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RAPID COMMUNICATION

Strain estimation from distorted vertebrate fossils: application of the Wellman method

JYOTI SHAH & DEEPAK C. SRIVASTAVA*
Department of Earth Sciences, Indian Institute of Technology Roorkee, Roorkee 247667, India

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Abstract

Distortion of the vertebral column in fossils can be used for the estimation of two-dimensional finite strain by a simple geometrical technique, namely the Wellman method. We demonstrate application of the Wellman method to the distorted vertebral columns of a reptile and a stem-chordate, and use the results to restore the undistorted fossil shapes by a computer graphic method. The Wellman method is particularly efficient in situations where independent evidence for the principal strain directions, or undistorted forms, are lacking. The method is purely geometrical, easy to use, and rapid. It involves relatively low error, and works even when only a small segment of the distorted vertebral column is preserved.

Keywords: vertebrate, distortion, finite strain analysis, restoration.

1. Introduction

Structural geologists routinely estimate strain in rocks to study the nature of deformation in orogenic belts, and get an insight into the mechanism of development of ductile structures (Burg & Laurent, 1978; Gray & Durney, 1979; Evans & Dunne, 1991; McNaught & Mitra, 1996). As the distorted fossils are potentially vulnerable to taxonomic errors, palaeontologists, too, need strain estimations for restoring the original morphology of the forms (Sharpe, 1847; Lake, 1943; Hughes & Jell, 1992). Choice of the method for determination of strain, however, depends on the initial shape and fabric of the distorted objects, or the strain markers.

Various graphical and numerical methods exist for estimation of the strain from the objects of initially circular or elliptical shapes, e.g. oolites, reduction spots, and conglomerate pebbles, and distorted fossils (Ramsay, 1967; Ramsay & Huber, 1983). Amongst these strain markers, bilaterally symmetric invertebrate fossils such as the brachiopod and the trilobite have been extensively used by structural geologists and palaeontogists for strain estimation and/or retrodeformation (Lake, 1943; Breddin, 1956; Wellman, 1962; Sdzuy, 1966; Cooper, 1990; Hughes & Rushton, 1990; Hughes & Jell, 1992; Rushton & Smith, 1993; Srivastava & Shah, 2006a). Relatively, there are fewer studies that use fossil vertebrates as strain markers (Jefferies, Lewis & Donovan, 1987; Motani, 1997), probably due to their complex morphology, and commonly disarticulated and fragmentary nature of preservation. However, a distinct advantage in using vertebrate fossils as strain markers is that the preservation of a small segment of the vertebral column is sufficient for the analysis, whereas in invertebrate fossils two or more complete forms are commonly required for the estimation of strain in situations where the rocks do not contain any independent evidence for the principal strain directions (Ramsay, 1967; Ramsay & Huber, 1983; Ragan, 1985; Treagus, 1987; Lisle, 1991).

A vertebral column consists of a set of centra that are similar in shape but that differ with respect to orientation (Fig. 1a). Distortion of the shapes of the variably oriented centra, due to homogeneous deformation, provides useful geometrical information sufficient for determining the axial ratio and the orientation of the finite strain ellipse.

Motani (1997) proposed two algebraic methods that use centra as strain markers for retrodeformation, and hence for the precise taxonomic identification of the distorted fossils. The first method involves geometrical measurements on a pair of centra, vector resolutions, construction of a two-by-two deformation matrix, and computations, leading to the determination of the eigenvalues and the eigenvectors. The eigenvectors are parallel to the principal strain directions, and the ratio of the two eigenvalues equals the axial ratio of the strain ellipse. In practice, this procedure is repeated on all available pairs of centra and the results are averaged to obtain the representative strain. The second method involves geometrical measurements on several centra, solution of simultaneous equations, and an algebraic search of a deformation matrix that minimizes the discrepancy among data. Both these methods require a series of mathematical operations. This paper shows that a simple geometrical technique, namely the Wellman method, can estimate strain by using the distorted shapes of centra. It demonstrates, with the help of two test examples of distorted vertebrae, that despite being simple and purely geometrical the Wellman method produces rapid results with very low errors.

