

Metabolism and Morphology

Architecture is on the cusp of systemic change, driven by the dynamics of climate and economy, of new technologies and new means of production. There is a growing interest in the dynamics of fluidity, in networks and in the new topologies of surfaces and soft boundaries. This is part of a general cultural response to the contemporary reconfiguration of the concept of 'nature' within the discourse of architecture; a change from metaphor to model, from 'nature' as a source of formal inspiration to 'nature' as a mine of interrelated dynamic processes that are available for analysis and digital simulation. **Michael Weinstock** presents an account of the dynamics of natural metabolisms, and suggests an agenda for the development of metabolic morphologies of buildings and cities.

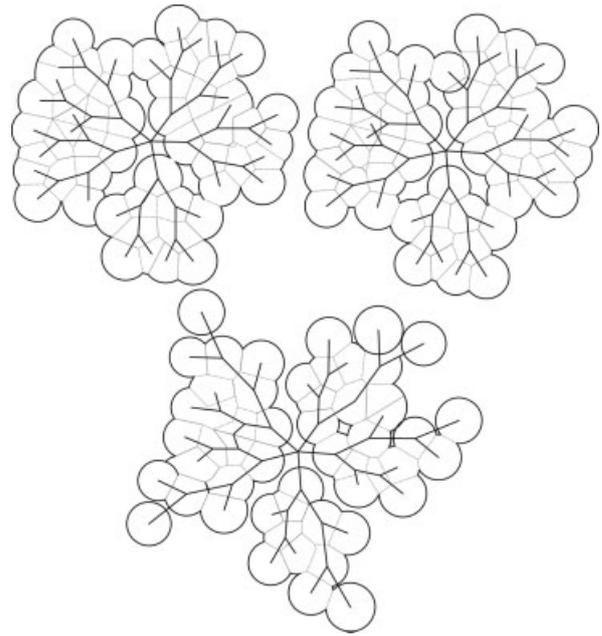


Form has been a central focus in the theories and practice of architecture throughout history, and over time has been aligned with many different ideologies and methods of generating the shape of buildings. The design of surfaces that capture or modify light, the design of heat-generation and transportation systems, and of systems for the movement of air are applied to forms that have been designed according to other criteria. In built architecture, morphology is prior to and separate from metabolism. In city morphologies, the designation of parks and other spaces as the 'lungs' of cities is an inexact metaphor – and a metaphor chosen from the wrong metabolism.

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All living forms must acquire energy and materials from their environment, and transform this matter and energy within their bodies to construct their tissues, to grow, to reproduce and to survive. D'Arcy Wentworth Thompson argued in *On Growth and Form* that the morphology of living forms has a 'dynamical aspect, under which we deal with the interpretation, in terms of force, of the operations of Energy.'¹ Living forms are able to construct and dynamically maintain themselves by the exchange of energy and material through their surfaces, and in doing so excrete changed materials and energy back into the environment. Morphology and metabolism are intricately linked through the processing of energy and materials. Metabolism is the fire of life,² and occurs at all levels from the molecular to the intricate dynamics of ecological



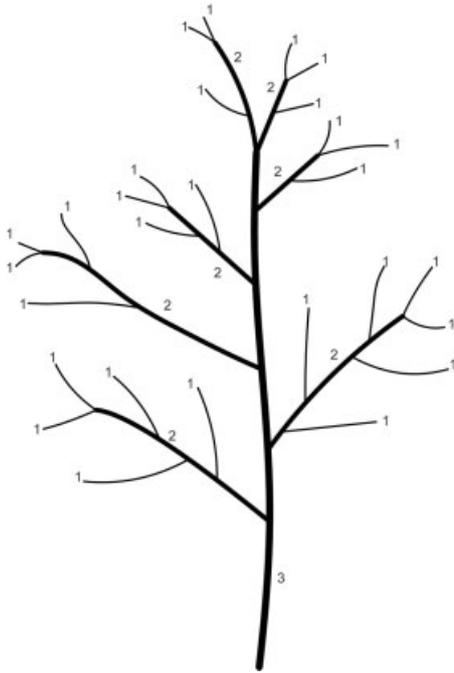
Theoretical optimal ratios of branch lengths produce the most equitable distribution of leaf clusters in computed branch systems, and are similar to the observed ratios in real trees.

systems. There are common metabolic characteristics for whole forms, in the relations between the geometry and overall size of the body plan, the internal operating temperature and the mode of existence in the environment.

