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Relationships between dimensionless models of ammonoid shell morphology

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In morphological studies the shape may be conveniently quantified by relative dimensions or dimensionless quantities. The analyses of shell morphology and morphospace occupation have been historically approached mainly by means of statistical analysis on classical dimensions (distance measurements: diameter, umbilical width, whorl width, whorl height and apertural whorl height), the Raup's coiling and expansion rate parameters and, more recently, by means of the ADA-model which conjugates the classical variables in a single simple equation. Relationships between these studies should be possible based on mathematical equivalences between classical dimensions and those of coiling and expansion rates. These equivalences, which are presented in this paper, have been obtained on the basis of the ADA-model and a new general method for deriving dimensionless models of morphology based on exponential trajectories as a function of a rotational angle.

Introduction

In morphological studies the shape may be conveniently quantified by relative dimensions or dimensionless quantities. This important point was discussed and developed in two recent papers (Parent and Greco 2007; Parent et al. 2010) where it was proposed a dimensionless treatment of the ammonite morphology. The model, called the ADA-model, was analyzed and used for the exploration of shell morphology and morphospace occupation in Mesozoic planispiral ammonoids. Some interesting results include evidence that the apertural whorl height relative to the size or diameter is an important dimension which not only defines a large part of the shell morphology and constrains the size, but also was shown to be the link between coiling and inflation of the shell.

There is an important body of published work about the analysis of shell morphology and morphospace occupation. The morphometric analysis has been widely based on statistical procedures on the classical dimensions (Fig. 1A), describing and comparing regressions representing differential allometry, mainly with respect to size (e.g., Thierry 1978). Morphospace occupation research has been largely based on the dimensions defined by Raup (1966, 1967), e.g., Dommergues et al. (1996). The ADA-model is defined on the basis of the classical dimensions so that the published statistical analyses may be directly related with the dimensionless analysis. Nevertheless the studies based on the Raup's dimensions (Fig. 1B) could be related with the ADA-model and with statistical studies on classical dimensions if equivalences between classical variables and Raup's dimensions are known. These equivalences had not been yet fully developed. They appear clearly useful after the discussion in Parent et al. (2010) where the reliability of the ADA-model has been shown on the basis of a large sample of Mesozoic ammonoids. (see SOM, Supplementary Online Material at http://app.pan.pl/SOM/app57-Parent_etal_SOM.pdf for an illustration about the generation of morphology and control of shell shape).

The objective of this paper is to present a general method for derivation of dimensionless models of morphology which is then used for obtaining an alternative derivation of the ADA-model. Finally, equivalences between the classical dimensions as represented in the ADA-model and those of Raup are presented, opening a new field of research where results from the different approaches may be combined.

An alternative derivation of the ADA-model

The ADA-model was originally derived from a model consisting of an ellipse spinning through a directional vector (Parent et al. 2010: fig. 3A). Alternatively the model may be derived independently of the directional vector as follows. We postulate that the shell grows such that all variables (distance measurements) X_i follow exponential trajectories $k_i e^{c\theta}$ as a function of rotational angle θ. The constant k, the value at the initial angle (θ = 0), is specific to each variable, while c is equal for all variables. Considering the exponential function $f(\theta) = e^{c\theta}$ and two arbitrary angles θ and θ', the angular dependence of any variable X_i can be written as:

$$X_i(\theta) = X_i(\theta' + \theta - \theta') = k_i e^{c\theta'} e^{c(\theta-\theta')} = X_i(\theta') f(\theta - \theta') \quad \text{(Eq. 1)}$$

For example, if we know the ammonoid shell diameter $D(\theta)$ at a given angle θ, we can obtain the corresponding diameter for any other angle θ' by means of $D(\theta') = D(\theta) f(\theta' - \theta)$. As a consequence the ratio between any pair of variables (dimensions) is independent of the angle, as follows:

$$\frac{X_1(\theta)}{X_2(\theta)} = \frac{X_1(\theta_0) f(\theta - \theta_0)}{X_2(\theta_0) f(\theta - \theta_0)} = \frac{X_1(\theta_0)}{X_2(\theta_0)} = \text{constant} \quad \text{(Eq. 2)}$$

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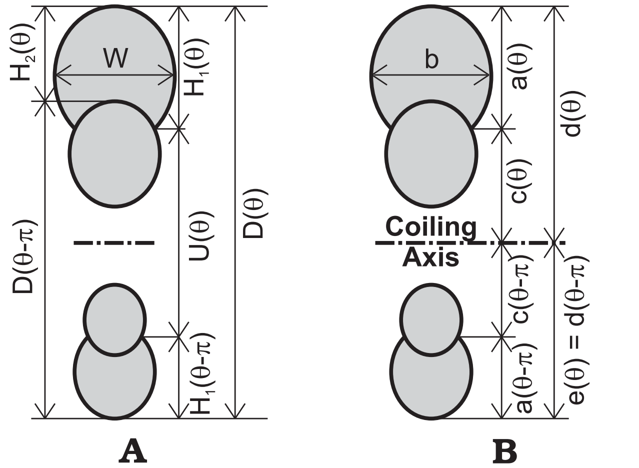

Fig. 1. **A**. Classical dimensions of the ammonite shell as considered in Parent et al. (2010). **B**. Dimensions of the ammonite shell considered by Raup (1967).

This property shows that the model is isometric.

