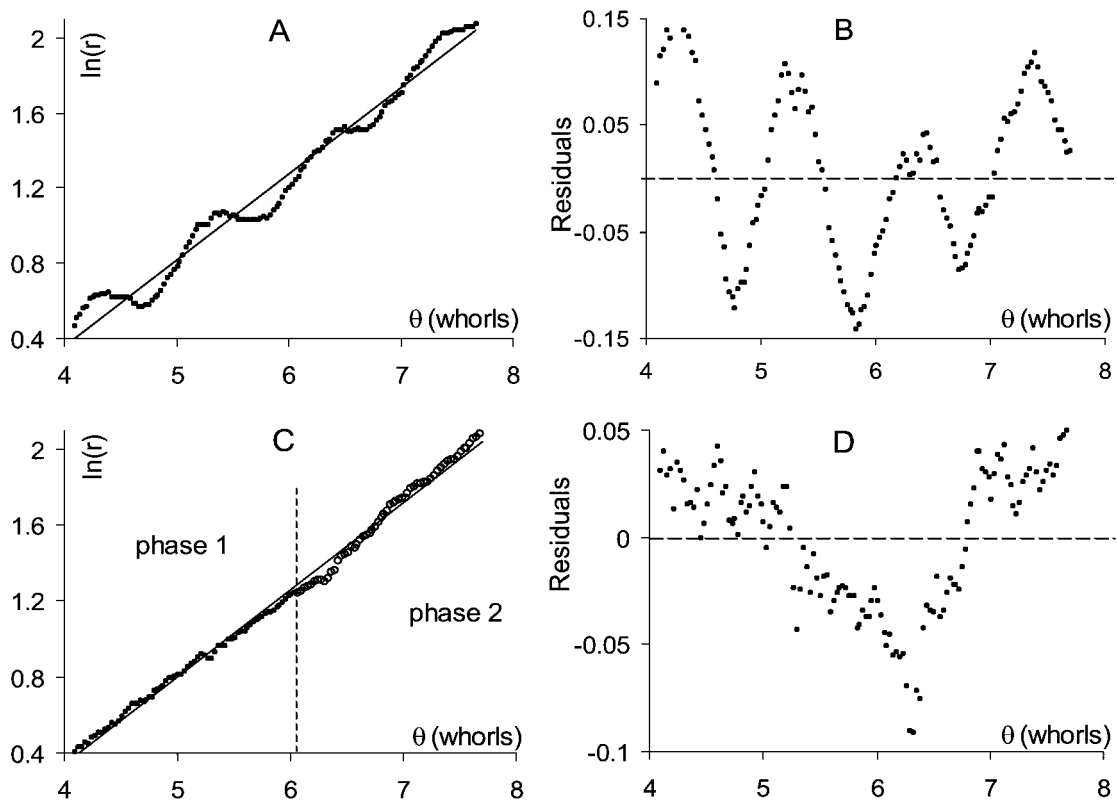
FIGURE 8. Teleoconch filament channel of one specimen of *Oliva porphyria*. A, Plot of ln $r = f(\theta)$ measured from an arbitrary origin, visually chosen as a best estimation of the pole of the spiral (taken every 10°). B, Residuals of the linear regression in A. Except for the sinusoidal component, no change in expansion rate is detectable. C, ln $r = f(\theta)$ for the same data set recalculated by the computing method ($r^2 = 99.54\%$, $a = 4.55°$, $b = -4.97°$, $x_p = 0.62$ mm, $y_p = 0.97$ mm). D, Residuals of the fitting for recalculated data. Two phases are now clearly visible.

$y_p = 0.08$ mm [not illustrated]); S_r of phase 2 = 1.71 ($r^2 = 99.80\%$ and random residuals; $a = 5.66°$, $b = -3.62°$, $x_p = 0.72$ mm, $y_p = 0.09$ mm [not illustrated]).

One could object that the reason one single, continuous spiral does not fit the complete suture is that the equations approximate the suture only in small domains. This can be disproved by outstanding fitting of several multispiral shells, such as the example given in Figure 1.