Performance has been a central concern of discourses on contemporary architecture, and it is clear that architects today are increasingly becoming engaged with the natural world. There is a new sensitivity to the 'life' of buildings, and an understanding that performance and behaviour can be inputs to the process of design rather than functions applied later to a form. The study of natural metabolisms is a significant resource for design as it reveals that shape or morphology is deeply integrated within the means of capturing and transmitting energy. The organisation and morphology of energy systems of the natural world provide a set of models for what will become the new 'metabolic morphologies' of future buildings, and ultimately of cities.

Metabolism determines the relations of individuals and populations of natural forms with their local environment. Higher levels of biological organisation emerge from metabolic processes, in the relations between species, and in the density and patterns of distribution of species across the surface of the earth. All metabolic processes stem from the sunlight that falls on the surface of the earth. A very small percentage, perhaps less than 2 per cent, of that light energy

Branching system, leafless tree in winter. In the anatomical organisation of trees, the transportation network for fluids and the structural support for the leaf array have evolved as a fully integrated morphology. Branch angles and the ratios of length in sequential 'mother to daughter' branches determine the effective leaf area and constrain the overall morphology of a tree. They are also intrinsic characteristics of a species, so that different angles and ratios appear in different species.



Horton's general hydrological classification of the hierarchy of stream networks. 'Horton's ratios' are morphometrics, constant ratios of bifurcation and the relative length of each segment.

enters ecological systems through the photosynthesis of plants. Light energy is transformed into chemical energy, bound in organic molecules, and used to construct the tissues of plants. The flow of energy through all living forms is often thought of as a food chain, and although this description is topologically inaccurate (web is a more accurate description than chain), it is a useful description of the general direction of energy flow. Plants produce biological materials that can be reprocessed to release energy, and all other forms of life consume them in sequence; herbivores feed on the plants, converting them into heat energy, and in turn carnivores feed on the herbivores or other carnivores, and humans consume all other forms of life. Dead organic matter is broken down by microbes and fungi into prebiotic molecules. At each level, energy is used up so that only a small percentage of the energy available at one level is transferred to the next level. Matter is recycled, but energy is dissipated, used up and lost to the system. All metabolic processes cease without a constant source of energy, although most living forms are capable of storing some energy in chemicals to survive temporary fluctuations in energy supply.

There are common features in all natural energy systems. All organisms must not only capture and produce energy, they must also transport it; and the morphology of branching networks is found in all forms of life. There is also a relationship between energy, lifespan and body mass; small organisms are typically more metabolically active than larger organisms, and the larger the organism, the slower the metabolism. Bigger organisms live longer than small

organisms. Metabolic relationships to mass and lifespan are complex, but a gram of living tissue consumes approximately the same amount of energy during its whole lifespan independently of the form or species of which it is part. Within any specific taxa, such as mammals or plants, the metabolic rate of activity will vary from species to species, but it is generally observed that the rate of energy consumption per unit of body mass declines as the body size increases. A gram of tissue in a mouse uses up 25 times more energy in any unit of time than a gram of tissue in an elephant, so that the mouse must eat much more frequently, and much larger quantities in relation to its body mass, than the elephant. But when unrelated taxa that differ greatly in size are compared, such as a comparison between bacteria and mammals, the metabolic activity per unit body mass is approximately the same. What varies is the lifespan, by many orders of magnitude. Bacteria may live for a few hours, a mouse two to three years, an elephant up to 60 years.

There are no comparable studies in the history of architecture, yet it is clear that the metabolic 'rate' of a building, and the relationship of that rate to the mass and form of the building will not only form a stable set of criteria for the evaluation of all buildings, but can also be inputs in the generative phase of design. Culture, climate and the economy of energy are today undergoing radical revision, and new instruments and precepts for future buildings and cities are essential. The study of natural metabolisms commences with their architecture; the spatial and material organisation of a system for capturing, transforming and transporting energy.

