

FLUID DYNAMICS OF THE GRAPTOLITE RHABDOSOME RECORDED BY LASER DOPPLER ANEMOMETRY

by BARRIE RICKARDS, SUSAN RIGBY, JERRY RICKARDS
and CHRIS SWALES

ABSTRACT. A precise laser based technique has been used to measure changes in fluid velocity over a range of graptolite models mounted in a wind tunnel. Results from this laser Doppler anemometer (LDA) show the flow to be altered significantly by spines on the sicula and by the morphology of the thecae. A single virgellar spine retards flow along the 'naked' (ventral) side of the sicula and directs it instead over the thecae. More complicated sicular spine arrays in Ordovician biserial graptolites produce trailing vortices and turbulence. These results are important for three reasons. First, they demonstrate that this tool offers a means of quantitatively and non-intrusively assessing the hydrodynamic function of aspects of graptolite morphology and has the potential to enable us to understand the specific oceanic conditions for which graptolites evolved. Second, they show that, with flow controlled by sicular and thecal morphology, the zooids were unlikely to have fed within the stagnant zones of the thecal apertures; it is more likely that they fed at some distance from these apertures, either with lophophores extended into the sea or having themselves crawled along spines. The stagnant or quiet zones provided a resting position. However, it remains to be tested if food particles have a tendency to accumulate in these stagnant zones. Third, as graptolite models are stable in fluids only when flow is from sicula to nema, it seems likely that graptolites with relatively simple metathecae arrayed themselves in this fashion relative to motion in the oceans.

FOR most of this century graptolite research has focused on the objective of understanding the rhabdosomal and thecal morphology of specimens which have usually suffered varied diagenetic and tectonic alteration. An important spin-off from this work has been an appreciation of evolutionary lineages and hence the determination of a precise biostratigraphy. But, until recent decades, attempts at an understanding of the functional morphology of the class Graptolithina, or of the hydrodynamics of the planktic order Graptoloidea, have been limited.

Some suggestions have been rather bizarre, such as that of Nimmo (1847) who considered that graptolite stipes were merely the serrated tail spines of *Raja pastinaca*, the sting ray. Of the serious hypotheses, that of Lapworth (1897) that the planktic forms were actually epiplanktic, enjoyed popularity in the first half of this century, but was eventually abandoned in view of the lack of evidence for any form of attachment: indeed synrhabdosomes could not be epiplanktic in any circumstances. Bulman (1955, 1964, 1970) and Kozłowski (1966, 1970) surveyed the body of evidence supporting the idea that the graptoloids were holoplanktic and acted in passive response to the vagaries of ocean currents. This was essentially the approach adopted by Rickards (1975), who tended to support Bulman's concept of vacuolated tissue rather than Kozłowski's (1970) concept of large gas-filled, bulbous membranes. The weakness of several of these arguments supporting passive response, especially of Bulman's (1964) model which argues against diurnal migration of the colonies, was highlighted in Kirk's (1969, 1972) papers, which pointed out that graptolites would have starved if they had not moved position relative to the enclosing water mass. Hence Kirk adopted an automobile model in which concerted zooidal activity moved the colonies by spiralling them up and down. Bulman (1964) was not opposed to spiral movements, comparing

the probable movement of *Cyrtograptus* to that of the living umbrella sponge *Axoniderma*, which spirals upwards in response to the slightest ocean turbulence, and then reverses the process as turbulence wanes. The arguments against the automobility hypothesis were discussed by Rickards (1975) and will not be repeated here. When Bulman was researching his 1964 paper, both researchers had extensive discussions with marine biologists working on planktic communities. Whilst these workers were wholly opposed to automobility and in favour of passive response and vacuolated tissue, they insisted that the colonies would have to move through the water in some fashion. It is important not to conflate the two arguments. Movement of graptoloids relative to water was clearly vital, but the method of movement remains in dispute.

An important effect of all these studies was to focus attention for the first time not merely upon the mode of life of graptolites but upon their possible hydrodynamic function. This was investigated further by Rigby (Rigby and Rickards 1989; Rigby 1991, 1992) who suggested, from testing graptolite models, that the rhabdosomal morphology itself caused spiral motion: thus multi-branched dichograptids as well as sparsely branched diplograptids and monograptids would have been capable of spiralling through sea water. More recently, Rickards (1996) outlined arguments for the nema and virgula being rotational agents. The work of Jenkins (in press) on turbulence in the ocean has demonstrated that finer scale features of the rhabdosome were important to graptolite hydrodynamics. The effect of these structures can only be assessed using physical models. The modelling by Rigby (in Rigby and Rickards 1989) and by Melchin and Doucet (1996) have provided useful insights into graptolite hydrodynamics but have failed to quantify accurately flow over a rhabdosome. We present such quantitative results here.

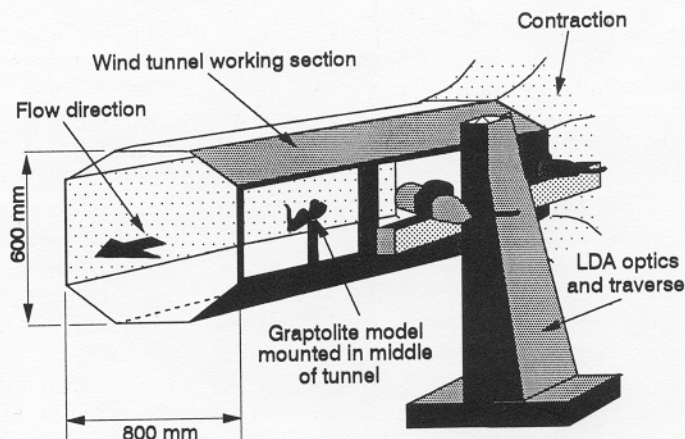
Experiments using accurate models of graptoloids in controlled conditions of fluid flow offer the possibility of assessing the effect of spines and thecal morphology on the movement of fluid over a rhabdosome. Such movement would have occurred regardless of whether the rhabdosome was still, with water passing over it, or in motion through still water. The effects would have had importance for the colony as a whole, in terms of the drag produced by the rhabdosome, and for the individual zooids which must have fed from water moving past the thecal apertures. In the present study, the impact of variations in thecal morphology and the effect of spines at the proximal end of graptolite colonies are assessed with respect to their effect on fluid dynamics.

PREVIOUS USE OF HYDRODYNAMIC ANALYSES

Relatively few studies have been undertaken in which models of fossils were tested for their hydrodynamic properties. Those which have been conducted have investigated two properties of fossil organisms; rates of feeding and rates, or means, of movement.

Feeding experiments were initiated by Rudwick and Cowen (1968), who analysed the likely feeding patterns of aberrant strophomenides through the construction of anatomical models. Later work, such as that of Melchin and Doucet (1996) on graptolites, has emphasized the potential of these methods. Melchin and Doucet reported that currents reaching a conical colony entered the cone via the sides, between the stipes, but left by the aperture of the cone (i.e. upwards).