2. Principle and methodology

Wellman (1962) demonstrated that the angles between the hinge lines and the median lines of distorted brachiopod fossils could be used for estimation of two-dimensional

*Author for correspondence:dpkesfes@iitr.ernet.in

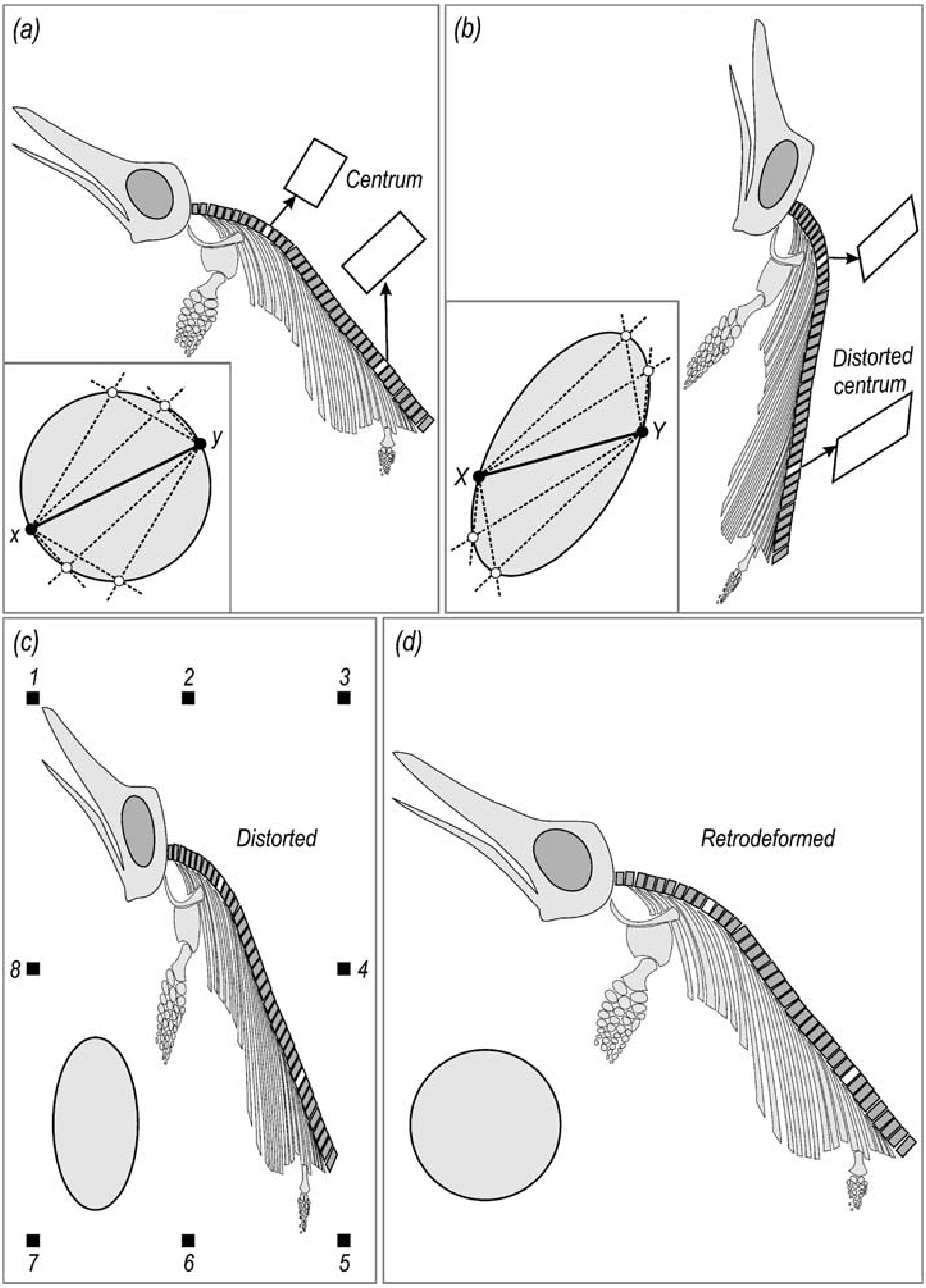

Figure 1. (a, b) Principle of the Wellman method. (a) Sketch of an ichthyosaur, *Stenopterygius*, showing rectangular shapes of centra in vertebral column (after illustration on p. 426 in Fenton & Fenton, 1989). Inset shows the rectangles obtained by drawing lines parallel to sides of the undistorted centra from the points *x* and *y*. *xy*: the common diagonal of rectangles, which equals the diameter of the circumscribing circle. (b) Distortion of *Stenopterygius* by 30 % shortening results in parallelogram-shaped geometry of the centra. Inset shows the parallelograms made by the lines paralleling sides of the distorted centra. Strain ellipse circumscribes all the parallelograms. *XY*: the common diagonal of parallelograms. (c, d) Procedure for retrodeformation. (c) Image of the distorted fossil, and the strain ellipse obtained by the Wellman method. The image has been rotated to make the major axis of strain ellipse vertical. Numbers *1* to *8*: dragging handles. (d) Shape restoration, by dragging handle *4* horizontally outwards until the strain ellipse transforms into circle. Note that centra return to rectangular shapes.