Photosynthetic Metabolism and Plant Morphologies

Plants are 'autotrophs', or self-feeders, constructing their own materials, molecule by molecule from sunlight, water and carbon dioxide, and a few trace minerals in tiny proportions from the soil. The process is a sequence of chemical reactions known as photosynthesis, and drives the metabolism of marine unicellular organisms including cyanobacteria and algae, and all the larger plants on the surface of the earth. Oxygen is the by product.³ Carbon dioxide enters the plant, and oxygen is excreted along with water vapour, through the stomata, the pores in leaves and stems.⁴

Plants that are adapted to hotter regimes, including many of the summer 'annual' plants, have evolved a faster-acting modified photosynthetic chemistry.⁵ The stomata stay open for shorter periods during the day to absorb carbon dioxide, and so less water is lost by transpiration. A third modification of photosynthetic metabolism⁶ is found in Crassulaceae and other cacti, succulents and bromeliads. The stomata open at night, minimising evaporation, and close during the day. In these plants metabolic activity may be internalised altogether in extremely arid conditions, and stomata are closed night and day. This enables the plant to survive dry spells, and when water is available again there is a rapid uptake of it and recovery occurs. The body of the plant includes specialised water-storage tissues, and some root systems are similarly adapted.

Leaf Arrays

The characteristic silhouette of trees, the outer boundary of the volume of leaves, is constrained by the shape and size of the individual leaf geometry specific to the species and the extent to which leaves shade each other from the light.⁷ In environments with high levels of light, several layers of leaves may be arrayed before the lowest leaf is so shaded that it cannot capture sufficient light for photosynthesis. It has been argued that 'pioneer' trees, the early species in developing forests, tended to have leaf arrays organised in deep multilayered crowns. In consequence, later 'climax' species adapting to the lower light environment between established species, reduce their self-shading by developing flatter, shallow monolayered crowns with a single layer of leaves on the boundary of the leaf volume.⁸ However, many trees appear to have stacked monolayers, one above the other, and other varied morphologies do not strictly conform to either organisation.

The arrangement of leaves on a twig or stem, phyllotaxis or leaf ordering, is significantly related to the avoidance of self-shading. Leaves spring from a twig or stem at more or less the same angle, but in sequence are rotated so that they are offset from each other. Elm trees, for example, have successive leaves on opposite sides of the twig, which is also expressed as an angle of offset, in this case 180° . On beech and hazel trees

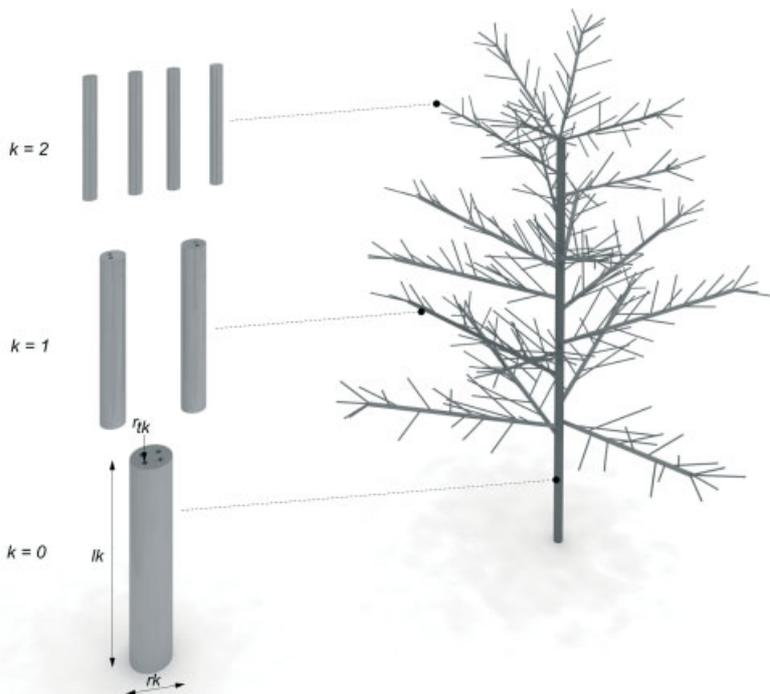
the leaves are rotated $1/3$ of the circumference of the twig, or 120° , on oak trees the rotation is $2/5$, or 144° , on poplar and pear trees it is $3/8$, or 135° , and on willow and almond trees it is $5/13$, or 130.46° . The fractional numbers are recognisable as quotients of alternative Fibonacci numbers,⁹ and are commonly found across many scales and in many different modular components, including petals and cones. Changes in leaf shape and orientation and in stem length can compensate for the negative effects of leaf overlap produced by phyllotactic patterns. The effectiveness of phyllotaxy in limiting self-shading is not absolute, and is modified by the shape and orientation of the leaves, and distance along the stem between leaves.¹⁰