Distinction of Protoconch and Teleoconch Sutures

Small, not visually detectable differences in the orientations of the teleoconch and the protoconch coiling axes can be shown and quantified by our method. For example, we have measured the suture of a specimen of *Achatina achatina* (L., 1758) where the transition from the protoconch to the teleoconch seems gradual. The sutures of both parts of the shell are not visually different (see Fig. 9G). After the location of the pole and the corrections for the projection are recalculated by the computing method in an apical view, the logarithmic spiral fits the teleoconch suture measurements well (residuals are random for the teleoconch and $r^2 = 99.86\%$; Fig. 9A,B). Plotting protoconch suture points (recalculated with the parameters obtained for the teleoconch) resulted in systematic deviations and oscillating components for the protoconch part of the shell (Fig. 9A,B). These could result from the inadequacy of the logarithmic spiral to fit the protoconch, from a poor location of its pole, or from an error in its projection. We then tried to fit the suture of the whole shell (teleoconch and protoconch). Despite a high r^2 (98.79%), the oscillating components were not eliminat-
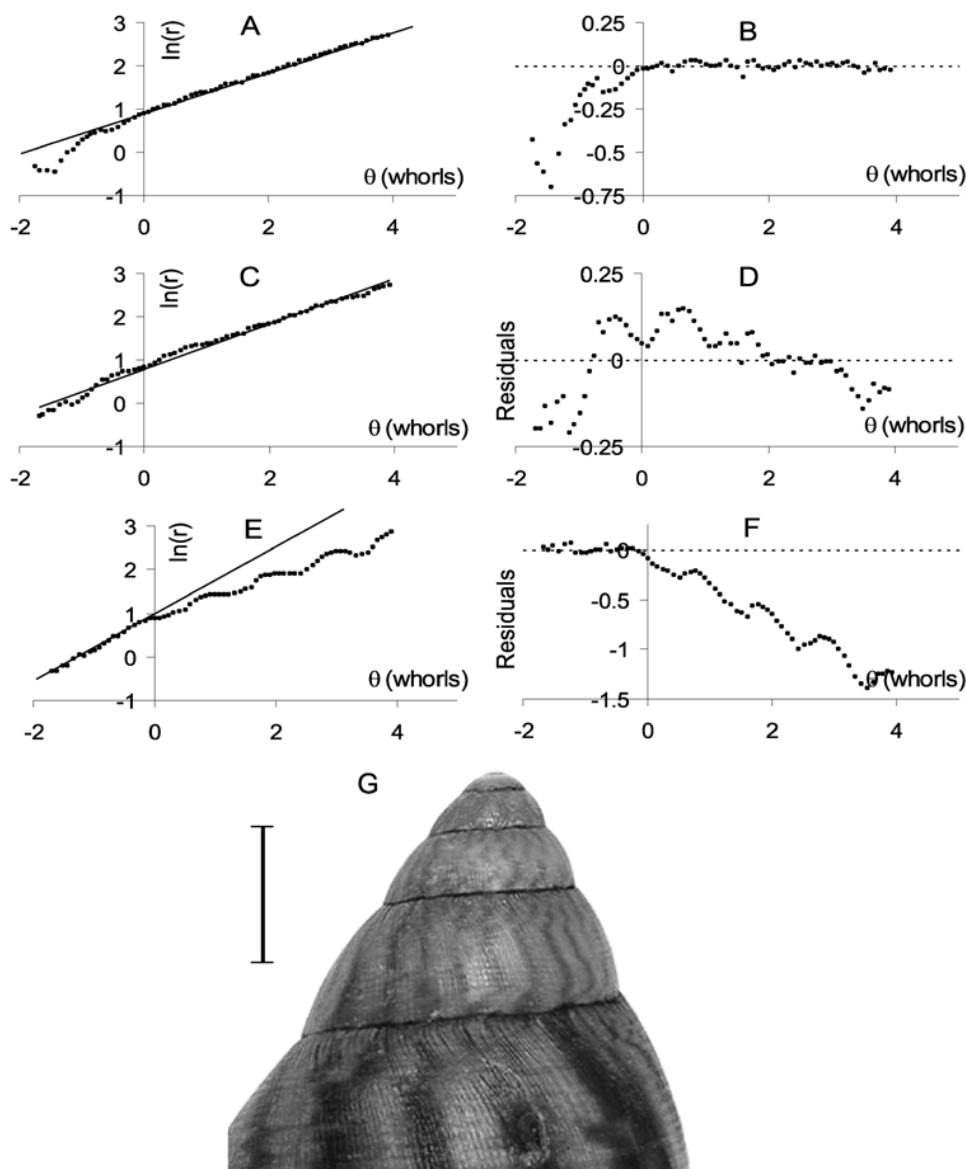
FIGURE 9. Suture of the whole shell of a specimen of *Achatina achatina*: consequence of selecting an origin and an apical projection for the teleoconch (A, B), the protoconch (E, F), or the whole shell (C, D). A, C, E, Plot of ln $r = f(\theta)$ for the data recalculated by the computing method (taken every 30°). B, D, F, Residuals of the respective linear regressions. A, Correction parameters deduced from the *teleoconch whorls only*: S_r of the teleoconch = 1.59, r^2 = 99.86%, a = 0.97°, b = 0.49°, x_p = −0.31 mm, y_p = −0.10 mm. C, Correction parameters deduced from the *whole shell whorls*: S_r of the whole shell = 1.69, r^2 = 98.79%, a = 1.92°, b = −0.52°, x_p = −0.07 mm, y_p = −0.20 mm. E, Correction parameters deduced from the *protoconch whorls only*: S_r of the protoconch = 2.22, r^2 = 99.42%, a = −4.78°, b = −1.80°, x_p = −0.05 mm, y_p = −0.24 mm. The suture of one part of the shell appears poorly represented by the equations (systematic deviations), by the pole and/or by the axis orientation (sinusoidal residuals) of the other part of the shell. G, Upper part of the shell: the difference in orientation of the coiling axes of the protoconch and the teleoconch is hardly detectable by eye (scale bar, 1 cm).

ed for any part of the shell (Fig. 9C,D), and no satisfactory solution was found. In contrast, if the whorls of the protoconch only are used, another pole, different from the one found for the teleoconch, is obtained. The calculated angles for the projection correction were also different. After recalculations, the logarithmic spiral appears now to fit the protoconch suture well (residuals are random for the protoconch and $r^2 = 99.42\%$, Fig. 9E,F).

Discussion

Logarithmic Helicospiral: Isometric or Allometric Growth?

The familiar equations (1) correspond to the general definition of logarithmic helicospirals (see, for instance, Prusinkiewicz and Fowler 1995). It is worth noting that these equations represent an allometric growth, *unless* S_r and S_z are equal. As allometry is the differential relative growth of variates (according to, amongst others, Futuyma 1986; Mayr and Aschlock 1991; Skelton 1993; Lawrence 1995), allometry is any growth that is not isometric (Huxley and Teissier 1936; Gould 1966). Some authors (Savazzi 1990; Stone 1996b; Tursch 1997) have already noted that most models, with constant parameters, imply initial isometric conditions (for example Raup 1966; McGhee 1978, 1980; Løvtrup and Løvtrup 1988; Cortie 1989; Savazzi 1990). Such models describe only true conical spires although allometry is the rule rather than the exception in actual gastropods (Gould 1992; Skelton 1993; Vermeij 1993).

