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Towards a morphospace for the Ediacara biota

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Abstract: The Ediacara biota of the late Neoproterozoic is justly famous as a biological puzzle. Studies of Ediacaran biology have commonly used analogy with living organisms as a cipher for the decoding of biological affinity, and consequently the life mode and habit. Here, we discuss the problems of using such analogous reasoning and put forward our alternative approach, that of using Morphospace Analysis for the study of growth, form and phylogeny. This tool, we suggest, has the potential to be used for testing the unity of an evolutionary clade, such as 'rangeomorphs' and 'dickinsoniomorphs'. Preliminary data from the members of the Ediacara biota do indeed show such a unity within our preliminary morphospace model (all k values are low). This method reveals no clear relationships, between these forms and more recent biological groups such as the sea pens or the Foraminifera.

The problems involved in deducing the biology of long extinct organisms are considerable. Fossils cannot move, reproduce, respire or do any of the things that living organisms do. Their activities can only be inferred from their morphology, from their inferred biological affinities and from the associated environmental information. These difficulties are well illustrated, for example, by the problem of inferring the mode of life in trilobite arthropods (Fortey 1985). As this long extinct group is not thought to be ancestral to any extant arthropod group, their life modes and habits have proved particularly challenging to address. Whereas we can make informed inferences about bivalves from the fossil record because many are alive today (using the principle of uniformity), uniformity cannot be applied directly in the case of a trilobite. There are, of course, living organisms (such as *Limulus*) that are closely related enough to fossil trilobites for us to seek useful *analogies* in both life cycle and behaviour. The study of trilobites is also blessed with detailed biostratigraphic constraints on their fossil record. Even so, the details of trilobite palaeobiology, such as agnostoids, are often moot.

The problems become acute, therefore, when we turn to a group of organisms whose biological affinities are completely uncertain, such as the Ediacara biota of the late Neoproterozoic (Glaessner 1966, 1984). Inferences about the life modes and habits of this biota are not easy to make. One problem here is that the rocks in which they occur are poorly constrained in terms of biostratigraphy and geochronology, so that it is hard to decode their evolutionary history. A second problem arises from the possibility that there were significant differences in the composition of the atmosphere,

hydrosphere, biosphere and lithosphere at the time of the Ediacara biota. Under such circumstances, analogies with modern ecosystems must be fraught with problems.

There are, of course, some things we know about the Ediacara biota that are beyond dispute. First, we have the geological information held within the sediments themselves. This means that we can make useful inferences about the associated facies (and hence make comparisons with modern environments), about sedimentary fabrics and taphonomic processes. Much of this has been done very fruitfully (e.g. Grazhdankin 2000, 2003, 2004), revealing a late Precambrian world that potentially was very different to the Phanerozoic world, which we inhabit. Second, we have the fossils themselves. Unfortunately, the number of analogies drawn between the Ediacaran fossils and living organisms are at least as many as there are authors writing upon the subject. With this methodology, the chosen analogue clearly determines the inference. For example, *Charniodiscus* has been reconstructed as feeding in bottom currents in the manner of modern sea-pens (Jenkins 1992), and *Dickinsonia* has been envisioned as stuck to the sediment surface, drawing in nutrients like a modern deep-sea protist (Seilacher *et al.* 2003).

Such an approach, using analogous reasoning, has a long and respectable history. Fortey (1985), for example, has advocated the use of a closely affiliated, extant organism as an analogue for the functional morphology and behaviour of extinct fossil groups and to increase understanding of their life habits. Unfortunately, we cannot expect the reverse reasoning to be true. That is to say, analogous life modes and habits cannot help to inform

us about taxonomic affinities. Further, no analogue in any situation can actually inform us with regard to the taxonomic position of our problematic fossil. Nor, indeed, can taphonomic studies help us greatly with taxonomic position of an extinct fossil group without the use of arguments themselves based upon analogy. These are real and difficult problems for us because the central question with regard to the Ediacara biota undoubtedly still concerns their taxonomic affinities. Answers to this question will help guide all our other Ediacaran problems.

A new approach

Few features are more useful for distinguishing between the higher taxa, such as classes, phyla and kingdoms, than are their differing modes of growth (see Antcliffe & Brasier 2007). Fortunately, an excellent tool for understanding the growth of long dead organisms is Morphospace Analysis. By this, we mean a graph in which each ordinate has geometric significance, and in which the geometry may be illustrated for selected ordinates at the ordinate point. Hitherto, such morphospace analysis has been undertaken on several groups: molluscs and brachiopods (Raup 1966), foraminiferans (Brasier 1980, 1982), graptolites (Fortey & Bell 1987), bryozoans (Gardiner & Taylor 1980, 1982; McKinney & Raup 1982), higher plants (Honda 1971) and even bird's feathers (Prum & Williamson 2001). Such morphospace studies provide a useful, theoretical structure for the quantification of form, for the accurate discussion of variations in form, and for generating pointed questions about the functional morphology of the group to be posed (such as 'why do these forms exist and not others?'). The most famous morphospace is, of course, that put forward for coiled shell morphology by Raup (1966) based on the logarithmic spiral mode of growth, following the pioneering work of Thompson (1917). This 'Raupian' morphospace was so constructed as to include all mollusc groups, as well as some rhizopod protists and some of the Lophotrochozoa.