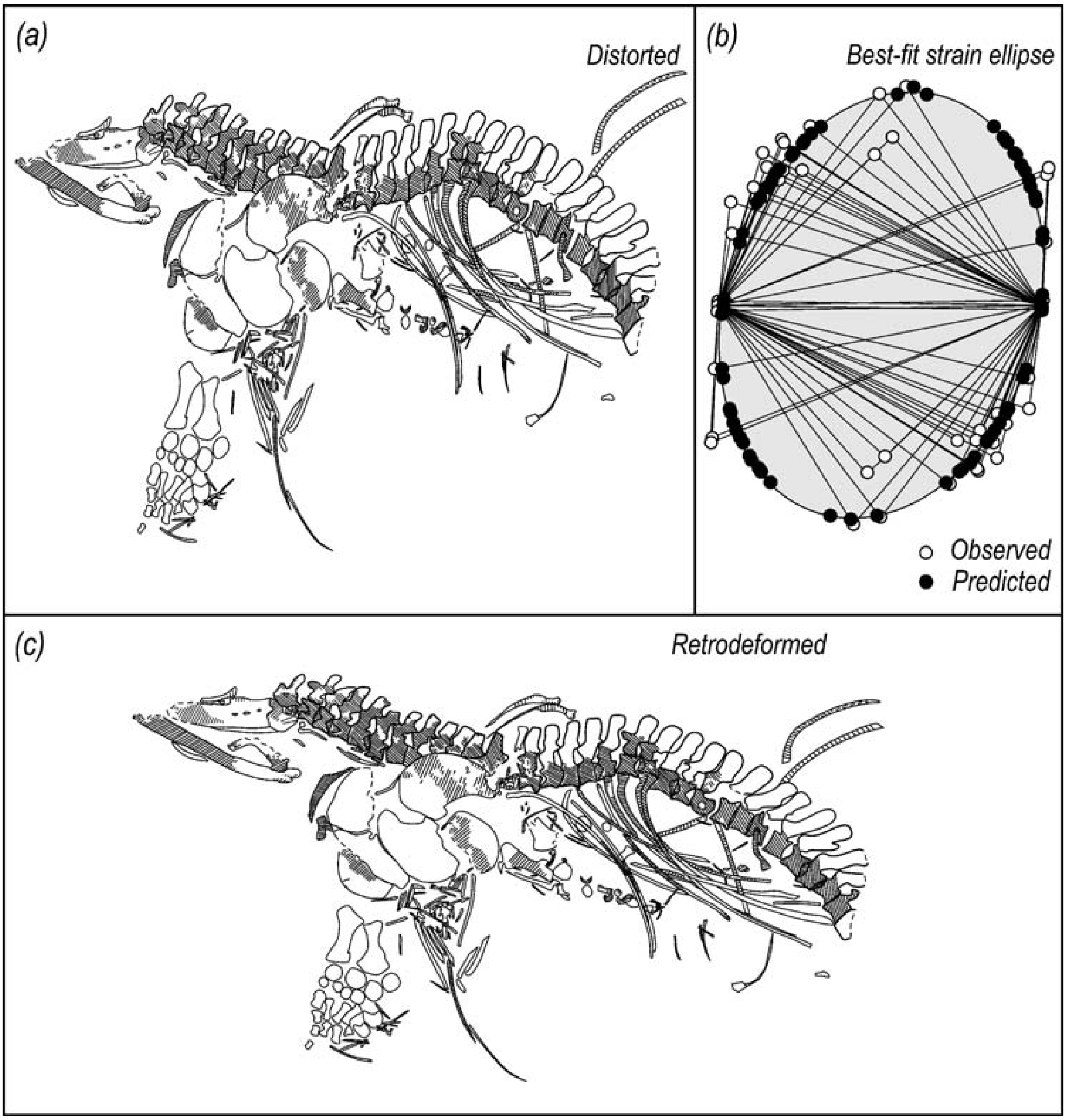

Figure 2. (a) Distorted ichthyosaur fossil (traced from fig. 1 in Brinkman, Zhao & Nicholls, 1992). (b) Strain ellipse obtained by the Wellman method. (c) Shape-restored image of the fossil in (a).

strain by a simple geometrical construction. His method involves: (i) drawing a pair of lines parallel to the hinge line and the median line of each distorted fossil from the two ends of an arbitrarily chosen reference line, and (ii) searching the best-fit ellipse through the intersections of the pairs of lines. More recently, Shah & Srivastava (2006) extended application of the Wellman method for estimation of strain in flattened parallel folds by using the angles between the isogons and the respective tangents. In this article, we use the Wellman method for estimation of strain in fossil vertebrates.

The shape of an undistorted vertebral centrum, in longitudinal section, is either rectangular or it can be circumscribed by a rectangle (Fig. 1a). The rectangles, drawn on a set of variably oriented centra, can be transferred in a common reference frame, and scaled such that an arbitrarily chosen reference line defines the common diagonal of all the rectangles. Such a transformation results in a geometrical condition where the common diagonal, xy, is the diameter of a reference circle that circumscribes all the rectangles obtained by drawing parallels to the sides of centra from points x and y (inset in Fig. 1a). Deformation by homogeneous strain distorts the geometry of a centrum from rectangular to parallelogram-shaped, and transforms the reference circle into a strain ellipse (Fig. 1b). In practice, the strain ellipse is traced by searching for the best-fit curve through vertices of the scaled and commonly referenced parallelograms (inset in Fig. 1b).

Once the strain ellipse is obtained by the Wellman method, the original shape of the distorted fossil can be restored with the help of most computer-aided graphics software, e.g. CorelDraw, Corel Photo-Paint, Adobe Illustrator, or

