

The Relation of the form of a Sponge to its Currents.

By

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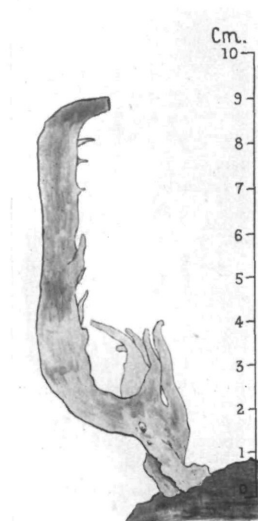
With 12 Text-figures.

ALL zoologists know that from the large holes, which we call oscula, on a sponge, an outgoing current may be detected in life. During several months in Naples I investigated this current, using litmus and carmine solutions, and carmine and indigo in suspension. I worked with two calcareous species of sponges, having oscula at the end of tubular prolongations, which reach the size and shape of a child's thumb in the case of *Leucaltis*, and of a child's finger in the case of *Leucandra aspera* (Text-fig. 1). The solutions were either placed on the surface of the sponge, to be sucked in by its currents (Text-fig. 2), or dropped by a pipette through an incision into the cloaca—the cavity of the tubular prolongation. In the latter case the time taken for the colour to be thrown out at the osculum, though liable to many corrections, afforded on the whole the most trustworthy determinations of oscular velocity: the cloaca being wider than the osculum, the observed

¹ This paper was read before the British Association at Hull, September 1922. A preliminary note was published in 'Proc. Camb. Phil. Soc.', 1888, vol. vi, p. 5. (See also 'Quart. Journ. Micr. Sci.', vol. 38, p. 28; 'Proc. Roy. Soc.', vol. 64, p. 61; and I. B. J. Sollas, 'Camb. Nat. Hist.', vol. i, p. 235.) The experiments were made in the Naples Zoological Station in 1887, 1888, and 1889, where I occupied the Cambridge University table, and in 1890, 1891, and 1892 at a table allowed me by the great kindness of the late Professor Anton Dohrn. For a long time I proposed to myself to make a further series of experiments to clear up doubtful points, but recognizing that I shall not now do so, I have reconsidered all the experiments this year (1922) and recalculated all results and formulae.

cloacal velocity would be multiplied by 4, 5, or 6, as the case might be, to obtain the oscular velocity. A pretty method was arrived at accidentally (Text-fig. 3), when I found the coloured jet marked by dark beads or nodes, caused by my pulse shaking

TEXT-FIG. 1.



Leucandra aspera var. *gigantea* (A. 11).¹

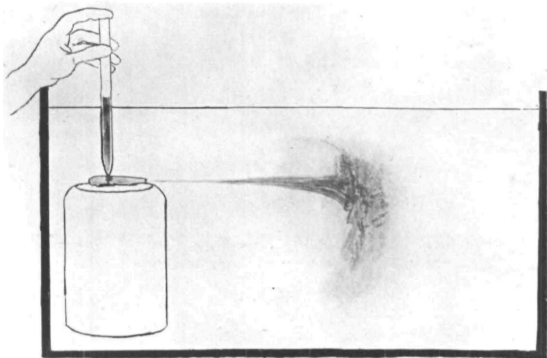
the pipette; the length between any two nodes, divided by three-quarters of a second, gives the core-velocity at that part of the jet.

The fastest oscular velocity recorded directly for the

¹ This sponge came from the Porto Militare, and I regret that I have drawn it erect instead of pendent. Vosmaer states that this metamp of *L. aspera* is found only on the keels of boats (cf. p. 314).

L. aspera of Text-fig. 1 was 7 cm. a second, and this was the basis adopted in the calculations of this paper. I have now changed them, in consequence of the conclusion that the actual mean oscular velocity when the sponge was in the sea was 8.5 cm. a second (Appendix, Note 1).¹ From Parker's experi-

TEXT-FIG. 2.



ments on the pressure in *Stylotella*, a siliceous sponge, its velocity is considerably higher than that of *Leucandra*; we shall see later that this could be conjectured from its structure.²

In quite still water such a current from *Leucandra* goes

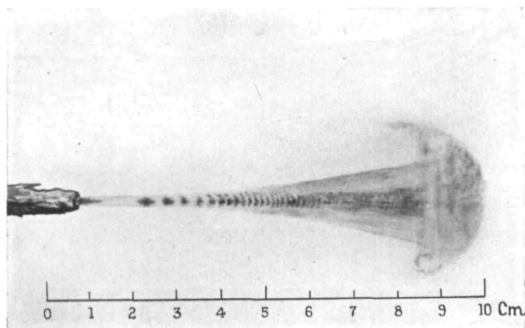
¹ This was the conclusion from observations of length of jet and velocity; I cannot put it forward as an exact physical measurement, but as a final judgement after considering upwards of 1,000 unsatisfactory and imperfect observations, of the nature described in the text. Note 6 (Appendix) indicates that the figure 8.5 was a lucky judgement, and is probably close to the true velocity.

² The velocity in *Stylotella* will be less than Parker calculates, as he does not allow for the friction in the canals of the sponge.

10 or even 20 inches before coming to rest.¹ Speaking exactly, it does not really come to rest at this distance, but reaches a velocity not higher than that of the slow return-current, slightly indicated in Text-figs. 2 and 3, which is necessarily established to fill up the region from which this water has been removed.

Text-fig. 4 is a diagram of the currents which must exist around a bath-sponge in still, deep water. The swift vertical jets from the oscula on the top surface carry the used and

TEXT-FIG. 3.



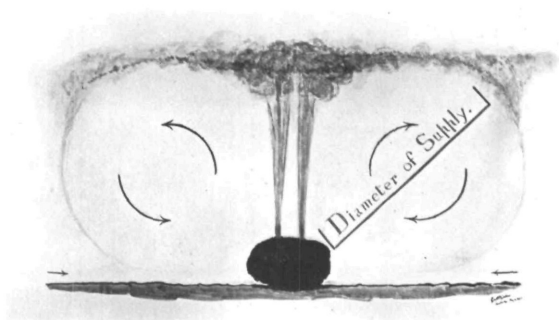
fouled water to a stratum some feet above the sponge; slow currents, in the plane at right angles to the jets, creep in from all directions along the sea-bottom to feed the intaking pores, which cover the general surface of the sponge. If the water be absolutely still, there is established between these afferent and efferent currents a re-entrant vortex, whose section is a circle in any radial plane through the osculum.