All transpiration takes place through the stomata, and they typically slow down diffusion of water vapour into the atmosphere; the resistance to the flow of liquids is typically hundreds of times greater in leaves than it is in the roots, stem and branches.¹¹ The pattern of veins for the movement of fluids within the leaf varies across the species, but the rate of flow of water through the tree is slowed and controlled by the leaf array. Both gases and water vapour are controlled by the stomata, so the rate of transpiration is closely coupled to the rate of exchange of gases. Both gas and fluid flow are highly dynamic, varying between night and day, between young leaves and old leaves, and generally in response to changes in temperature and in the water supply from the roots. It follows that the photosynthetic metabolism of a tree is a product of the total surface area and mass of leaves in the array, and the lifespan of the leaves, and that these have an intricate mathematical relationship with the fluid distribution network of the whole tree and its overall morphology.¹²

Branching Networks

Branching patterns have been studied intensively in many disciplinary fields. Two of the most cited works in geomorphology are studies of the geometrical properties of hydraulic branching networks of streams and river systems.¹³ In the anatomical organisation of trees, the transportation network for fluids and the structural support for the leaf array have evolved as a fully integrated morphology.¹⁴ Branch angles and the ratios of length in sequential 'mother to daughter' branches determine the effective leaf area¹⁵ and constrain the overall morphology of a tree. They are also intrinsic characteristics of a species, so that different angles and ratios appear in different species. The number and the position of a branch in the hierarchy of branches from the outermost twig to the trunk, and the length of each branch, are said to have a logarithmic relation.¹⁶

There are two elaborate branching networks of vessels that extend throughout the plant, from the roots to the stomata of the smallest leaf. One system, the 'xylem', consists of many bundles of narrow tubes, and water that is absorbed from the soil into the roots is drawn up through the plant to the leaves, where it evaporates through the stomata. The evaporation creates a negative water pressure in the column of water in



A script to generate a branching pattern was developed (in Maxscript 3D Studio Scripting Language) for a simple tree-like branching structure, using the West Brown Enquist theoretical model combined with the phyllotactical pattern of a pine tree, as defined by Turing. The base of the script is a Fibonacci sequence that has a random factor and a divergence angle of 137.51° . A radius differentiation of $1/4r$ was introduced to the branching hierarchies. Finally three additional parameters were defined: to control the total height, the amount of medium-scale branches, and the quantity of small branchings.

the xylem tubes. The other system, the 'phloem', moves the carbohydrates that are assembled in the leaves to other metabolically active parts of the plant. Water is needed to maintain the pressure inside the living cells, and most of the metabolic processes of the cells require water molecules. However, almost all of the water that enters the plant system is 'transpired', or evaporated from the leaves, and this movement of cool water up from the soil regulates the internal temperature of the plant. The humidity and temperature of the air around the plant will affect the rate of transpiration. Low temperatures or high humidity slow transpiration, and high temperatures or low humidity accelerate transpiration. Very little of the energy that falls on a plant is used for the metabolic assembly of complex molecules; some light energy is reflected, but most, up to 75 per cent, is dissipated as latent heat in the water vapour that evaporates from the stomata.

There is relationship between the total mass¹⁷ of a plant form and its lifespan.¹⁸ Big plants live longer than small ones, and this appears to be true for all plants, from phytoplankton that live for one day to giant sequoia which may live for up to three thousand years.¹⁹ Size is a critical factor in the rate of metabolism, and the geometry of the vascular network scales with the size, volume and mass of the plant form.²⁰ There are invariant ratios across the diversity of plant morphologies, relationships between the surface area of leaves, the total volume the plant occupies, the geometry of its branching networks, and the metabolic rate and lifespan. Variations of these characteristics are all dependent on the size, or rather the total mass, of the plant form. The relationship of any morphological or metabolic characteristic to mass is known as allometry.²¹ For example, the number and mass of leaves in a plant, the rate of fluid flow in the vascular network, and the total carbon assimilation or gross photosynthesis scale proportionally to each other. They all scale at the quarter power of the mass.