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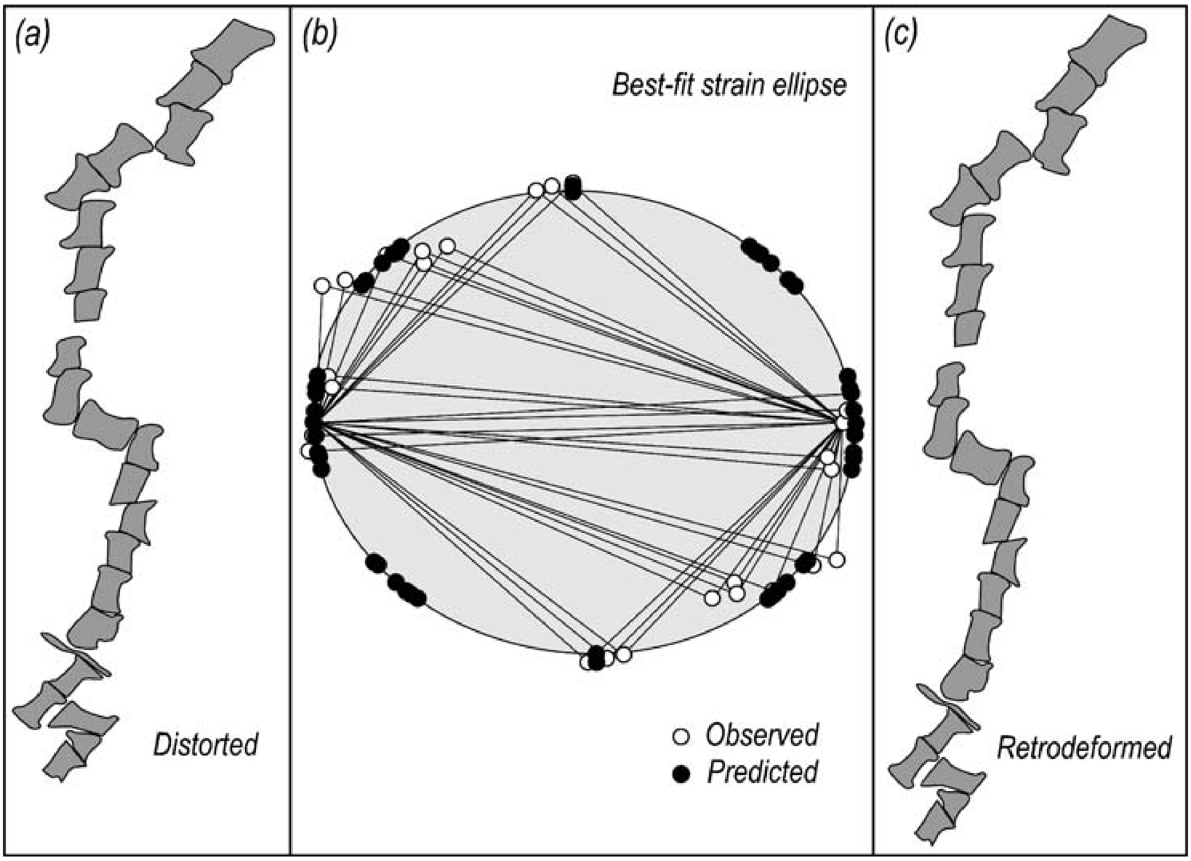

Figure 3. (a) Distorted centra of a stem-group chordate (traced from fig. 1 in plate 57 of Jefferies, Lewis & Donovan, 1987). (b) Strain ellipse obtained by the Wellman method. (c) Shape-restored image of the fossil in (a).

Smartdraw. A step-by-step procedure for strain estimation by the Wellman method, and subsequent restoration of the distorted fossil shape by a technique suggested initially for destraining the flattened parallel fold (Srivastava & Shah, 2006b), is outlined as follows:

(i) Draw different parallelograms, each tracing or circumscribing a centrum (Fig. 1b).

(ii) Draw parallels to adjacent sides of each parallelogram from the ends *X* and *Y* of an arbitrary line *XY* of any convenient length and orientation (inset in Fig. 1b). This step scales the parallelograms in a common reference frame such that the line *XY* becomes the common diagonal.

(iii) Find the best-fit ellipse passing through the vertices of all the parallelograms either by visual best fit, or by least-squares fitting depending on required level of accuracy.

(iv) For retrodeformation, import the image of the distorted fossil and the strain ellipse obtained by the Wellman method into the graphic software, and group these two objects.

(v) Rotate the grouped objects until the major axis of the strain ellipse becomes vertical. Using the pick tool, select the image to display eight dragging handles, *1* to *8* (Fig. 1c).