Several important conclusions can be drawn from the morphospace of Raup (1966), that are hugely important in evolutionary terms, but which have received scant notice. First, and remarkably, all of the univalved and bivalved molluscs fit into this morphospace. Second, the presence of nearly all molluscs within this morphospace can be taken to imply their unity as a clade. In other words, limited exploitation of morphological possibilities may be taken to imply shared evolutionary constraints from a common ancestry. Those that are absent from this morphospace (for instance the heteromorph ammonoids and vermetid gastropods) are

members that have diverged in their mode of growth from the molluscan 'archetype' described by the Raupian model. It could therefore be argued that the Raupian morphospace provides an incomplete description of the Mollusca. However, it does contain all major molluscan groups—it is only derived subgroups within these that depart from the rules of Raupian morphospace. Third, the mode of growth described in the Raupian morphospace may be representative of the initial conditions for the molluscan growth system.

Morphospace analysis is surely a valuable tool that may yet be shown to have the potential for discrimination between higher taxonomic units. Exceptions that depart from a prescribed morphospace (see above) should not, of course, be taken to imply the formation of new, higher taxa. Like any other feature in phylogenetic analysis, a distinction needs to be made between those situations in which the mode of growth can be considered as a homology, and those in which it would tend to mislead our interpretation of higher taxonomy as a result of homoplasious behaviour. Such a situation is seen, for example, in the heteromorph ammonites and vermetid gastropods previously mentioned. Here, the novel feature of uncoiling is swamped by other homologies (such as embryology, mantle and gills) that clearly imply that these forms are indeed molluscs. Patterson (1982) has helpfully discussed the kinds of criteria needed to establish a given feature as a homology. One criterion is that of 'ontogenetic procedures', notably those of embryonic development, which are likely to be closely linked to the modes of growth. Clearly, the use of homologous growth modes for the determination of higher taxonomic affinities is an interesting, but complex, issue. For the present, we are content to draw attention to the idea that mode of growth is, potentially, a very informative feature for the decoding of long extinct organisms.

There is, of course, little value in developing a morphospace that cannot be easily related to the actual geometry of organisms (McGhee 2001). Thus, the development of a morphospace must be intimately connected to realistic methods for the actual measurement of form. There has been a growing movement over the last decade to quantify morphology in detail. These measurement methodologies have arisen largely in response to the populational approach demanded by evolutionary theory. These methods, termed morphometrics ('measurements of form'), have proven very successful at revealing natural groupings and evolutionary trends (e.g. Hughes 1999). McGhee (2001) has discussed the derivation of morphospaces and their integration with morphometric methods to provide what he termed 'a (complete) integrated theoretical morphometry' of the

organism. Although such studies are currently unusual, they clearly point the way forward for palaeobiological research.

Most morphospaces (certainly any biological ones, as opposed to ones quantifying Neolithic axe heads for instance) so far developed make assumptions about the mode of growth. Such morphospaces cannot, however, be directly applied to any group of organisms for which we do not know the mode of growth. We can turn the problem around, however. Rather than using a model of growth to derive a morphospace, we can use a general morphospace (where growth is not an assumed factor) to learn about the mode of growth and thereby make reasoned biological inferences. This is the essential paradigm of our methodology. In such a morphospace, the organisms will 'grow' through the space rather than being confined to a particular point throughout its ontogeny. In this way, the pathways that extinct fossil organisms mark out through their growth may be able to reveal something valuable about the developmental procedures of their group. The greater the number of forms that are parametricised and 'fitted in' to the morphospace, the more robust will be the conclusions that may be drawn.

Formulation—a theoretical morphospace for the Ediacara biota

Here, the formulation of a theoretical morphospace that has general applicability is outlined as is its potential to describe taxa of the Ediacara biota and their possible relatives. The derivation begins with an appreciation of how to define the relationships between points in space.

Mode of line origination (M)

The parameter *M* describes how any given line originates and terminates. This can be best displayed by illustrating *M* as a 'branching tree'. This should not be taken to infer a bifurcating system, though this is allowed by the system. Given a line in space with an origination point and a termination point, then *M* describes how another line in space relates to this line.

In order to do this, we require that there is also another point (termed a node) that lies somewhere on the line defined by the two points. At this node, another line finds its origination point (see Fig. 1b).

After a node, it is necessary to define whether there are additional nodes between node 1 and the termination point on the original line, and whether

there are any nodes on the new line. This is what is formalized by the parameter here called *M*.