The diameter of that circle I call the Diameter of Supply; and the angle between the directions of the intake and outflow currents, which in sessile sponges (Text-fig. 4) is a right-angle, and in pedunculated sponges (Text-figs. 9 and 10) is 110° to 120° or more, I call the Angle of Supply.

¹ See Note 5, (12).

On these two factors depends the life of the sponge, or of any other fixed or stationary organism in still water. The outgoing current carries with it water which has been filtered of food, in which carbonic acid has been substituted for oxygen, into which the poisonous products of metabolism have been excreted. In still, or nearly still water, the angle of supply and the diameter of the circle of supply measure the chance that some convection current or drift will carry away that water,

TEXT-FIG. 4.



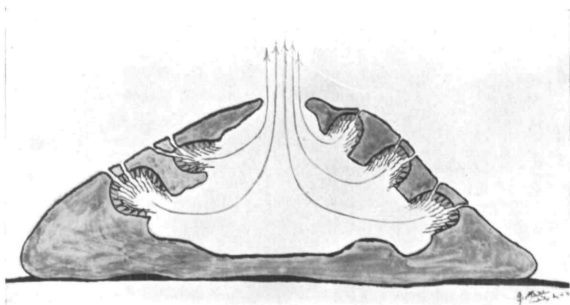
useless for life, before the slow eddy of return brings it down to the plane of the ingoing current. According to the distance to which it is so carried is the percentage of clean, unused water which enters the organism, and according to this percentage is the chance of life of the organism; and in a slow tidal channel it is clear that the distance to which the foul water will be carried by the tide before it is drawn back to the plane of the ingoing currents, depends directly upon the length of the oscular jet.

The length of this jet was shown by the experiments to vary as the initial velocity—a result to be expected by elementary theory, though a full theory would be difficult. With jets of the same initial velocity, but from oscula of different size,

the distance carried appeared to be proportional to the diameter of the osculum, although, in consequence of the oscula used having small range in size, this result was not so certain. The rough formula indicated by the experiments is that, using centimetres and seconds, the length of the jet approximates numerically to twelve times the product of its initial velocity and the diameter of the osculum.

That among jets of equal velocity the distance carried should

TEXT-FIG. 5.



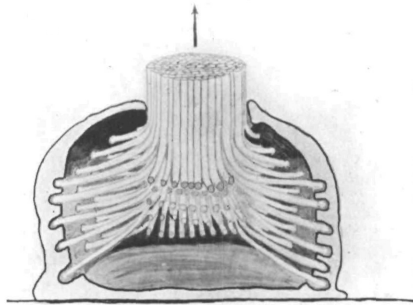
Rhagon.

be proportional to the oscular diameter, might also be expected by elementary theory; since per centimetre of length the weight of water increases as the square of the diameter, while the surface exposed to friction increases only as the diameter. Consequently the ratio of the moving weight to the resisting surface increases as the diameter, and with equal velocity a jet 4 mm. wide may be expected to go twice as far as a jet 2 mm. wide.

This consideration enables us to understand the advantage gained by the union of many unicellular flagellates to make one thimble-shaped Olynthus, or by the union of many Olynthi opening into a central cloacal cavity to form a Rhagon (Text-fig. 5) or a Sycon. Suppose, in Text-fig. 6, we unite a hundred

Olynthi, each ejecting an efferent stream 1 mm. wide, and raise up their colonial wall to enclose a common efferent aperture 1 cm. wide, thus forming a hypothetical Rhagon with an efferent aperture having its area equal to the aggregate oscular area of the 100 Olynthi. We can visualize the stream from each Olynthus as a thread, and the stream from the Rhagon as a cord of a hundred threads issuing side by side. We see at once

TEXT-FIG. 6.



Efferent streams. Hypothetical Rhagon with wide aperture.

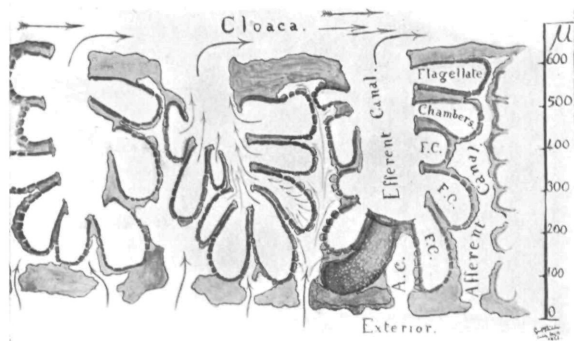
that most of the threads lie altogether inside the cord, with their surfaces entirely protected by other moving threads from friction against still water. The mass and initial velocity of the Rhagon's jet is that of its 100 constituent jets; but for each centimetre of length the external surface of the Rhagon's jet is only one-tenth of the total surface of the constituent jets, consequently the friction to which it is exposed is one-tenth of their friction, and the combined jet will travel about ten times as far as each of the constituent jets would go separately.

Coalescence is therefore advantageous in increasing the diameter of supply; and, as in all living things and in the

works of engineers, absolute magnitudes are determined by the relations of the consequences of increase in length to the consequences respectively of increases in area and in volume.

But sponges are not mere coalesced Protista: they have varied cellular differentiation and at least two organs. The first is the perforated membrane of tissue which is formed by the flagellate cells, or on which they stand (Text-fig. 8), thereby ensuring to them absolute separation of the water which leaves

TEXT-FIG. 7.

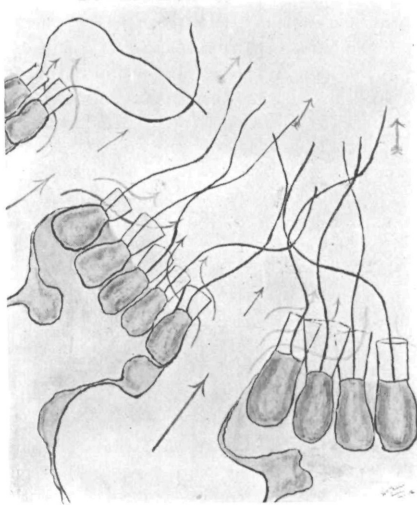
Wall of *Leucandra aspera*.

them from the water which supplies them; this organ is possessed by no choanoflagellate, and characterizes the sponges. The second is the canal system, which we may better call the hydraulic organ, in which the form of every part is wonderfully modified for the advantage of the whole aggregate. In the canal system all agree that progressive changes have occurred again and again in similar order along many lines of descent in sponges. We can show these changes to have as one of their necessary consequences large increase in oscular velocity, with consequent increase in the diameter of supply, and that therefore each successive change has left the sponge a more self-

sufficient food-catching machine than its ancestors, so as eventually to make a fixed organism which is independent of chance currents from waves and tides.