The observed deviations from ideal isometric logarithmic helicospirals are sometimes attributed to ''non-fit'' or ''inadequacy of the logarithmic spiral'' (Raup 1966; Vermeij 1993) and ''allometric growth is obtained by changing the values of one or more parameters during growth'' (Savazzi 1990: p. 197). These assumptions are not always necessary, because *unconstrained* logarithmic helicospirals ($S_r \neq S_z$) account for many extraconical (allometric) forms without any change in parameter values during growth (see the examples given in Figs. 2, 5). It is also not necessary to use allometric equations (instead of eq. 1) to fit (or model) such forms (see Stone 1995, 1996a,

1997). Allometric equations start exactly at the origin ($\theta = 0$, $r = 0$, $z = 0$), contrary to the logarithmic helicospiral ($\theta = 0$, $r = r_0$, $z = z_0$). The use of allometric equations results in loose (unattached) early whorls in simulated shells (see the figures in Stone 1995, 1996a, 1997).

Other departures from isometry can be illustrated by the transition from the protoconch to the teleoconch (Fig. 9) or by the succession of different growth phases during postmetamorphic life (e.g., the biphasic teleoconch of *O. porphyria* [Fig. 8]). These departures could coincide with a change in the mode of life, for example such as from planktonic to benthic mode of life (Raup 1966) or sexual maturity.

Nevertheless, the logarithmic helicospiral equations do not necessarily account for all types of allometry. They can be used only when both r and z increase with θ. Deviations from this model are to be expected. An example is given by sutures moving away from the axis (increase of r values) then moving closer (decrease of r values), such as the last growth phase of *Cerion* shells. Another example is represented by spirals going down (increase of z-coordinates) then going up (decrease of z-coordinates), such as the uncommon case of fully grown specimens of *Oliva concavospira*.

Location of the Coiling Axis

Apical Projection.—Schindel (1990) has used the first whorl of the protoconch to ''construct'' five different ''rules'' to estimate the position of the coiling axis of the whole shell in apical view. The plots of $\ln r = f(\theta)$ measured from any of the five positions present oscillating error terms (see his Fig. 10.5). These origins are thus inadequate, because the ''rules'' were inexact and/or only the protoconch was used only to locate the pole of the suture of the whole shell.

The graphical construction proposed here to locate the pole in apical view is not a convention but a nonarbitrary method based on the well-known equiangular property of the logarithmic spiral. This method does not require many whorls (one is theoretically sufficient) and thus remains valid for damaged

specimens or for specimens having the spire partially covered. The pole is determined with high accuracy only if (1) the radial growth of the suture conforms to the logarithmic spiral, (2) the suture effectively coils around a single linear axis, and (3) the projection plane is perpendicular to the coiling axis of the suture. Conversely, imprecise location of the pole indicates one or several violations of these assumptions.

The computing method could be applied to any type of spiral by choosing adequate equations (for example arithmetic spiral for some protoconchs). The graphical method is simpler and can be applied with minimal equipment but is restricted to the logarithmic helicospiral only. The graphical method does not make any correction, so it does not eliminate the sinusoidal components due to slight errors of the visual orientation for the projection.

Lateral Projection.—For practical morphometrical studies, different conventions have been proposed to approximate the coiling axis in an apertural view (see for example Kohn and Riggs 1975; Harasewych 1981; Goodfriend 1983; Boulding and Hay 1993). In contrast to these conventions, the graphical and computing methods we propose to locate the coiling axis in a lateral view are defined by the suture itself and are not arbitrary. They are independent of the aperture position and can be applied for any lateral position.

Both approaches (graphical and computing) lead to highly similar, if not identical, axes (see Fig. 5). Slight differences appear when some particularities of the shell (different growth phases, distinction between protoconch and teleoconch part of the shell, etc.) are not taken into account. Specimens having the suture hidden by the whorls in the apical view can still be measured in lateral projection.

In lateral view, the graphical approach has the advantage over the computing method by requiring only elementary calculations and no specific computer hardware and software (data processing, image acquisition, etc.). The advantages of the computing method are (1) faster analysis and (2) no requirement of the apical view analysis to locate the axis. The computing method facilitates the analysis of any image of shells (obtained by video capture, by scanning of illustrations or drawings, etc., as in Figs. 5, 7). The computing method allows a rapid determination of a reference system. The location of the coiling axis takes less than one minute with ShellAxis on an Intel Pentium 166 Mhz computer. ShellAxis will facilitate measurements on the numerous specimens required for elaborate morphometrical studies often considered too time consuming. In our laboratory, 28 shell measurements were performed in less than ten minutes for each specimen.

Determination of the Suture Expansion Parameters (S_r and S_z)

Radial Expansion Parameter.—Determination of the radial expansion rate (S_r) should preferably be performed in apical view because it affords more points (every 45° or less) than the few available (every 180°) in the lateral position. Both methods give statistically equivalent values for S_r (see Table 1, *F*-test for equality of slopes at the level $\alpha = 0.01$).