The first and seminal work using models to assess the hydrodynamics of movement in fossils was that of Jefferies and Minton (1965), who tested aluminium models of the bivalve *Bositra* to estimate sinking rates of this form. In these experiments, fluids of different viscosities and models of fixed size were used to estimate sinking velocities of bivalves with different sizes and densities. Based on their results, Jefferies and Minton were able to suggest that the presence of tentacles might have enabled *Bositra* to sink slowly at all growth stages. This was considered positive evidence for an epiplanktic mode of life when considered with other lines of argument. Later work on trilobites (Fortey 1985) has used models of species with different body shapes to assess the likelihood of a nektic mode of life from the frictional drag created by each shape. Real size models of the trilobites were suspended in water, moving at varying speeds. Displacement of the model was used to calculate drag and dye streams were used to visualize the wakes created by the models.



TEXT-FIG. 1. Bristol University wind tunnel, showing the configuration of the model in an air stream, within the working section of the array.

Simple modelling of graptoloids (Rigby and Rickards 1989) demonstrated that a variety of shapes of rhabdosome created a spiralling motion which would have been advantageous to a living graptoloid colony. Models of real size and likely density were allowed to fall through fresh water and sea water (see Rickards and Rigby in press) and their rates of fall and orientations during movement recorded visually and with video cameras.

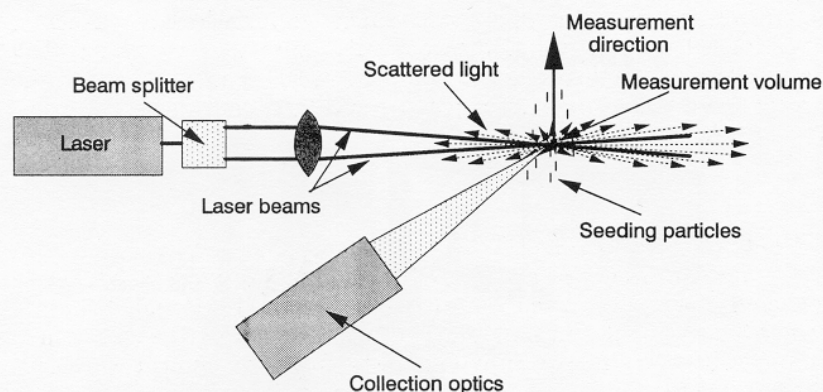
Each of these studies has demonstrated the value of physical modelling in assessing the likely hydrodynamic properties of fossil organisms. However, in a sense, all have been qualitative guides rather than quantitative assessments of the flow. The problem has been resolved in the present study by the use of laser Doppler anemometry, a technique which offers the potential to collect large amounts of accurate velocity data from the flow around models of fossils.

EXPERIMENTAL TECHNIQUE

The above discussion has highlighted the need for a better understanding of the nature of fluid flow around graptolites. In order to simplify the acquisition of flow velocity measurements in the region of the thecae and around the sicular aperture, larger scale models of graptolites were used for this work. In order to avoid the difficulties of taking measurements on an object as it moves through a fluid (Bradshaw 1970) the experiments were performed in a wind tunnel. A wind tunnel provides a uniform stream of air over a fixed model placed in the working section, hence giving equivalent conditions to the model moving through a stationary fluid. Text-figure 1 shows the principal components of the low speed wind tunnel employed for these tests (Department of Aerospace Engineering, University of Bristol). Simple numerical conversions render measurements in air comparable to those in water.

Measurement of fluid flow

Numerous techniques are available for the investigation of airflows. Most methods are qualitative in nature, providing only a visual indication of the flow behaviour, and consequently are limited in their value. However, they are easy to employ and cheap, and are thus still widely used. Examples include the injection of dyes/pigments or smoke into the flow to indicate its overall direction, and the use of tufts attached to surfaces which move to align themselves with the flow.



TEXT-FIG. 2. Introduction to LDA theory. Seeding particles are counted and their velocity and direction measured by their scattering effect on light collected from three mutually orthogonal laser pairs.

In addition, there are several quantitative techniques which are available for flow measurement. The two most commonly used quantitative techniques are pitot-static probes, relying on measurement of dynamic air pressure which is proportional to the square of the velocity, and hot-wire anemometers. A hot-wire anemometer consists of a very fine wire, typically $5 \mu\text{m}$ in diameter, which is heated by an electric current and mounted on the prongs of a small 'fork' positioned in the airflow. As the air flows over the wire it tends to cool it down, thus reducing its electrical resistance. Consequently the wire can be calibrated to indicate velocity in terms of the additional current required to maintain the wire at a constant temperature.

Optical methods of flow measurement have been in use for around 30 years but it is only recently that reliable commercial systems have become available. Laser Doppler anemometry (LDA) is probably the most commonly used of these due to its excellent reliability and accuracy. Most current LDAs operate by the Differential Doppler technique (Drain 1980). In this method two laser beams overlap to form a small region known as the *measurement volume*. When small seeding particles (typically around $1 \mu\text{m}$ diameter), which are injected into the flow, pass through the measurement volume they scatter two distinct frequencies of light. This Doppler effect is due to the difference in relative velocity between the seeding particle and the point of origin of each of the two laser beams. When the scattered light is collected by a photodetector the two light signals interfere with each another, producing a 'burst', the frequency of which is directly proportional to the velocity of the particle and hence the airflow. The measured velocity vector is in the plane of the two intersecting laser beams and perpendicular to their bisector (Text-fig. 2).

The three component Dantec LDA system used for these tests has three such pairs of beams, each pair of different wavelength, and therefore three velocity components can be acquired simultaneously from which the magnitude of the flow in any direction can then be determined. The three pairs of beams are emitted from two optic heads mounted on a triaxial traverse mechanism and are focused to a single common measurement volume which is approximately spherical and less than 0.1 mm in diameter. The traverse mechanism can position the measurement volume at any point in space within a $0.6 \text{ m} \times 0.6 \text{ m} \times 0.6 \text{ m}$ virtual cube, to a resolution better than 0.01 mm . Each optic head is able to receive scattered light as well as to transmit the laser beams. This collected light is passed via fibre-optic cables to three photomultipliers, which convert the scattered light into electrical signals. These signals are processed to obtain the Doppler frequency and hence the flow velocity by three Burst Spectrum Analysers, one for each wavelength.

The LDA has several advantages over pitot-static probes and hot-wires. The technique is non-invasive; in other words, it does not affect the flow it is trying to measure. In addition, it is able to

measure both the direction and magnitude of the velocity vector, which is essential in regions where reversed flow is expected, such as around thecae. Furthermore, the 3 component LDA system used in this work is able to measure three velocity components simultaneously and at the same point in space. Other techniques cannot offer true spatial coincidence and thus cannot match the spatial resolution of the LDA.

Experimental set-up and the graptolite models

Scale models of graptolites were tested within Bristol University's low speed, low turbulence wind tunnel as is generally the case in wind tunnel testing. Vogel (1981) stated that 'it is possible to compare flow over bodies of different sizes, and between air and water, as long as there is a similarity of Reynolds number between the two situations'. The Reynolds number is a dimensionless index which helps to describe the interaction between solids and fluids. It can be defined as:

$$Re = lU/u$$

where l = characteristic length of the model (or the real specimen) in the direction of flow, U = velocity and u = kinematic viscosity of the fluid. The kinematic viscosity of sea water at 20 °C is $1.047 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$, while for air at the same temperature it is $1.5 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$.