The ADA-model is based on the equation presented in Parent et al. (2010: 88), cf. Fig. 1A:

$$\frac{U}{D} = 1 - 2\frac{H_1}{D} + \left(\frac{H_1}{D}\right)^2 \frac{H_2}{H_1} \qquad \text{(Eq. 3)}$$

This equation may be alternatively derived from the general function presented above (Eq. 1), considering $H_2(\theta) = D(\theta) - D(\theta-\pi)$ (see Fig. 1A). From Eq. 1 we have $D(\theta-\pi) = D(\theta)f(-\pi)$, i.e.,

$$f(-\pi) = 1 - \frac{H_2}{D} \qquad \text{(Eq. 4)}$$

Another relationship observable in Fig. 1A is $D(\theta) = H_1(\theta) + H_1(\theta-\pi) + U(\theta)$ from which, using Eq. 1, we obtain

$$1 = \frac{H_1}{D}\left[1 + f(-\pi)\right] + \frac{U}{D} \qquad \text{(Eq. 5)}$$

Finally, introducing Eq. 4 into Eq. 5, we arrive at Eq. 3, which is the equation on which the ADA-model is based.

Relationship between the ADA-model and Raup's dimensions

The dimensions used by Raup (1967) for describing the ammonoid morphology are: *a*, *b*, *c*, *d*, and *e* (see Fig. 1B) with which he defined the coiling and expansion rates $W_R = (d/e)^2$, $D_R = c/d$ and $S = b/a$ (the subscript R is not original, but added herein for avoiding confusion with *W* and *D* defined in Fig. 1A).

From Fig. 1A it is evident that $U(\theta) = c(\theta) + c(\theta-\pi)$ and $D(\theta) = d(\theta) + d(\theta-\pi)$, from which

$$\frac{U}{D} = \frac{c(\theta) + c(\theta-\pi)}{d(\theta) + d(\theta-\pi)}.$$

Using Eq. 1 on $c(\theta-\pi)$ and $d(\theta-\pi)$we obtain

$$\frac{U}{D} = \frac{c}{d} = D_R \qquad \text{(Eq. 6)}$$

From the definition of W_R,

$$W_R = \left[\frac{d(\theta)}{e(\theta)}\right]^2 = \left[\frac{d(\theta)}{d(\theta-\pi)}\right]^2$$

where we have replaced $e(\theta)$ by $d(\theta-\pi)$. Using Eq. 1 on $d(\theta-\pi)$ results in

$$W_R = \left[\frac{d(\theta)}{d(\theta)f(-\pi)}\right]^2 = \left[f(-\pi)\right]^{-2}$$

In order to relate with the variables (dimensions) of the ADA-model we recall Eq. 4:

$$W_R = \left[1 - \frac{H_2}{D}\right]^{-2} \qquad \text{(Eq. 7)}$$

From Eqs. 5–7 the dimensionless H_1/D, H_2/D and H_2/H_1 can be written in terms of W_R and D_R as follows:

$$\frac{H_2}{D} = 1 - \frac{1}{\sqrt{W_R}} \qquad \text{(Eq. 8)}$$

$$\frac{H_1}{D} = \frac{1 - D_R}{1 + \frac{1}{\sqrt{W_R}}} \qquad \text{(Eq. 9)}$$

$$\frac{H_2}{H_1} = \frac{1 - \frac{1}{W_R}}{1 - D_R} \qquad \text{(Eq. 10)}$$

Discussion and conclusion

The equivalences between the variables of the ADA-model (Parent et al. 2010) and those of Raup (1967) are presented by means of Eqs. 8–10 above. From these equivalences the plots of Raup (1967: figs. 4, 8) may be transformed into the morphospace (H_2/H_1, H_1/D) defined by Parent et al. (2010), as shown in Fig. 2.

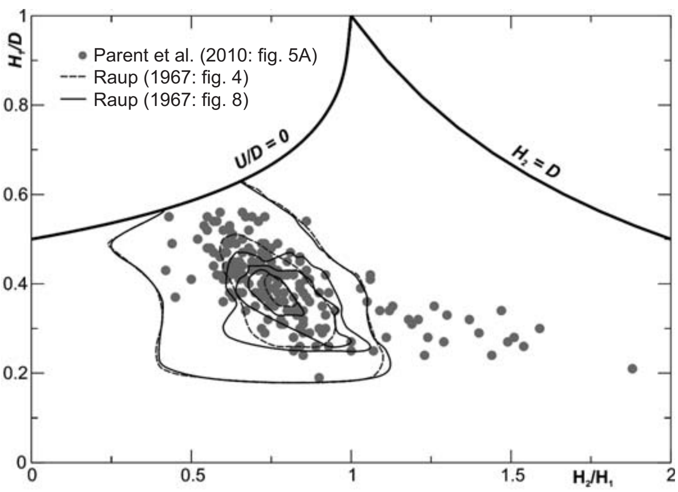

Fig. 2. Plot of a sample of 1222 observations from 201 species of Mesozoic planispiral ammonites in the morphospace (H_2/H_1, H_1/D), modified from Parent et al. (2010). The closed curves are the contours shown in Raup (1967: figs. 4, 8) as explained in text.

However, beyond these equivalences the ADA-model possesses the following advantages for the study of the shell morphology: (i) all the variables are simultaneously related in a single simple equation (Eq. 3), and (ii) the model is written using classical dimensions (Fig. 1A) which can be measured in almost every piece of ammonite and have direct meaning in visualization and literal descriptions (see SOM). The relationships between the variables of the morphospaces of both models are not linear (Eqs. 8–10). These constraints are originated in the strong dependence on the position of the coiling axis.

It is hoped that the simplicity of the ADA-model facilitates studies on morphology and evolution of ammonites, taking advantage of that most of the biometry in the literature is based on measurements of the classical dimensions. On the other hand, the equivalences presented open a new field of research where results from the different approaches may be combined.

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