ON
GROWTH AND FORM

BY
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A new edition

CAMBRIDGE: AT THE UNIVERSITY PRESS
NEW YORK: THE MACMILLAN COMPANY
1945
CHAPTER II
ON MAGNITUDE

To terms of magnitude, and of direction, must we refer all our conceptions of Form. For the form of an object is defined when we know its magnitude, actual or relative, in various directions; and Growth involves the same concepts of magnitude and direction, related to the further concept, or "dimension," of Time. Before we proceed to the consideration of specific form, it will be well to consider certain general phenomena of spatial magnitude, or of the extension of a body in the several dimensions of space.

We are taught by elementary mathematics—and by Archimedes himself—that in similar figures the surface increases as the square, and the volume as the cube, of the linear dimensions. If we take the simple case of a sphere, with radius \( r \), the area of its surface is equal to \( 4\pi r^2 \), and its volume to \( \frac{4}{3}\pi r^3 \); from which it follows that the ratio of its volume to surface, or \( V/S \), is \( \frac{1}{3}r \). That is to say, \( V/S \) varies as \( r \); or, in other words, the larger the sphere by so much the greater will be its volume (or its mass, if it be uniformly dense throughout) in comparison with its superficial area. And, taking \( L \) to represent any linear dimension, we may write the general equations in the form

\[
S \propto L^2, \quad V \propto L^3,
\]

or

\[
S = kL^2, \quad V = k'L^3,
\]

where \( k, k' \), are "factors of proportion,"

and

\[
\frac{V}{S} \propto L, \quad \text{or} \quad \frac{V}{S} = \frac{k}{k'} L = KL.
\]

So, in Lilliput, "His Majesty's Ministers, finding that Gulliver's stature exceeded theirs in the proportion of twelve to one, concluded from the similarity of their bodies that his must contain at least 1728 [or 12\(^3\)] of theirs, and must needs be rationed accordingly*."

* Likewise Gulliver had a whole Lilliputian hogshead for his half-pint of wine: in the due proportion of 1728 half-pints, or 108 gallons, equal to one pipe or
From these elementary principles a great many consequences follow, all more or less interesting, and some of them of great importance. In the first place, though growth in length (let us say) and growth in volume (which is usually tantamount to mass or weight) are parts of one and the same process or phenomenon, the one attracts our *attention* by its increase very much more than the other. For instance a fish, in doubling its length, multiplies its weight no less than eight times; and it all but doubles its weight in growing from four inches long to five.

In the second place, we see that an understanding of the correlation between length and weight in any particular species of animal, in other words a determination of *k* in the formula \( W = k \cdot L^3 \), enables us at any time to translate the one magnitude into the other, and (so to speak) to weigh the animal with a measuring-rod; this, however, being always subject to the condition that the animal shall in no way have altered its form, nor its specific gravity. That its specific gravity or density should materially or rapidly alter is not very likely; but as long as growth lasts changes of form, even though inappreciable to the eye, are apt and likely to occur. Now weighing is a far easier and far more accurate operation than measuring; and the measurements which would reveal slight and otherwise imperceptible changes in the form of a fish—slight relative differences between length, breadth and depth, for instance—would need to be very delicate indeed. But if we can make fairly accurate determinations of the length, which is much the easiest linear dimension to measure, and correlate it with the weight, then the value of *k*, whether it varies or remains constant, will tell us at once whether there has or has not been a tendency to alteration in the general form, or, in other words, a difference in the rates of growth in different directions. To this subject we shall return, when we come to consider more particularly the phenomenon of *rate of growth*.

double-hogshead. But Gilbert White of Selborne could not see what was plain to the Lilliputians; for finding that a certain little long-legged bird, the stilt, weighed 4½ oz. and had legs 8 in. long, he thought that a flamingo, weighing 4 lbs., should have legs 10 ft. long, to be in the same proportion as the stilt’s. But it is obvious to us that, as the weights of the two birds are as 1:15, so the legs (or other linear dimensions) should be as the cube-roots of these numbers, or nearly as 1:2½. And on this scale the flamingo’s legs should be, as they actually are, about 20 in. long.
We are accustomed to think of magnitude as a purely relative matter. We call a thing big or little with reference to what it is wont to be, as when we speak of a small elephant or a large rat; and we are apt accordingly to suppose that size makes no other or more essential difference, and that Lilliput and Brobdignag\(^*\) are all alike, according as we look at them through one end of the glass or the other. Gulliver himself declared, in Brobdignag, that "undoubtedly philosophers are in the right when they tell us that nothing is great and little otherwise than by comparison": and Oliver Heaviside used to say, in like manner, that there is no absolute scale of size in the Universe, for it is boundless towards the great and also boundless towards the small. It is of the very essence of the Newtonian philosophy that we should be able to extend our concepts and deductions from the one extreme of magnitude to the other; and Sir John Herschel said that "the student must lay his account to finding the distinction of great and little altogether annihilated in nature."

All this is true of number, and of relative magnitude. The Universe has its endless gamut of great and small, of near and far, of many and few. Nevertheless, in physical science the scale of absolute magnitude becomes a very real and important thing; and a new and deeper interest arises out of the changing ratio of dimensions when we come to consider the inevitable changes of physical relations with which it is bound up. The effect of scale depends not on a thing in itself, but in relation to its whole environment or milieu; it is in conformity with the thing's "place in Nature," its field of action and reaction in the Universe. Everywhere Nature works true to scale, and everything has its proper size accordingly. Men and trees, birds and fishes, stars and star-systems, have their appropriate dimensions, and their more or less narrow range of absolute magnitudes. The scale of human observation and experience lies within the narrow bounds of inches, feet or miles, all measured in terms drawn from our own selves or our own doings. Scales which include light-years, parsecs, Angström units, or atomic

\(^*\) Swift paid close attention to the arithmetic of magnitude, but none to its physical aspect. See De Morgan, on Lilliput, in \textit{N. and Q.} (2), vi, pp. 123–125, 1858. On relative magnitude see also Berkeley, in his \textit{Essay towards a New Theory of Vision}, 1709.
and sub-atomic magnitudes, belong to other orders of things and other principles of cognition.

A common effect of scale is due to the fact that, of the physical forces, some act either directly at the surface of a body, or otherwise in proportion to its surface or area; while others, and above all gravity, act on all particles, internal and external alike, and exert a force which is proportional to the mass, and so usually to the volume of the body.

A simple case is that of two similar weights hung by two similar wires. The forces exerted by the weights are proportional to their masses, and these to their volumes, and so to the cubes of the several linear dimensions, including the diameters of the wires. But the areas of cross-section of the wires are as the squares of the said linear dimensions; therefore the stresses in the wires per unit area are not identical, but increase in the ratio of the linear dimensions, and the larger the structure the more severe the strain becomes:

\[
\frac{\text{Force}}{\text{Area}} \propto \frac{l^2}{l^2} \propto l,
\]

and the less the wires are capable of supporting it.

In short, it often happens that of the forces in action in a system some vary as one power and some as another, of the masses, distances or other magnitudes involved; the "dimensions" remain the same in our equations of equilibrium, but the relative values alter with the scale. This is known as the "Principle of Similitude," or of dynamical similarity, and it and its consequences are of great importance. In a handful of matter cohesion, capillarity, chemical affinity, electric charge are all potent; across the solar system gravitation* rules supreme; in the mysterious region of the nebulae, it mayhap be that gravitation grows negligible again.

To come back to homelier things, the strength of an iron girder obviously varies with the cross-section of its members, and each cross-section varies as the square of a linear dimension; but the weight of the whole structure varies as the cube of its linear dimen-

* In the early days of the theory of gravitation, it was deemed especially remarkable that the action of gravity "is proportional to the quantity of solid matter in bodies, and not to their surfaces as is usual in mechanical causes; this power, therefore, seems to surpass mere mechanism" (Colin Maclaurin, on Sir Isaac Newton's Philosophical Discoveries, iv, 9).
sions. It follows at once that, if we build two bridges geometrically similar, the larger is the weaker of the two*, and is so in the ratio of their linear dimensions. It was elementary engineering experience such as this that led Herbert Spencer to apply the principle of similitude to biology†.

But here, before we go further, let us take careful note that increased weakness is no necessary concomitant of increasing size. There are exceptions to the rule, in those exceptional cases where we have to deal only with forces which vary merely with the area on which they impinge. · If in a big and a little ship two similar masts carry two similar sails, the two sails will be similarly strained, and equally stressed at homologous places, and alike suitable for resisting the force of the same wind. Two similar umbrellas, however differing in size, will serve alike in the same weather; and the expanse (though not the leverage) of a bird’s wing may be enlarged with little alteration.

The principle of similitude had been admirably applied in a few clear instances by Lesage‡, a celebrated eighteenth-century physician, in an unfinished and unpublished work. Lesage argued, for example, that the larger ratio of surface to mass in a small animal would lead to excessive transpiration, were the skin as “porous” as our own; and that we may thus account for the hardened or thickened skins of insects and many other small terrestrial animals. Again, since the weight of a fruit increases as the cube of its linear dimensions, while the strength of the stalk increases as the square, it follows that the stalk must needs grow out of apparent due proportion to the fruit: or, alternatively, that tall trees should not bear large


† Herbert Spencer, The form of the earth, etc., Phil. Mag. xxx, pp. 194–6, 1847; also Principles of Biology, pt. ii, p. 123 seq., 1864.

fruit on slender branches, and that melons and pumpkins must lie upon the ground. And yet again, that in quadrupeds a large head must be supported on a neck which is either excessively thick and strong like a bull's, or very short like an elephant's*.

But it was Galileo who, wellnigh three hundred years ago, had first laid down this general principle of similitude; and he did so with the utmost possible clearness, and with a great wealth of illustration drawn from structures living and dead†. He said that if we tried building ships, palaces or temples of enormous size, yards, beams and bolts would cease to hold together; nor can Nature grow a tree nor construct an animal beyond a certain size, while retaining the proportions and employing the materials which suffice in the case of a smaller structure‡. The thing will fall to pieces of its own weight unless we either change its relative proportions, which will at length cause it to become clumsy, monstrous and inefficient, or else we must find new material, harder and stronger than was used before. Both processes are familiar to us in Nature and in art, and practical applications, undreamed of by Galileo, meet us at every turn in this modern age of cement and steel§.

Again, as Galileo was also careful to explain, besides the questions of pure stress and strain, of the strength of muscles to lift an increasing weight or of bones to resist its crushing stress, we have the important question of bending moments. This enters, more or less, into our whole range of problems; it affects the whole form of the skeleton, and sets a limit to the height of a tall tree||.

† Discorsi e Dimostrazioni matematiche, intorno à due nuove scienze attenenti alla Mecanica ed ai Muovimenti Locali: appresso gli Elzevirii, 1638; Operé, ed. Favaro, viii, p. 169 seq. Transl. by Henry Crew and A. de Salvio, 1914, p. 130.
‡ So Werner remarked that Michael Angelo and Bramanti could not have built of gypsum at Paris on the scale they built of travertin at Rome.
§ The Chrysler and Empire State Buildings, the latter 1048 ft. high to the foot of its 200 ft. "mooring mast," are the last word, at present, in this brobdingngarian architecture.
|| It was Euler and Lagrange who first shewed (about 1776-1778) that a column of a certain height would merely be compressed, but one of a greater height would be bent by its own weight. See Euler, De altitudine columnarum etc., Acta Acad. Sci. Imp. Petropol. 1778, pp. 163-193; G. Greenhill, Determination of the greatest height to which a tree of given proportions can grow, Camb. Phil. Soc. Proc. iv, p. 65, 1881, and Chree, ibid. vii, 1892.
We learn in elementary mechanics the simple case of two similar beams, supported at both ends and carrying no other weight than their own. Within the limits of their elasticity they tend to be deflected, or to sag downwards, in proportion to the squares of their linear dimensions; if a match-stick be two inches long and a similar beam six feet (or 36 times as long), the latter will sag under its own weight thirteen hundred times as much as the other. To counteract this tendency, as the size of an animal increases, the limbs tend to become thicker and shorter and the whole skeleton bulkier and heavier; bones make up some 8 per cent. of the body of mouse or wren, 13 or 14 per cent. of goose or dog, and 17 or 18 per cent. of the body of a man. Elephant and hippopotamus have grown clumsy as well as big, and the elk is of necessity less graceful than the gazelle. It is of high interest, on the other hand, to observe how little the skeletal proportions differ in a little porpoise and a great whale, even in the limbs and limb-bones; for the whole influence of gravity has become negligible, or nearly so, in both of these.

In the problem of the tall tree we have to determine the point at which the tree will begin to bend under its own weight if it be ever so little displaced from the perpendicular*. In such an investigation we have to make certain assumptions—for instance that the trunk tapers uniformly, and that the sectional area of the branches varies according to some definite law, or (as Ruskin assumed) tends to be constant in any horizontal plane; and the mathematical treatment is apt to be somewhat difficult. But Greenhill shewed, on such assumptions as the above, that a certain British Columbian pine-tree, of which the Kew flag-staff, which is 221 ft. high and 21 inches in diameter at the base, was made, could not possibly, by theory, have grown to more than about 300 ft. It is very curious that Galileo had suggested precisely the same height (ducento braccie alta) as the utmost limit of the altitude of a tree. In general, as Greenhill shewed, the diameter of a tall homogeneous body must increase as the power 3/2 of its height, which accounts for the slender proportions of young trees compared with the squat

* In like manner the wheat-straw bends over under the weight of the loaded ear, and the cat's tail bends over when held erect—not because, they "possess flexibility," but because they outstrip the dimensions within which stable equilibrium is possible in a vertical position. The kitten's tail, on the other hand, stands up spiky and straight.
OF THE HEIGHT OF A TREE

or stunted appearance of old and large ones*. In short, as Goethe
says in *Dichtung und Wahrheit*, "Es ist dafür gesorgt dass die Bäume
nicht in den Himmel wachsen."