In the continual bifurcation, each line originating from the node has another node somewhere along its length before termination. The nature of termination in such bifurcating systems was discussed by Fortey & Bell (1987) with respect to multiramous graptolites, though it should be noted that they did not formalise the line origination in this manner, since they had no need to do so for the purpose of their study.

The inter-point function, $F(x, y, z)$

In the discussion above, the form of the line between the origination and termination points was assumed to be linear. This form is again shown below, but now with the addition of Cartesian axes. In the general case, $F(x, y, z)$ may be a complex function in three dimensions. That is, it may not entirely lie in the x - y plane. In any case, the form of the inter-point function can be described by a Fourier series, though it may differ as to whether a two- or three-dimensional form is required.

Additionally, it would be possible for the inter-point function to take an ellipsoidal or other closed form (any polygon). This would allow a very accurate description of segmented and septated forms. Again, this could be achieved by Fourier series and effectively incorporates the field of outline analysis (as in studies by Foote 1989; Harper & Owen 1999). The linear form is here taken for the inter-point function. This is a reasonable approximation for most of the forms to be considered, and it is certainly a sensible starting point. However, the natural extension of the work to more complex forms of the inter-point function needs to be noted. Though these will not necessarily alter any of the evolutionary interpretations that can be made, they will make the 'morphospace individuals' look more like real fossil specimens.

The position of the node—the k ratio

The position of the node along the line can now be outlined for the general case. The k ratio for a given node is defined as follows:

$$k = \ell / L$$

Where: L is the linear distance measured between the two adjacent nodes (or an equivalent termination/origination point) on the line, as shown in Fig. 1e, ℓ is the distance between the node in question and the previous node on the line (or origination point is here called ℓ). Note that by definition, there cannot be another node after the termination point.