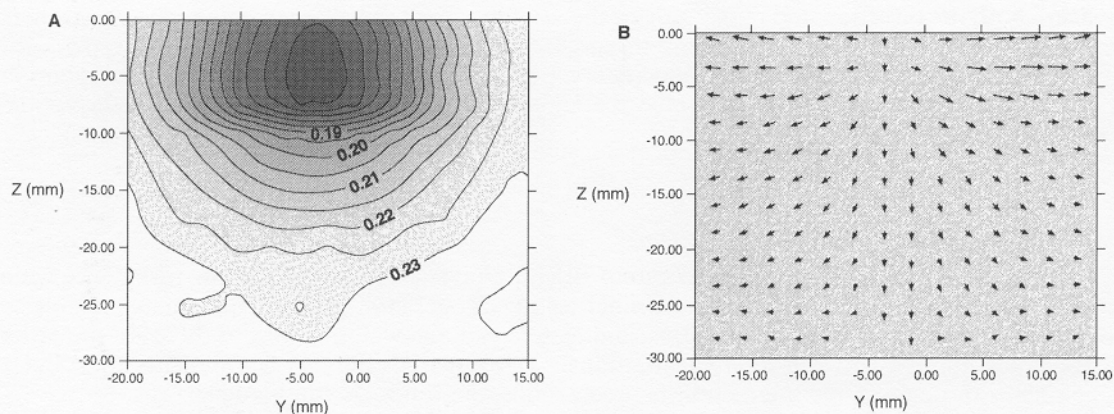
Essentially, the principle of dynamic similarity has been used in these experiments to ensure that comparison is valid between the models and reality. However, the velocity of a graptolite in seawater is an unknown in this equation, and would clearly have varied with oceanographic conditions. It is necessary to estimate likely speeds, and to establish extremes beyond which a graptolite would have been unlikely to go during normal conditions. The simplest method of estimating likely graptolite velocities is by analogy with modern plankton. Diel migration is almost ubiquitous in this group and most movement is of the order of 50–400 m in 12 hours (Raymont 1983). As they move both up and down in this time, these figures are effectively doubled and give velocities of $2.3 \times 10^{-3} \text{ ms}^{-1}$ to $2 \times 10^{-2} \text{ ms}^{-1}$ (Raymont 1983). In reality, this is probably the lower end of the velocity spectrum which graptolites experienced, as turbulence in the sea water surrounding them would have subjected them to velocities which were orders of magnitude greater than this. Although the overall movement might have been relatively small, an object suspended in sea water would be extensively buffeted in most conditions so that the total movement would be much larger than the apparent distance covered.

The wind tunnel used in this series of experiments runs at a minimum velocity of 0.1 ms^{-1} . For the model of *Amplexograptus maxwelli*, this gives a Reynolds number for the model of 1733, which is dynamically similar to a real specimen moving at a velocity of 0.28 ms^{-1} . This is higher than the minimum values predicted from considerations of the modern system, but well within the range of velocities encountered by plankton in modern oceans (Raymont 1983). Although not ideal, this is considered a good first approximation. The same reasoning also applies to the other two models.

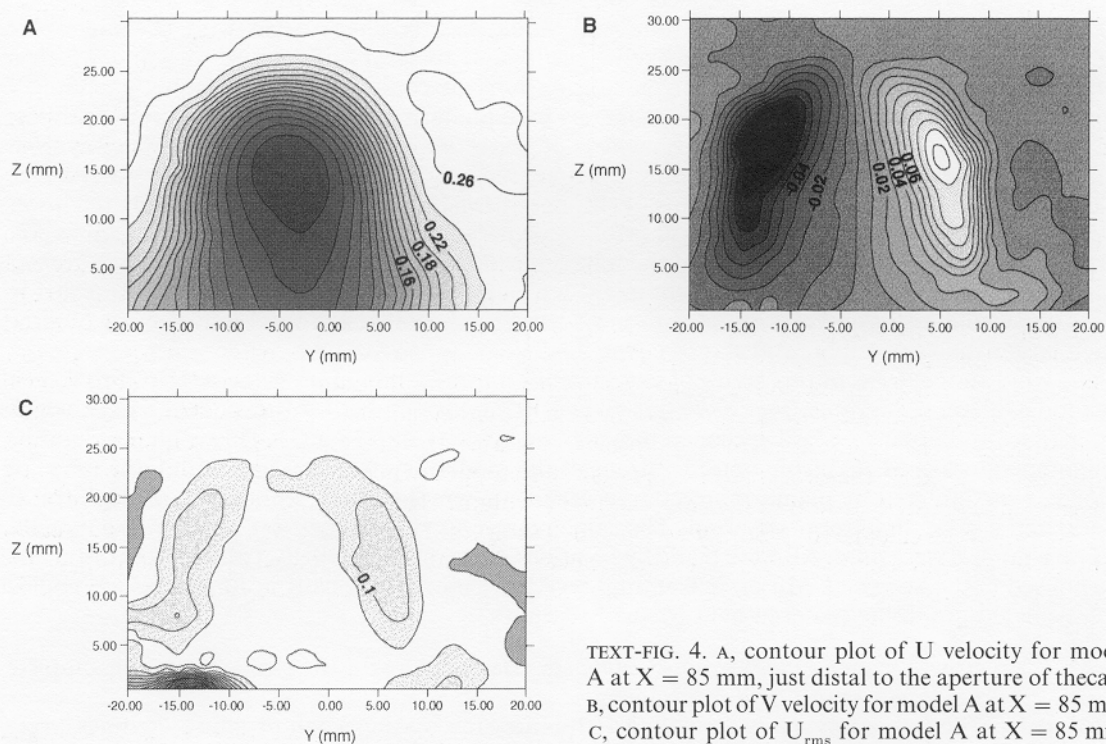
Three models were used. All were made by Cynthia Clarkson in the 1950s, from a waxy resin, and are housed in the Sedgwick Museum, Cambridge. All are morphologically accurate and are copied from isolated graptolite material held by the Museum:

1. An early growth stage of *Saetograptus chimaera* (Barrande) with the sicula and an incomplete th1, 75 times larger than the real specimen.
2. A model of *Saetograptus chimaera* with three thecae, each bearing a pair of spines, 75 times larger than actual size.
3. A model of *Amplexograptus maxwelli* with six thecae, of which th2³ is incomplete, 40 times larger than actual size.