But the tapering pine-tree is but a special case of a wider problem.
The oak does not grow so tall as the pine-tree, but it carries a heavier
load, and its boll, broad-based upon its spreading roots, shews a
different contour. Smeaton took it for the pattern of his lighthouse,
and Eiffel built his great tree of steel, a thousand feet high, to a
similar but a stricter plan. Here the profile of tower or tree follows,
or tends to follow, a logarithmic curve, giving equal strength
throughout, according to a principle which we shall have occasion
to discuss later on, when we come to treat of form and mechanical
efficiency in the skeletons of animals. In the tree, moreover,
anchoring roots form powerful wind-struts, and are most de-
veloped opposite to the direction of the prevailing winds; for the
lifetime of a tree is affected by the frequency of storms, and its
strength is related to the wind-pressure which it must needs with-
stand†.

Among animals we see, without the help of mathematics or of
physics, how small birds and beasts are quick and agile, how slower
and sedater movements come with larger size, and how exaggerated
bulk brings with it a certain clumsiness, a certain inefficiency, an
element of risk and hazard, a preponderance of disadvantage. The
case was well put by Owen, in a passage which has an interest of
its own as a premonition, somewhat like De. Candolle's, of the
"struggle for existence." Owen wrote as follows‡: "In proportion
to the bulk of a species is the difficulty of the contest which, as a
living organised whole, the individual of each species has to maintain
against the surrounding agencies that are ever tending to dissolve
the vital bond, and subjugate the living matter to the ordinary
chemical and physical forces. Any changes, therefore, in such
external conditions as a species may have been originally adapted

* The stem of the giant bamboo may attain a height of 60 metres while not more
than about 40 cm. in diameter near its base, which dimensions fall not far short
xi, pp. 277-285, 1930. Also an interesting paper by James Macdonald, on The
form of coniferous trees, *Forestry*, vi, 1 and 2, 1931/2.
to exist in, will militate against that existence in a degree proportionate, perhaps in a geometrical ratio, to the bulk of the species. If a dry season be greatly prolonged, the large mammal will suffer from the drought sooner than the small one; if any alteration of climate affect the quantity of vegetable food, the bulky Herbivore will be the first to feel the effects of stinted nourishment."

But the principle of Galileo carries us further and along more certain lines. The strength of a muscle, like that of a rope or girder, varies with its cross-section; and the resistance of a bone to a crushing stress varies, again like our girder, with its cross-section. But in a terrestrial animal the weight which tends to crush its limbs, or which its muscles have to move, varies as the cube of its linear dimensions; and so, to the possible magnitude of an animal, living under the direct action of gravity, there is a definite limit set. The elephant, in the dimensions of its limb-bones, is already shewing signs of a tendency to disproportionate thickness as compared with the smaller mammals; its movements are in many ways hampered and its agility diminished: it is already tending towards the maximal limit of size which the physical forces permit*. The spindleshanks of gnat or daddy-long-legs have their own factor of safety, conditional on the creature's exiguous bulk and weight; for after their own fashion even these small creatures tend towards an inevitable limitation of their natural size. But, as Galileo also saw, if the animal be wholly immersed in water like the whale, or if it be partly so, as was probably the case with the giant reptiles of the mesozoic age, then the weight is counterpoised to the extent of an equivalent volume of water, and is completely counterpoised if the density of the animal's body, with the included air, be identical (as a whale's very nearly is) with that of the water around†. Under these circumstances there is no longer the same physical barrier to the indefinite growth of the animal. Indeed, in the case of the aquatic animal, there is, as Herbert Spencer pointed out,

† Cf. W. S. Wall, A New Sperm Whale etc., Sydney, 1851, p. 64: "As for the immense size of Cetacea, it evidently proceeds from their buoyancy in the medium in which they live, and their being enabled thus to counteract the force of gravity."
a distinct advantage, in that the larger it grows the greater is its speed. For its available energy depends on the mass of its muscles, while its motion through the water is opposed, not by gravity, but by "skin-friction," which increases only as the square of the linear dimensions*: whence, other things being equal, the bigger the ship or the bigger the fish the faster it tends to go, but only in the ratio of the square root of the increasing length. For the velocity \( V \) which the fish attains depends on the work \( W \) it can do and the resistance \( R \) it must overcome. Now we, have seen that the dimensions of \( W \) are \( l^3 \), and of \( R \) are \( l^2 \); and by elementary mechanics

\[
W \propto R V^2, \quad \text{or} \quad V^2 \propto \frac{W}{R}.
\]

Therefore

\[
V^2 \propto \frac{l^3}{l^2} = l, \quad \text{and} \quad V \propto \sqrt{l}.
\]

This is what is known as Froude's Law, of the correspondence of speeds—a simple and most elegant instance of "dimensional theory†."

But there is often another side to these questions, which makes them too complicated to answer in a word. For instance, the work (per stroke) of which two similar engines are capable should vary as the cubes of their linear dimensions, for it varies on the one hand with the area of the piston, and on the other with the length of the stroke; so is it likewise in the animal, where the corresponding ratio depends on the cross-section of the muscle, and on the distance through which it contracts. But in two similar engines, the available horse-power varies as the square of the linear dimensions, and not as the cube; and this for the reason that the actual energy developed depends on the heating-surface of the boiler‡. So likewise must

* We are neglecting "drag" or "head-resistance," which, increasing as the cube of the speed, is a formidable obstacle to an unstreamlined body. But the perfect streamlining of whale or fish or bird lets the surrounding air or water behave like a perfect fluid, gives rise to no "surface of discontinuity," and the creature passes through it without recoil or turbulence. Froude reckoned skin-friction, or surface-resistance, as equal to that of a plane as long as the vessel's water-line, and of area equal to that of the wetted surface of the vessel.

† Though, as Lanchester says, the great designer "was not hampered by a knowledge of the theory of dimensions."

‡ The analogy is not a very strict or complete one. We are not taking account, for instance, of the thickness of the boiler-plates.
there be a similar tendency among animals for the rate of supply of kinetic energy to vary with the surface of the lung, that is to say (other things being equal) with the square of the linear dimensions of the animal; which means that, caeteris paribus, the small animal is stronger (having more power per unit weight) than a large one. We may of course (departing from the condition of similarity) increase the heating-surface of the boiler, by means of an internal system of tubes, without increasing its outward dimensions, and in this very way Nature increases the respiratory surface of a lung by a complex system of branching tubes and minute air-cells; but nevertheless in two similar and closely related animals, as also in two steam-engines of the same make, the law is bound to hold that the rate of working tends to vary with the square of the linear dimensions, according to Froude's law of steamship comparison. In the case of a very large ship, built for speed, the difficulty is got over by increasing the size and number of the boilers, till the ratio between boiler-room and engine-room is far beyond what is required in an ordinary small vessel*; but though we find lung-space increased among animals where greater rate of working is required, as in general among birds, I do not know that it can be shewn to increase, as in the "overboilered" ship, with the size of the animal, and in a ratio which outstrips that of the other bodily dimensions. If it be the case then, that the working mechanism of the muscles should be able to exert a force proportionate to the cube of the linear bodily dimensions,

* Let \( L \) be the length, \( S \) the (wetted) surface, \( T \) the tonnage, \( D \) the displacement (or volume) of a ship; and let it cross the Atlantic at a speed \( V \). Then, in comparing two ships, similarly constructed but of different magnitudes, we know that \( L = V^2 \), \( S = L^2 = V^4 \), \( D = T = L^3 = V^6 \); also \( R \) (resistance) = \( S \cdot V^2 = V^8 \); \( H \) (horse-power) = \( R \cdot V = V^7 \); and the coal (\( C \)) necessary for the voyage = \( H/V = V^6 \). That is to say, in ordinary engineering language, to increase the speed across the Atlantic by 1 per cent. the ship's length must be increased 2 per cent., her tonnage or displacement 6 per cent., her coal-consumption also 6 per cent., her horse-power, and therefore her boiler-capacity, 7 per cent. Her bunkers, accordingly, keep pace with the enlargement of the ship, but her boilers tend to increase out of proportion to the space available. Suppose a steamer 400 ft. long, of 2000 tons, 2000 h.p., and a speed of 14 knots. The corresponding vessel of 800 ft. long should develop a speed of 20 knots (1 : 2 : 14 : 20), her tonnage would be 16,000, her h.p. 25,000 or thereby. Such a vessel would probably be driven by four propellers instead of one, each carrying 8000 h.p. See (int. al.) W. J. Millar, On the most economical speed to drive a steamer, Proc. Edin. Math. Soc. vii, pp. 27-29, 1889; Sir James R. Napier, On the most profitable speed for a fully laden cargo steamer for a given voyage, Proc. Phil. Soc., Glasgow, vi, pp. 33-38, 1865.
while the respiratory mechanism can only supply a store of energy at a rate proportional to the square of the said dimensions, the singular result ought to follow that, in swimming for instance, the larger fish ought to be able to put on a spurt of speed far in excess of the smaller one; but the distance travelled by the year's end should be very much alike for both of them. And it should also follow that the curve of fatigue is a steeper one, and the staying power less, in the smaller than in the larger individual. This is the case in long-distance racing, where neither draws far ahead until the big winner puts on his big spurt at the end; on which is based an aphorism of the turf, that "a good big 'un is better than a good little 'un." For an analogous reason wise men know that in the 'Varsity boat-race it is prudent and judicious to bet on the heavier crew.

Consider again the dynamical problem of the movements of the body and the limbs. The work done \( W \) in moving a limb, whose weight is \( p \), over a distance \( s \), is measured by \( ps \); \( p \) varies as the cube of the linear dimensions, and \( s \) in ordinary locomotion, varies as the linear dimensions, that is to say as the length of limb:

\[
W \propto ps \propto l^3 \times l = l^4.
\]

But the work done is limited by the power available, and this varies as the mass of the muscles, or as \( l^2 \); and under this limitation neither \( p \) nor \( s \) increase as they would otherwise tend to do. The limbs grow shorter, relatively, as the animal grows bigger; and spiders, daddy-long-legs and such-like long-limbed creatures attain no great size.

Let us consider more closely the actual energies of the body. A hundred years ago, in Strasburg, a physiologist and a mathematician were studying the temperature of warm-blooded animals*. The heat lost must, they said, be proportional to the surface of the animal: and the gain must be equal to the loss, since the temperature of the body keeps constant. It would seem, therefore, that the heat lost by radiation and that gained by oxidation vary both alike, as the surface-area, or the square of the linear dimensions, of the animal. But this result is paradoxical; for whereas the heat lost

may well vary as the surface-area, that produced by oxidation ought rather to vary as the bulk of the animal: one should vary as the square and the other as the cube of the linear dimensions. Therefore the ratio of loss to gain, like that of surface to volume, ought to increase as the size of the creature diminishes. Another physiologist, Carl Bergmann*, took the case a step further. It was he, by the way, who first said that the real distinction was not between warm-blooded and cold-blooded animals, but between those of constant and those of variable temperature: and who coined the terms \textit{homoeothermic} and \textit{poecilothermic} which we use today. He was driven to the conclusion that the smaller animal does produce more heat (per unit of mass) than the large one, in order to keep pace with surface-loss; and that this extra heat-production means more energy spent, more food consumed, more work done†. Simplified as it thus was, the problem still perplexed the physiologists for years after. The tissues of one mammal are much like those of another. We can hardly imagine the muscles of a small mammal to produce more heat (\textit{caeteris paribus}) than those of a large; and we begin to wonder whether it be not nervous excitation, rather than quality of muscular tissue, which determines the rate of oxidation and the output of heat. It is evident in certain cases, and may be a general rule, that the smaller animals have the bigger brains; "plus l'animal est petit," says M. Charles Richet, "plus il a des échanges chimiques actifs, et plus son cerveau est volumineux‡." That the smaller animal needs more food is certain and obvious. The amount of food and oxygen consumed by a small flying insect is enormous; and bees and flies and hawkmoths and humming-


† The metabolic activity of sundry mammals, per 24 hours, has been estimated as follows:

<table>
<thead>
<tr>
<th>Animal</th>
<th>Weight (kilo.)</th>
<th>Calories per kilo.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Guinea-pig</td>
<td>0.7</td>
<td>223</td>
</tr>
<tr>
<td>Rabbit</td>
<td>2</td>
<td>58</td>
</tr>
<tr>
<td>Man</td>
<td>70</td>
<td>33</td>
</tr>
<tr>
<td>Horse</td>
<td>600</td>
<td>22</td>
</tr>
<tr>
<td>Elephant</td>
<td>4000</td>
<td>13</td>
</tr>
<tr>
<td>Whale</td>
<td>150000</td>
<td>\textit{circa} 1.7</td>
</tr>
</tbody>
</table>

birds live on nectar, the richest and most concentrated of foods*. Man consumes a fiftieth part of his own weight of food daily, but a mouse will eat half its own weight in a day; its rate of living is faster, it breeds faster, and old age comes to it much sooner than to man. A warm-blooded animal much smaller than a mouse becomes an impossibility; it could neither obtain nor yet digest the food required to maintain its constant temperature, and hence no mammals and no birds are as small as the smallest frogs or fishes. The disadvantage of small size is all the greater when loss of heat is accelerated by conduction as in the Arctic, or by convection as in the sea. The far north is a home of large birds but not of small; bears but not mice live through an Arctic winter; the least of the dolphins live in warm waters, and there are no small mammals in the sea. This principle is sometimes spoken of as Bergmann's Law.

The whole subject of the conservation of heat and the maintenance of an all but constant temperature in warm-blooded animals interests the physicist and the physiologist alike. It drew Kelvin's attention many years ago†, and led him to shew, in a curious paper, how larger bodies are kept warm by clothing while smaller are only cooled the more. If a current be passed through a thin wire, of which part is covered and part is bare, the thin bare part may glow with heat, while convection-currents streaming round the covered part cool it off and leave it in darkness. The hairy coat of very small animals is apt to look thin and meagre, but it may serve them better than a shaggier covering.

Leaving aside the question of the supply of energy, and keeping to that of the mechanical efficiency of the machine, we may find endless biological illustrations of the principle of similitude. All through the physiology of locomotion we meet with it in various ways: as, for instance, when we see a cockchafer carry a plate many times its own weight upon its back, or a flea jump many inches high. "A dog," says Galileo, "could probably carry two or three such dogs upon his back; but I believe that a horse could not carry even one of his own size."