It is clear that a metabolic system for buildings and cities can begin with the development of systems that are conceptually and mathematically related to the metabolic morphologies of plants. The metabolic imperative is identical in plants and buildings: the spatial organisation of large surface areas to capture light and for the exchange of gases, the structural system for the deployment of those surfaces, and an internal transportation system for moving water (and heat) or metabolic products. In plants and buildings, the need to deploy the maximum surface area for photosynthesis or light is constrained by the necessity for a stable structural configuration that will be strong enough to resist buckling under its own weight, and to resist additional imposed loads such as snow and wind pressure from all directions. The structural properties and the morphology of trees emerge from the interaction of the volumetric array of leaves and the patterns of branching networks that support them and enable their metabolisms. Developing comparable metabolic morphological systems for buildings will necessarily include

other interactions, with differing volumetric and material constraints, but the metabolic imperatives are consistent across the different domains.

Thermal Metabolisms and Animal Morphologies

Animal metabolisms process the chemical energy stored in plants, or in the flesh of other animals. They are thermal or heat-producing metabolisms, and are characterised by the relationship of their internal body temperature to the temperature of their immediate environment. It was once common to refer to 'hot blooded' or 'cold blooded' animals, but this is inaccurate. For example, the body temperature of 'cold blooded' reptiles can be extremely high when they are in sunlight for any length of time. Animal metabolisms may either maintain a constant internal temperature regardless of the ambient temperatures, or they may allow their internal temperature to vary according to the rise and fall of the temperature of their environment. Most animal metabolisms are predominately one or the other regime, but combine some behavioural aspects of both regimes.

Endotherms generate heat internally to maintain their body temperature. Maintaining a constant body temperature is a demanding energy regime for a living form. The rate of metabolic activity is high and the majority of food must be used as fuel for body temperature, with little left over to be converted into body tissues or mass. Food consumption is up to ten times more than a comparable-size animal with a variable temperature metabolism, and elaborate morphological and system adaptations are necessary. This in turn presents difficulties when the external temperature rises and falls through seasonal variation. Constant temperature metabolisms have the advantage of remaining active in very cold climates, by increasing the rate of metabolism, but of course they do need to do so in order to acquire food to maintain their energy regime. The development of enhanced insulation in layers of fat, fur and feathers increases the retention of heat, but there are far fewer adaptations that enhance the shedding of heat. Few animals with constant body temperature metabolisms can survive in very hot environments.

Ectotherms absorb heat from their environment to raise their body temperatures. Variable temperature regimes, such as the metabolisms of most amphibians and reptiles, are less energy demanding. Metabolic activity is more chemically complex, but the rate of activity is slower, and heat production is so low that the external environment effectively regulates the body temperature a little below the environmental temperature. High body temperatures are achieved by basking in the sun, for example lizards or snakes resting on warm rocks in the hot sun. Much more of their food intake can be converted into body mass. They are less active as the temperature drops, but do not need to be so active to acquire food. In fact they can survive long periods without food, and some can reduce their metabolic rate when food is scarce. They cannot survive in very cold environments.



X-ray of *Coleus* leaf, showing branching system of venation. The pattern of veins for the movement of fluids within the leaf varies across the species, but the rate of flow of water through the tree is slowed and controlled by the leaves. The photosynthetic metabolism of a tree is a product of the total surface area and mass of leaves, and the lifespan of the leaves. They have an intricate mathematical relationship with the fluid distribution network of the whole tree and its overall morphology.

The energy requirements of amphibian and reptilian metabolisms are lower than those of birds and mammals by a whole order of magnitude.

The difference in energy production capacity between the two regimes is apparent in the organisation of body organs and tissues. The endothermic of mammalian and bird forms have larger internal organs than amphibian and reptilian forms, the organs have a far greater density of mitochondria, and the mitochondria themselves have a greater surface area.²² It is clear that the constant temperature metabolisms of mammals and birds are energetically very demanding, and that the ectothermic metabolisms, with their fluctuating internal temperatures, provide an interesting model for architecture that is not constrained by very low temperatures.