(vi) Drag handle *4* horizontally to the right until the strain ellipse transforms into a circle (Fig. 1d). At this stage all the parallelograms become rectangles, and the fossil recovers its undistorted shape.

3. Examples

We demonstrate the application of the Wellman method on a distorted ichthyosaur fossil from the Lower Triassic siltstone beds of the Sulphur Mountain Formation, British Columbia, Canada (Fig. 2a, traced from fig. 1 in Brinkman, Zhao & Nicholls, 1992), and a stem-group chordate, *Protocystites menevensis* from the Middle Cambrian of South Wales (Fig. 3a, traced from fig. 1 in plate 57 of Jefferies, Lewis & Donovan, 1987). The ichthyosaur example is particularly selected because it has already been treated for strain estimation by the two algebraic methods of Motani (1997). Testing this example, therefore, facilitates a ready comparison between the Wellman method and the algebraic methods.

If the opposite sides of the centra were not exactly parallel to each other, the points of intersection of the lines, paralleling the adjacent sides of centra, would not lie on a unique ellipse in the Wellman construction. To minimize this error, we have obtained the least-squares best-fit ellipse by a user-defined MATLAB function that minimizes the sum of squares of the residuals, where a residual is the difference between the observed and the predicted values (Figs 2b and 3b). For each ellipse, the goodness-of-fit is calculated in terms of *E*, the root mean square error (Table 1). The strain analysis on the ichthyosaur fossil reveals that the axial ratio (R) and the orientation (θ) of the best-fit ellipse given by the Wellman method compare very closely with those obtained by the application of rigorous mathematical methods (Table 1). The reason for slight discrepancy between the results obtained by the two approaches is, however, not clear because it is not

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Table 1 Results of the Wellman method and the algebraic methods

Source	Fossil	Algebraic methods (Motani, 1997) Method 1 R	$\theta°$	Method 2 R	$\theta°$	Wellman method (this study) R	$\theta°$	E	n
figure 1 in Brinkman, Zhao & Nicholls, 1992	Ichthyosaur (TMP 89.127.3)	1.29	84	1.33	79.7	1.38	75	0.101	44 (21)
figure 1 in plate 57 of Jefferies, Lewis & Donovan, 1987	Stem-group chordate	*na*	*na*	*na*	*na*	1.17	−8	0.007	28 (13)

TMP: Royal Tyrrell Museum of Palaeontology, Alberta; R: axial ratio of the strain ellipse; $\theta°$: angle between major axis and the horizontal reference line; E: root mean square error, a measure of goodness-of-fit, n: number of points used for the best-fit; intrabracket numbers: number of centra; *na*: not available.

known which particular centra were used by Motani (1997). This limitation also precludes the estimation of errors in the application of the algebraic methods on the ichthyosaur example.

Increasing the number of points for searching the best-fit ellipse can further minimize the error E. One way of obtaining more points is to use both the diagonals XY and AB of the parallelogram obtained from the first centrum, instead of one diagonal XY, for scaling and drawing parallels to the sides of other centra (Fig. 4). This simple geometrical arrangement increases the total number of available points from $2 + 2(n)$ to $4(n)$, where n is the number of centra. Similarly, the number of points can be further increased by successively considering diagonals of different parallelograms as the reference line. We have, however, not increased the number of points for the sake of retaining the original method proposed by Wellman (1962). The other errors, such as measuring errors, and the errors due to oblique sectioning, or projection of centra on a single plane, can also be minimized by multiple measurements and geometrical projections depending on the required level of accuracy.

Both the examples of distorted fossils tested in this study have been retrodeformed by using the results of the Wellman method and applying the computer graphic technique explained in the steps (iv) to (vi) of Section 2. In the retrodeformed images, all the centra restore their rectangular shapes approximately (Figs 2c, 3c). The retrodeformed ichthyosaur fossil (Fig. 2c) is notably similar to the retrodeformed shape of this fossil as depicted in figure 3a of Motani (1997).