Such problems were admirably treated by Galileo and Borelli, but many writers remained ignorant of their work. Linnaeus remarked that if an elephant were as strong in proportion as a stag-beetle, it would be able to pull up rocks and level mountains; and Kirby and Spence have a well-known passage directed to shew that such powers as have been conferred upon the insect have been withheld from the higher animals, for the reason that had these latter been endued therewith they would have "caused the early desolation of the world*." 

Such problems as that presented by the flea’s jumping powers†, though essentially physiological in their nature, have their interest for us here: because a steady, progressive diminution of activity with increasing size would tend to set limits to the possible growth in magnitude of an animal just as surely as those factors which tend to break and crush the living fabric under its own weight. In the case of a leap, we have to do rather with a sudden impulse than with a continued strain, and this impulse should be measured in terms of the velocity imparted. The velocity is proportional to the impulse \( (x) \), and inversely proportional to the mass \( (M) \) moved: \( V = x/M \). But, according to what we still speak of as "Borelli’s law," the impulse (i.e. the work of the impulse) is proportional to the volume of the muscle by which it is produced‡, that is to say (in similarly constructed animals) to the mass of the whole body; for the impulse is proportional on the one hand to the cross-section of the muscle, and on the other to the distance through which it 

* Introduction to Entomology, II, p. 190, 1826. Kirby and Spence, like many less learned authors, are fond of popular illustrations of the "wonders of Nature," to the neglect of dynamical principles. They suggest that if a white ant were as big as a man, its tunnels would be "magnificent cylinders of more than three hundred feet in diameter"; and that if a certain noisy Brazilian insect were as big as a man, its voice would be heard all the world over, "so that Stentor becomes a mute when compared with these insects!" It is an easy consequence of anthropomorphism, and hence a common characteristic of fairy-tales, to neglect the dynamical and dwell on the geometrical aspect of similarity.

† The flea is a very clever jumper; he jumps backwards, is stream-lined accordingly, and alights on his two long hind-legs. Cf. G. I. Watson, in Nature, 21 May 1938.

‡ That is to say, the available energy of muscle, in ft.-lbs. per lb. of muscle, is the same for all animals: a postulate which requires considerable qualification when we come to compare very different kinds of muscle, such as the insect’s and the mammal’s.
contracts. It follows from this that the velocity is constant, whatever be the size of the animal.

Putting it still more simply, the work done in leaping is proportional to the mass and to the height to which it is raised, \( W \propto mH \).

But the muscular power available for this work is proportional to the mass of muscle, or (in similarly constructed animals) to the mass of the animal, \( W \propto m \).

It follows that \( H \) is, or tends to be, a constant. In other words, all animals, provided always that they are similarly fashioned, with their various levers in like proportion, ought to jump not to the same relative but to the same actual height*. The grasshopper seems to be as well planned for jumping as the flea, and the actual heights to which they jump are much of a muchness; but the flea’s jump is about 200 times its own height, the grasshopper’s at most 20–30 times; and neither flea nor grasshopper is a better but rather a worse jumper than a horse or a man†.

As a matter of fact, Borelli is careful to point out that in the act of leaping the impulse is not actually instantaneous, like the blow of a hammer, but takes some little time, during which the levers are being extended by which the animal is being propelled forwards; and this interval of time will be longer in the case of the longer levers of the larger animal. To some extent, then, this principle acts as a corrective to the more general one, and tends to leave a certain balance of advantage in regard to leaping power on the side of the larger animal‡. But on the other hand, the question of strength of materials comes in once more, and the factors of stress and strain and bending moment make it more and more difficult for nature to endow the larger animal with the length of lever with which she has provided the grasshopper or the flea. To Kirby and Spence it seemed that “This wonderful strength of insects is doubtless the result of something peculiar in the structure and arrangement of their muscles, and principally their extraordinary

* Borelli, Prop. clxxvii. Animalia minora et minus ponderosa majores saltus efficient respectu sui corporis, si caetera fuerint paria.
† The high jump is nowadays a highly skilled performance. For the jumper contrives that his centre of gravity goes under the bar, while his body, bit by bit, goes over it.
‡ See also (int. al.), John Bernoulli, De Motu Musculorum, Basil., 1694; Chabry, Mécanisme du saut, J. de l’Anat. et de la Physiol. xix, 1883; Sur la longueur des membres des animaux sauteurs, ibid. xxv, p. 356, 1885; Le Hello, De l’action des organes locomoteurs, etc., ibid. xxix, pp. 65–93, 1893; etc.
power of contraction.” This hypothesis, which is so easily seen on physical grounds to be unnecessary, has been amply disproved in a series of excellent papers by Felix Plateau*.

From the impulse of the preceding case we may pass to the momentum created (or destroyed) under similar circumstances by a given force acting for a given time: \( mv = Ft \).

We know that \( m \propto l^2 \), and \( t = \frac{1}{v} \), so that \( Fv = \frac{Fl}{v} \), or \( v^2 = \frac{F}{l^2} \).

But whatsoever force be available, the animal may only exert so much of it as is in proportion to the strength of his own limbs, that is to say to the cross-section of bone, sinew and muscle; and all of these cross-sections are proportional to \( l^2 \), the square of the linear dimensions. The maximal force, \( F_{\text{max}} \), which the animal dare exert is proportional, then, to \( l^2 \); therefore

\[
F_{\text{max}}/l^2 = \text{constant.}
\]

And the maximal speed which the animal can safely reach, namely \( V_{\text{max}} = \frac{F_{\text{max}}}{l} \), is also constant, or independent (ceteris paribus) of the dimensions of the animal.

A spurt or effort may be well within the capacity of the animal but far beyond the margin of safety, as trainer and athlete well know. This margin is a narrow one, whether for athlete or racehorse; both run a constant risk of overstrain, under which they may "pull" a muscle, lacerate a tendon, or even "break down" a bone†.

It is fortunate for their safety that animals do not jump to heights proportional to their own. For conceive an animal (of mass \( m \)) to jump to a certain altitude, such that it reaches the ground with a velocity \( v \); then if \( c \) be the crushing strain at any point of the sectional area \( (A) \) of the limbs, the limiting condition is that \( mv = cA \).

If the animal vary in magnitude without change in the height to which it jumps (or in the velocity with which it descends), then

\[
c \propto \frac{m}{A} \propto \frac{l^3}{l^2} \quad \text{or} \quad l.
\]

The crushing strain varies directly with the linear dimensions of the animal; and this, a dynamical case, is identical with the usual statical limitation of magnitude.


But if the animal, with increasing size or stature, jump to a correspondingly increasing height, the case becomes much more serious. For the final velocity of descent varies as the square root of the altitude reached, and therefore as the square root of the linear dimensions of the animal. And since, as before,

\[ c \propto mv \propto \frac{l^3}{t^2} V, \]

\[ c \propto \frac{l^3}{t^2} \sqrt{t}, \quad \text{or} \quad c \propto l. \]

If a creature’s jump were in proportion to its height, the crushing strains would so increase that its dimensions would be limited thereby in a much higher degree than was indicated by statical considerations. An animal may grow to a size where it is unstable dynamically, though still on the safe side statically—a size where it moves with difficulty though it rests secure. It is by reason of dynamical rather than of statical relations that an elephant is of graver deportment than a mouse.

An apparently simple problem, much less simple than it looks, lies in the act of walking, where there will evidently be great economy of work if the leg swing with the help of gravity, that is to say, at a pendulum-rate. The conical shape and jointing of the limb, the time spent with the foot upon the ground, these and other mechanical differences complicate the case, and make the rate hard to define or calculate. Nevertheless, we may convince ourselves by counting our steps, that the leg does actually tend to swing, as a pendulum does, at a certain definite rate*. So on the same principle, but to the slower beat of a longer pendulum, the scythe swings smoothly in the mower’s hands.

To walk quicker, we “step out”; we cause the leg-pendulum to describe a greater arc, but it does not swing or vibrate faster until we shorten the pendulum and begin to run. Now let two similar individuals, A and B, walk in a similar fashion, that is to say with a similar angle of swing (Fig. 1). The arc through which the leg swings, or the amplitude of each step, will then vary as the length of leg (say as \( a/b \)), and so as the height or other linear dimension (l) of the man†. But the time of swing varies inversely as the square

* The assertion that the limb tends to swing in pendulum-time was first made by the brothers Weber (Mechanik der menschl. Gehwerkzeuge, Göttingen, 1836). Some later writers have criticised the statement (e.g. Fischer, Die Kinematik des Beinschwingens etc., Abh. math. phys. Kl. k. Sächs. Ges. xxv-xxviii, 1899-1903), but for all that, with proper and large qualifications, it remains substantially true.

† So the stride of a Brobdingnagian was 10 yards long, or just twelve times the 2 ft. 6 in., which make the average stride or half-pace of a man.
root of the pendulum-length, or $\sqrt{a}/\sqrt{b}$. Therefore the velocity, which is measured by amplitude/time, or $a/b \times \sqrt{b}/\sqrt{a}$, will also vary as the square root of the linear dimensions; which is Froude’s law over again.

The smaller man, or smaller animal, goes slower than the larger, but only in the ratio of the square roots of their linear dimensions; whereas, if the limbs moved alike, irrespective of the size of the animal—if the limbs of the mouse swung no faster than those of the horse—then the mouse would be as slow in its gait or slower than the tortoise. M. Delisle* saw a fly walk three inches in half-a-second; this was good steady walking. When we walk five miles an hour we go about 88 inches in a second, or $88/6 = 14.7$ times the pace of M. Delisle’s fly. We should walk at just about the fly’s pace if our stature were $1/(14.7)^2$, or $1/216$ of our present height—say 72/216 inches, or one-third of an inch high. Let us note in passing that the number of legs does not matter, any more than the number of wheels to a coach; the centipede runs none the faster for all his hundred legs.

But the leg comprises a complicated system of levers, by whose various exercise we obtain very different results. For instance, by being careful to rise upon our instep we increase the length or amplitude of our stride, and improve our speed very materially; and it is curious to see how Nature lengthens this metatarsal joint, or instep-lever, in horse† and hare and greyhound, in ostrich and in kangaroo, and in every speedy animal. Furthermore, in running we bend and so shorten the leg, in order to accommodate it to a quicker rate of pendulum-swing‡. In short the jointed structure

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* Quoted in Mr John Bishop’s interesting article in Todd’s *Cyclopaedia*, iii, p. 443.
† The “cannon-bones” are not only relatively longer but may even be actually longer in a little racehorse than a great carthorse.
‡ There is probably another factor involved here: for in bending and thus shortening the leg, we bring its centre of gravity nearer to the pivot, that is to say to the joint, and so the muscle tends to move it the more quickly. After all,
of the leg permits us to use it as the shortest possible lever while it is swinging, and as the longest possible lever when it is exerting its propulsive force.

The bird’s case is of peculiar interest. In running, walking or swimming, we consider the speed which an animal can attain, and the increase of speed which increasing size permits of. But in flight there is a certain necessary speed—a speed (relative to the air) which the bird must attain in order to maintain itself aloft, and which must increase as its size increases. It is highly probable, as Lanchester remarks, that Lilienthal met his untimely death (in August 1896) not so much from any intrinsic fault in the design or construction of his machine, but simply because his engine fell somewhat short of the power required to give the speed necessary for its stability.

Twenty-five years ago, when this book was written, the bird, or the aeroplane, was thought of as a machine whose sloping wings, held at a given angle and driven horizontally forward, deflect the air downwards and derive support from the upward reaction. In other words, the bird was supposed to communicate to a mass of air a downward momentum equivalent (in unit time) to its own weight, and to do so by direct and continuous impact. The downward momentum is then proportional to the mass of air thrust downwards, and to the rate at which it is so thrust or driven: the mass being proportional to the wing-area and to the speed of the bird, and the rate being again proportional to the flying speed; so that the momentum varies as the square of the bird’s linear dimensions and also as the square of its speed. But in order to balance its weight, this momentum must also be proportional to the cube of the bird’s linear dimensions; therefore the bird’s necessary speed, such as enables it to maintain level flight, must be proportional to the square root of its linear dimensions, and the whole work done must be proportional to the power 3\(\frac{1}{2}\) of the said linear dimensions.

The case stands, so far, as follows: \(m\), the mass of air deflected downwards; \(M\), the momentum so communicated; \(W\), the work done—all in unit time; \(w\), the weight, and \(V\), the velocity of the

we know that the pendulum theory is not the whole story, but only an important first approximation to a complex phenomenon.
bird; \( l \), a linear dimension, the form of the bird being supposed constant.

\[ M = w = l^3, \text{ but } M = mV, \text{ and } m = l^2V. \]

Therefore

\[ M = l^2V^2 = l^3, \]

and therefore

\[ V = \sqrt{l} \]

and

\[ W = MV = l^3. \]

The gist of the matter is, or seems to be, that the work which can be done varies with the available weight of muscle, that is to say, with the mass of the bird; but the work which has to be done varies with mass and distance; so the larger the bird grows, the greater the disadvantage under which all its work is done*. The disproportion does not seem very great at first sight, but it is quite enough to tell. It is as much as to say that, every time we double the linear dimensions of the bird, the difficulty of flight, or the work which must needs be done in order to fly, is increased in the ratio of \( 2^3 \) to \( 2^{3.4} \), or \( 1 : \sqrt{2} \), or say \( 1 : 1.4 \). If we take the ostrich to exceed the sparrow in linear dimensions as \( 25 : 1 \), which seems well within the mark, the ratio would be that between \( 25^{3.4} \) and \( 25^3 \), or between \( 5^7 \) and \( 5^8 \); in other words, flight would be five times more difficult for the larger than for the smaller bird.