The model graptolites were mounted on a slim strut in the centre of the wind tunnel working section (Text-fig. 1), with optical access for the laser beams provided through a glass window. The

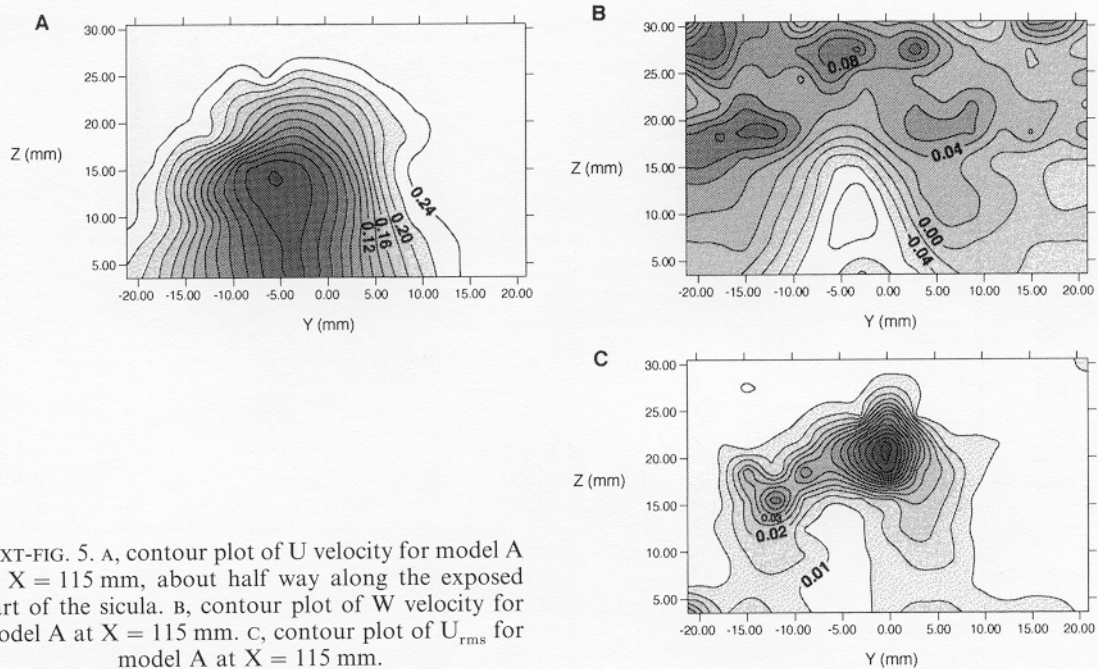


TEXT-FIG. 3. A, contour plot of U velocity for model A at $X = 16.5$ mm, just proximal to the sicular aperture. In all of these figures, the X axis runs parallel to the long axis of the colony, beginning at the tip of the virgular spine and ending at the tip of the sicula. Y and Z axes are mutually orthogonal to this, the Z axis being vertical. B, vector plot in YZ plane for model A at $X = 16.5$ mm.



TEXT-FIG. 4. A, contour plot of U velocity for model A at $X = 85$ mm, just distal to the aperture of theca 1. B, contour plot of V velocity for model A at $X = 85$ mm. C, contour plot of U_{rms} for model A at $X = 85$ mm.

models were positioned in the wind tunnel so that fluid flow was from the sicula to the nema as this is believed to be the only hydrodynamically stable position for a body of this shape. The axis system was such that the X direction was horizontal, the Y and Z axes formed an orthogonal grid at right



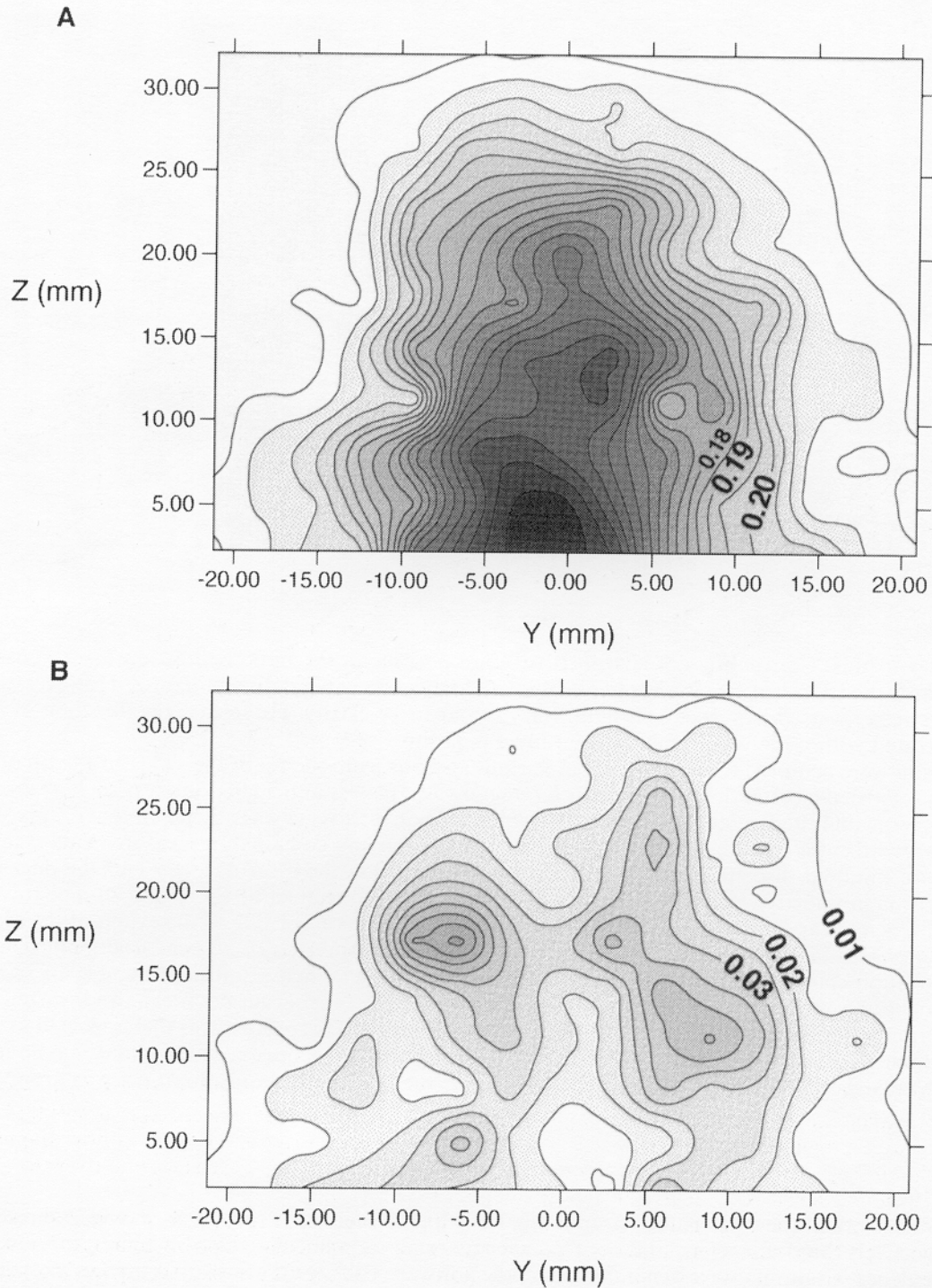
TEXT-FIG. 5. A, contour plot of U velocity for model A at $X = 115$ mm, about half way along the exposed part of the sicula. B, contour plot of W velocity for model A at $X = 115$ mm. C, contour plot of U_{rms} for model A at $X = 115$ mm.

angles to this. Conventions of sign in Bristol are positive in the upflow direction for X , positive towards the LDA traverse for Y and positive in a vertical downward direction for Z . However, these have been reversed in subsequent figures in this paper for clarity (i.e. so that the direction of flow generated within the main body of the tunnel is positive).