4. Discussion and conclusions

Whereas the algebraic methods of Motani (1997) assume an equidimensional nature of two diagonals of an undistorted centrum, the Wellman method assumes rectangular shape of centra. Most methods of strain analysis and retrodeformation, including the Wellman method, assume a constant volume homogeneous deformation. Because the Wellman method plots the strain ellipse directly, it provides a way for testing the assumption of homogeneous strain. In general, a good fit of the ellipse, through the vertices of the parallelograms, justifies the assumption of homogeneous strain.

One practical limitation in using the Wellman method is that all the centra in a distorted vertebral column may not be parallelogram-shaped due to inherent biological reasons. The occurrence of a few irregularly shaped centra is, in fact, quite common. In such situations, we recommend the consideration of only those centra that are parallelogram-

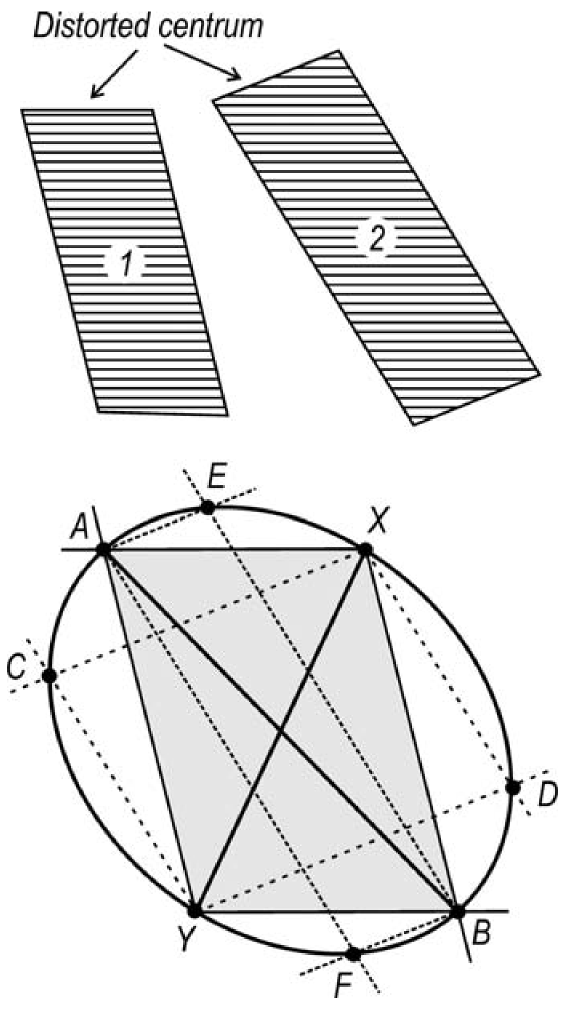

Figure 4. Increasing number of points for searching the best-fit ellipse. *AXBY* and *CXDY* are two parallelograms obtained by drawing parallels to the sides of the two distorted centra *1* and *2*, from the two ends of an arbitrary reference line that defines the common diagonal *XY*. Lines parallel to the sides of second centra *2* from the two ends of the diagonal *AB* produce two additional intersection points *E* and *F* on the ellipse. This geometrical arrangement gives eight points from two centra.

shaped. Because the fossil vertebrates are commonly large in size, a significant competency contrast may exist between the fossil and the rock. In such instances, shape analysis

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of the distorted centra underestimates, or overestimates, the bulk strain depending on whether the fossil is more, or less, competent than the rock.

The retrodeformation procedure also has a limitation because all the parallelogram-shaped centra may not restore to perfect rectangular shapes with any particular amount of stretching of the image. In such situations, the optimal amount of stretching, which restores or nearly restores rectangular geometry in most of the centra, produces the most likely image of the retrodeformed fossil.

A strong merit of both the Wellman method and the numerical methods of Motani (1997) is that these techniques do not require an *a priori* knowledge of the principal strain directions. These methods work even when the distorted vertebral column contains only two parallelogram-shaped centra. The Wellman method is a simple geometrical alternative to rigorous algebraic methods of strain analyses in fossil vertebrates.

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