But this whole explanation is doubly inadequate. For one thing, it takes no account of gliding flight, in which energy is drawn from the wind, and neither muscular power nor engine power are employed; and we see that the larger birds, vulture, albatross or solan-goose, depend on gliding more and more. Secondly, the old simple account of the impact of the wing upon the air, and the manner in which a downward momentum is communicated and support obtained, is now known to be both inadequate and erroneous. For the science of flight, or aerodynamics, has grown out of the older science of hydrodynamics; both deal with the special properties of a fluid, whether water or air; and in our case, to be content to think of the air as a body of mass \( m \), to which a velocity \( v \) is imparted, is to neglect all its fluid properties. How the

* This is the result arrived at by Helmholtz, Ueber ein Theorem geometrisch-ähnliche Bewegungen flüssiger Körper betreffend, nebst Anwendung auf das Problem Luftballons zu lenken, Monatsber. Akad. Berlin, 1873, pp. 501–514. It was criticised and challenged (somewhat rashly) by K. Müllenhof, Die Grösse der Flugflächen etc., Pflüger's Archiv, xxxv, p. 407; xxxvi, p. 548, 1885.
fish or the dolphin swims, and how the bird flies, are up to a certain point analogous problems; and *stream-lining* plays an essential part in both. But the bird is much heavier than the air, and the fish has much the same density as the water, so that the problem of keeping afloat or aloft is negligible in the one, and all-important in the other. Furthermore, the one fluid is highly compressible, and the other (to all intents and purposes) incompressible; and it is this very difference which the bird, or the aeroplane, takes special advantage of, and which helps, or even enables, it to fly.

It remains as true as ever that a bird, in order to counteract gravity, must cause air to move downward and obtains an upward reaction thereby. But the air displaced downward beneath the wing accounts for a small and varying part, perhaps a third perhaps a good deal less, of the whole force derived; and the rest is generated above the wing, in a less simple way. For, as the air streams past the slightly sloping wing, as smoothly as the stream-lined form and polished surface permit, it swirls round the front or "leading" edge*, and then streams swiftly over the upper surface of the wing; while it passes comparatively slowly, checked by the opposing slope of the wing, across the lower side. And this is as much as to say that it tends to be compressed below and rarefied above; in other words, that a partial vacuum is formed above the wing and follows it wherever it goes, so long as the stream-lining of the wing and its angle of incidence are suitable, and so long as the bird travels fast enough through the air.

The bird's weight is exerting a downward force upon the air, in one way just as in the other; and we can imagine a barometer delicate enough to shew and measure it as the bird flies overhead. But to calculate that force we should have to consider a multitude of component elements; we should have to deal with the stream-lined tubes of flow above and below, and the eddies round the fore-edge of the wing and elsewhere; and the calculation which was too simple before now becomes insuperably difficult. But the principle of necessary speed remains as true as ever. The bigger the bird

* The arched form, or "dipping front edge" of the wing, and its use in causing a vacuum above, were first recognised by Mr H. F. Phillips, who put the idea into a patent in 1884. The facts were discovered independently, and soon afterwards, both by Lilienthal and Lanchester.
becomes, the more swiftly must the air stream over the wing to give rise to the rarefaction or negative pressure which is more and more required; and the harder must it be to fly, so long as work has to be done by the muscles of the bird. The general principle is the same as before, though the quantitative relation does not work out as easily as it did. As a matter of fact, there is probably little difference in the end; and in aeronautics, the "total resultant force" which the bird employs for its support is said, empirically, to vary as the square of the air-speed: which is then a result analogous to Froude’s law, and is just what we arrived at before in the simpler and less accurate setting of the case.

But a comparison between the larger and the smaller bird, like all other comparisons, applies only so long as the other factors in the case remain the same; and these vary so much in the complicated action of flight that it is hard indeed to compare one bird with another. For not only is the bird continually changing the incidence of its wing, but it alters the lie of every single important feather; and all the ways and means of flight vary so enormously, in big wings and small, and Nature exhibits so many refinements and "improvements" in the mechanism required, that a comparison based on size alone becomes imaginary, and is little worth the making.

The above considerations are of great practical importance in aeronautics, for they shew how a provision of increasing speed must accompany every enlargement of our aeroplanes. Speaking generally, the necessary or minimal speed of an aeroplane varies as the square root of its linear dimensions; if (ceteris paribus) we make it four times as long, it must, in order to remain aloft, fly twice as fast as before*. If a given machine weighing, say, 500 lb. be stable at 40 miles an hour, then a geometrically similar one which weighs, say, a couple of tons has its speed determined as follows:

\[ W : w :: L^3 : l^3 :: 8 : 1. \]

Therefore \[ L : l :: 2 : 1. \]

But \[ V^2 : v^2 :: L : l. \]

Therefore \[ V : v :: \sqrt{2} : 1 = 1.414 : 1. \]

That is to say, the larger machine must be capable of a speed of
40 × 1.414, or about 56\(\frac{1}{2}\) miles per hour.

An arrow is a somewhat rudimentary flying-machine; but it is
capable, to a certain extent and at a high velocity, of acquiring
"stability," and hence of actual flight after the fashion of an aero-
plane; the duration and consequent range of its trajectory are
vastly superior to those of a bullet of the same initial velocity.

Coming back to our birds, and again comparing the ostrich with
the sparrow, we find we know little or nothing about the actual
speed of the latter; but the minimal speed of the swift is estimated
at 100 ft. per second, or even more—say 70 miles an hour. We
shall be on the safe side, and perhaps not far wrong, to take 20 miles
an hour as the sparrow's minimal speed; and it would then follow
that the ostrich, of 25 times the sparrow's linear dimensions, would
have to fly (if it flew at all) with a minimum velocity of 5 × 20, or
100 miles an hour*.

The same principle of necessary speed, or the inevitable relation
between the dimensions of a flying object and the minimum velocity
at which its flight is stable, accounts for a considerable number of

* Birds have an ordinary and a forced speed. Meinertzhagen puts the ordinary
flight of the swift at 68 m.p.h., which tallies with the old estimate of Athanasius
Kircher (Physiologia, ed. 1680, p. 65) of 100 ft. per second for the swallow. Abel
Chapman (Retrospect, 1928, ch. xiv) puts the gliding or swooping flight of the swift
at over 150 m.p.h., and that of the griffon vulture at 180 m.p.h.; but these skilled
fliers doubtless far exceed the necessary minimal speeds which we are speaking of.

An airman flying at 70 m.p.h. has seen a golden eagle fly past him easily; but
even this speed is exceptional. Several observers agree in giving 50 m.p.h. for
grouse and woodcock, and 30 m.p.h. for starling, chaffinch, quail and crow. A
migrating flock of lapwing travelled at 41 m.p.h., ten or twelve miles more than the
usual speed of the single bird. Lanchester, on theoretical considerations,
estimates the speed of the herring gull at 26 m.p.h., and of the albatross at about
34 miles. A tern, a very skilful flier, was seen to fly as slowly as 15 m.p.h.
A hornet or a large dragonfly may reach 14 or 18 m.p.h.; but for most insects
2-4 metres per sec., say 4-9 m.p.h., is a common speed (cf. A. Magnan, Vol.
des Insectes, 1834, p. 72). The larger diptera are very swift, but their speed is much
exaggerated. A deerfly (Cephenomyia) has been said to fly at 400 yards per second,
or say 800 m.p.h., an impossible velocity (Irving Langmuir, Science, March 11, 1938).

It would mean a pressure on the fly's head of half an atmosphere, probably enough
to crush the fly; to maintain it would take half a horsepower; and this would need
a food-consumption of 1\(\frac{1}{2}\) times the fly's weight per second! 25 m.p.h. is a more
reasonable estimate. The naturalist should not forget, though it does not touch
our present argument, that the aeroplane is built to the pattern of a beetle rather
than of a bird; for the elytra are not wings but planes. Cf. int. al., P. Amans,
Géométrie... des ailes rigides, C.R. Assoc. Franç. pour l'avancement des Sc. 1901.
observed phenomena. It tells us why the larger birds have a marked difficulty in rising from the ground, that is to say, in acquiring to begin with the horizontal velocity necessary for their support; and why accordingly, as Mouillard* and others have observed, the heavier birds, even those weighing no more than a pound or two, can be effectually caged in small enclosures open to the sky. It explains why, as Mr Abel Chapman says, "all ponderous birds, wild swans and geese, great bustard and capercailzie, even blackcock, fly faster than they appear to do," while "light-built types with a big wing-area†, such as herons and harriers, possess no turn of speed at all." For the fact is that the heavy birds must fly quickly, or not at all. It tells us why very small birds, especially those as small as humming-birds, and à fortiori the still smaller insects, are capable of "stationary flight," a very slight and scarcely perceptible velocity relatively to the air being sufficient for their support and stability. And again, since it is in all these cases velocity relatively to the air which we are speaking of, we comprehend the reason why one may always tell which way the wind blows by watching the direction in which a bird starts to fly.

The wing of a bird or insect, like the tail of a fish or the blade of an oar, gives rise at each impulsion to a swirl or vortex, which tends (so to speak) to cling to it and travel along with it; and the resistance which wing or oar encounter comes much more from these vortices than from the viscosity of the fluid.‡ We learn as a corollary to this, that vortices form only at the edge of oar or wing—it is only the length and not the breadth of these which matters. A long narrow oar outpaces a broad one, and the efficiency of the long, narrow wing of albatross, swift or hawkmoth is so far accounted for. From the length of the wing we can calculate approximately its rate of swing, and more conjecturally the dimensions of each vortex, and finally the resistance or lifting power of the stroke; and the result shews once again the advantages of the small-scale

* Mouillard, L'empire de l'air; essai d'ornithologie appliquée à l'aviation, 1881; transl. in Annual Report of the Smithsonian Institution, 1892.
† On wing-area in relation to weight of bird see Lendenfeld in Naturw. Wochenschr. Nov. 1904, transl. in Smithsonian Inst. Rep. 1904; also E. H. Hankin, Animal Flight, 1913; etc.
‡ Cf. V. Bjerknes, Hydrodynamique physique, ii, p. 293, 1934.
mechanism, and the disadvantage under which the larger machine or larger creature lies.

<table>
<thead>
<tr>
<th></th>
<th>Weight gm.</th>
<th>Length of wing m.</th>
<th>Beats per sec.</th>
<th>Speed of wing-tip m./s.</th>
<th>Radius of vortex*</th>
<th>Force of wing-beat gm.</th>
<th>Specific force $F/W$</th>
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(From V. Bjerknes)

* Conjectural.

A bird may exert a force at each stroke of its wing equal to one-half, let us say for safety one-quarter, of its own weight, more or less; but a bee or a fly does twice or thrice the equivalent of its own weight, at a low estimate. If stork, gull or pigeon can thus carry only one-fifth, one-third, one-quarter of their weight by the beating of their wings, it follows that all the rest must be borne by sailing-flight between the wing-beats. But an insect’s wings lift it easily and with something to spare; hence sailing-flight, and with it the whole principle of necessary speed, does not concern the lesser insects, nor the smallest birds, at all; for a humming-bird can “stand still” in the air, like a hover-fly, and dart backwards as well as forwards, if it please.

There is a little group of Fairy-flies (Mymaridae), far below the size of any small familiar insects; their eggs are laid and larvae reared within the tiny eggs of larger insects; their bodies may be no more than $\frac{1}{2}$ mm. long, and their outspread wings 2 mm. from tip to tip (Fig. 2). It is a peculiarity of some of these that their little wings are made of a few hairs or bristles, instead of the continuous membrane of a wing. How these act on the minute quantity of air involved we can only conjecture. It would seem that that small quantity reacts as a viscous fluid to the beat of the wing; but there are doubtless other unobserved anomalies in the mechanism and the mode of flight of these pigmy creatures†.

The ostrich has apparently reached a magnitude, and the moa certainly did so, at which flight by muscular action, according to

† It is obvious that in a still smaller order of magnitude the Brownian movement would suffice to make flight impossible.
the normal anatomy of a bird, becomes physiologically impossible. The same reasoning applies to the case of man. It would be very difficult, and probably absolutely impossible, for a bird to flap its way through the air were it of the bigness of a man; but Borelli, in discussing the matter, laid even greater stress on the fact that a man’s pectoral muscles are so much less in proportion than those of a bird, that however we might fit ourselves out with wings, we could never expect to flap them by any power of our own weak muscles. Borelli had learned this lesson thoroughly, and in one of his chapters he deals with the proposition: *Est impossible ut homines propriis viribus artificiose volare possint*. But gliding flight, where wind-force and gravitational energy take the place of muscular power, is another story, and its limitations are of another kind. Nature has many modes and mechanisms of flight, in birds of one kind and another, in bats and beetles, butterflies, dragonflies and what not; and gliding seems to be the common way of birds, and the flapping flight (*remigio alarum*) of sparrow and of crow to be the exception rather than the rule. But it were truer to say that gliding and soaring, by which energy is captured from the wind, are modes of flight little needed by the small birds, but more and more essential to the large. Borelli had proved so convincingly that we could never hope to fly *propriis viribus*, that all through the eighteenth century men tried no more to fly at all. It was in trying to glide that the pioneers of aviation, Cayley, Wenham and Mouillard,

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* Giovanni Alfonso Borelli, *De Motu Animalium*, i, Prop. cciv, p. 243, edit. 1685. The part on *The Flight of Birds* is issued by the Royal Aeronautical Society as No. 6 of its *Aeronautical Classics*. 

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![Fig. 2. Fairy-flies (Mymaridae): after F. Enock. ×20.](image-url)
Langley, Lilienthal and the Wrights—all careful students of birds—renewed the attempt*; and only after the Wrights had learned to glide did they seek to add power to their glider. Flight, as the Wrights declared, is a matter of practice and of skill, and skill in gliding has now reached a point which more than justifies all Leonardo da Vinci’s attempts to fly. Birds shew infinite skill and instinctive knowledge in the use they make of the horizontal acceleration of the wind, and the advantage they take of ascending currents in the air. Over the hot sands of the Sahara, where every here and there hot air is going up and cooler coming down, birds keep as best they can to the one, or glide quickly through the other; so we may watch a big dragonfly planing slowly down a few feet above the heated soil, and only every five minutes or so regaining height with a vigorous stroke of his wings. The albatross uses the upward current on the lee-side of a great ocean-wave; so, on a lesser scale, does the flying-fish; and the seagull flies in curves, taking every advantage of the varying wind-velocities at different levels over the sea. An Indian vulture flaps his way up for a few laborious yards, then catching an upward current soars in easy spirals to 2000 feet; here he may stay, effortless, all day long, and come down at sunset. Nor is the modern sail-plane much less efficient than a soaring bird; for a skilful pilot in the tropics should be able to roam all day long at will†.