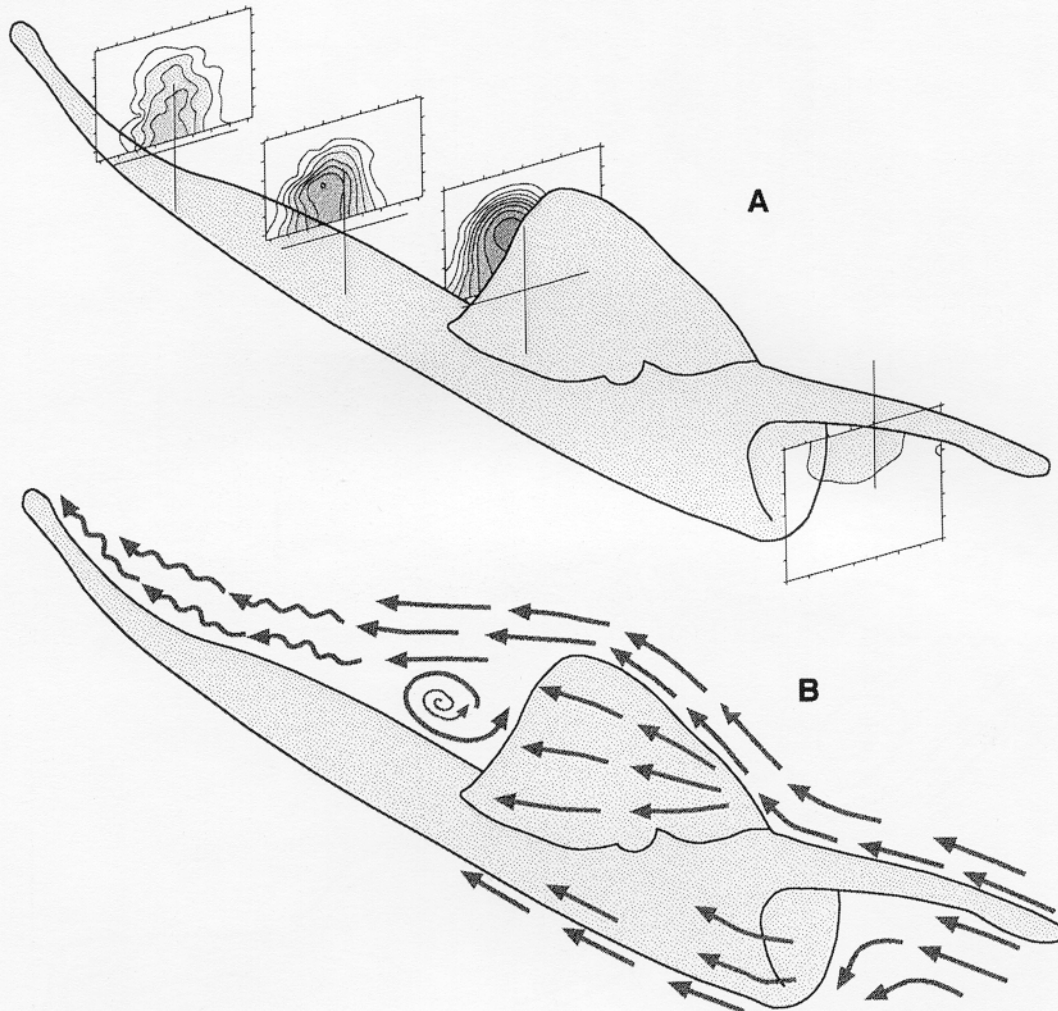
Data were acquired for each model at various stations from the tip of the sicula to the tip of the nema. Particular attention was paid to the regions of greatest anticipated interest such as around the thecae and the sicular aperture. Each two dimensional traverse was aligned in the YZ plane, in other words at a fixed distance downstream of the sicula, and consisted of measurements taken at several hundred discrete stations. At each traverse position the mean velocity and the degree of variation in velocity were measured in each component of flow direction (X , Y and Z). The traverse grid spacing was generally 2 mm, although the spacing varied according to the extent of the region of interest and the required resolution. Once a suitable traverse had been programmed, data acquisition started at the first traverse position and stopped when a sufficient number of seeding particles had passed through the measurement volume for accurate mean and turbulence information to be calculated, typically around 3000 samples. This process was then repeated at each subsequent measurement position. The time required for data acquisition was about one hour for each traverse program, that is at each X -position: the total data acquisition time was around 20 hours.

Plotting of results

Results were plotted as contour graphs for U , V and W velocities (in the X , Y and Z directions respectively) and for U_{rms} , the root mean square of U velocity which indicates the level of turbulence. Contours were generated using the software package, Surfer for Windows (Copyright Golden Software, Inc. 1994), and the data points were manipulated into contour form by kriging with a linear variogram. Vector plots were also produced for V and W velocities. These have been synthesized into diagrams which show flow patterns over the whole rhabdosome for each model.



TEXT-FIG. 6. A, contour plot of U velocity for model A at $X = 147$ mm, towards the closed tip of the sicula. B, contour plot of U_{rms} for model A at $X = 147$ mm.



TEXT-FIG. 7. Graptolite model A, with U velocity contour plots, and a sketch showing flow over the model.