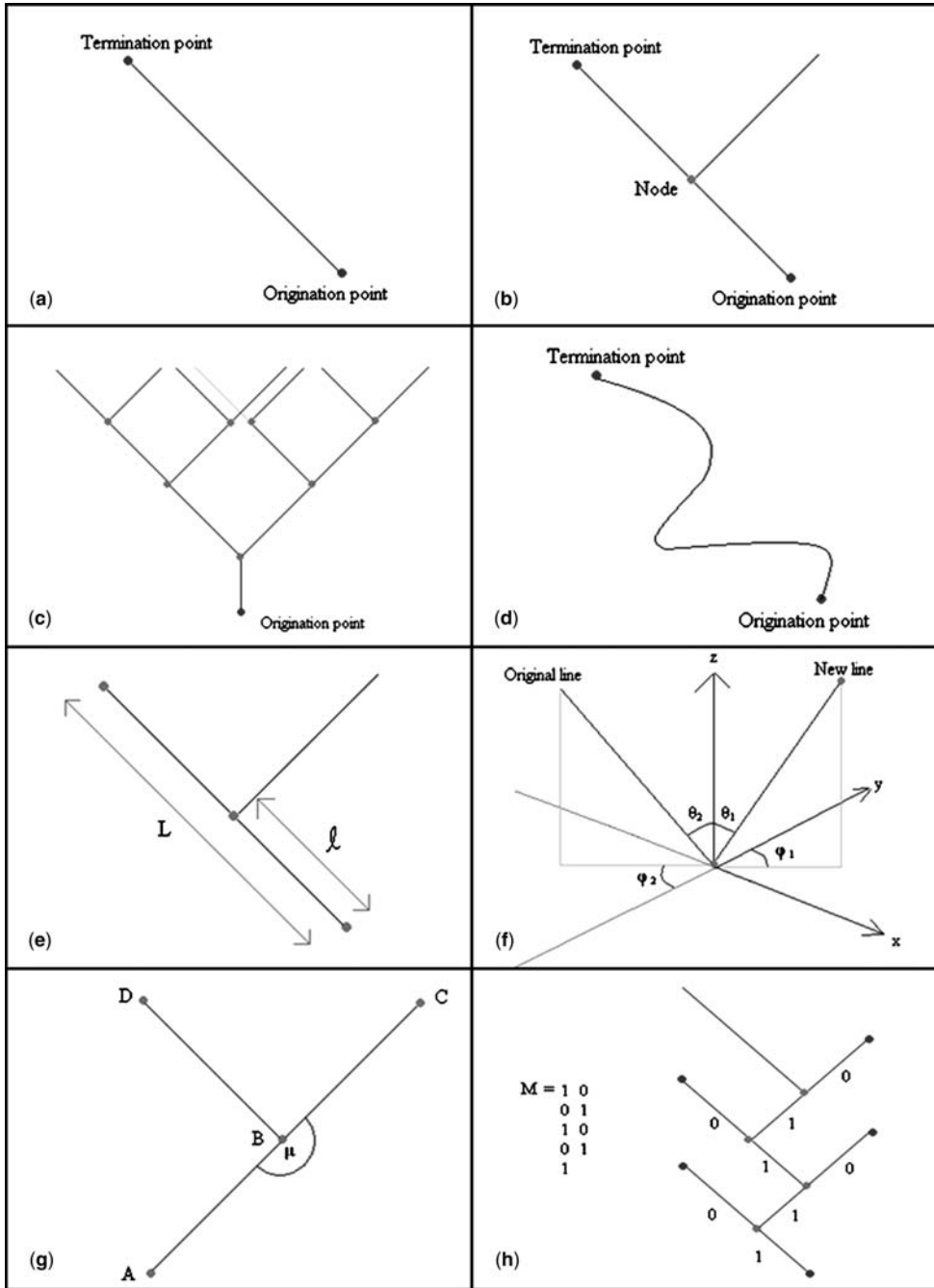


Fig. 1. (a) A line in space defined by an origination point and a termination point. The form of the line between these two points requires another parameter to describe it. (b) The same line in space but with another line originating along its length. (c) The form of M determines the style of line origination and thus influences the overall topology of the form. (d) A more complex form of the inter-point function. (e) Illustrating the measurement of L and ℓ so as to allow the calculation of the parameter k . (f) The angular relations of the two lines. (g) The orientation of the original line after a node must be specified—this is achieved with parameter μ . (h) The statement of M applicable to geometry removes a large range of potential forms from the morphospace—for instance, all bifurcating perpetuating systems (e.g. as in multiramous graptolites, trees).

By taking the ratio of these two lengths, we have produced a dimensionless parameter that will not be altered by the size of the organism *per se* but may vary throughout ontogeny as a result of the mode of growth.

The position of the new line

The new line takes its origination point at a node on the previous line, as described by k . We require, however, another point to define this new line uniquely in space. This point is the termination point or the first node on the next line. The position of this line in relation to the previous one can be described uniquely in space by the presence of just four angles (see Fig. 1f).

Note that the origin lies at the node from which the new line originates. The orientation of the z -axis is problematic. It could be taken to be the long axis of the organism in question, which would be applicable to many forms. However, the long axis may be obscure in several easily imaginable ways. A slightly more applicable (if less detailed) approach is to assume that ϕ_1 and ϕ_2 are equal (so that the form can be described with only two axes) and that θ_1 and θ_2 are equal (and so we take half the angle between the two lines to get θ values.) This allows a logical extension of the study to understand the nature of the z -axis in any forms where it was forced to distort from node to node and through ontogeny.

Orientation of the original line after a node— μ

Consider Fig. 1g. The orientation of the line BD has been determined with respect to the line BC. However this needs to be calibrated by stating the orientation of BC with respect to AB. After all, there is no particular reason that ABD could not be considered the original line and B the node for the origination of the new line BC. By making the following definition, this ambiguity can be removed. The original line is that which continues through the node, with μ closest to 180° . Note that it is not necessary to specify the Cartesian geometry in this case, because for any two lines that share a common point (the node) in space, there is a unique plane that contains both lines— μ is measured in this plane.

A plane for Ediacaran geometry

By taking several particular cases to the treatment above, it is possible to define a plane of the morphospace that will clarify the geometry of many members of the Ediacara biota. It is also possible to define (M) so that is applicable to many

members of the Ediacaran biota, as illustrated is Fig. 1h.

Note that the value of μ is shown to be 180° ; hence this parameter need not be considered further in relation to our Ediacaran geometry. The structure above is planar, so there is also no need to specify values of ϕ (and the associated complexity of determining an appropriate x - y plane). We have already stated that the inter-node function, (F), shall not be considered further in this work. Thus, a plane for Ediacaran geometry can be defined with only k and θ as variables. It should not be forgotten, of course, that this is a 'morphospace creature' and not a real one. It need not necessarily look exactly like a particular form in any given case. Further, the choice of the origination point, nodes, and terminations points is effectively arbitrary. It is simply required for them to have some consistency across the study, and it is sensible to choose a particular point that can be located on all forms of interest (there is an extensive literature on landmarks as homologies and we refer the reader to Macleod 2001 and Zelditch *et al.* 2001). Thus the line represented by $F(x,y,z)$ does not have to correspond to any given line of actual organism geometry.

It is now essential to relate these parameters to actual organism geometry, by choosing the location of the morphospace nodes using morphometric landmark analysis (*sensu* Bookstein 1991). The example shown is that of *Phyllozoon hanseni* (Fig. 2a, b), which is deliberately chosen because it is a distorted specimen that requires additional treatment before the morphospace, parameters can be extracted. Landmarks are selected that define the geometry of the specimen (Fig. 2b)—consistent with the extraction of the morphospace parameters. An origin for a coordinate system is selected (the top left pixel of the image—this is rather arbitrary and has no effect on results) such that the landmarks can be described by coordinates. The coordinates are then placed into a spreadsheet and viewed without the fossil (Fig. 2c). The approach is comparable to that of Hughes (1999). Regression lines are then fitted to this data to show where the form departs from the ideal (see Fig. 2d). The central axis should be straight; the trend lines quantify how the form departs from the ideal.