A bird’s sensitiveness to air-pressure is indicated in other ways besides. Heavy birds, like duck and partridge, fly low and apparently take advantage of air-pressure reflected from the ground. Water-hen and dipper follow the windings of the stream as they fly up or down; a bee-line would give them a shorter course, but not so smooth a journey. Some small birds—wagtails, woodpeckers and a few others—fly, so to speak, by leaps and bounds; they fly briskly

* Sir George Cayley (1774–1857), father of British aeronautics, was the first to perceive the capabilities of rigid planes, and to experiment on gliding flight. He anticipated all the essential principles of the modern aeroplane, and his first paper “On Aerial Navigation” appeared in Nicholson’s Journal for November 1809. F. H. Wenham (1824–1908) studied the flight of birds and estimated the necessary proportion of surface to weight and speed; he held that “the whole secret of success in flight depends upon a proper concave form of the supporting surface.” See his paper “On Aerial Locomotion” in the Report of the Aeronautical Society 1806.

for a few moments, then close their wings and shoot along*. The flying-fishes do much the same, save that they keep their wings outspread. The best of them "taxi" along with only their tails in the water, the tail vibrating with great rapidity, and the speed attained lasts the fish on its long glide through the air†.

Flying may have begun, as in Man's case it did, with short spells of gliding flight, helped by gravity, and far short of sustained or continuous locomotion. The short wings and long tail of Archaeopteryx would be efficient as a slow-speed glider; and we may still see a Touraco glide down from his perch looking not much unlike Archaeopteryx in the proportions of his wings and tail. The small bodies, scanty muscles and narrow but vastly elongated wings of a Pterodactyl go far beyond the limits of mechanical efficiency for ordinary flapping flight; but for gliding they approach perfection‡. Sooner or later Nature does everything which is physically possible; and to glide with skill and safety through the air is a possibility which she did not overlook.

Apart from all differences in the action of the limbs—which apart from differences in mechanical construction or in the manner in which the mechanism is used—we have now arrived at a curiously simple and uniform result. For in all the three forms of locomotion which we have attempted to study, alike in swimming and in walking, and even in the more complex problem of flight, the general result, obtained under very different conditions and arrived at by different modes of reasoning, shews in every case that speed tends to vary as the square root of the linear dimensions of the animal.

While the rate of progress tends to increase slowly with increasing size (according to Froude's law), and the rhythm or pendulum-rate of the limbs to increase rapidly with decreasing size (according to Galileo's law), some such increase of velocity with decreasing

* Why large birds cannot do the same is discussed by Lanchester, op. cit. Appendix iv.
† Cf. Carl L. Hubbs, On the flight of...the Cypselurinae, and remarks on the evolution of the flight of fishes, Papers of the Michigan Acad. of Sci. xvii, pp. 575-611, 1933. See also E. H. Hankin, P.Z.S. 1920, pp. 467-474; and C. M. Breeder, On the structural specialisation of flying fishes from the standpoint of aerodynamics, Copeia, 1930, pp. 114-121.
‡ The old conjecture that their flight was helped or rendered possible by a denser atmosphere than ours is thus no longer called for.
magnitude is true of all the rhythmic actions of the body, though for reasons not always easy to explain. The elephant’s heart beats slower than ours*, the dog’s quicker; the rabbit’s goes pit-a-pat; the mouse’s and the sparrow’s are too quick to count. But the very “rate of living” (measured by the O consumed and CO₂ produced) slows down as size increases; and a rat lives so much faster than a man that the years of its life are three, instead of threescore and ten.

From all the foregoing discussion we learn that, as Crookes once upon a time remarked †, the forms as well as the actions of our bodies are entirely conditioned (save for certain exceptions in the case of aquatic animals) by the strength of gravity upon this globe; or, as Sir Charles Bell had put it some sixty years before, the very animals which move upon the surface of the earth are proportioned to its magnitude. Were the force of gravity to be doubled our bipedal form would be a failure, and the majority of terrestrial animals would resemble short-legged saurians, or else serpents. Birds and insects would suffer likewise, though with some compensation in the increased density of the air. On the other hand, if gravity were halved, we should get a lighter, slenderer, more active type, needing less energy, less heat, less heart, less lungs, less blood. Gravity not only controls the actions but also influences the forms of all save the least of organisms. The tree under its burden of leaves or fruit has changed its every curve and outline since its boughs were bare, and a mantle of snow will alter its configuration again. Sagging wrinkles, hanging breasts and many another sign of age are part of gravitation’s slow relentless handiwork.

There are other physical factors besides gravity which help to limit the size to which an animal may grow and to define the conditions under which it may live. The small insects skating on a pool have their movements controlled and their freedom limited by the surface-tension between water and air, and the measure of that tension determines the magnitude which they may attain. A man coming wet from his bath carries a few ounces of water, and is perhaps 1 per cent. heavier than before; but a wet fly weighs twice as much as a dry one, and becomes a helpless thing. A small

* Say 28 to 30 beats to the minute.
† Proc. Psychical Soc. xii, p. 338-355, 1897.
insect finds itself imprisoned in a drop of water, and a fly with two feet in one drop finds it hard to extricate them.

The mechanical construction of insect or crustacean is highly efficient up to a certain size, but even crab and lobster never exceed certain moderate dimensions, perfect within these narrow bounds as their construction seems to be. Their body lies within a hollow shell, the stresses within which increase much faster than the mere scale of size; every hollow structure, every dome or cylinder, grows weaker as it grows larger, and a tin canister is easy to make but a great boiler is a complicated affair. The boiler has to be strengthened by "stiffening rings" or ridges, and so has the lobster's shell; but there is a limit even to this method of counteracting the weakening effect of size. An ordinary girder-bridge may be made efficient up to a span of 200 feet or so; but it is physically incapable of spanning the Firth of Forth. The great Japanese spider-crab, *Macrocheira*, has a span of some 12 feet across; but Nature meets the difficulty and solves the problem by keeping the body small, and building up the long and slender legs out of short lengths of narrow tubes. A hollow shell is admirable for small animals, but Nature does not and cannot make use of it for the large.

In the case of insects, other causes help to keep them of small dimensions. In their peculiar respiratory system blood does not carry oxygen to the tissues, but innumerable fine tubules or tracheae lead air into the interstices of the body. If we imagine them growing even to the size of crab or lobster, a vast complication of tracheal tubules would be necessary, within which friction would increase and diffusion be retarded, and which would soon be an inefficient and inappropriate mechanism.

The vibration of vocal chords and auditory drums has this in common with the pendulum-like motion of a limb that its rate also tends to vary inversely as the square root of the linear dimensions. We know by common experience of fiddle, drum or organ, that pitch rises, or the frequency of vibration increases, as the dimensions of pipe or membrane or string diminish; and in like manner we expect to hear a bass note from the great beasts and a piping treble from the small. The rate of vibration (\(N\)) of a stretched string depends on its tension and its density; these being equal, it varies inversely as its own length and as its diameter. For similar
strings, \( N \propto 1/l^2 \), and for a circular membrane, of radius \( r \) and thickness \( e \), \( N \propto 1/(r^2 \sqrt{e}) \).

But the delicate drums or tympana of various animals seem to vary much less in thickness than in diameter, and we may be content to write, once more, \( N \propto 1/r^2 \).

Suppose one animal to be fifty times less than another, vocal chords and all: the one’s voice will be pitched 2500 times as many beats, or some ten or eleven octaves, above the other’s; and the same comparison, or the same contrast, will apply to the tympanic membranes by which the vibrations are received. But our own perception of musical notes only reaches to 4000 vibrations per second, or thereby; a squeaking mouse or bat is heard by few, and to vibrations of 10,000 per second we are all of us stone-deaf. Structure apart, mere size is enough to give the lesser birds and beasts a music quite different to our own: the humming-bird, for aught we know, may be singing all day long. A minute insect may utter and receive vibrations of prodigious rapidity; even its little wings may beat hundreds of times a second*. Far more things happen to it in a second than to us; a thousandth part of a second is no longer negligible, and time itself seems to run a different course to ours.

The eye and its retinal elements have ranges of magnitude and limitations of magnitude of their own. A big dog’s eye is hardly bigger than a little dog’s; a squirrel’s is much larger, proportionately, than an elephant’s; and a robin’s is but little less than a pigeon’s or a crow’s. For the rods and cones do not vary with the size of the animal, but have their dimensions optically limited by the interference-patterns of the waves of light, which set bounds to the production of clear retinal images. True, the larger animal may want a larger field of view; but this makes little difference, for but a small area of the retina is ever needed or used. The eye, in short, can never be very small and need never be very big; it has its own conditions and limitations apart from the size of the animal. But the insect’s eye tells another story. If a fly had an eye like ours, the pupil would be so small that diffraction would render a clear image impossible. The only alternative is to unite a number

* The wing-beats are said to be as follows: dragonfly 28 per sec., bee 190, housefly 330; cf. Erhard, Verh. d. d. zool. Gesellschaft. 1913, p. 206.
of small and optically isolated simple eyes into a compound eye, and in the insect Nature adopts this alternative possibility*.

Our range of vision is limited to a bare octave of "luminous" waves, which is a considerable part of the whole range of light-heat rays emitted by the sun; the sun's rays extend into the ultra-violet for another half-octave or more, but the rays to which our eyes are sensitive are just those which pass with the least absorption through a watery medium. Some ancient vertebrate may have learned to see in an ocean which let a certain part of the sun's whole radiation through, which part is our part still; or perhaps the watery media of the eye itself account sufficiently for the selective filtration. In either case, the dimensions of the retinal elements are so closely related to the wave-lengths of light (or to their interference patterns) that we have good reason to look upon the retina as perfect of its kind, within the limits which the properties of light itself impose; and this perfection is further illustrated by the fact that a few light-quanta, perhaps a single one, suffice to produce a sensation†. The hard eyes of insects are sensitive over a wider range. The bee has two visual optima, one coincident with our own, the other and principal one high up in the ultra-violet‡. And with the latter the bee is able to see that ultra-violet which is so well reflected by many flowers that flower-photographs have been taken through a filter which passes these but transmits no other rays§.

When we talk of light, and of magnitudes whose order is that of a wave-length of light, the subtle phenomenon of colour is near at hand. The hues of living things are due to sundry causes; where they come from chemical pigmentation they are outside our theme, but oftentimes there is no pigment at all, save perhaps as a screen or background, and the tints are those proper to a scale of wave-lengths or range of magnitude. In birds these "optical colours" are of two chief kinds. One kind include certain vivid blues, the

blue of a blue jay, an Indian roller or a macaw; to the other belong
the iridescent hues of mother-of-pearl, of the humming-bird, the
peacock and the dove: for the dove's grey breast shews many
colours yet contains but one—colores inesse plures nec esse plus uno,
as Cicero said. The jay's blue feather shews a layer of enamel-like
cells beneath a thin horny cuticle, and the cell-walls are spongy
with innumerable tiny air-filled pores. These are about 0·3 μ in
diameter, in some birds even a little less, and so are not far from
the limits of microscopic vision. A deeper layer carries dark-brown
pigment, but there is no blue pigment at all; if the feather be dipped
in a fluid of refractive index equal to its own, the blue utterly
disappears, to reappear when the feather dries. This blue is like
the colour of the sky; it is "Tyndall's blue," such as is displayed
by turbid media, cloudy with dust-motes or tiny bubbles of a size
comparable to the wave-lengths of the blue end of the spectrum.
The longer waves of red or yellow pass through, the shorter violet
rays are reflected or scattered; the intensity of the blue depends
on the size and concentration of the particles, while the dark pigment-
screen enhances the effect.

Rainbow hues are more subtle and more complicated; but in the
peacock and the humming-bird we know for certain* that the
colours are those of Newton's rings, and are produced by thin plates
or films covering the barbules of the feather. The colours are such
as are shewn by films about ½ μ thick, more or less; they change
towards the blue end of the spectrum as the light falls more and
more obliquely; or towards the red end if you soak the feather
and cause the thin plates to swell. The barbules of the peacock's
feather are broad and flat, smooth and shiny, and their cuticular
layer splits into three very thin transparent films, hardly more than
1 μ thick, all three together. The gorgeous tints of the humming-
birds have had their places in Newton's scale defined, and the
changes which they exhibit at varying incidence have been predicted

* Rayleigh, Phil. Mag. (6), xxxvii, p. 98, 1919. For a review of the whole
subject, and a discussion of its many difficulties, see H. Onslow, On a periodic
structure in many insect scales, etc., Phil. Trans. (B), cxxi, pp. 1–74, 1921;
butterflies); also B. Reusch and Th. Elsasser in Journ. f. Ornithologie, lxxiii,
1925; etc.
and explained. The thickness of each film lies on the very limit of microscopic vision, and the least change or irregularity in this minute dimension would throw the whole display of colour out of gear. No phenomenon of organic magnitude is more striking than this constancy of size; none more remarkable than that these fine lamellae should have their tenuity so sharply defined, so uniform in feather after feather, so identical in all the individuals of a species, so constant from one generation to another.

A simpler phenomenon, and one which is visible throughout the whole field of morphology, is the tendency (referable doubtless in each case to some definite physical cause) for mere bodily surface to keep pace with volume, through some alteration of its form. The development of villi on the lining of the intestine (which increase its surface much as we enlarge the effective surface of a bath-towel), the various valvular folds of the intestinal lining, including the remarkable "spiral valve" of the shark's gut, the lobulation of the kidney in large animals*, the vast increase of respiratory surface in the air-sacs and alveoli of the lung, the development of gills in the larger crustacea and worms though the general surface of the body suffices for respiration in the smaller species—all these and many more are cases in which a more or less constant ratio tends to be maintained between mass and surface, which ratio would have been more and more departed from with increasing size, had it not been for such alteration of surface-form†. A leafy wood, a grassy sward, a piece of sponge, a reef of coral, are all instances of a like phenomenon. In fact, a deal of evolution is involved in keeping due balance between surface and mass as growth goes on.