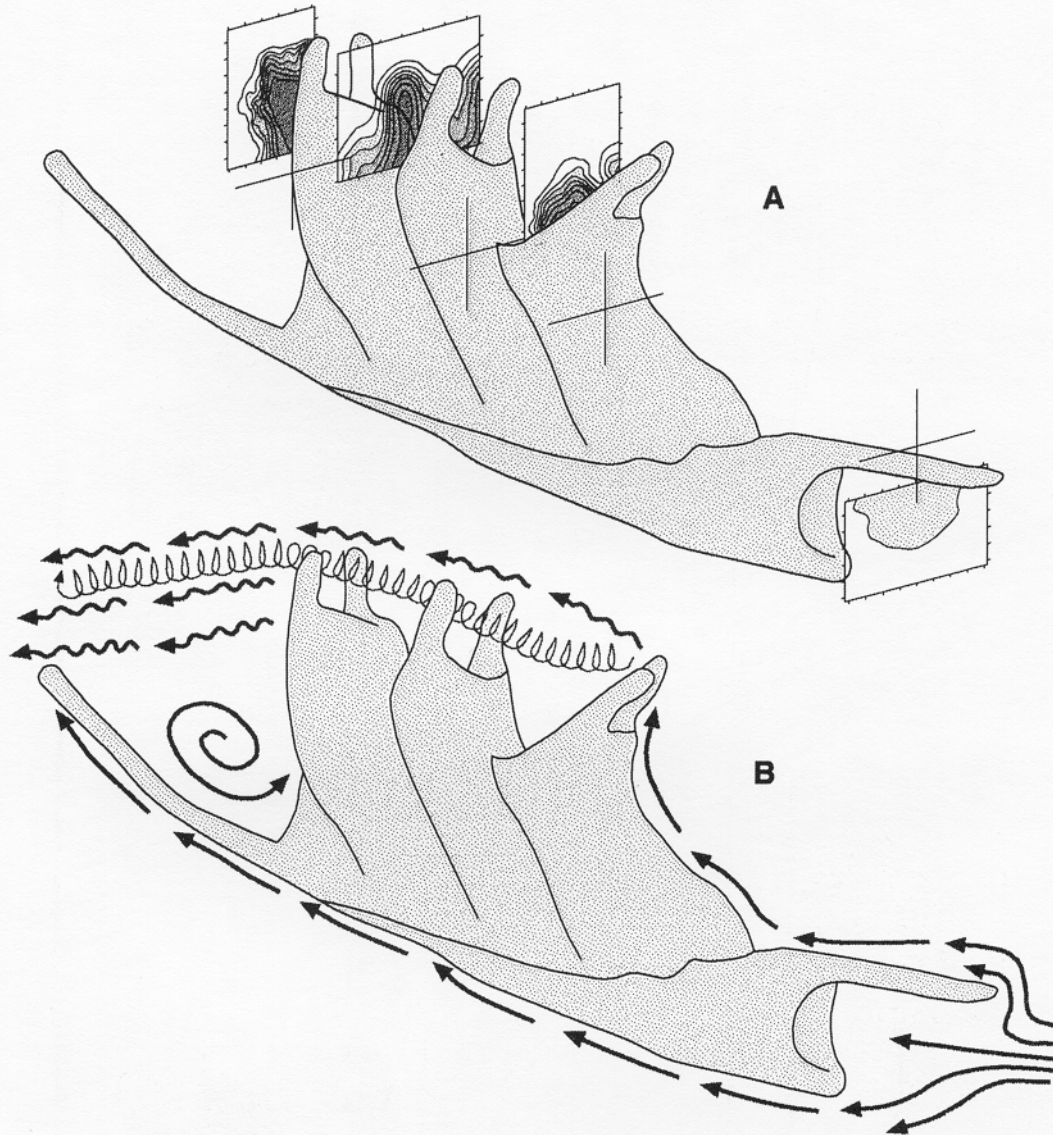
RESULTS

Saetograptus chimaera (Barrande), model A

Four traverses were made of this model, one close to the sicular opening, one just distally of the thecal aperture and two along the length of the nema. The most proximal traverse shows that fluid is deflected around the sicular aperture, partly by the action of the virgella, with flow stagnating within the aperture itself. Flow is directed around the rhabdosome, to the sides and over the theca. Flow along the sicula is retarded by the virgella (Text-fig. 3).

The second traverse, made immediately distally of the aperture of th1 shows that as fluid encounters the thecal aperture, velocity decreases in a zone immediately downstream or distal of it. This is caused by recirculation of fluid in this region and it is therefore a relatively quiet, low velocity region. Fluid also contracts into this region from the sides. Turbulence increases distally of the thecal rim (Text-fig. 4).

At traverse three, the recirculating pocket of fluid generated by the theca is still visible. Flow is



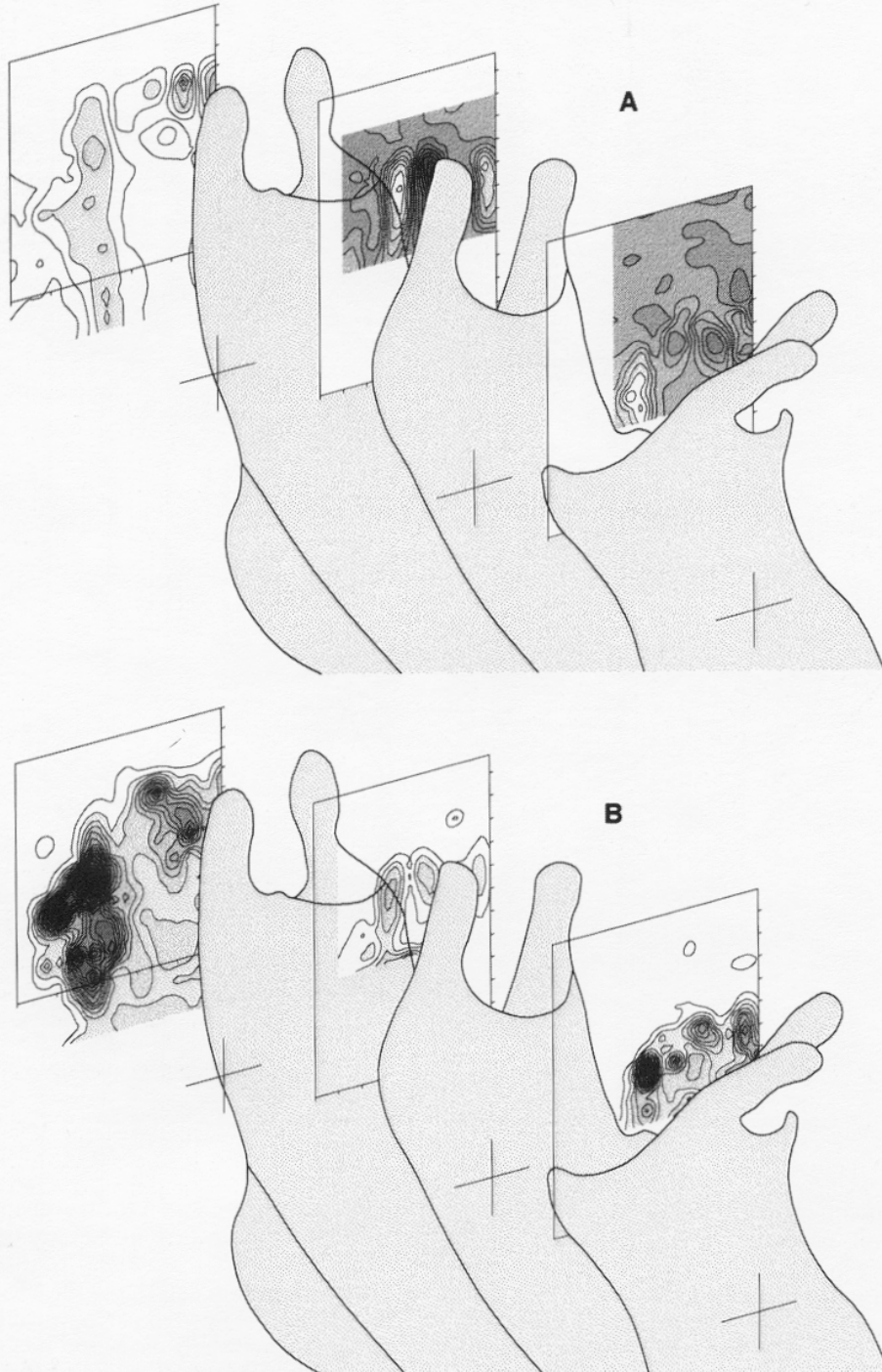
TEXT-FIG. 8. Graptolite model B, with U contour plots, and a sketch showing flow over the model.

directed along the nema and turbulence has increased here to about four times the level in the freestream (Text-fig. 5). This pattern is maintained to traverse four, at which point turbulence has increased to between eight and ten times the undisturbed level and the 'shadow' of the theca as recorded by U velocity is beginning to decay (Text-fig. 6).