Watching under the microscope a flagellum with such a rapid period of vibration that the eye only sees a mist

TEXT-FIG. 8.



Wall of flagellate chamber, with two afferent pores.

terminated by the two extreme positions, we are apt to think, and to say, that the flagellum is moving rapidly; and much theory has been written about the mechanics of the collar-cells and choanoflagellates, on the assumption that food-particles are thrown through the water at express-train speed by this rapidly moving flagellum, as a savage hurls a projectile with a throwing-stick, or as civilized man drives a ball with a club.

Really, far from express-train speed, no part of the most rapidly moving flagellum ever attains the rapidity of motion of a snail. We forget, as we look through a microscope magnifying 1,000 diameters, that though distance is magnified, time is not magnified, and therefore any velocity is $\frac{1}{1000}$ what it appears to be. I have estimated the vibrations of the flagella in healthy and lively collar-cells at twenty to the second.¹ The flagellum is 30μ long; therefore if it vibrates through an angle of 60° , its tip travels 30μ each half-vibration and 60μ each complete vibration, making twenty vibrations 1.2 mm. per second; which is 14 ft. an hour. This is the speed of only the extreme tip of the flagellum, the base being motionless; so that some 7 ft. an hour is the mean speed of the middle point of this invisibly rapid flagellum.

I confess that I have often adduced this calculation to show why there are no flagella in the cloaca of *Leucandra*, where the mean velocity is $1\frac{1}{2}$ centimetres a second, or twenty times the speed of the flagellum. But, really, viscous flow at a mean velocity of 1 cm. means an axial velocity of 2 cm. diminishing gradually to zero on the walls. The bareness of the cloaca we must attribute to the fact that the sponge flagella do not, and cannot, act like oars, an action which requires direction of movement and nervous co-ordination. All observers agree that the movements of sponge-flagella are neither co-ordinated, synchronous, nor in parallel planes.² A collar-cell flagellate surface is comparable mechanically to a seine-net with a number of fishes fixed by their gills in the meshes. Their movements cannot establish a current along the face of the net: that would involve their tails all striking strongly in the same direction and weakly in its opposite. But if the net be fixed, the uncoordinated movement of their tails will draw water through the net from the side on which are their noses. Sponge collar-cells are similarly capable of

¹ 'Quart. Journ. Micr. Sci.', vol. 38, p. 17.

² Permanent sections of *Oscarella* show the pinacocytal flagella of the afferent canals looking as if they work as oars, and far enough apart to do so without collision; say, one to the area of 30 collar-cells.

drawing water through the perforated membrane on which they stand ; from its position the walls of the cloaca cannot be so perforated, so it bears no collar-cells. It is true that sponge-flagella can accelerate a current down which they lie, but for this their position is least useful when they stand on a wall parallel to the current, and most useful on a wall at right angles to it. To this latter position they become more and more limited in the progressive development of the canal system, in which flagellate tubes become progressively shortened until only the perforated hemispherical end of the chamber is left.

The remarkable achievement of the perfected hydraulic organ in sponges is that from this waving of hairs $\frac{1}{8}$ of an inch in thickness at a mean speed of 7 feet an hour, there is produced an oscular jet with an axial velocity of over half a foot a second (280 times the speed of the flagellum), which in *Leucandra* throws to the distance of 9 inches five gallons a day or a ton in six weeks (Appendix, Note 3).

It is, of course, clear that when we combine many slow streams into one narrow channel the velocity is increased. I computed in several sponges the aggregate cross-section of the stream through the body in various parts of its course. In the *Leucandra* of Text-figs. 1 and 7, 10 cm. long, there were about $2\frac{1}{2}$ million flagellate chambers, with a total transverse area of $52\frac{1}{2}$ sq. cm., or 1,700 times the area of the osculum, which is 0.031 sq. cm.; so that the mean velocity at the osculum is 1,700 times as high as in the chambers.

At $8\frac{1}{2}$ cm. a second, a quarter of a cubic centimetre (0.26 c.c.) will issue from the osculum each second, and to replace it a quarter of a cubic centimetre must have passed through the $2\frac{1}{2}$ million chambers, that is $\frac{1}{8}$ of a cubic millimetre through each, or 116,000 cubic μ ; which through a chamber 54μ diameter (transverse area 2,300 sq. μ) implies a rate of flow of 50 μ a second, or $\frac{1}{17}$ of that at the osculum, as above.

The flagellate chamber (Text-fig. 7) is a blind, thimble-shaped tube, the water entering through perforations in the walls. The total area of the wall-surface is eight times the cross-

section of the tube, so that the water entering has this transverse area of channel as it passes the flagella (Text-fig. 8), and therefore the velocity of only 6μ a second.¹ Below the flagella half the channel is occupied by the necks of the collars, so that between them the water moves at the rate of 12μ a second, and a particle of food takes a second to travel the length of a cell.

Slow as we thought the movement of the flagella, at $\frac{1}{2}$ mm. a second, the water on which they act is stationary by comparison, and they can get on their full work. And the remarkable anomaly in sponges, that through considerable evolution their motor-cells remain their ingestive cells, ceases to be surprising when we realize that both functions are alike localized at the position where the current is slowest.

The one second during which a food-particle is passing the collar-cell is not such a short time for its capture as would at first appear. It allows of a good many events in the cell's life: we know of twenty double vibrations of the flagellum, with the metabolic cycles which they imply. The biological magnitude of an interval of time is measured by the number of events which can happen in it; and since every event requires the motion of something from one position to another, therefore where the distances between positions are smaller, events can happen more rapidly. Every motion is produced by an acceleration—such as gravity, or the stress of contracting protoplasm—and with a given acceleration the time required to move over a certain distance from rest is as the square root of that distance: a stone takes a second to fall 16 ft., but to fall a quarter that distance takes half a second. Therefore in a biological world whose linear dimensions are $\frac{1}{1000}$ those of our own, there will be some thirty times as many events in a second as in our own, since thirty-two times thirty-two is a thousand; and I suggest that in the biological time of the flagellate cell the one second during which a particle of food is passing would compare with half a minute in our external life. (We must put the adjective 'external', because our psychical events which happen 'with the speed of thought', are events

¹ Note 6 gives reason for supposing double these velocities in full health.

in a cellular or intracellular world where distances may be even smaller than those about a flagellate cell. Hence, always, their rapidity has been noted as of a different order to that of common external events.)