The illustrated form departs from ideal by 12° at around $x = 250$. A simple rotational matrix can be used to transform the data set so that no points are in 'incorrect positions'. It should be noted that this kind of work varies specimen-by-specimen and so the method has to be subtly adapted to suit the nature of the deformation. The restored form can be seen in Fig. 2e.

It needs to be stated that while the form still appears to be asymmetric, this cannot be assumed

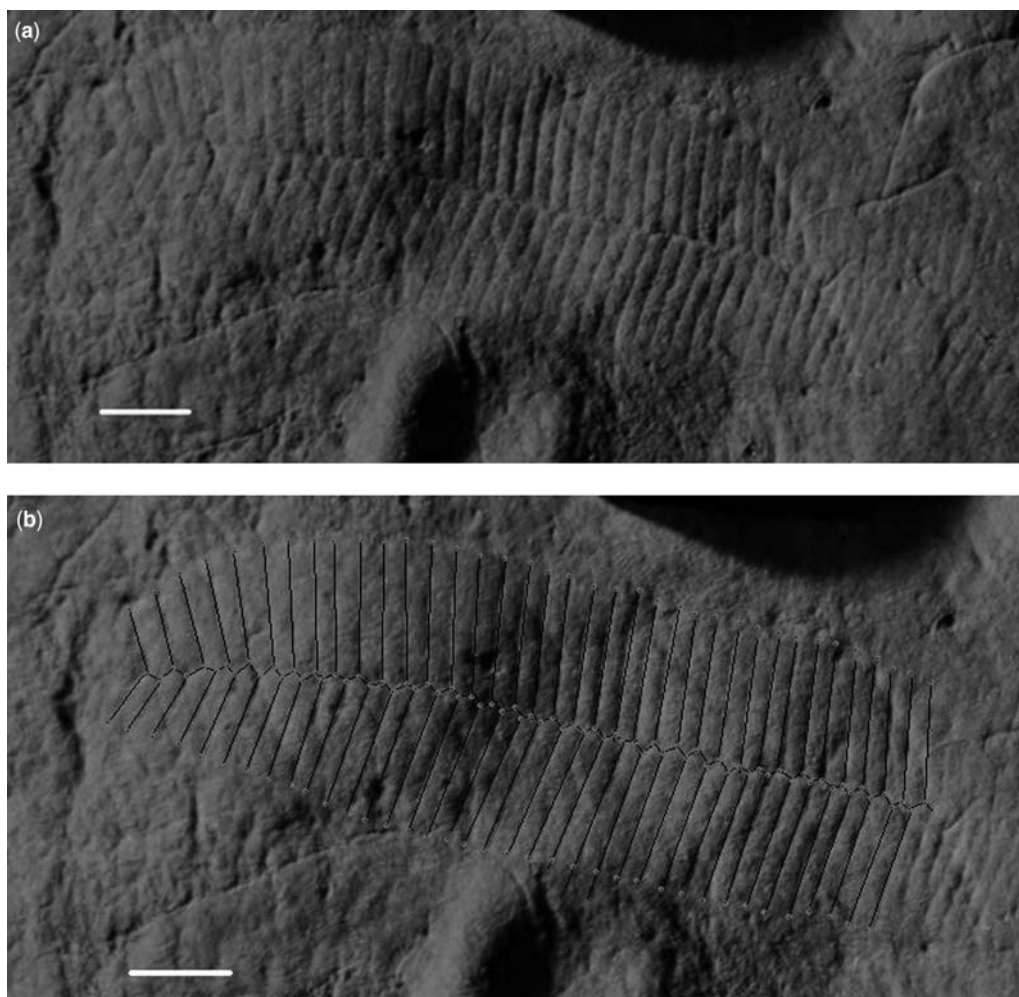


Fig. 2. (a) An image of *Phyllozoon hanseni* from the Flinders Ranges. Photograph: M. D. Brasier. Scale: 1 cm. (b) The same image with morphometric landmarks to define the geometry. Scale: 1 cm. (c) Landmarks are extracted for numerical analysis. (d) Regression analysis of the landmark data. (e) The form after it has been undeformed. It is also a reflection of the image as was previously shown. (f) Illustrating how morphospace parameters are extracted from the restored form.

to be a taphonomic effect because the asymmetry may represent the actual organism geometry. Indeed, Seilacher (1989) and many others have suggested that this asymmetry is a characteristic of Vendobionta construction. From this, the points can be reconnected and the appropriate morphospace parameters extracted. If deformation is not removed, we find that there is little effect upon the morphospace parameters for the majority of the specimens because only those nodes with $x < 250$ have been altered.