In the case of very small animals, and of individual cells, the principle becomes especially important, in consequence of the molecular forces whose resultant action is limited to the superficial layer. In the cases just mentioned, action is facilitated by increase of surface: diffusion, for instance, of nutrient liquids or respiratory gases is rendered more rapid by the greater area of surface; but

† For various calculations of the increase of surface due to histological and anatomical subdivision, see E. Babak, Ueber die Oberflächenentwicklung bei Organismen, Biol. Centralbl. xxx, pp. 225–239, 257–267, 1910.
there are other cases in which the ratio of surface to mass may change the whole condition of the system. Iron rusts when exposed to moist air, but it rusts ever so much faster, and is soon eaten away, if the iron be first reduced to a heap of small filings; this is a mere difference of degree. But the spherical surface of the rain-drop and the spherical surface of the ocean (though both happen to be alike in mathematical form) are two totally different phenomena, the one due to surface-energy, and the other to that form of mass-energy which we ascribe to gravity. The contrast is still more clearly seen in the case of waves: for the little ripple, whose form and manner of propagation are governed by surface-tension, is found to travel with a velocity which is inversely as the square root of its length; while the ordinary big waves, controlled by gravitation, have a velocity directly proportional to the square root of their wave-length. In like manner we shall find that the form of all very small organisms is independent of gravity, and largely if not mainly due to the force of surface-tension: either as the direct result of the continued action of surface-tension on the semi-fluid body, or else as the result of its action at a prior stage of development, in bringing about a form which subsequent chemical changes have rendered rigid and lasting. In either case, we shall find a great tendency in small organisms to assume either the spherical form or other simple forms related to ordinary inanimate surface-tension phenomena, which forms do not recur in the external morphology of large animals.

Now this is a very important matter, and is a notable illustration of that principle of similitude which we have already discussed in regard to several of its manifestations. We are coming to a conclusion which will affect the whole course of our argument throughout this book, namely that there is an essential difference in kind between the phenomena of form in the larger and the smaller organisms. I have called this book a study of Growth and Form, because in the most familiar illustrations of organic form, as in our own bodies for example, these two factors are inseparably associated, and because we are here justified in thinking of form as the direct resultant and consequence of growth: of growth, whose varying rate in one direction or another has produced, by its gradual and unequal increments, the successive stages of development and
the final configuration of the whole material structure. But it is by no means true that form and growth are in this direct and simple fashion correlative or complementary in the case of minute portions of living matter. For in the smaller organisms, and in the individual cells of the larger, we have reached an order of magnitude in which the intermolecular forces strive under favourable conditions with, and at length altogether outweigh, the force of gravity, and also those other forces leading to movements of convection which are the prevailing factors in the larger material aggregate.

However, we shall require to deal more fully with this matter in our discussion of the rate of growth, and we may leave it meanwhile, in order to deal with other matters more or less directly concerned with the magnitude of the cell.

The living cell is a very complex field of energy, and of energy of many kinds, of which surface-energy is not the least. Now the whole surface-energy of the cell is by no means restricted to its outer surface; for the cell is a very heterogeneous structure, and all its protoplasmic alveoli and other visible (as well as invisible) heterogeneities make up a great system of internal surfaces, at every part of which one "phase" comes in contact with another "phase," and surface-energy is manifested accordingly. But still, the external surface is a definite portion of the system, with a definite "phase" of its own, and however little we may know of the distribution of the total energy of the system, it is at least plain that the conditions which favour equilibrium will be greatly altered by the changed ratio of external surface to mass which a mere change of magnitude produces in the cell. In short, the phenomenon of division of the growing cell, however it be brought about, will be precisely what is wanted to keep fairly constant the ratio between surface and mass, and to retain or restore the balance between surface-energy and the other forces of the system*. But when a germ-cell divides or "segments" into two, it does not increase in mass; at least if there be some slight alleged tendency for the egg to increase in

* Certain cells of the cucumber were found to divide when they had grown to a volume half as large again as that of the "resting cells." Thus the volumes of resting, dividing and daughter cells were as $1:1.5:0.75$; and their surfaces, being as the power $2/3$ of these figures, were, roughly, as $1:1.3:0.8$. The ratio of $S/V$ was then as $1:0.9:1.1$, or much nearer equality. Cf. F. T. Lewis, *Anat. Record*, xlvii, pp. 59-99, 1930.
mass or volume during segmentation it is very slight indeed, generally imperceptible, and wholly denied by some*. The growth or development of the egg from a one-celled stage to stages of two or many cells is thus a somewhat peculiar kind of growth; it is growth limited to change of form and increase of surface, unaccompanied by growth in volume or in mass. In the case of a soap-bubble, by the way, if it divide into two bubbles the volume is actually diminished, while the surface-area is greatly increased†; the diminution being due to a cause which we shall have to study later, namely to the increased pressure due to the greater curvature of the smaller bubbles.

An immediate and remarkable result of the principles just described is a tendency on the part of all cells, according to their kind, to vary but little about a certain mean size, and to have in fact certain absolute limitations of magnitude. The diameter of a large parenchymatous cell is perhaps tenfold that of a little one; but the tallest phanerogams are ten thousand times the height of the least. In short, Nature has her materials of predeterminate dimensions, and keeps to the same bricks whether she build a great house or a small. Even ordinary drops tend towards a certain fixed size, which size is a function of the surface-tension, and may be used (as Quincke used it) as a measure thereof. In a shower of rain the principle is curiously illustrated, as Wilding Köllner and V. Bjerknes tell us. The drops are of graded sizes, each twice as big as another, beginning with the minute and uniform droplets of an impalpable mist. They rotate as they fall, and if two rotate in contrary directions they draw together and presently coalesce; but this only happens when two drops are falling side by side, and since the rate of fall depends on the size it always is a pair of coequal drops which so meet, approach and join together. A supreme instance of constancy or quasi-constancy of size, remote from but yet analogous to the size-limitation of a rain-drop or a cell, is the fact that the stars of heaven (however else one differeth from another), and even the nebulae themselves, are all wellnigh co-equal in mass. Gravity draws matter together, condensing it into a world

* Though the entire egg is not increasing in mass, that is not to say that its living protoplasm is not increasing all the while at the expense of the reserve material.
† Cf. P. G. Tait, Proc. R.S.E. v, 1866 and vi, 1868.
or into a star; but ethereal pressure is an opponent force leading to disruption, negligible on the small scale but potent on the large. High up in the scale of magnitude, from about \(10^{33}\) to \(10^{35}\) grams of matter, these two great cosmic forces balance one another; and all the magnitudes of all the stars lie within or hard by these narrow limits.

In the living cell, Sachs pointed out (in 1895) that there is a tendency for each nucleus to gather around itself a certain definite amount of protoplasm*. Driesch †, a little later, found it possible, by artificial subdivision of the egg, to rear dwarf sea-urchin larvae, one-half, one-quarter or even one-eighth of their usual size; which dwarf larvae were composed of only a half, a quarter or an eighth of the normal number of cells. These observations have been often repeated and amply confirmed: and Loeb found the sea-urchin eggs capable of reduction to a certain size, but no further.

In the development of *Crepidula* (an American "slipper-limpet," now much at home on our oyster-beds), Conklin‡ has succeeded in rearing dwarf and giant individuals, of which the latter may be five-and-twenty times as big as the former. But the individual cells, of skin, gut, liver, muscle and other tissues, are just the same size in one as in the other, in dwarf and in giant§. In like manner


§ Thus the fibres of the crystalline lens are of the same size in large and small dogs, Rabl, Z. f. u. Z. lxvii, 1899. Cf. (int. al.) Pearson, On the size of the blood-corpuscles in Rana, Biometrika, vi, p. 403, 1909. Dr Thomas Young caught sight of the phenomenon early in last century: "The solid particles of the blood do not by any means vary in magnitude in the same ratio with the bulk of the animal," Natural Philosophy, ed. 1845, p. 466; and Leeuwenhoek and Stephen Hales were aware of it nearly two hundred years before. Leeuwenhoek indeed had a very good idea of the size of a human blood-corpuscle, and was in the habit of using its diameter—about 1/3000 of an inch—as a standard of comparison. But though the blood-corpuscles shew no relation of magnitude to the size of the animal, they are related without doubt to its activity; for the corpuscles in the
the leaf-cells are found to be of the same size in an ordinary water-lily, in the great *Victoria regia*, and in the still huger leaf, nearly 3 metres long, of *Euryale ferox* in Japan*. Driesch has laid particular stress upon this principle of a "fixed cell-size," which has, however, its own limitations and exceptions. Among these exceptions, or apparent exceptions, are the giant frond-like cell of a *Caulerpa* or the great undivided plasmodium of a *Myxomycete*. The flattening of the one and the branching of the other serve (or help) to increase the ratio of surface to content, the nuclei tend to multiply, and streaming currents keep the interior and exterior of the mass in touch with one another.

![Cell Diagram](image)

**Fig. 3.** Motor ganglion-cells, from the cervical spinal cord.
From Minot, after Irving Hardesty.

We get a good and even a familiar illustration of the principle of size-limitation in comparing the brain-cells or ganglion-cells, whether of the lower or of the higher animals†. In Fig. 3 we shew certain identical nerve-cells from various mammals, from mouse to elephant, all drawn to the same scale of magnification; and we see that they are all of much the same order of magnitude. The nerve-cell of the elephant is about twice that of the mouse in linear

sluggish Amphibia are much the largest known to us, while the smallest are found among the deer and other agile and speedy animals (cf. Gulliver, *P.Z.S.* 1875, p. 474, etc.). This correlation is explained by the surface condensation or adsorption of oxygen in the blood-corpuscles, a process greatly facilitated and intensified by the increase of surface due to their minuteness.

dimensions, and therefore about eight times greater in volume or in mass. But making due allowance for difference of shape, the linear dimensions of the elephant are to those of the mouse as not less than one to fifty; and the bulk of the larger animal is something like 125,000 times that of the less. It follows, if the size of the nerve-cells are as eight to one, that, in corresponding parts of the nervous system, there are more than 15,000 times as many individual cells in one animal as in the other. In short we may (with Enriques) lay it down as a general law that among animals, large or small, the ganglion-cells vary in size within narrow limits; and that, amidst all the great variety of structure observed in the nervous system of different classes of animals, it is always found that the smaller species have simpler ganglia than the larger, that is to say ganglia containing a smaller number of cellular elements*. The bearing of such facts as this upon the cell-theory in general is not to be disregarded; and the warning is especially clear against exaggerated attempts to correlate physiological processes with the visible mechanism of associated cells, rather than with the system of energies, or the field of force, which is associated with them. For the life of the body is more than the sum of the properties of the cells of which it is composed: as Goethe said, “Das Lebendige ist zwar in Elemente zerlegt, aber man kann es aus diesen nicht wieder zusammenstellen und beleben.”

Among certain microscopic organisms such as the Rotifer a (which have the least average size and the narrowest range of size of all the Metazoa), we are still more palpably struck by the small number of cells which go to constitute a usually complex organ, such as kidney, stomach or ovary; we can sometimes number them in a few

* While the difference in cell-volume is vastly less than that between the volumes, and very much less also than that between the surfaces, of the respective animals, yet there is a certain difference; and this it has been attempted to correlate with the need for each cell in the many-celled ganglion of the larger animal to possess a more complex “exchange-system” of branches, for intercommunication with its more numerous neighbours. Another explanation is based on the fact that, while such cells as continue to divide throughout life tend to uniformity of size in all mammals, those which do not grow, and in particular the ganglion cells, continue to grow, and their size becomes, therefore, a function of the duration of life. Cf. G. Levi, Studi sulla grandezza delle cellule, Arch. Ital. di Anat. e di Embriol. v, p. 291, 1906; cf. also A. Berezowski, Studien iiber die Zellgrösse, Arch. f. Zellforsch. v, pp. 375-384, 1910.
units, in place of the many thousands which make up such an organ in larger, if not always higher, animals. We have already spoken of the Fairy-flies, a few score of which would hardly weigh down one of the larger rotifers, and a hundred thousand would weigh less than one honey-bee. Their form is complex and their little bodies exquisitely beautiful; but I feel sure that their cells are few, and their organs of great histological simplicity. These considerations help, I think, to shew that, however important and advantageous the subdivision of the tissues into cells may be from the constructional, or from the dynamic, point of view, the phenomenon has less fundamental importance than was once, and is often still, assigned to it.

Just as Sachs shewed there was a limit to the amount of cytoplasm which could gather round a nucleus, so Boveri has demonstrated that the nucleus itself has its own limitations of size, and that, in cell-division after fertilisation, each new nucleus has the same size as its parent nucleus*; we may nowadays transfer the statement to the chromosomes. It may be that a bacterium lacks a nucleus for the simple reason that it is too small to hold one, and that the same is true of such small plants as the Cyanophyceae, or blue-green algae. Even a chromatophore with its "pyrenoids" seems to be impossible below a certain size†.

Always then, there are reasons, partly physiological but in large part purely physical, which define or regulate the magnitude of the organism or the cell. And as we have already found definite limitations to the increase in magnitude of an organism, let us now enquire whether there be not also a lower limit below which the very existence of an organism becomes impossible.