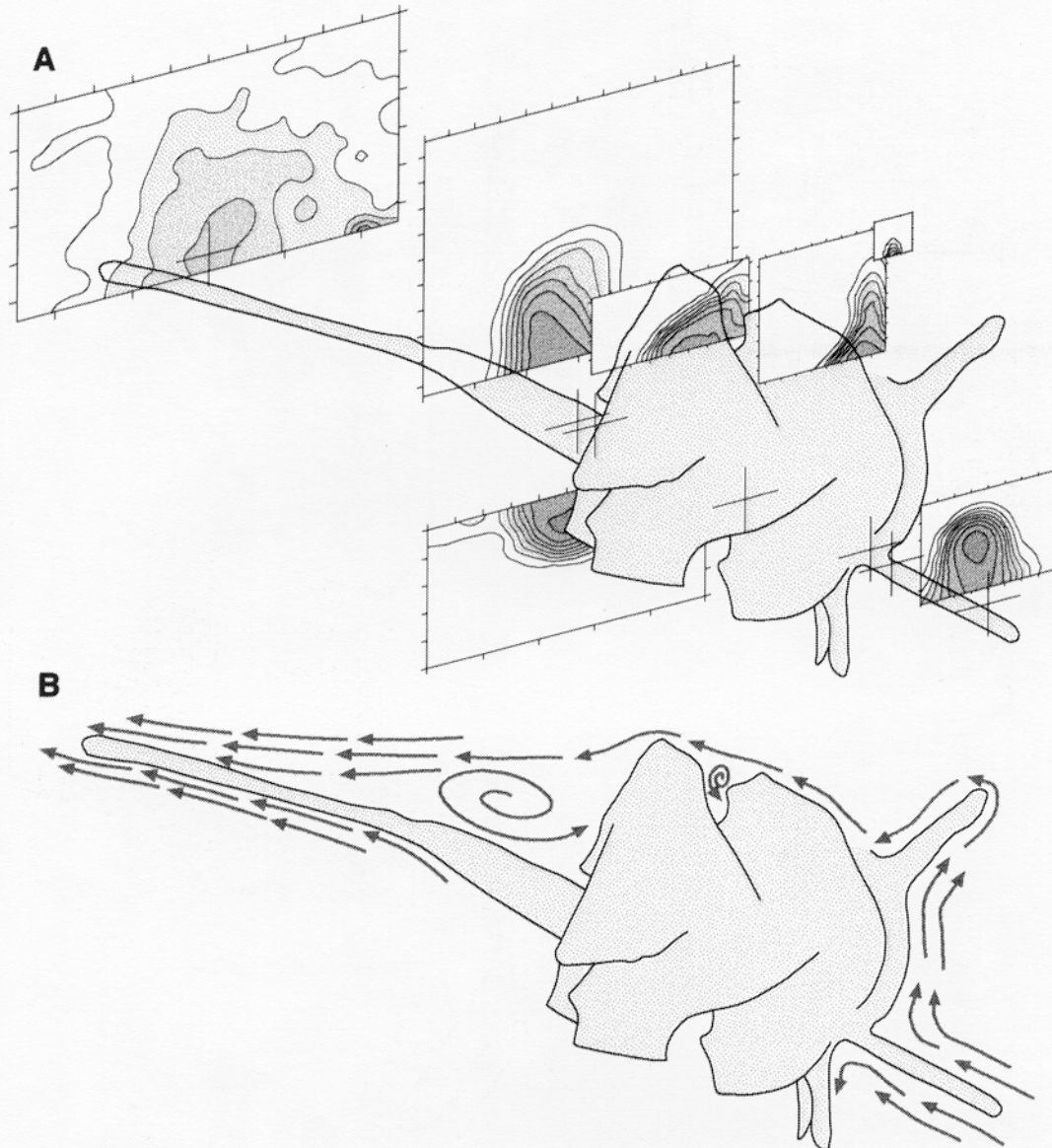
These observations are summarized in Text-figure 7, and summaries alone are provided for subsequent models.

Saetograptus chimaera (Barrande), model B

Four traverses were made along the length of this graptolite, as shown in Text-figure 8. A broadly similar pattern of flow was measured over this model as was found for model A. Distinct differences



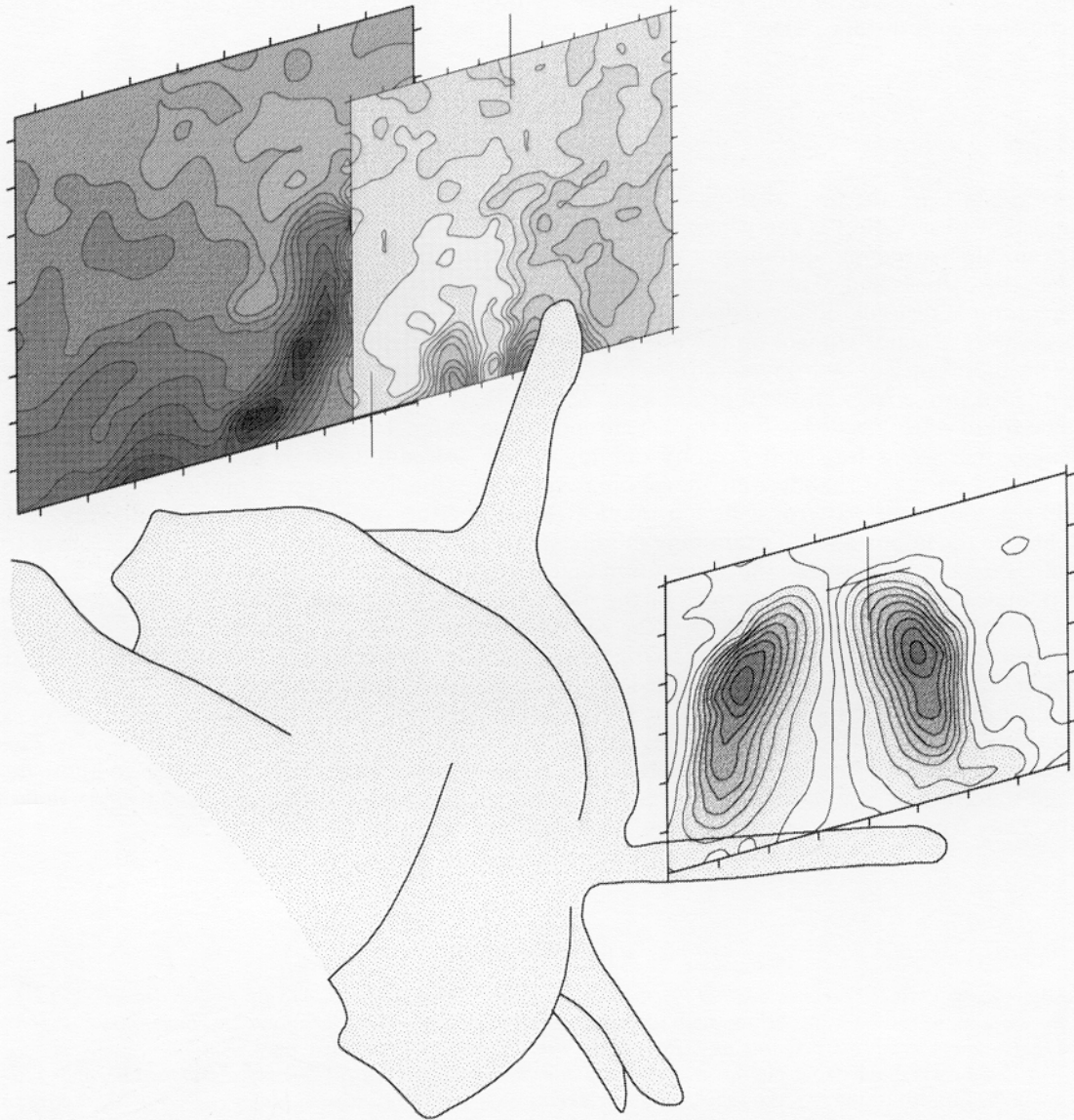
TEXT-FIG. 9. Contours plots of A, V velocity, and B, U_{rms} for model B, showing the effect of paired thecal spines.