Since least-squares linear regression is sensitive to extreme values, incomplete sinusoidal periods (corresponding to a non-integer number of whorls) can produce a bias in the evaluation of S_r. This bias is particularly important when only a few whorls are measured or measurable. It is a considerable problem with mollusk shells that coil for less than one whorl (for example bivalves and scaphopods) and also with brachiopod shells. To give one example (a different case is given in Table 1), choosing the umbo as the origin of measurements of brachiopods' valves has led McGhee (1980) to conclude that their expansion rate decreases with growth (see Fig. 10A) and that the ''ontogenic change in whorl expansion rates is widespread in the Brachiopoda . . . .'' Two remarks can be made: On the one hand, the pole of a logarithmic spiral is not located on the actual shell spiral ($r = r_0 \neq 0$ for $\theta = 0$; $r = 0$ for $\theta = -\infty$). There is no reason to designate arbitrarily one point on the shell (or on the suture of gastropods) as its pole. On the other hand, accurate relocation of the origin (being recalculated by the computing method) shows that all measurements of his illustrated example (his Fig. 2, our Fig. 10A,B) are well fitted by a logarithmic spiral with constant ex-

TABLE 1. Comparison of the radial expansion parameter values estimated by the graphical and computing methods in both apical and lateral views (*n* stands for the number of points used, *nw* stands for number of whorls taken into account). In lateral view, the graphical and computing methods lead to similar values of S_r. Differences between the values estimated by the apical and lateral methods appear when only a few points are available in the lateral view. In apical view, all r^2 values are higher with the computing method (recalculated data). The graphical and computing methods lead to similar values for S_r, except for *O. concavospira,* for which the measurements were made on less than one whorl. A small error in the location of the pole in the graphical method results in a biased parameter value ($x_p = 0.09$ mm; $y_p = -0.10$ mm) (case similar to the brachiopod; see Fig. 10 and Discussion).

		Apical view			Lateral view		
	nw	*n*	S_r	r^2(%)	*n*	S_r	r^2(%)
Graphical method							
Conus consors Sowerby I, 1833	4.25	33	1.39	99.30	10	1.45	99.39
Helix pomatia L., 1758	2.37	20	2.05	99.37	4	2.12	99.66
Anctus angiostoma (J. A. Wagner, 1827)	3.80	92	1.42	99.56	7	1.43	99.18
Nerita peloronta L., 1758	1.50	28	2.98	99.75	4	2.79	99.76
Oliva parkinsoni Prior, 1975	3.00	25	1.75	99.68	7	1.76	99.25
Oliva concavospira Sowerby, 1914	0.67	12	1.77	98.66	—	—	—
Murex brandaris L., 1758	2.50	20	1.95	99.49	6	2.09	96.34
Computing method							
Conus consors Sowerby I, 1833	4.25	33	1.39	99.88	10	1.44	99.37
Helix pomatia L., 1758	2.37	20	2.03	99.96	4	2.11	99.77
Anctus angiostoma (J. A. Wagner, 1827)	3.80	92	1.43	99.92	7	1.43	99.68
Nerita peloronta L., 1758	1.50	28	2.99	99.79	4	2.93	99.69
Oliva parkinsoni Prior, 1975	3.00	25	1.76	99.74	7	1.73	99.90
Oliva concavospira Sowerby, 1914	0.67	12	1.83	99.74	—	—	—
Murex brandaris L., 1758	2.50	20	1.97	99.88	6	2.12	97.61

pansion rate (Fig. 10C,D). The relocation of the origin influences not only the interpretation of shell growth but also the evaluation of the radial expansion parameter. McGhee's conclusions have been aptly reconsidered in the recent paper of Aldridge (1998).

It could be tempting to evaluate S_r by using the ratio of successive radii, or by using the average of several such ratios (a method similar to that of Kohn and Riggs [1975] and Harasewych [1981] for the determination of Raup's *W* parameter). Taking successive ratios along one single radius (or several radii), can result in biased values for S_r or in rejecting the use of the logarithmic helicospiral (ratios not constant), as these ratios are very sensitive to small measurements errors (see Fig. 11). The incorporation of even a few points of the protoconch can similarly lead to large errors.

Longitudinal Expansion Parameter.—The longitudinal expansion rate S_z can be evaluated in a lateral view in a very similar way to S_r by the linear regression of ln $z = f(\theta)$. Nevertheless, an unbiased estimation of S_z must take into account an appropriate origin of longitudinal measurements (see next section). More than four points allows statistical testing of

the fitting and a better estimation of the parameters. The more points available, the better the precision in estimating the expansion parameters (also in locating the coiling axis). In order to increase the precision for S_z when determined on lateral views (this remark is also valid for S_r), one could add more points by using several lateral views rotated by a known angle, or by using a device that directly performs a three-dimensional analysis (three-dimensional scanner or the Reflex microscope cited in Johnston et al. 1991). Radial distances are hardly altered by a small misorientation of the shell in lateral view. Longitudinal measurements are slightly underestimated when the coiling axis of the shell is not perfectly perpendicular to the optical axis. However, this underestimation remains negligible for the typical error range that occurs during visual orientation of the shell (an unusually important misorientation of 10° leads to an underestimation of longitudinal distances of only 1.5%).