For every node, there is a value of k and θ . The orientation of the nodes describes the entire

geometry of the form, thus the k and θ pairs for every node will also describe the whole organism. By plotting k against θ , it is thereby possible to characterize morphology of many Ediacaran organisms.

Results and discussion

Preliminary morphospace results are here presented, (see Fig. 3; plots of k against θ) for taxa in the Ediacaran biota; *Charnia masoni* (holotype), *Phyllozoon hanseni* and *Charniodiscus* sp.

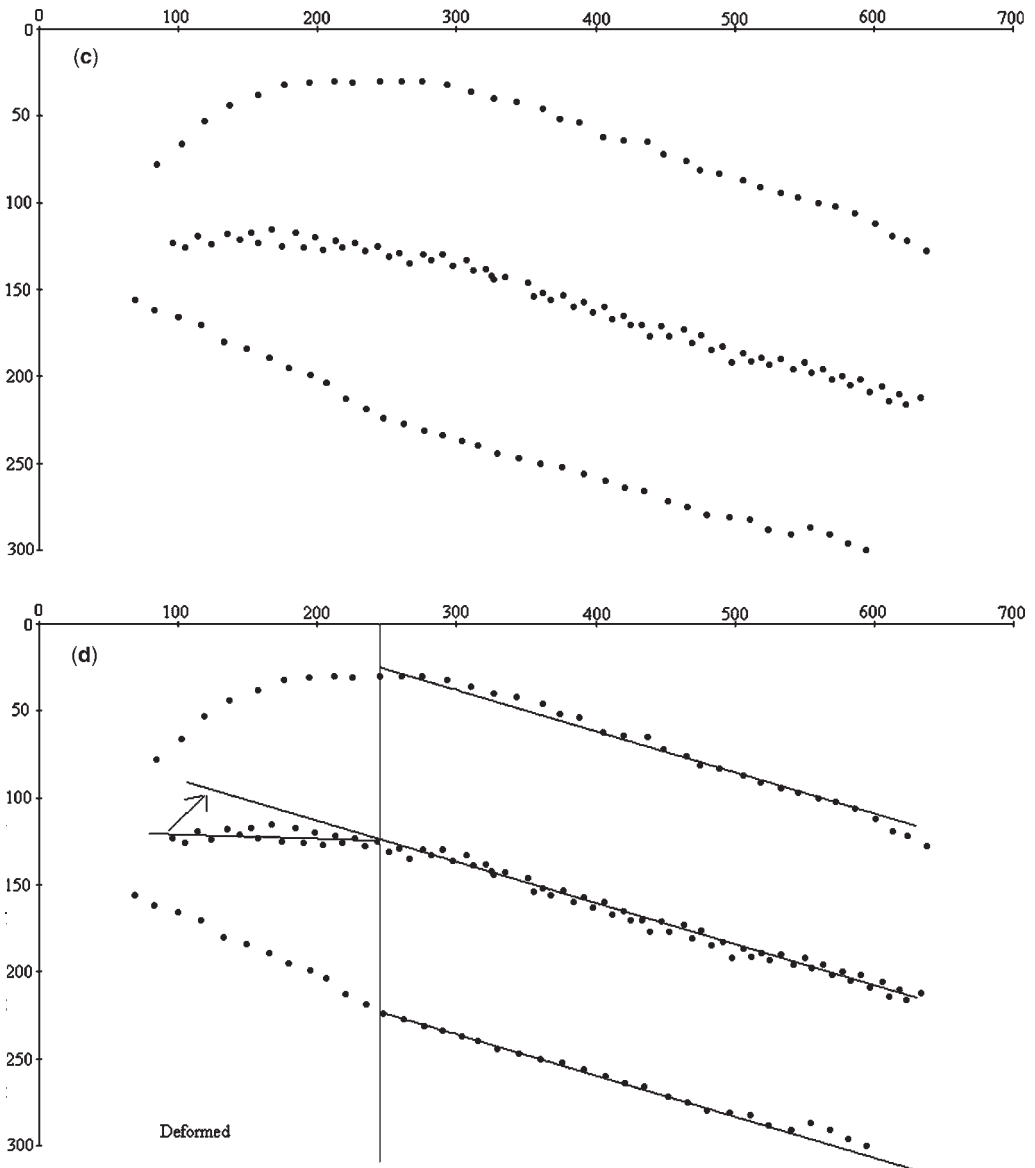


Fig. 2. (Continued).