† The size of the nucleus may be affected, even determined, by the number of chromosomes it contains. There are giant races of Oenothera, Primula and Solanum whose cell-nuclei contain twice the normal number of chromosomes, and a dwarf race of a little freshwater crustacean, Cyclops, has half the usual number. The cytoplasm in turn varies with the amount of nuclear matter, the whole cell is unusually large or unusually small; and in these exceptional cases we see a direct relation between the size of the organism and the size of the cell. Cf. (int. al.) R. P. Gregory, Proc. Camb. Phil. Soc. xv, pp. 239-246, 1909; F. Keeble, Journ. of Genetics, ii, pp. 163-188, 1912.
A bacillus of ordinary size is, say, 1 μ in length. The length (or height) of a man is about a million and three-quarter times as great, i.e. 1.75 metres, or 1.75 × 10^6 μ; and the mass of the man is in the neighbourhood of 5 × 10^18 (five million, million, million) times greater than that of the bacillus. If we ask whether there may not exist organisms as much less than the bacillus as the bacillus is less than the man, it is easy to reply that this is quite impossible, for we are rapidly approaching a point where the question of molecular dimensions, and of the ultimate divisibility of matter, obtrudes itself as a crucial factor in the case. Clerk Maxwell dealt with this matter seventy years ago, in his celebrated article Atom*. Kolli (or Colley), a Russian chemist, declared in 1893 that the head of a spermatozoon could hold no more than a few protein molecules; and Errera, ten years later, discussed the same topic with great ingenuity†. But it needs no elaborate calculation to convince us that the smaller bacteria or micrococci nearly approach the smallest magnitudes which we can conceive to have an organised structure. A few small bacteria are the smallest of visible organisms, and a minute species associated with influenza, B. pneumosinter, is said to be the least of them all. Its size is of the order of 0.1 μ, or rather less; and here we are in close touch with the utmost limits of microscopic vision, for the wave-lengths of visible light run only from about 400 to 700 mμ. The largest of the bacteria, B. megatherium, larger than the well-known B. anthracis of splenic fever, has much the same proportion to the least as an elephant to a guinea-pig‡.

Size of body is no mere accident. Man, respiring as he does, cannot be as small as an insect, nor vice versa; only now and then, as in the Goliath beetle, do the sizes of mouse and beetle meet and overlap. The descending scale of mammals stops short at a weight of about 5 grams, that of beetles at a length of about half a millimetre, and every group of animals has its upper and its lower limitations of size. So, not far from the lower limit of our vision, does the long series of bacteria come to an end. There remain still smaller particles which the ultra-microscope in part reveals; and

* Encyclopaedia Britannica, 9th edition, 1875.
‡ Cf. A. E. Boycott, The transition from live to dead, Proc. R. Soc. of Medicine, xxii (Pathology), pp. 55-69, 1928.
here or hereabouts are said to come the so-called viruses or "filter-passer," brought within our ken by the maladies, such as hydrophobia, or foot-and-mouth disease, or the mosaic diseases of tobacco and potato, to which they give rise. These minute particles, of the order of one-tenth the diameter of our smallest bacteria, have no diffusible contents, no included water—whereby they differ from every living thing. They appear to be inert colloidal (or even crystalloid) aggregates of a nucleo-protein, of perhaps ten times the diameter of an ordinary protein-molecule, and not much larger than the giant molecules of haemoglobin or haemocyanin*.

Bejerinck called such a virus a *contagium vivum*; "infective nucleo-protein" is a newer name. We have stepped down, by a single step, from living to non-living things, from bacterial dimensions to the molecular magnitudes of protein chemistry. And we begin to suspect that the virus-diseases are not due to an "organism, capable of physiological reproduction and multiplication, but to a mere specific chemical substance, capable of catalysing pre-existing materials and thereby producing more and more molecules like itself. The spread of the virus in a plant would then be a mere autocatalysis, not involving the transport of matter, but only a progressive change of state in substances already there†."  

But, after all, a simple tabulation is all we need to shew how nearly the least of organisms approach to molecular magnitudes. The same table will suffice to shew how each main group of animals has its mean and characteristic size, and a range on either side, sometimes greater and sometimes less.

Our table of magnitudes is no mere catalogue of isolated facts, but goes deep into the relation between the creature and its world. A certain range, and a narrow one, contains mouse and elephant, and all whose business it is to walk and run; this is our own world,

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with whose dimensions our lives, our limbs, our senses are in tune. The great whales grow out of this range by throwing the burden of their bulk upon the waters; the dinosaurs wallowed in the swamp, and the hippopotamus, the sea-elephant and Steller’s great sea-cow pass or passed their lives in the rivers or the sea. The things which

Linear dimensions of organisms, and other objects

<table>
<thead>
<tr>
<th>cm.</th>
<th>Description</th>
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<tbody>
<tr>
<td>(10,000\ \text{km.})</td>
<td>(10^7) A quadrant of the earth’s circumference</td>
</tr>
<tr>
<td>(1000\ \text{km.})</td>
<td>(10^6) Orkney to Land’s End</td>
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<tr>
<td>(10^5)</td>
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<tr>
<td>(10^4)</td>
<td></td>
</tr>
<tr>
<td>(10^3)</td>
<td>Mount Everest</td>
</tr>
<tr>
<td>(10^2)</td>
<td>Giant trees: <em>Sequoia</em></td>
</tr>
<tr>
<td>(10^1)</td>
<td>Large whale</td>
</tr>
<tr>
<td>(10^0)</td>
<td>Basking shark</td>
</tr>
<tr>
<td>(10^{-1})</td>
<td>Elephant; ostrich; man</td>
</tr>
<tr>
<td>(10^{-2})</td>
<td>Dog; rat; eagle</td>
</tr>
<tr>
<td>(10^{-3})</td>
<td>Small birds and mammals; large insects</td>
</tr>
<tr>
<td>(10^{-4})</td>
<td>Small insects; minute fish</td>
</tr>
<tr>
<td>(10^{-5})</td>
<td>Minute insects</td>
</tr>
<tr>
<td>(10^{-6})</td>
<td>Protozoa; pollen-grains</td>
</tr>
<tr>
<td>(10^{-7})</td>
<td>Large bacteria; human blood-corpuscles</td>
</tr>
<tr>
<td>(10^{-8})</td>
<td>Minute bacteria</td>
</tr>
<tr>
<td>(10^{-9})</td>
<td>Limit of microscopic vision</td>
</tr>
<tr>
<td>(10^{-10})</td>
<td>Viruses, or filter-passers</td>
</tr>
<tr>
<td>(10^{-11})</td>
<td>Giant albuminoids, casein, etc.</td>
</tr>
<tr>
<td>(\text{micron. } \mu)</td>
<td>Cells</td>
</tr>
<tr>
<td>(10^{-6})</td>
<td>Colloid particles</td>
</tr>
<tr>
<td>(10^{-7})</td>
<td>Starch-molecule</td>
</tr>
<tr>
<td>(10^{-8})</td>
<td>Water-molecule</td>
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<tr>
<td>(\text{m} \mu)</td>
<td></td>
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<tr>
<td>(10^{-9})</td>
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fly are smaller than the things which walk and run; the flying birds are never as large as the larger mammals, the lesser birds and mammals are much of a muchness, but insects come down a step in the scale and more. The lessening influence of gravity facilitates flight, but makes it less easy to walk and run; first claws, then hooks and suckers and glandular hairs help to secure a foothold,
until to creep upon wall or ceiling becomes as easy as to walk upon the ground. Fishes, by evading gravity, increase their range of magnitude both above and below that of terrestrial animals. Smaller than all these, passing out of our range of vision and going down to the least dimensions of living things, are protozoa, rotifers, spores, pollen-grains* and bacteria. All save the largest of these float rather than swim; they are buoyed up by air or water, and fall (as Stokes’s law explains) with exceeding slowness.

There is a certain narrow range of magnitudes where (as we have partly said) gravity and surface tension become comparable forces, nicely balanced with one another. Here a population of small plants and animals not only dwell in the surface waters but are bound to the surface film itself—the whirligig beetles and pond-skaters, the larvae of gnat and mosquito, the duckweeds (Lemna), the tiny Wolffia, and Azolla; even in mid-ocean, one small insect (Halobates) retains this singular habitat. It would be a long story to tell the various ways in which surface-tension is thus taken full advantage of. Gravitation not only limits the magnitude but controls the form of things. With the help of gravity the quadruped has its back and its belly, and its limbs upon the ground; its freedom of motion in a plane perpendicular to gravitational force; its sense of fore-and-aft, its head and tail, its bilateral symmetry. Gravitation influences both our bodies and our minds. We owe to it our sense of the vertical, our knowledge of up-and-down; our conception of the horizontal plane on which we stand, and our discovery of two axes therein, related to the vertical as to one another; it was gravity which taught us to think of three-dimensional space. Our architecture is controlled by gravity, but gravity has less influence over the architecture of the bee; a bee might be excused, might even be commended, if it referred space to four dimensions instead of three!† The plant has its root and its stem; but about this vertical or

* Pollen-grains, like protozoa, have a considerable range of magnitude. The largest, such as those of the pumpkin, are about 200μ in diameter; these have to be carried by insects, for they are above the level of Stokes’s law, and no longer float upon the air. The smallest pollen-grains, such as those of the forget-me-not, are about 4½ μ in diameter (Wodehouse).

† Corresponding, that is to say, to the four axes which, meeting in a point, make co-equal angles (the so-called tetrahedral angles) one with another, as do the basal angles of the honeycomb. (See below, chap. VII.)
gravitational axis its radiate symmetry remains, undisturbed by directional polarity, save for the sun. Among animals, radiate symmetry is confined to creatures of no great size; and some form or degree of spherical symmetry becomes the rule in the small world of the protozoon—unless gravity resume its sway through the added burden of a shell. The creatures which swim, walk or run, fly, creep or float are, so to speak, inhabitants and natural proprietors of as many distinct and all but separate worlds. Humming-bird and hawkmoth may, once in a way, be co-tenants of the same world; but for the most part the mammal, the bird, the fish, the insect and the small life of the sea, not only have their zoological distinctions, but each has a physical universe of its own. The world of bacteria is yet another world again, and so is the world of colloids; but through these small Lilliputs we pass outside the range of living things.

What we call mechanical principles apply to the magnitudes among which we are at home; but lesser worlds are governed by other and appropriate physical laws, of capillarity, adsorption and electric charge. There are other worlds at the far other end of the scale, in the uttermost depths of space, whose vast magnitudes lie within a narrow range. When the globular star-clusters are plotted on a curve, apparent diameter against estimated distance, the curve is a fair approximation to a rectangular hyperbola; which means that, to the same rough approximation, the actual diameter is identical in them all*

It is a remarkable thing, worth pausing to reflect on, that we can pass so easily and in a dozen lines from molecular magnitudes† to the dimensions of a Sequoia or a whale. Addition and subtraction, the old arithmetic of the Egyptians, are not powerful enough for such an operation; but the story of the grains of wheat upon the chessboard shewed the way, and Archimedes and Napier elaborated

† We may call (after Siedentopf and Zsigmondi) the smallest visible particles microns, such for instance as small bacteria, or the fine particles of gum-mastich in suspension, measuring 0·5 to 1·0μ; sub-microns are those revealed by the ultramicroscope, such as particles of colloid gold (2–15mμ), or starch-molecules (5mμ); amicrons, under 1mμ, are not perceptible by either method. A water-molecule measures, probably, about 0·1mμ.
the arithmetic of multiplication. So passing up and down by easy steps, as Archimedes did when he numbered the sands of the sea, we compare the magnitudes of the great beasts and the small, of the atoms of which they are made, and of the world in which they dwell*.

While considerations based on the chemical composition of the organism have taught us that there must be a definite lower limit to its magnitude, other considerations of a purely physical kind lead us to the same conclusion. For our discussion of the principle of similitude has already taught us that long before we reach these all but infinitesimal magnitudes the dwindling organism will have experienced great changes in all its physical relations, and must at length arrive at conditions surely incompatible with life, or what we understand as life, in its ordinary development and manifestation.

We are told, for instance, that the powerful force of surface-tension, or capillarity, begins to act within a range of about $1/500,000$ of an inch, or say $0.05\mu$. A soap film, or a film of oil on water, may be attenuated to far less magnitudes than this; the black spots on a soap bubble are known, by various concordant methods of measurement, to be only about $6 \times 10^{-7}$ cm., or about $6 m\mu$ thick, and Lord Rayleigh and M. Devaux have obtained films of oil of $2 m\mu$, or even $1 m\mu$ in thickness. But while it is possible for a fluid film to exist of these molecular dimensions, it is certain that long before we reach these magnitudes there arise conditions of which we have little knowledge, and which it is not easy to imagine. A bacillus lives in a world, or on the borders of a world, far other than our own, and preconceptions drawn from our experience are not valid there. Even among inorganic, non-living bodies, there comes a certain grade of minuteness at which the ordinary properties become modified. For instance, while under ordinary circumstances crystallisation starts in a solution about a minute solid fragment or crystal

* Observe that, following a common custom, we have only used a logarithmic scale for the round numbers representing powers of ten, leaving the interspaces between these to be filled up, if at all, by ordinary numbers. There is nothing to prevent us from using fractional indices, if we please, throughout, and calling a blood-corpuscle, for instance, $10^{-3.2}$ cm. in diameter, a man $10^{2.25}$ cm. high, or Sibbald's Rorqual $10^{1.48}$ metres long. This method, implicit in that of Napier of Merchiston, was first set forth by Wallis, in his *Arithmetica infinitorum*.
of the salt, Ostwald has shewn that we may have particles so minute that they fail to serve as a nucleus for crystallisation—which is as much as to say that they are too small to have the form and properties of a "crystal." And again, in his thin oil-films, Lord Rayleigh noted the striking change of physical properties which ensues when the film becomes attenuated to one, or something less than one, close-packed layer of molecules, and when, in short, it no longer has the properties of matter in mass.

These attenuated films are now known to be "monomolecular," the long-chain molecules of the fatty acids standing close-packed, like the cells of a honeycomb, and the film being just as thick as the molecules are long. A recent determination makes the several molecules of oleic, palmitic and stearic acids measure 10·4, 14·1 and 15·1 cm. in length, and in breadth 7·4, 6·0 and 5·5 cm., all by 10⁻⁸: in good agreement with Lord Rayleigh and Devaux's lowest estimates (F. J. Hill, Phil. Mag. 1929, pp. 940–946). But it has since been shewn that in aliphatic substances the long-chain molecules are not erect, but inclined to the plane of the film; that the zig-zag constitution of the molecules permits them to interlock, so giving the film increased stability; and that the interlock may be by means of a first or second zig-zag, the measured area of the film corresponding precisely to these two dimorphic arrangements. (Cf. C. G. Lyons and E. K. Rideal, Proc. R.S. (A), cxxvii, pp. 468–473, 1930.) The film may be lifted on to a polished surface of metal, or even on a sheet of paper, and one monomolecular layer so added to another; even the complex protein molecule can be unfolded to form a film one amino-acid molecule thick. The whole subject of monomolecular layers, the nature of the film, whether condensed, expanded or gaseous, its astonishing sensitivity to the least impurities, and the manner of spreading of the one liquid over the other, has become of great interest and importance through the work of Irving Langmuir, Devaux, N. K. Adam and others, and throws new light on the whole subject of molecular magnitudes*.