TEXT-FIG. 10. Graptolite model C, with U velocity contour plots and a sketch showing flow over the model.

were caused by the greater number of thecae and by the presence of spines on the thecal apertures. The overall pattern of flow is shown in Text-figure 8 and new features of interest are described below.

Traverse two was taken between the first and second thecal apertures and shows the effect of the two spines which characterize the thecal apertures of this species. Two vortices are created by these spines and shed downstream. The third and fourth traverses, taken distally of the second and third thecae, show that these vortices interfere with those created by subsequent spines so that a wide turbulent zone is created (Text-fig. 9).



TEXT-FIG. 11. V velocity contour plots over the proximal region of model C.

Amplexograptus maxwelli Decker, model C

Eight traverses were made around this model, most of which had their shape defined by the complicated morphology of the graptolite which limited the areas where the lasers could penetrate. The positions of these traverses are shown in Text-figure 10.

Flow encounters both the sicular aperture and the smooth bend of $th1^1$. Flow is smooth over this theca to begin with, but it forms vortices as it encounters the thecal spine. The vortices are still effective as they encounter traverse three, which is distal to the aperture of $th1^1$ (Text-fig. 11).

Further along the model, flow resembles that observed for model 1, but with increasing turbulence with distance along the rhabdosome (Text-fig. 10).

CONCLUSIONS

These results are the first to show details of fluid flow over a graptolite rhabdosome. The most important observation is the general one that many aspects of rhabdosome morphology have a measurable hydrodynamic function which has not previously been recognized. The generation, by spines, of vortices and of increasing turbulence along the rhabdosome is one such observation. The generation of recirculation cells distal to thecal apertures is another. This implies that hydrodynamic effects were a major control on the evolution of different morphologies of graptolites.

The importance of hydrodynamic effects to a graptolite colony would have been two-fold and can be divided into effects on the functioning of the entire colony in the water and on the effects on a single zooid which needed to feed from surrounding sea water. Turbulent wakes would have had the result of increasing drag on the colony and might have slowed it down. However, an assessment of the overall effects of rhabdosome morphology on colony function requires more experimentation.

For a zooid, the pattern of flow around a thecal aperture would have been vital. This study highlights the importance of examining modifications to the thecal apertures of graptolites in more detail. For simple apertures, the observation that flow rate in the aperture itself is low, and that fluid recirculates into the thecal apertures of the models suggests that feeding did not occur within the thecae. Instead, it seems probable that the zooids extended into the surrounding water, or climbed spines where these were present near to the thecal apertures, in order to feed. Modern pterobranchs feed in this manner in order to avoid the low-flow region close to the sea bed (Rigby 1993). Feeding would probably not have occurred in the stagnant area created at the sicular aperture of *S. chimaera*, implying either great mobility of this zooid, its mortality as the colony grew or its lack of feeding function. A second possible function of the virgellar spine might have been to allow this zooid to feed upstream of the stagnant region, although a prime function must have been to deflect flow away from the sicular aperture and along the metatheca of th1.

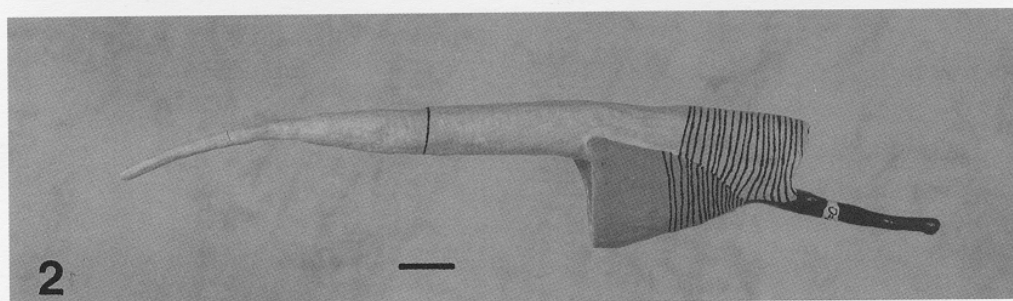
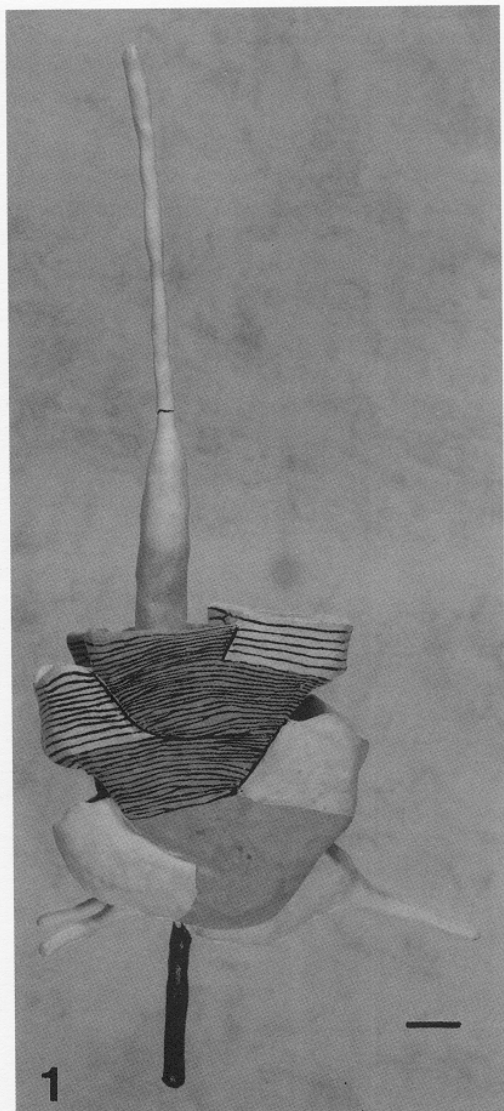
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EXPLANATION OF PLATE 1

Fig. 1. Model of *Amplexograptus maxwelli*.

Figs 2–3. Models of *Saetograptus chimaera*. 3, early growth stage. Scale bars represent 10 mm. Growth lines are slightly schematic, drawn on to the models.



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BARRIE RICKARDS

Department of Earth Sciences
University of Cambridge
Downing Street
Cambridge CB2 3EQ, UK

SUSAN RIGBY

Department of Geology and Geophysics
Grant Institute
University of Edinburgh
West Mains Road
Edinburgh EH9 3JW, UK

JERRY RICKARDS

TWR Group plc.
Leafield Technical Centre
Leafield, Witney
Oxon. OX8 5PF, UK

CHRIS SWALES

Department of Aerospace Engineering
Queen's Building
University Walk
Bristol BS8 1TR, UK

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