There is also a purely physical point deserving attention in the conditions of the world under an immersion lens. When we watch flagella working under a high power, the water seems to have lost its fluidity: a particle moved with apparent swiftness by a flagellum loses its motion at once. The general appearance is as if the flagella were labouring in thick gum, or treacle; and to understand microscopic physics it is a serviceable short-cut to think of the water as treacle. The energy of a projectile to overcome the resistance of the medium through which it is thrown is as its mass multiplied by the square of its velocity; loss of energy from the resistance is as its surface multiplied by the velocity and by the distance traversed. We magnify its apparent mass as the cube of the magnification, and the square of its apparent velocity as the square of the magnification; so that the apparent energy of the projectile is magnified as the fifth power; but the energy lost, measured by surface multiplied by velocity and distance traversed, is only magnified as the fourth power. Consequently, with 1,000 diameters, the water offers a thousand times the retarding effect which we expect, on the projectile which we think we see; and the ratio is even higher with the small projectiles which concern us.¹ With velocities among which 25 ft. an hour is the swiftest, at distances among which $\frac{1}{1000}$ of an inch is very great, the viscosity of water is the predominant phenomenon; and this world at which we are looking is a world of pushing, not of throwing.

When the flagellum pushes in with its stroke a minute drop-let of water into the flagellate chamber (Text-fig. 8), it creates

¹ Sir J. J. Thomson kindly informed me that, according to Stokes's law, the resistance of water to the movement of a minute sphere is proportional to the diameter, not to the square of the diameter. This would make the apparent retardation under the microscope a million instead of a thousand times the expected retardation.

a pressure there which forces an equal amount of water out into the efferent canal (Text-fig. 7), and so the pressure created in the chamber is transmitted to the efferent canal, and thence, with a loss by friction, to the cloaca. The chamber is distended by this flagellar pressure, as the elastic bag of a squeeze-pump is distended, and the stretching of the chamber-walls is resisted by the surface tension and elasticity of the tissue, as the stretching of a soap bubble is resisted by the surface tension of soapy water in air. The text-books have long pointed out that, as the canal system is specialized, the diameter of the chambers become smaller, and they change from cylinders to hemispheres and spheres. This change, therefore, directly increases the possible pressure in the chambers, and therefore the diameter of supply. There is twice the pressure in a soap bubble 1 in. in diameter that there is in a soap bubble 2 in. in diameter; and similarly, reduction in the size of flagellate chambers proportionally increases the pressure which their tension can balance. In *Leucandra* I calculate from computation of the oscular current¹ and the friction in the canals that the pressure is between $\frac{2}{3}$ mm. and $1\frac{1}{5}$ mm. of water in the cylindrical flagellate chambers $54\ \mu$ wide. The same tension would support double the pressure in spherical chambers of the same diameter, and four times the pressure in spherical chambers of half the diameter; so that from my results the pressure in a sponge with spherical chambers $27\ \mu$ in diameter would be $2\frac{1}{2}$ to 5 mm. of water, and in $35\ \mu$ chambers would be 2 to 4 mm. In spherical chambers of $35\ \mu$, by direct experiment, Parker found the pressure of $3\frac{1}{2}$ to 4 mm. of water in *Stylotella*. We may therefore conclude with some safety that the pressure in *Leucandra* is close to 1 mm. of water, and that the healthy tension of the chamber-wall tissue is nearly alike in this and in *Stylotella* (for the latter 0.00034 gm. weight per centimetre, or less than $\frac{1}{50}$ of the surface tension of petroleum in water). In the smaller spherical chambers of *Stylotella* this tension can support three times the pressure of the large cylinders of *Leucandra*, and so

¹ See Appendix, Note 6.

we may expect nearly twice the oscular velocity, and consequently nearly twice the diameter of supply, with this admittedly more specialized type of canal system.

This pressure of 1 mm. water is transmitted, with a loss from friction, through the efferent canals and cloaca to the open osculum, where the potential energy of the compressed water is converted into the kinetic energy of the swift oscular jet.

We are familiar with such conversion of the potential energy of compressed air in an air-gun into the kinetic energy of the escaping bullet, and of the potential energy of the compressed water at the bottom of a cistern, converted into the kinetic energy of the jet from a garden-hose. We know well, with the garden-hose, that when the water will only go 3 ft. from the open hose, it will throw a jet 30 ft. from a fine tube-nozzle. This is because with the open pipe, delivering perhaps 10 gallons a minute, there is a flow of 5 ft. a second through the 1 in. hose-pipe, with great loss of energy in every foot of the pipe from friction. Putting on a nozzle which will only deliver 1 gallon a minute, the velocity within the hose is lowered to 6 in. a second, $\frac{1}{2}$ of the loss by friction is avoided, and the potential energy of the cistern is transmitted almost undiminished through the hose, in any part of which there is nearly the full pressure of the cistern. If we stop the nozzle with the finger, we have the full pressure of the cistern throughout the hose, and can feel it on the finger. This is not perceptibly diminished by allowing a fine thread of water to escape, and its velocity of issue approximates to the full theoretic velocity due to the cistern head, but it does not travel far owing to the smallness of its mass compared with the surface of friction it exposes to the air. As the jet is allowed to increase in volume, so does the velocity increase in the hose-pipe, and the consequent successive loss of energy in each yard of its length; and we can feel the pressure on the finger noticeably diminish and can see that the velocity of the jet consequently decreases, though with its greater volume it travels farther.

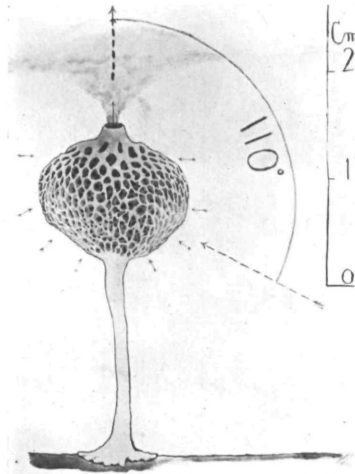
So with the sponge. The narrow osculum, 2 mm. diameter, in