The Origin of Longitudinal Coordinates: a Pitfall That Could Lead to Confusion with Allometry.—Radial coordinates are defined orthogonal to the coiling axis, which is the unambig-
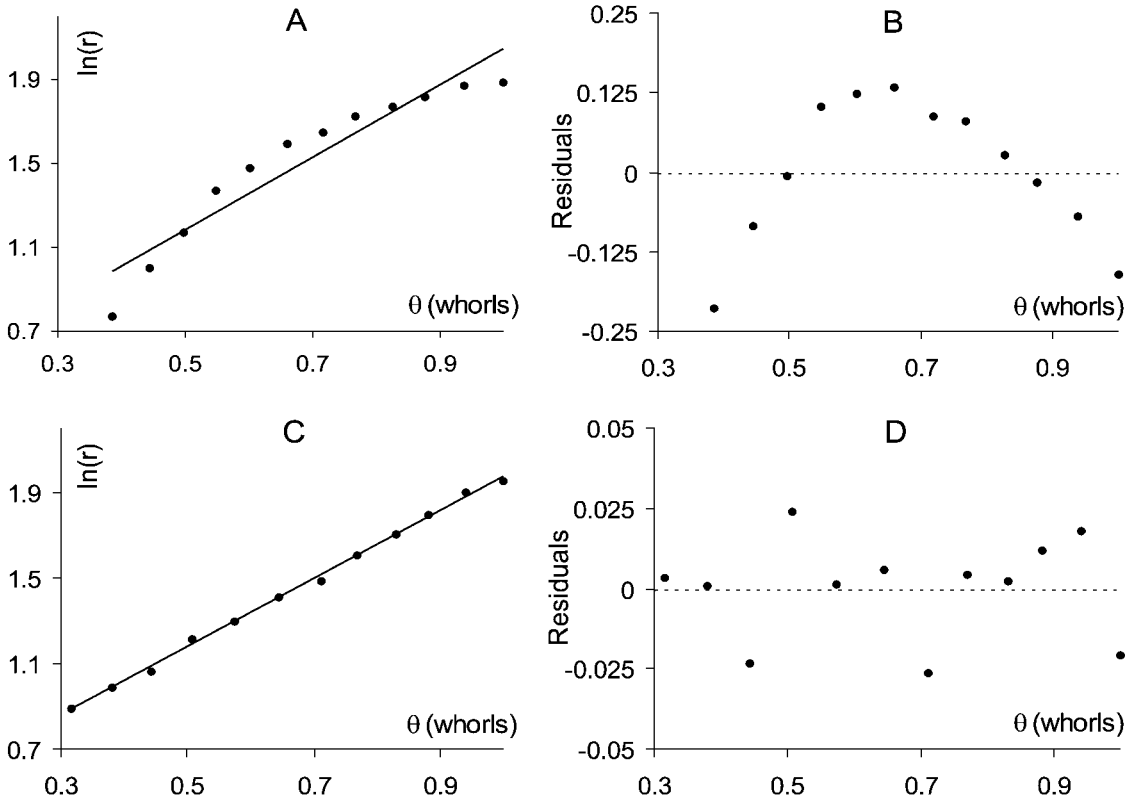
FIGURE 10. Dorsal valve of one pentameride brachiopod *Lycophoria nucella* (Dalman). A, ln $r = f(\theta)$ (taken from McGhee 1980: Fig. 2) illustrates the curvilinear ''decrease'' of the whorl expansion rate during ontogeny ($r^2 = 90.11\%$). B, Residuals of the linear regression. C, A linear relationship is determined after the relocation of the pole by the computing method ($r^2 = 99.80\%$). D, Residuals of the linear regression represented in C (random distribution and weaker amplitude—note the change of scale). Although the corrections for the translation of the origin to the pole are weak ($x_p = -0.43$ mm; $y_p = -0.69$ mm), no ''variation'' of the growth rate is apparent any more. The expansion rate parameter on the original data (A) is biased and is 5.60, while it is 4.89 for the recalculated data (C).

uous origin of these measurements. Usually the apex of the shell, i.e., the posteriormost part of the protoconch, is chosen as the origin of longitudinal measurements of the teleoconch (see, for example, Stone 1995, 1997), but this practice remains problematic. The longitudinal coordinates cannot be measured from an obvious origin along the axis and cannot be chosen arbitrarily (the origin of longitudinal measurements is different from—and must not be confused with—z_0, one of the four parameters of eq. 1).

Longitudinal coordinates of a logarithmic helicospiral were generated by equations (1) with arbitrary fixed parameters (plausible values: $S_z = S_r = 2$, $z_0 = 1.2$ mm; Fig. 12). The logarithmic transformations of the data are perfectly linear (ln $z = f(\theta)$ in Fig. 12). For the sake of argument, an isometric helicospiral

was chosen although the same conclusions are reached with a nonisometric one. An error in the choice of the longitudinal origin is equivalent to a translation of the origin along the z-axis by an amount z_s:

$$z' = z - z_s = z_0 \cdot S_z{}^\theta - z_s \qquad (15)$$

The logarithmic transformations of the new coordinates z' are not linear any more (ln $z' = f(\theta)$ in Fig. 12). A curvilinear relationship is obtained whose concavity points upward or downward depending on the sign of z_s. The curvature increases with the absolute value of z_s. Such nonlinear relationships have sometimes been erroneously attributed to allometry or to nonconstant longitudinal expansion parameters. Some polynomial regressions have been proposed to fit such data, includ-
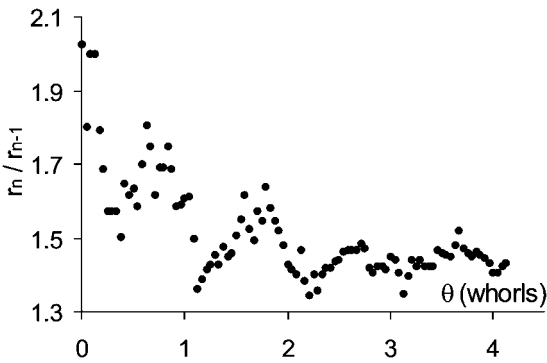
FIGURE 11. Measurements of the suture of a specimen of *Anctus angiostomus* (the same specimen used for Fig. 1 and also illustrated in Fig. 5). Radial expansion growth parameter (S_r for the suture) are sometimes estimated by ratios of successive radii (r_n/r_{n-1}). The values obtained by this method are not consistent without corrections for either the projection plane or the origin of measurements (128 ratios, max = 2.02, min = 1.33). One can wrongly conclude that the same logarithmic helicospiral is not valid, because the ratios are not constant. S_r value obtained after recalculation by the computing method is 1.43 ($r^2 = 99.92\%$) (see also Table 1).
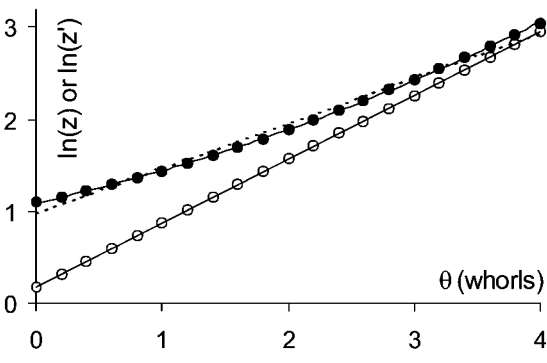

FIGURE 12. Consequences of an error on the longitudinal origin of measurements. Longitudinal coordinates were generated using an isometric logarithmic helicospiral (eq. 1 with $S_z = S_r = 2$, $z_0 = 1.2$ mm. Open circles: $\ln z = f(\theta)$, a perfect linear relationship is obtained. Dark circles: $\ln z' = f(\theta)$, i.e., corresponding to the same data measured from another origin along the coiling axis ($z' = z - z_s$ with $z_s = -1.8$ mm < 10% of the total height [19.2 mm]). The points are not linearly aligned any more. A linear regression (dotted line, $r^2 = 98.97\%$) or a polynomial regression (continuous line, $r^2 > 99.99\%$,) leads to biased estimates of S_z (1.63 and 1.36, respectively).

ing, for example, the following equation used by Schindel (1990):

$$\ln z' = a_1 \cdot \theta + a_2 \cdot \theta^2 + b \qquad (16)$$

The fit of our arbitrary data with equation (16) is very highly significant ($r^2 > 99.99\%$, *F*-test: $p < 0.0001$; Fig. 12), although this equation does not depict logarithmic growth coordinates translated by a small amount. In our example, the shift of $z_s = -1.8$ mm represents less than 10% of the total longitudinal growth of the suture after four whorls. Such a small shift could correspond to the choice of the actual apex as the origin of the teleoconch helicospiral in real shells.

The effect of a wrong origin along the z-axis is even more insidious. The estimation of S_z is heavily biased both with a linear and with a polynomial regression (Schindel [1990] considered the parameter a_1 of equation (16) equal to ln S_z). There is only one origin of longitudinal measurements to which a given logarithmic helicospiral could be referred (in the case of an isometric logarithmic helicospiral, it is called the center of similitude [Prusinkiewicz and Fowler 1995]). It can be determined by iterative calculations of z_s that lead to the best linearization of ln $z = f(\theta)$ (one starts in practice with longitudinal coordi-

nates z' shifted by an a priori unknown amount z_s). This calculation is included in the computing method in lateral view, and z_s is equal to z_p in equations (13).

Here also, it could be tempting to evaluate the origin of longitudinal measurements (or also S_z) by using the ratio of a few intersutural distances. Sean Rice (personal communication 1998) suggested rapid location of the origin from ratios of the distances, along the z-axis, between points on the suture:

$$z_s = \frac{(z_\theta' - z_{\theta-1/2}')^2}{(z_\theta' - z_{\theta-1/2}') - (z_{\theta-1/2}' - z_{\theta-1}')} - z_\theta' \qquad (17)$$

where $z'_{\theta-1}$, $z'_{\theta-1/2}$ and z'_θ are z-coordinates of any three sutural points measured every 180° in the lateral projection, considered from an arbitrary longitudinal origin along the coiling axis. Differences between longitudinal coordinates (such $z'_\theta - z'_{\theta-1/2}$) are insensitive to a correct origin and z_s should represent the exact distance from the origin.

Equation (17) is theoretically correct but is not applicable in practice, as it is too sensitive to slight measurement errors. This could lead to erroneous conclusions (similar to the ones explained for the determination of S_r by sim-

ilar methods) because the estimation of z_s (or S_z) is variable with the chosen triplets.

Protoconch and Teleoconch Differences

The protoconch and the teleoconch correspond to different stages of the life history of a mollusk and could therefore be expected to be subjected to different ''developmental constraints'' (sensu Gould 1989, 1992; Stone 1996a). Few authors (Cox 1955; Savazzi 1990; Johnston et al. 1991) have highlighted the common difference in the direction of the coiling axes of the protoconch and the teleoconch in cases other than heterostrophic protoconchs (for heterostrophy, see, for example, Robertson 1974 and Bouchet 1987). Analyses performed with our method suggest that the protoconch and the teleoconch often differ in their coiling axis and by different expansion parameters (see Fig. 9). Such differences seem to be widespread. For some *Oliva* species, an arithmetic helicospiral appears to be more representative of the protoconch suture, whereas the logarithmic helicospiral remains the best model for the teleoconch (unpublished results).

Therefore, there is no reason to consider a priori that the sutures of both parts of the shell (i.e., the protoconch *and* the teleoconch) necessarily match the same continuous growth pattern. Their separate treatment appears indispensable. The use of the shell apex (the top of the protoconch) as the origin of teleoconch measurements is thus error-prone.