(holotype). We also plot, for comparison, the plant leaves of living angiosperms *Musa* sp. (banana plant), *Calathea* sp., *Piper* sp., *Alocasia* sp. and *Curculigo* sp. A plot for the biserial foraminiferid *Brizalina* sp. (following the model from Brasier 1982) is also shown. It can be seen from this figure that many disparate Ediacara fossil forms (e.g. *Charnia* sp., *Dickinsonia* sp. and *Phyllozoon* sp.) share fundamentally similar morphospace parameters (k values are all confined to values

between 2 and 5, which is not true for any other group plotted). They are distinguished as a unique group within a morphospace plane and, significantly, they are not closely approached by many putatively similar groups such as the fronds of sea pens, biserial Foraminifera, and plant leaves. The latter show an interesting area of overlap but their total morphospace is much larger. We find that many other groups with suggested affinity to the Ediacara biota,

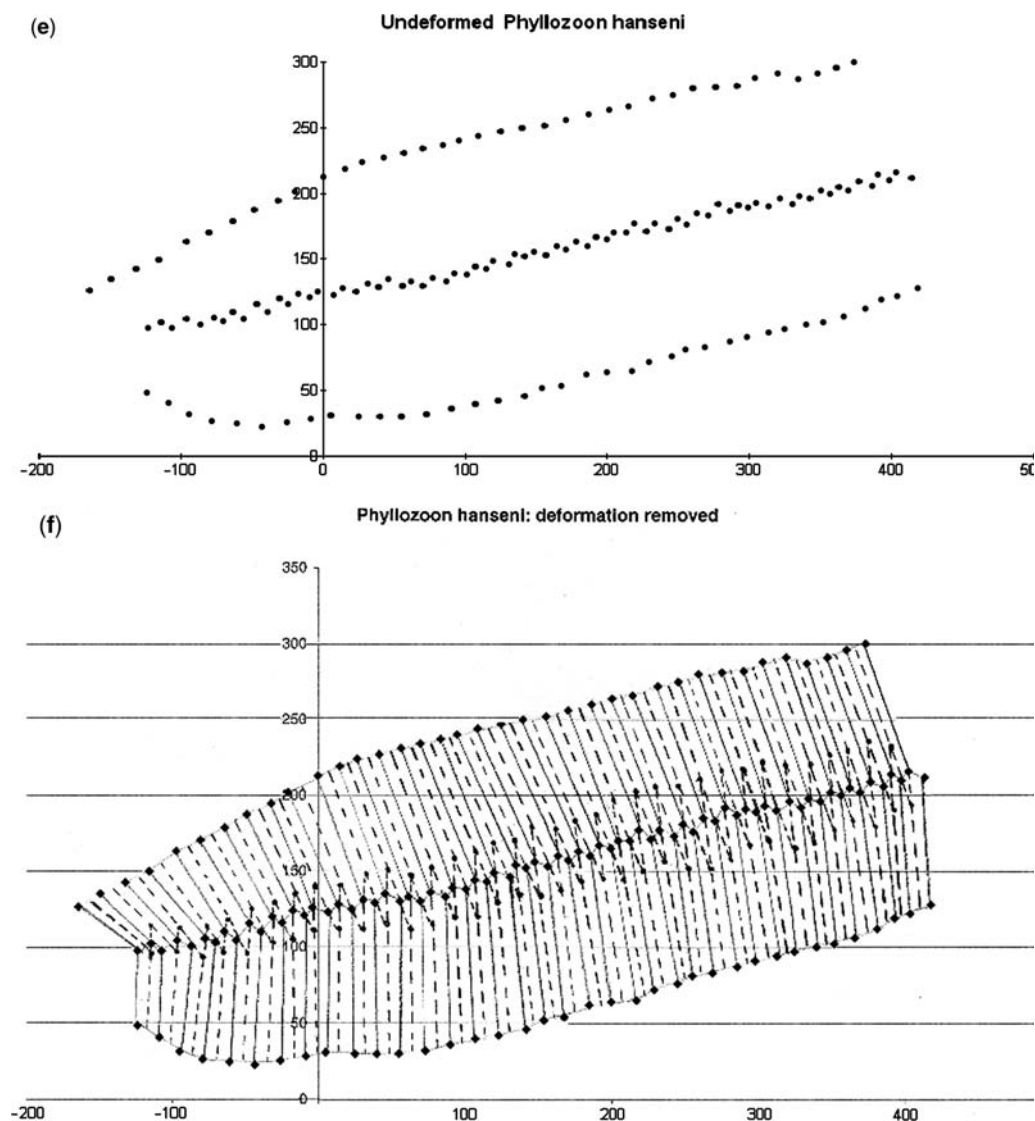


Fig. 2. (Continued).

particularly the xenophyophore foraminiferids (Seilacher *et al.* 2003) require very different parameters to describe them and do not plot in the same morphospace plane (except artificially by parameter projection—like a vector trace). Further morphospace work is required, using the best preserved fossil material, in order to determine the significance of the gaps in morphospace between the extinct Ediacara biota and putatively similar looking groups that are alive today. This should, ultimately, allow us to determine a viable

mode of growth for Ediacaran organisms and, therefore, test the potential higher taxonomic standing of this enigmatic group. At a lower taxonomic level, however, that is within the Ediacara biota, we may now tentatively begin to consider the significance of these early morphospace results. If members of the Ediacara biota are indeed closely related, then there should be a viable evolutionary progression with corresponding alterations in morphospace from the earliest forms to the later ones.