Leucandra is comparable to the tube-nozzle on the hose. It means that pressure is transmitted from the flagella through the water of the canals, the water moving so slowly that loss in friction still leaves enough energy at the osculum to make a strong stream. As with the hose-pipe, were we to close the osculum more, there would be less energy lost, and the velocity at the osculum would rise, with a pin-point hole, from $8\frac{1}{2}$ cm. to 13 cm. a second, but the tiny jet could barely travel $1\frac{1}{2}$ cm. instead of 24 cm., while the quantity would not be a hundredth of that necessary for nourishment. With the osculum half its existing diameter, the velocity would be increased to 11 cm. instead of $8\frac{1}{2}$ cm., but the length of the jet reduced to three-quarters and the quantity of water to only one-third what we now find them. On the other hand, were the same *Leucandra* shaped like a cornucopia, with the widest part of its cloaca as osculum, the quantity of water passing would be increased by one-sixth of the existing quantity, but the velocity would be only $1\frac{1}{2}$ cm. a second, and the jet consequently less than half the present length. For a given pressure, acting through a given length of channel of fixed width, there is an optimum value for the size of the osculum (as we have all found with the garden-hose) above and below which it will not carry so far; with measurements of the flagellar pressure, and of the number and dimensions of the canals, an equation can be made to determine this optimum value. I have calculated it for the *Leucandra* of Text-fig. 1 (Note 5), but my computations of the canals and currents are not close enough to say more than that the theoretically best diameter for the osculum of this specimen is $2.6 \text{ mm.} \pm \frac{1}{4} \text{ mm.}$; the preserved diameter being 2 mm. Rough computations for other specimens, and for a *Sycön*, confirmed the conclusion that the osculum is always at any rate near to the optimum size for producing the greatest diameter of supply; and that this is the explanation of the small and definite oscula which we have all noted as characteristic of the majority of sponges with high canal system.

The secret of the repeated development of this common type of sponge is the reduction of internal velocities, so that

a larger proportion of the energy produced by the flagella is transmitted to the osculum in the untaxed form of pressure. The cloaca must be much wider than the osculum for the cloacal current to be slow; hence the bottle-shaped cloaca with a small orifice, which led our forefathers to compare to the stomach and mouth of animals the pressure-chamber

TEXT-FIG. 9.



Clathrina blanca. Angle of supply 110° .

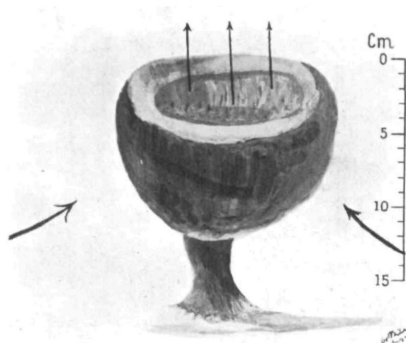
and vent of the hydraulic organ of sponges, evolved with the advantage, not of the retention and digestion of food, but of the forcible removal of excreta.

I shall not here discuss the sluggish currents of *Clathrina* and *Leucosolenia*; nor the evolution of subdermal spaces, and their possible development as muscular pumps with the collars acting as valves (as in the strange reversed canal

system described by Vosmaer in *Spirastrella*).¹ But modifications concerned with the angle of supply demand brief notice in regard to our main thesis.

Stalks of greater or less length (Text-fig. 9) increase the angle of supply in many sponges, and when this is the case in sponges of any size, the osculum opens out, as admixture of incoming and outgoing streams becomes less probable, and oscular velocity therefore less important. This gives rise to the

TEXT-FIG. 10.



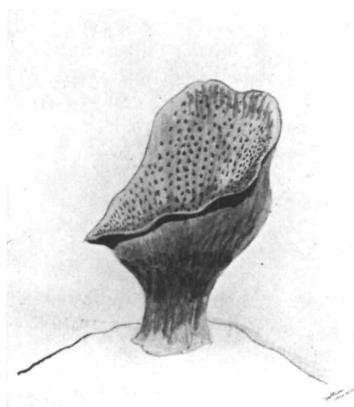
Calyx lieberkuhnii (modified from O. Schmidt).

well-known Neptune's-cup form (Text-fig. 10), found in many groups, and the expanded lip intervenes between the two streams.

If this cup becomes set on one side (Text-fig. 11), the efferent stream passes away forwards, while the intake is at the back of the cup, and the angle of supply approaches to 180°. In still water, with the oscular jet horizontal, the length of the jet becomes infinite, whatever its velocity; because with the angle of supply 180° there is no back eddy, and the friction on the surrounding water serves by degrees to set it in motion

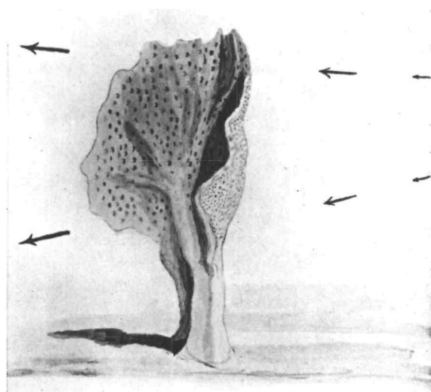
¹ Siboga-Expeditie, 'The Genus *Spirastrella*', p. 49.

TEXT-FIG. 11.



Phakellia ventila brum (combined from Johnston and Bowerbank).

TEXT-FIG. 12.



Phakellia conulosa (reconstructed from Dendy).

in the direction of the jet. So, since maintenance of oscular velocity is now of no advantage, the osculum opens out completely to allow the maximum quantity of flow regardless of oscular energy. The cloaca becomes a flat surface (Text-fig. 12), and the whole sponge a disk or fan with one intake face and one outflow face. If such a sponge be in really still water the surrounding water will by degrees be all set into slow motion, in the direction from intake to outflow, and the condition of life approaches that of the deep-sea sponges and polypes.

It is a puzzling fact at first that in most of the Hexactinellida we can detect no hydraulic evolution nor hydraulic efficiency; puzzling until we remember that in the great depths where they live, an unchanging current sweeps slowly from the poles to the equator. They have but to spread a net across it, and, whatever their mechanical inefficiency, they have incoming and outgoing streams 180° apart; the flagella have only to work the water through the many meshes formed by the feet of the collar-cells. The cavity of the Hexactinellida is no pressure-chamber: it is even perforated to let the onflowing water sweep out that which is befouled. Food is brought to them, waste is taken away. For them in their eternal abyss, with its time-like stream, there is no hurry, there is no return. Such an organism becomes a mere living screen between the used half of the universe and the unused half—a moment of active metabolism between the unknown future and the exhausted past.

APPENDIX.

NOTE 1. THE VELOCITY OF A JET OF MEASURED LENGTH.

The empiric formula, in centimetres and seconds,

$$L = (12 \pm 2) V.B. \times \{1 - 0.023 (20 - t)\}$$

where L is the length of the oscular jet,

V its mean velocity at the osculum,

B the diameter of the osculum,

t the temperature in degrees Centigrade,

may be of use to naturalists who are able to observe in a large tank the length of the jet from a mollusc or other fixed organism, and the width of the aperture. It is thus possible, for jets not exceeding 180 cm., to obtain a value for the approximate issuing velocity, and therefore of the quantity of water filtered by the animal and of the effective work performed by its cilia. The correction for temperature is theoretical.