Conclusions

Unexpectedly, the suture of a majority of shells can be described by simple equations with only a few parameters. The logarithmic helicospiral cannot be disassociated from a coiling axis and the suture has been shown to allow location of the coiling axis in gastropod shells. The coiling axis thus appears post facto as a secondarily derived feature of the morphogenetic program (Ackerly 1989b). The coiling axis of the suture could be considered as a nonarbitrary internal reference and is not only an artificial construction useful for orienting shells and characterizing their geometry. Such an internal reference is independent of a few particular landmarks on the shell and

therefore could provide a reliable reference frame for morphometric and systematic studies. An accurate reference system is the first minimum requirement to compare real and computer-simulated shells.

Precise analysis of the suture (e.g., in apical view with the computing method) is a useful and sensitive tool for detecting and characterizing otherwise unnoticeable changes in the ontogeny of the shell. The study of sutures appears to be an interesting complementary tool for investigating constraints in the evolution of coiled shells.

The assumption of the equality of the expansion rate parameters (isometric growth) of the logarithmic helicospiral and some experimental and/or methodological errors have yielded considerable misinterpretations that must be reconsidered.

Literature Cited

Ackerly, S. C. 1989a. Shell coiling in gastropods: analysis by stereographic projection. Palaios 4:374–378.

———. 1989b. Kinematics of accretionary shell growth, with examples from brachiopods and molluscs. Paleobiology 15: 147–164.

Aldridge, A. E. 1998. Brachiopod outline and the importance of the logarithmic spiral. Paleobiology 24:215–226.

Bookstein, F. L. 1982. Foundations of morphometrics. Annual Review of Ecology and Systematics 13:451–470.

———. 1993. A brief history of the morphometric synthesis. Pp. 14–40 *in* L. F. Marcus, E. Bello, and A. Garcia-Valdecasas, eds. Contributions to morphometrics. Monografías Museo Nacional de Ciencias Naturales, Madrid.

Bouchet, P. 1987. La protoconque des gastéropodes: aspects biologiques, taxonomiques et évolutifs. Thèse de Doctorat d'Etat. Université Pierre et Marie Curie, Paris.

Boulding, E. G., and T. K. Hay. 1993. Quantitative genetics of

shell form of an intertidal snail: constraints on short-term response to selection. Evolution 47:576–592.

Chiba, S. 1993. Modern and historical evidence for natural hybridization between sympatric species in *Mandarina* (Pulmonata: Camaenidae). Evolution 47:1539–1556.

Coppois, G., and C. Glowacki. 1982. Bulimulid land snails from the Galapagos. 1. Factor analysis of Santa Cruz Island species. Malacologia 23:209–219.

Cortie, M. B. 1989. Models for mollusc shell shape. South African Journal of Science 85:454–460.

Cox, L. R. 1955. Observations on gastropod descriptive terminology. Proceedings of the Malacological Society of London 31:190–202.

D'Arcy Thompson, W. 1961. On growth and form, 4th ed. Cambridge University Press, Cambridge.

Dawkins, R. 1996. Climbing mount improbable. Penguin, London.

Ekaratne, S.U.K., and D. J. Crisp. 1983. A geometrical analysis of growth in gastropod shells, with particular reference to turbinate forms. Journal of the Marine Biological Association of the United Kingdom 63:777–797.

Futuyma, D. J. 1986. Evolutionary biology, 2d ed. Sinauer, Sunderland, Mass.

Galler, L., and S. J. Gould. 1979. The morphology of a ''hydrid zone'' in *Cerion* variation, clines and an ontogenic relationship between two ''species'' in Cuba. Evolution 33:714–727.

Goodfriend, G. A. 1983. Some new methods for morphometric analysis of gastropod shells. Malacological Review 16:79–86.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. Biological Reviews 41:587–640.

———. 1989. A developmental constraint in *Cerion* with comments on the definition and interpretation of constraint in evolution. Evolution 43:516–539.

———. 1992. Constraint and the square snail: life at the limit of a covariance set. The normal teratology of *Cerion* disform. Biological Journal of the Linnean Society 47:407–437.

Grahame, J., and P. J. Mill. 1989. Shell shape variation in *Littorina saxatilis* and *L. arcana*: a case of character displacement? Journal of the Marine Biological Association of the United Kingdom 69:837–855.

Harasewych, M. G. 1981. Mathematical modeling of the shells of higher prosobranchs. Bulletin of the American Malacological Union 1981:6–10.

Heath, D. J. 1985. Whorl overlap and the economical construction of the gastropod shell. Biological Journal of the Linnean Society 24:165–174.

Huxley, J. S., and G. Teissier. 1936. Terminologie et notation dans la description de la croissance relative. Comptes Rendus des Séances de la Société de Biologie et ses filiales 121:934–936.

Illert, C. 1989. Formulation and solution of the classical seashell problem. II. Tubular three-dimensional seashell surfaces. Il Nuevo Cimento 11:761–780.

Janson, K., and P. Sundberg. 1983. Multivariate morphometric analysis of two varieties of *Littorina saxatilis* from the Swedish west coast. Marine Biology 74:49–53.

Johannesson, B., and K. Johannesson. 1990. *Littorina neglecta* Bean, a morphological form within the variable species *Littorina saxatilis* (Olivi)? Hydrobiologia 193:71–87.

Johnston, M. R., R. E. Tobachnick, and F. L. Bookstein. 1991. Landmark-based morphometric of spiral accretionary growth. Paleobiology 17:19–36.

Kohn, A. J., and A. C. Riggs. 1975. Morphometry of the *Conus* shell. Systematic Zoology 24:346–359.