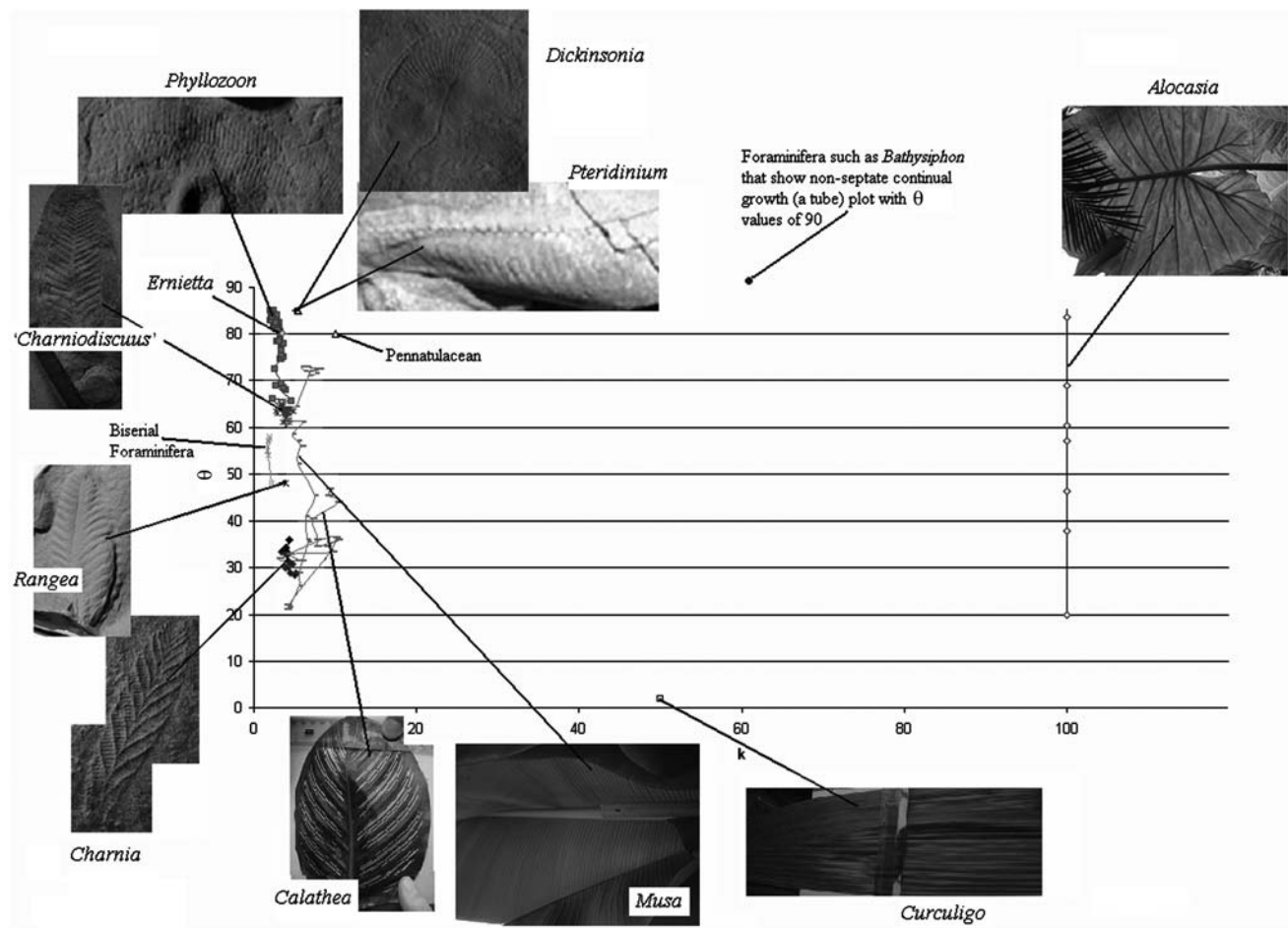


Fig. 3. Illustrates the paths in morphospace required to describe the following forms uniquely: *Charnia masoni* (holotype), *Phyllozoon hansenii* and *Charniodiscus concentricus* (holotype). Plant leaves of the following forms are also shown for geometrical comparison—*Musa* sp. (banana plant), *Calathea* sp., *Piper* sp., *Alocasia* sp. and *Curculigo* sp. A biserial foraminiferid following the model from Brasier (1982) is shown as well. It can be seen that many disparate Ediacara fossil forms (e.g. *Charnia* sp., *Dickinsonia* sp. and *Phyllozoon* sp.) occupy a similar region of the morphospace plane. Further, the interrelationships between members of the Ediacara taxa are only beginning to be understood.

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