Thus the figure of 8.5 ± 1.5 cm. per second, which I have finally adopted as the mean oscular velocity, at 18°C ., of *Leucandra aspera gigantea* (Text-fig. 1), healthy and in natural conditions, is deduced from the oscular streams of 30 cm. and even 45 cm. long, measured from recently gathered sponges. These indicate a mean oscular velocity of 8 cm. per second, and from the reduction which this undergoes under the best aquarium conditions, it may be concluded that the velocity of any gathered sponge is less than in the sea.¹

The formula was deduced from measurements of velocity on sponges some time in the tanks whose streams had shortened to 15 cm., 10 cm., 5 cm., or even 1 cm. ; such languid velocities being more easy to measure. The constant (12 ± 2) has been adopted as a compromise between a group of experiments by different methods which agree on the value $L/VB = 10.5 \pm 1$ and several experiments which group themselves about $L/VB = 14$.² The distance to which the cloud drifts will obviously be affected by the position of the jet with reference to the walls of the tank : with accurate physical experiment and definition of the conditions a closer result could be obtained ; but for aquarium observations it is probable that the conditions cannot be sufficiently identical to reduce greatly the probable error of the ratio L/VB .

¹ In cold water, flagella have a lower metabolism with which to drive a more viscous fluid, and the energy of the oscular current is less. When increase of temperature first becomes injurious, diminishing vitality is compensated by diminishing viscosity ; with still higher temperatures the change in viscosity is less and the injury greater (cf. 'Linn. Soc. J.', 34, p. 317).

² Experiments in June and July, temperature unfortunately not observed.

NOTE 2. REGULATION OF THE SIZE OF THE OSCULUM.

In two examples of *Leucandra aspera* (one with an iris-like oscular sphincter) I cut off the oscular end for preservation, and observed that the aperture contracted to one-third of its normal diameter. Mechanical stimulation failed to induce further contraction.

There was more than once evidence that the oscular aperture contracted when the current through it grew feebler, though the contraction was not sufficient to keep from diminution either the oscular velocity or the length of the jet. In a *Leucaltis*, observed over 24 days, the osculum contracted to half its original diameter, while the length of the jet diminished from 18 cm. to 1 cm. I give this series of measurements, which shows also that when the current recovered (probably with a lower temperature) the osculum widened again.

<i>July</i>	7,	7,	8,	9,	9,	11,	11,	11,	20,	21,	22,	23,	29,	29,	30,	30,	30,	31
Diameter of osculum	.38	.35	.30	.25	.18	.32	.28	.25	.20	.205	.20	.20	.17	.16	.18	.18	.18	—
Length of jet	15+	9	7	6.5	2	13	8	7½	6.5	6.7	.62	4.4	.9	.5	1.6	1.0	.5	.7

Parker found in *Stylorella* ('Journ. Exp. Zool.', 8, p. 784) that the oscula close when the external water is still; this may be called 'Parker's reaction'. In *Leucandra* and *Leucaltis* it is shown by the sphincter of the osculum being inhibited from contraction by the movement of water over its internal surface. If the reaction is such that there is neither contraction nor relaxation in response to the velocity characteristic of the species (Note 5 (12)) the optimum osculum will be maintained at all stages of growth.

NOTE 3. DELIVERY OF WATER AND SECRETION OF LIME.

In the *Leucandra aspera* of Text-fig. 1, taking the mean oscular velocity at 8.5 cm. per second (see Note 1), the area of the osculum being 0.031 sq. cm., the delivery per second was 0.26 c.cm., or 16 c.cm. per minute; that is .9 litre an hour, 90 litres in 4 days, and a ton in 45 days (see Note 6).

This sponge was gathered on May 20, and from Vosmaer ('Mitth. Z. S. Neapel', v, pp. 486, 487) was probably only a month old, during which time its volume and the volume of its delivery must be supposed to have increased by some 40 per cent. every day in geometrical progression. Then the total amount of water passed during its whole life would be the equivalent of $3\frac{1}{2}$ days of its final delivery, and it would have extracted food from a total weight of 80 kg. of water.

By weighing the preserved sponge alternately in alcohol and water I found the total volume 0.31 c.cm., weight 0.59 gm., sp. gr. 1.9. Allowing 2.5 for the sp. gr. of the spicules and 1.4 for that of the dry protoplasm, this gives

	<i>Total Volume.</i>	<i>Dry Weight.</i>
	<i>c.cm.</i>	<i>gm.</i>
Spicules of <i>Leucandra aspera</i> (Text-fig. 1)	.15	.38
Protoplasm	.16	.21
	.31	.59

Therefore from 80 kg. of water the sponge abstracted a total weight of 0.38 gm. of carbonate of lime, or 0.005 gm. per kg., or about one-third of the amount of carbonate of lime which can be dissolved in pure water free from carbonic acid, and about one-twelfth of the total lime in an average sample of sea-water. If we suppose the sponge's life to have been longer, or the osculum to have been more dilated (Note 6), the percentage proportion of lime extracted is proportionately less.

NOTE 4. FAN-SHAPED SPONGES.

There is a possibility that these, like the Hexactinellids, are found always in a permanent current, on which they depend for subsistence.

After this paper was read at the British Association, Sir W. Herdman kindly informed me that in the deeps off Scotland (where the sponges were found from the figures of which Text-fig. 11 was made) there are many places where the current sets only one way. And Professor Stanley Gardiner added that in 30 fathoms off the Seychelles (where the sponge

was found of Text-fig. 12) there is a constant current down the slope away from the shore. The hypothesis is possible that the fan-shaped form only occurs in response to the stimulus of a constant current (compare Note 2) across which its plane is extended; but that if the current turns tidally from all points of the compass, the fan grows up across each direction in turn, so that an open cup is formed.

The advantage of the fan in still water is shown in the text, but in a current turning tidally the efferent stream will be driven back on the sponge for half the day. In such a position the vertical oscular stream is the common form, because this forms an equal angle with the supply from whatever point it comes. Oyster-shaped sponges, with oscula on the edges, are possibly from a channel where the tide runs alternately from two opposite points; they may be called 'pectinate'.

Sponges living always in the surf, or long flexible sponges, such as *Chalina oculata*, which point downstream from their stalks, have of course no need to do more than to lift the outflowing water sufficiently from their surface for the current down which they lie to bear it free of their more apical parts.