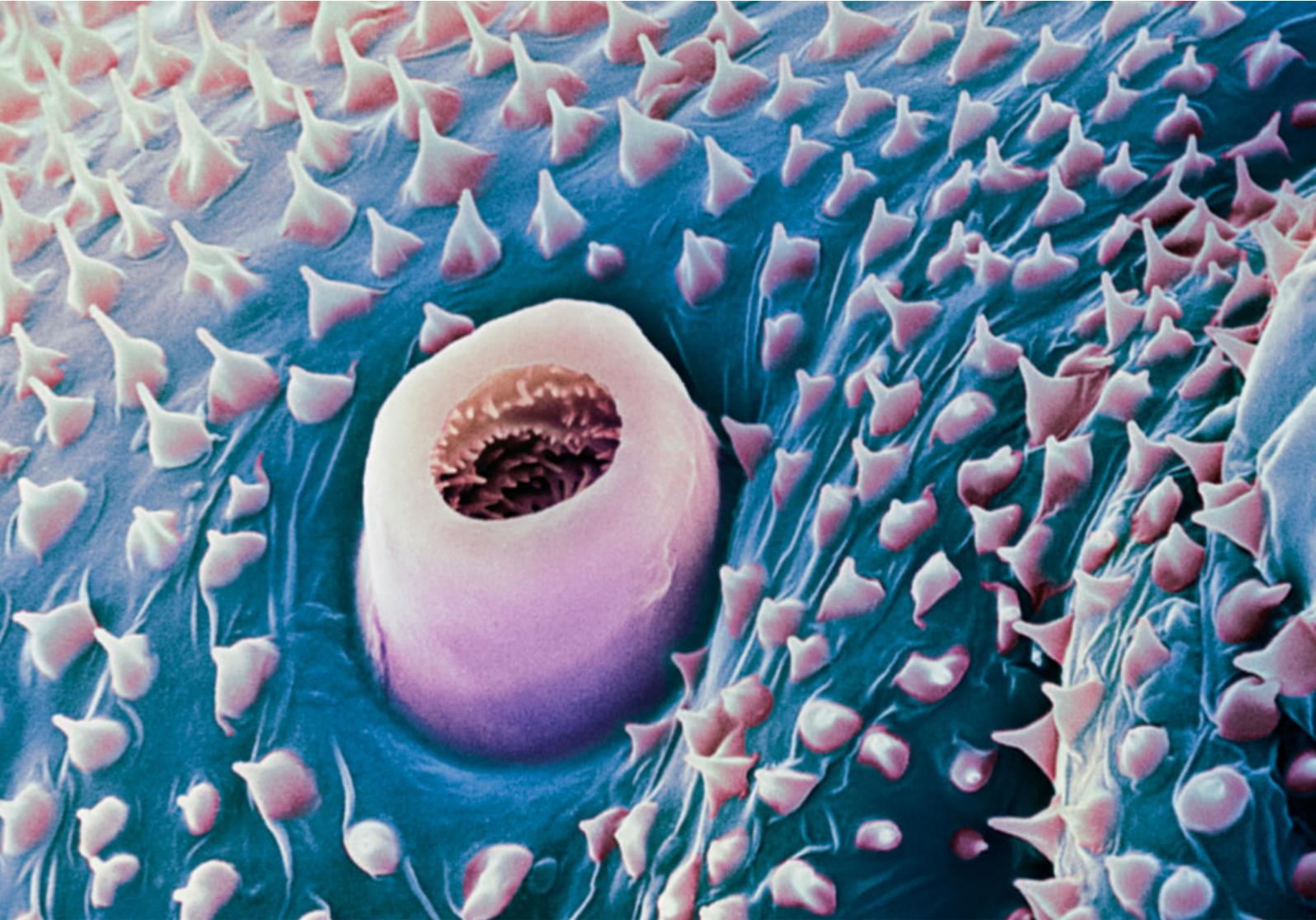
Body Size, Surfaces and Metabolic Rate

Metabolic processes have a relation to body mass; fluid energy transportation in particular is an essential determinant of body plan and overall morphology, and the size of elements within the transportation network, such as aortas, lung branches and tree trunks scale at the quarter power of body mass. Size is critical²³ in so far as it changes the ratio of the surface area to the volume enclosed by that surface. Heat loss is directly related to surface area, so the larger the surface

area the greater the heat loss. It follows that overall morphology is a significant strategy; conserving heat in cold climates is best done by large rounded forms, as proportionally they have a greater enclosed volume for their surface area. In hot climates, smaller and narrow morphologies shed heat more easily, as proportionally they have more surface area for enclosed volumes.