Kristensen, T. K., and A. G. Christensen. 1989. *Bulinus africanus*-group species in West Africa differentiated by morphometric analysis (Gastropoda, Planorbidae). Journal of Molluscan Studies 55:103–110.

Lawrence, E. 1995. Henderson's dictionary of biological terms, 11th ed. Longman, Harlow, England.

Lison, L. 1949. Recherches sur la forme et la mécanique de développement des coquilles des Lamellibranches. Mémoires de l'Institut Royal des Sciences Naturelles de Belgique 2:3–87.

Løvtrup, S., and M. Løvtrup. 1988. The morphogenesis of molluscan shells: a mathematical account using biological parameters. Journal of Morphology 197:53–62.

Mayr, E., and P. D. Aschlock. 1991. Principles of systematic zoology, 2d ed. McGraw-Hill, Singapore.

McGhee, G. R., Jr. 1978. Analysis of shell torsion phenomenon in the Bivalvia. Lethaia 11:315–329.

———. 1980. Shell form in the biconvex articulate Brachiopoda: a geometric analysis. Paleobiology 6:57–76.

———. 1991. Theoretical morphology: the concept and its applications. Analytical Paleobiology 4:87–102.

Murray, T. 1982. Morphological characterization of the *Littorina scutulata* species complex. Veliger 24:233–238.

Nemeschkal, H. L. 1990. Uber die form der Schneckenschale: Morphometrische Grundlagen und Vorbereitungen für ein statistisches Taxonmodell. Zoologische Jahrbüch für Systematik 117:491–534.

Nemeschkal, H. L., and H. Kothbauer. 1989. Zur Spirale der Schneckenschale: Eine Varianz-Kovarianzuntersuchung bei *Arianta* (Gastropoda, Helicidae). Zoologische Jahrbüch für Systematik 116:391–409.

Okamoto, T. 1988. Analysis of heteromorph ammonoids by differential geometry. Paleontology 33:35–52.

Prusinkiewicz, P., and D. R. Fowler. 1995. Shells models in three dimensions. Pp. 163–181 *in* H. Meinhart, ed. The algorithmic beauty of sea shells. Springer, Berlin.

Raup, D. M. 1961. The geometry of coiling in gastropods. Proceedings of the National Academy of Sciences USA 47:602–609.

———. 1962. Computer as aid in describing form in gastropods shells. Science 138:150–152.

———. 1966. Geometric analysis of shell coiling: general problems. Journal of Paleontology 40:1178–1190.

Raup, D. M., and A. Michelson. 1965. Theoretical morphology of the coiled shell. Science 147:1294–1295.

Robertson, R. 1974. Marine prosobranch gastropods: larval studies and systematics. Thalassia Yugoslavia 10:213–238.

Rohlf, F. J. 1990. Morphometrics. Annual Review of Ecology and Systematics 21:299–316.

Savazzi, E. 1990. Biological aspects of theoretical shell morphology. Lethaia 23:195–212.

Schindel, D. E. 1990. Unoccupied morphospace and the coiled geometry of gastropods: architectural constraint or geometric covariation. Pp. 270–304 *in* R. M. Ross and W. D. Allmon, eds. Causes of evolution: a paleontological perspective. University of Chicago Press, Chicago.

Sedgewick, R. 1988. Algorithms, 2d ed. Addison Wesley, Reading, Mass.

Sen, A., and M. Srivastava. 1990. Regression analysis. Theory methods and applications. Springer, New York.

Sheldon, P. 1993. The evolution of form. Pp. 668–742 *in* P. Skelton, ed. Evolution: a biological and paleontological approach. Open University Press, Wokingham, England.

Skelton, P. 1993. The fossil record of evolution in species. Pp. 445–508 *in* P. Skelton, ed. Evolution: a biological and paleontological approach. Open University Press, Wokingham, England.

Stepczak, K. 1988. Correlation between measurable features of *Helix pomatia* L. (Gastropoda), useful in the investigation of the snail. Bulletin de la Société des Amis des Sciences et des Lettres de Poznan 26:115–124.

Stone, J. R. 1995. Cerioshell: a computer program designed to simulate variation in shell form. Paleobiology 21:509–519.

———. 1996a. Computer-simulated shell size and shape variation in the Caribbean land snail genus *Cerion*: a test of geometrical constraints. Evolution 50:341–347.

———. 1996b. The evolution of ideas: a phylogeny of shell models. American Naturalist 148:904–929.

———. 1997. Using shell parameters as complementary data in phylogenetic systematic analyses: evolution of form in five species of littorinids (Mollusca: Gastropoda). Veliger 40:12–22.

Tursch, B. 1997. Spiral growth: ''The Museum of All Shells'' revisited. Journal of Molluscan Studies 63:581–588.

———. 1998. A simple shell model: applications and implications. Apex 13:161–176.

Van Osselaer, C., and B. Tursch. 1994. Studies on Olividae. XIX. Where is the suture of *Oliva* shells? Apex 9:47–50.

Verduin, A. 1982. How complete are diagnoses of coiled shells of regular build? A mathematical approach. Basteria 45:127–142.

Vermeij, G. J. 1971. Gastropod evolution and morphological diversity in relation to shell geometry. Journal of Zoology 163:15–23.

———. 1993. A natural history of shells. Princeton University Press, Princeton, N.J.

Wagner, P. J. 1996. Morphologic diversification of early Paleozoic ''archaeogastropods.'' Pp. 161–169 *in* J. D. Taylor, ed. Origin and evolutionary radiation of the Mollusca. Oxford University Press, Oxford.