The conditions discussed in this paper affect sponges which are left long in tide-pools, and sponges which inhabit depths where there is inappreciable wave-motion, and where currents are feeble.

NOTE 5. CALCULATIONS OF PRESSURE AND OPTIMUM SIZE
OF OSCULUM.

(Mathematical basis of the paper.)

The loss of energy in a tube from resistance due to viscosity in unit of time is

$$8\pi\mu u^2b,$$

where u = velocity,
 b = length of tube,
 μ = index of viscosity.

Therefore if E be the loss of energy per second in N similar tubes,

$$E = 8\pi\mu \cdot Nv^2b.*$$

Let q be the quantity of water passing per second through the N tubes in parallel, the loss of energy per second is

$$\epsilon = 8\pi\mu \cdot Nb \frac{q^2}{a^2},$$

where a is the aggregate area of the cross-sections of the tubes.

In the sponge the whole of the water passes in succession through

- | | |
|--------------------------|----------------------|
| (1) Afferent canals; | (3) Efferent canals; |
| (2) Flagellate chambers; | (4) The cloaca. |

For the whole system, therefore, the loss of energy due to resistance is the sum of the losses in these four systems, which may be represented

$$\sum \epsilon = 8\pi\mu \left(\sum \frac{N \cdot b}{a^2} \right) q^2.$$

$$\text{Let } 8\pi\mu \left(\sum \frac{N \cdot b}{a^2} \right) = F. \quad (1)$$

Then the energy reaching the osculum per second is

$$E = Pq - Fq^2, \quad (2)$$

where P is the pressure maintained by the action of the flagella.

But if v be the velocity at the osculum, the energy of the jet per second is

$$E = \rho \cdot q \frac{v^2}{2}, \quad (3)$$

where ρ is the density of the water; and if x be the diameter of the osculum

$$q = \frac{\pi}{4} x^2 \cdot v.$$

* It was the late Professor Sir G. G. Stokes, in 1888, who supplied me with this formula, and a clearly written exposition of its meaning, which could be understood by the ignorant. I cannot allow my use of it to appear in print without a tribute to his kindness to a then young man, unknown to him, with no recommendation but a somewhat shameless request for assistance.

Therefore from (2) and (3)

$$\rho \frac{v^2}{2} = P - Fq, \quad (4)$$

$$= P - \frac{\pi}{4} Fx^2 v.$$

$$v^2 + \frac{\pi}{2} \cdot \frac{F}{\rho} \cdot x^2 v = 2 \frac{P}{\rho}. \quad (5)$$

If l be the length of the oscular jet, I find by experiment (p. 298 and Note 1) that

$$l = Cv_x. \quad (6)$$

* Substitute $\frac{l}{Cx} = v$ in (5), therefore

$$\frac{l^2}{c^2 x^2} + \frac{\pi}{2} \cdot \frac{F}{\rho} \cdot \frac{x^2 l}{Cx} = \frac{2P}{\rho}, \quad (7)$$

$$\therefore \frac{2}{C^2} + \frac{\pi}{2} \cdot \frac{F}{\rho} \cdot \frac{x^3 l}{C} = \frac{2Px^2}{\rho}. \quad (8)$$

Now l has a maximum or minimum when $\frac{dl}{dx} = 0$. Differentiating (8),

$$\frac{2l}{C^2} \cdot \frac{dl}{dx} + \frac{\pi}{2} \cdot \frac{F}{\rho C} (3x^2 l + x^3 \frac{dl}{dx}) = \frac{4Px}{\rho}.$$

$$\text{Therefore when } \frac{dl}{dx} = 0, \quad \frac{\pi}{2} \cdot \frac{F}{\rho C} \cdot 3l = \frac{4P}{\rho x}.$$

$$\frac{l}{C} = \frac{8P}{3\pi Fx}.$$

Substitute this value in (7), therefore l has a maximum or minimum when

$$\left(\frac{8P}{3\pi F}\right)^2 \cdot \frac{1}{x^4} + \frac{4P}{3\rho} = \frac{2P}{\rho},$$

* I have to thank Mr. G. I. Taylor, F.R.S., who has very kindly read the first proof-sheets of this paper, for giving me this simple demonstration of (9), from (5) and (6), to replace my own very clumsy differentiation.—June 8, 1923.

$$\text{or} \quad \left(\frac{8P}{3\pi F}\right)^2 \cdot \frac{1}{x^4} = \frac{P}{\rho} \left(2 - \frac{4}{3}\right) = \frac{2}{3} \frac{P}{\rho}.$$

$$\therefore \text{when} \quad x^4 = \frac{64P^2}{9\pi^2 F^2} \cdot \frac{3\rho}{2P} = \frac{32P}{3\pi^2 F^2}. \quad (9)$$

(Note that the value of C is not involved in this equation.)

$$\therefore x^4 = 1.081\rho \frac{P}{F^2}, \text{ or taking } \rho = 1.025, x^4 = 1.11 \frac{P}{F^2}.$$

The negative and imaginary roots do not concern us, for x is necessarily rational and positive; and since P and F are finite and positive, this equation gives a finite and rational value for x , and therefore, from (5), l is also rational, positive and finite.

But there is no jet from an aperture of infinite radius, because the velocity is zero, and there can be no jet from a closed aperture;

therefore when $x = \infty$, $l = 0$; and when $x = 0$, $l = 0$;

therefore the value of x given by (9) corresponds to a greater value of l than that when $x = 0$, or when $x = \infty$; and as it is the only positive and finite value for x for which $\frac{dl}{dx} = 0$,

therefore the corresponding value of l is the only positive maximum of l , and the length of the oscular jet has its greatest value when the diameter of the osculum has the value X , where

$$X = \sqrt[4]{1.11 \frac{P}{F^2}} = 1.03 \sqrt{\frac{\sqrt{P}}{F}}. \quad (10)$$

If a second sponge precisely similar to A. 11 were to have the oscular end of its cloaca united with the oscular end of the cloaca of A. 11, to make a twin sponge with a single osculum, we should have twice the number of afferent and efferent canals, &c., and two cloacae; so that in the computation of F , N and a would both be doubled, with the result that, comparing F_2 for the twin sponge with F of the original sponge, by (1)

$$F_2 = 8\pi\mu \left(\sum \frac{2Nb}{4a^2} \right) = \frac{F}{2}.$$

With twice the number of flagellate chambers, q_2 will be approximately equal to $2q$, therefore $F_2 q_2 = Fq$. The pressure in the flagellate chamber depends solely on the structure and vigour of the flagellate cells, velocity there being so slow that kinetic energy is always negligible, therefore $P_2 = P$, whatever the number of chambers.