The surface-tension of a drop (as Laplace conceived it) is the cumulative effect, the statistical average, of countless molecular attractions, but we are now entering on dimensions where the molecules are few†. The free surface-energy of a body begins to vary with the radius, when that radius is of an order comparable to inter-molecular distances; and the whole expression for such energy tends to vanish away when the radius of the drop or particle is less than 0·01 μ, or 10 mμ. The qualities and properties of our

particle suffer an abrupt change here; what then can we attribute, in the way of properties, to a corpuscle or organism as small or smaller than, say, 0.05 or 0.03 μ? It must, in all probability, be a homogeneous structureless body, composed of a very small number of albumenoid or other molecules. Its vital properties and functions must be extremely limited; its specific outward characters, even if we could see it, must be nil; its osmotic pressure and exchanges must be anomalous, and under molecular bombardment they may be rudely disturbed; its properties can be little more than those of an ion-laden corpuscle, enabling it to perform this or that specific chemical reaction, to effect this or that disturbing influence, or produce this or that pathogenic effect. Had it sensation, its experiences would be strange indeed; for if it could feel, it would regard a fall in temperature as a movement of the molecules around, and if it could see it would be surrounded with light of many shifting colours, like a room filled with rainbows.

The dimensions of a cilium are of such an order that its substance is mostly, if not all, under the peculiar conditions of a surface-layer, and surface-energy is bound to play a leading part in ciliary action. A cilium or flagellum is (as it seems to me) a portion of matter in a state sui generis, with properties of its own, just as the film and the jet have theirs. And just as Savart and Plateau have told us about jets and films, so will the physicist some day explain the properties of the cilium and flagellum. It is certain that we shall never understand these remarkable structures so long as we magnify them to another scale, and forget that new and peculiar physical properties are associated with the scale to which they belong*.

As Clerk Maxwell put it, “molecular science sets us face to face with physiological theories. It forbids the physiologist to imagine that structural details of infinitely small dimensions (such as Leibniz assumed, one within another, ad infinitum) can furnish an explanation of the infinite variety which exists in the properties and functions of the most minute organisms.” And for this reason Maxwell reprobates, with not undue severity, those advocates of pangenesis

* The cilia on the gills of bivalve molluscs are of exceptional size, measuring from say 20 to 120 μ long. They are thin triangular plates, rather than filaments; they are from 4 to 10 μ broad at the base, but less than 1 μ thick. Cf. D. Atkins, Q.J.M.S., 1938, and other papers.
and similar theories of heredity, who "would place a whole world of wonders within a body so small and so devoid of visible structure as a germ." But indeed it scarcely needed Maxwell's criticism to shew forth the immense physical difficulties of Darwin's theory of pangenesis: which, after all, is as old as Democritus, and is no other than that Promethean particula undique desecta of which we have read, and at which we have smiled, in our Horace.

There are many other ways in which, when we make a long excursion into space, we find our ordinary rules of physical behaviour upset. A very familiar case, analysed by Stokes, is that the viscosity of the surrounding medium has a relatively powerful effect upon bodies below a certain size. A droplet of water, a thousandth of an inch (25μ) in diameter, cannot fall in still air quicker than about an inch and a half per second; as its size decreases, its resistance varies as the radius, not (as with larger bodies) as the surface; and its "critical" or terminal velocity varies as the square of the radius, or as the surface of the drop. A minute drop in a misty cloud may be one-tenth that size, and will fall a hundred times slower, say an inch a minute; and one again a tenth of this diameter (say 0.25μ, or about twice as big as a small micro-coccus) will scarcely fall an inch in two hours*. Not only do dust-particles, spores† and bacteria fall, by reason of this principle, very slowly through the air, but all minute bodies meet with great proportionate resistance to their movements through a fluid. In salt water they have the added influence of a larger coefficient of friction than in fresh ‡; and even such comparatively large organisms as the diatoms and the foraminifera, laden though they are with a heavy shell of flint or lime, seem to be poised in the waters of the ocean, and fall with exceeding slowness.

* The resistance depends on the radius of the particle, the viscosity, and the rate of fall (V); the effective weight by which this resistance is to be overcome depends on gravity, on the density of the particle compared with that of the medium, and on the mass, which varies as r³. Resistance = krV, and effective weight = k'r²; when these two equal one another we have the critical or terminal velocity, and V ∝ r².
† A. H. R. Buller found the spores of a fungus (Collybia), measuring 5 × 3μ, to fall at the rate of half a millimetre per second, or rather more than an inch a minute; Studies on Fungi, 1909.
When we talk of one thing touching another, there may yet be a distance between, not only measurable but even large compared with the magnitudes we have been considering. Two polished plates of glass or steel resting on one another are still about \(4\mu\) apart—the average size of the smallest dust; and when all dust-particles are sedulously excluded, the one plate sinks slowly down to within \(0.3\mu\) of the other, an apparent separation to be accounted for by minute irregularities of the polished surfaces*.

The Brownian movement has also to be reckoned with—that remarkable phenomenon studied more than a century ago by Robert Brown†, Humboldt’s \textit{facile princeps botanicorum}, and discoverer of the nucleus of the cell‡. It is the chief of those fundamental phenomena which the biologists have contributed, or helped to contribute, to the science of physics.

The quivering motion, accompanied by rotation and even by translation, manifested by the fine granular particle issuing from a crushed pollen-grain, and which Brown proved to have no vital significance but to be manifested by all minute particles whatsoever, was for many years unexplained. Thirty years and more after Brown wrote, it was said to be “due, either directly to some calorical changes continually taking place in the fluid, or to some obscure chemical action between the solid particles and the fluid which is indirectly promoted by heat§.” Soon after these words were


‡ The “nucleus” was first seen in the epidermis of Orchids; but “this areola, or nucleus of the cell as perhaps it might be termed, is not confined to the epidermis,” etc. See his paper on Fecundation in Orchideae and Asclepiadaceae, \textit{Trans. Linn. Soc.} xvi, 1829-33, also \textit{Proc. Linn. Soc.} March 30, 1832.

§ Carpenter, \textit{The Microscope}, edit. 1862, p. 185.
written it was ascribed by Christian Wiener * to molecular movements within the fluid, and was hailed as visible proof of the atomistic (or molecular) constitution of the same. We now know that it is indeed due to the impact or bombardment of molecules upon a body so small that these impacts do not average out, for the moment, to approximate equality on all sides †. The movement becomes manifest with particles of somewhere about 20μ, and is better displayed by those of about 10μ, and especially well by certain colloid suspensions or emulsions whose particles are just below 1μ in diameter ‡. The bombardment causes our particles to behave just like molecules of unusual size, and this behaviour is manifested in several ways.§ Firstly, we have the quivering movement of the particles; secondly, their movement backwards and forwards, in short, straight disjoined paths; thirdly, the particles rotate, and do so the more rapidly the smaller they are: and by theory, confirmed by observation, it is found that particles of 1μ in diameter rotate on an average through 100° a second, while particles of 13μ turn through only 14° a minute. Lastly, the very curious result appears, that in a layer of fluid the particles are not evenly distributed, nor do they ever fall under the influence of gravity to the bottom. For here gravity and the Brownian movement are rival powers, striving for equilibrium; just as gravity is opposed in the atmosphere by the proper motion of the gaseous molecules. And just as equilibrium is attained in the atmosphere when the molecules are so distributed that the density (and therefore the number of molecules per unit volume) falls off in geometrical


† Perrin, Les preuves de la réalité moléculaire, Ann. de Physique, xvii, p. 549, 1905; xix, p. 571, 1906. The actual molecular collisions are unimaginably frequent; we see only the residual fluctuations.

‡ Wiener was struck by the fact that the phenomenon becomes conspicuous just when the size of the particles becomes comparable to that of a wave-length of light.

§ For a full, but still elementary, account, see J. Perrin, Les Atomes; cf. also Th. Svedberg, Die Existenz der Moleküle, 1912; R. A. Millikan, The Electron, 1917, etc. The modern literature of the Brownian movement (by Einstein, Perrin, de Broglie, Smoluchowski and Millikan) is very large, chiefly owing to the value which the phenomenon is shewn to have in determining the size of the atom or the charge on an electron, and of giving, as Ostwald said, experimental proof of the atomic theory.
progression as we ascend to higher and higher layers, so is it with our particles within the narrow limits of the little portion of fluid under our microscope.

It is only in regard to particles of the simplest form that these phenomena have been theoretically investigated*, and we may take it as certain that more complex particles, such as the twisted body of a Spirillum, would shew other and still more complicated manifestations. It is at least clear that, just as the early microscopists in the days before Robert Brown never doubted but that these phenomena were purely vital, so we also may still be apt to confuse, in certain cases, the one phenomenon with the other. We cannot, indeed, without the most careful scrutiny, decide whether the movements of our minutest organisms are intrinsically "vital" (in the sense of being beyond a physical mechanism, or working model) or not. For example, Schaudinn has suggested that the undulating movements of Spirochaete pallida must be due to the presence of a minute, unseen, "undulating membrane"; and Doflein says of the same species that "sie verharrt oft mit eigenthümlich zitternden Bewegungen zu einem Orte." Both movements, the trembling or quivering movement described by Doflein, and the undulating or rotating movement described by Schaudinn, are just such as may be easily and naturally interpreted as part and parcel of the Brownian phenomenon.

While the Brownian movement may thus simulate in a deceptive way the active movements of an organism, the reverse statement also to a certain extent holds good. One sometimes lies awake of a summer’s morning watching the flies as they dance under the ceiling. It is a very remarkable dance. The dancers do not whirl or gyrate, either in company or alone; but they advance and retire; they seem to jostle and rebound; between the rebounds they dart hither or thither in short straight snatches of hurried flight, and turn again sharply in a new rebound at the end of each little rush†.

† As Clerk Maxwell put it to the British Association at Bradford in 1873, “We cannot do better than observe a swarm of bees, where every individual bee is flying furiously, first in one direction and then in another, while the swarm as a whole is either at rest or sails slowly through the air.”
Their motions are erratic, independent of one another, and devoid of common purpose*. This is nothing else than a vastly magnified picture, or simulacrum, of the Brownian movement; the parallel between the two cases lies in their complete irregularity, but this in itself implies a close resemblance. One might see the same thing in a crowded market-place, always provided that the bustling crowd had no business whatsoever. In like manner Lucretius, and Epicurus before him, watched the dust-motes quivering in the beam, and saw in them a mimic representation, rei simulacrum et imago, of the eternal motions of the atoms. Again the same phenomenon may be witnessed under the microscope, in a drop of water swarming with Paramoecia or such-like Infusoria; and here the analogy has been put to a numerical test. Following with a pencil the track of each little swimmer, and dotting its place every few seconds (to the beat of a metronome), Karl Przibram found that the mean successive distances from a common base-line obeyed with great exactitude the "Einstein formula," that is to say the particular form of the "law of chance" which is applicable to the case of the Brownian movement†. The phenomenon is (of course) merely analogous, and by no means identical with the Brownian movement; for the range of motion of the little active organisms, whether they be gnats or infusoria, is vastly greater than that of the minute particles which are passive under bombardment; nevertheless Przibram is inclined to think that even his comparatively large infusoria are small enough for the molecular bombardment to be a stimulus, even though not the actual cause, of their irregular and interrupted movements‡.

* Nevertheless there may be a certain amount of bias or direction in these seemingly random divagations: cf. J. Brownlee, Proc. R.S.E. xxxi, p. 262, 1910–11; F. H. Edgeworth, Metron, i, p. 75, 1920; Lotka, Elem. of Physical Biology, 1925, p. 344.

† That is to say, the mean square of the displacements of a particle, in any direction, is proportional to the interval of time. Cf. K. Przibram, Ueber die ungeordnete Bewegung niederer Tiere, Pflüger’s Archiv, cliii, pp. 401–405, 1913; Arch. f. Entw. Mech. xliii, pp. 20–27, 1917.

‡ All that is actually proven is that "pure chance" has governed the movements of the little organism. Przibram has made the analogous observation that infusoria, when not too crowded together, spread or diffuse through an aperture from one vessel to another at a rate very closely comparable to the ordinary laws of molecular diffusion.
George Johnstone Stoney, the remarkable man to whom we owe the name and concept of the *electron*, went further than this; for he supposed that molecular bombardment might be the source of the life-energy of the bacteria. He conceived the swifter moving molecules to dive deep into the minute body of the organism, and this in turn to be able to make use of these importations of energy*.

We draw near the end of this discussion. We found, to begin with, that “scale” had a marked effect on physical phenomena, and that increase or diminution of magnitude might mean a complete change of statical or dynamical equilibrium. In the end we begin to see that there are discontinuities in the scale, defining phases in which different forces predominate and different conditions prevail. Life has a range of magnitude narrow indeed compared to that with which physical science deals; but it is wide enough to include three such discrepant conditions as those in which a man, an insect and a bacillus have their being and play their several roles. Man is ruled by gravitation, and rests on mother earth. A water-beetle finds the surface of a pool a matter of life and death, a perilous entanglement or an indispensable support. In a third world, where the bacillus lives, gravitation is forgotten, and the viscosity of the liquid, the resistance defined by Stokes's law, the molecular shocks of the Brownian movement, doubtless also the electric charges of the ionised medium, make up the physical environment and have their potent and immediate influence on the organism. The predominant factors are no longer those of our scale; we have come to the edge of a world of which we have no experience, and where all our preconceptions must be recast.

* Phil. Mag. April 1890.