$$\text{But, from (4),} \quad P = \frac{\rho v^2}{2} + Fq. \quad (11)$$

$$P_2 = \frac{\rho (v_2)^2}{2} + F_2 q_2.$$

Therefore $v^2 = v_2^2$, and the velocity from the osculum is the same in sponges of similar canal systems, irrespective of size; that is, of the number of similar units which are grouped to expel water by one osculum; and for *Leucandra aspera gigantea* in health, from Note 1,

$$L = 12 \times 8.5 B = 100 B. \quad (12)$$

$$\text{Now by (10)} \quad X = 1.03 \sqrt{\frac{\sqrt{P}}{F}}.$$

Therefore for the twin sponge

$$X_2 = 1.03 \sqrt{\frac{\sqrt{P_2}}{F_2}} = 1.03 \sqrt{\frac{2\sqrt{P}}{F}} = X \sqrt{2}.$$

Similarly, if m similar units, for each of which the optimum oscular diameter is X , be united to one osculum, and X_m be the optimum diameter of this, then

$$X_m = X \sqrt{m}.$$

With similar sponges the external volume may be taken as the approximate measure of the number of similar units aggregated into one individual; or, more conveniently, the product of length, breadth, and thickness may be taken as the measure. Calling this product M , its value for *A. 11* is 4.1 c.c., and we shall find in Note 6 that for *A. 11* $X = .25 \pm .03$.

Therefore, for *Leucandra aspera gigantea* of similar canal-system, the optimum diameter of the osculum in centimetres is numerically

$$X_m = .25 \sqrt{\frac{M}{4.1}} = .12 \sqrt{M},$$

and generally for any one species and metamp

$$X_m = \alpha \sqrt{M},$$

the area of the osculum varying as the volume of the sponge.

For a sponge like the bath-sponge, with N oscula, the sum of whose diameters is $\sum X$, approximately,

$$\sum X = N \alpha \sqrt{\frac{M}{N}} = \alpha \sqrt{NM}.$$

NOTE 6. ARITHMETICAL TESTS, DATA, AND CONCLUSIONS.

From camera lucida drawings of the canals and their apertures in the *Leucandra aspera* of Figs. 1 and 7 ('A. 11' of my records) F is computed in the table below to be 180 ± 30 , the relative velocities being confirmed by the times taken by litmus to pass through the walls of the sponge and through its cloaca (p. 293). Using this value in (11), with $\rho = 1.025$, $v = 8.5 \pm 1.5$, we find for A. 11 the equation

$$P = 37.0 \pm 14 + (1200 \pm 420)x^2, \quad (13)$$

so that, if $x = .20$, the diameter of the osculum measured in spirit, then

$$P = 85 \pm 30 = .9 \text{ mm.} \pm 3 \text{ mm. of water;}$$

and by equation (10), the optimum diameter of the osculum

$$X = .235 \pm .025.$$

Note 2 shows the need of a probable correction in the value of x . The *Leucandra* 'A. 11' was 4 hrs. under experiment before being preserved, and its velocity had sunk to less than half its original value. If we may reason from the observations on *Leucaltis* we should expect the diameter of the osculum to have been reduced by 30 per cent., and therefore that for a velocity of 8.5 cm. it had been .28 cm. wide, instead of the .20 cm. measured after preservation.

With $x = .28$,

$$P = 131 \pm 45 = 1.33 \text{ mm.} \pm .46 \text{ mm. of water,}$$

$$X = .26 \pm .03.$$

The conditions under which the diameter of the osculum is equal to the theoretically best diameter are found by substituting the value of X in (10) for x in (11), giving the relations

$$\left. \begin{aligned} P &= 1.55 v^2 \\ x^2 &= 1.33 \frac{v}{\bar{F}} \end{aligned} \right\} \quad (14)$$

So that, with $F = 180$,

$$\text{if } v = 8.5; x = X = .251, P = 112;$$

$$v = 9.0; x = X = .258, P = 126;$$

the latter being acceptable values. On the other hand, we may ascertain what error is indicated in F , if we assume that in healthy life x was .28 cm. as suggested above, and that P (cf. p. 306) was exactly proportional to the pressure of 370 ± 25 found by Parker in the 35μ spherical chambers of *Stylo-tella*:

The chambers of *Leucandra* being cylindrical and 54μ in diameter,

$$P = (370 \pm 25) \times \frac{1}{2} \times \frac{34}{34} = 120 \pm 8.$$

$$\text{By (14)} \quad v = \sqrt{\frac{P}{1.55}} = \sqrt{\frac{120 \pm 8}{1.55}} = 8.84 \pm .3;$$

by assumption $x = .28$;

$$\text{by (14)} \quad F = \frac{4}{3} \cdot \frac{v}{x^2} = \frac{4}{3} \times \frac{8.84}{.0784} = 150.$$

The diminution of viscosity with warmth would reduce F from 180 at 15°C . to 150 at 22°C . This is no unlikely temperature for the *Porto Militare* in the summer, so that the investigation shows the data in harmony with each other and with the theories of the paper.

The arithmetical coincidence suggests that the probable errors of the observations are overstated. The errors could not be calculated statistically, and I could not estimate them at smaller figures. I much regret having been unable to claim greater exactitude.

TABLE OF DATA FOR CALCULATION OF VELOCITIES AND RESISTANCE (*L. aspera*. 'A. 11').

	Number.	Mean length.	Aggregate transverse area.	$\therefore F = .28 \frac{N}{a^2} \dagger$	Velocity.	
					(1)	(2)
Afferent canals . .	81000	.06	4.2	99	.06	.13
Subchoanal space . .	—	—	200	—	.0013	.0026
Flagellate chambers .	2,250000	$.019 \times \frac{1}{3}^*$	52.5	1	.005	.010
Efferent canals . .	5200	.08	2.5	47	.10	.21
Cloaca . .	1	$10 \times \frac{1}{2}^*$.21	33	1.3	2.5
Osculum . .	1	—	{(1).031} {(2).062}	—	8.5	8.5
Whole sponge. .				180		

Therefore, for A. 11, $F = (180 \pm 30) \times \{1 - .024(t - 15)\}$, where t° is the temperature Centigrade.

* The factors $\frac{1}{3}$ and $\frac{1}{2}$ allow for the water-entering by holes along the walls.

† At 15° C. From equation (1).

(1) Calculated for oscular diameter .20, area .031, delivery .26.

(2) Calculated for oscular diameter .28, area .062, delivery .53.