The body plan of living forms and the organisation of surfaces for metabolic exchange change as size increases. Thermal metabolisms evolve their long intestinal tube with its large number of convolutions to increase the surface area, and use muscles to accelerate the passage of food. The evolution of greater surface areas for respiration is a similar strategy, with the branching networks of lungs enabling very large surface areas. The evolution of body plans has been driven by natural selection acting on metabolisms, and has resulted in the organisation of systems that are simultaneously morphological and metabolic, for the capture of light and heat, for the exchange of gases, for the transportation of energy, and for structural stability.

Metabolic rates, the speed of energy and material transactions scale at the three-quarters power of the body mass. Other anatomical organisations and metabolic processes also scale in relation to mass. These allometric relations have long been studied, but the comprehensive model developed by



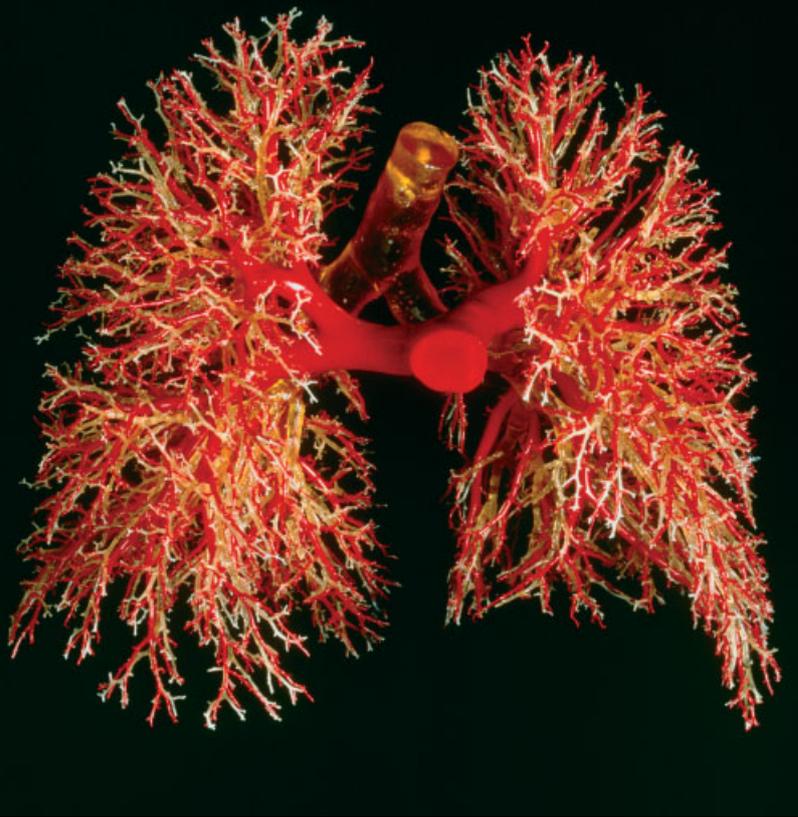
Branching network: insect respiration. Coloured scanning electron micrograph (SEM) of a spiracle of a garden tiger moth caterpillar (*Arctia caja*). Air diffuses into the spiracle and is carried around the body by a network of tubes called tracheae. Oxygen diffuses from the tracheae directly into the tissues, and carbon dioxide exits the tissues by the same system. Spiracles are found in pairs on either side of most body segments. Magnification: x 1130 when printed at 10 centimetres (3.9 inches) wide.

West, Brown and Enquist demonstrates that the geometry of branching networks for transporting energy and materials determines many morphological parameters across all species and taxa. For example, the scaling laws of branching networks occur in both the vascular system of trees and in the cardiovascular and respiratory system of mammals. The model characterises both structure and function, and demonstrates that the scaling of many ecological processes and patterns of distribution²⁴ occur in relation to the mass or size of an organism, including the patterns of plant populations and communities. The application of this mathematical model to buildings and cities has barely begun, and necessarily crosses the boundaries of many disciplines.

Conclusion

The dynamics of change in the natural world are being accelerated and perturbed by human activities at an unprecedented scale. Global climate change is upon us, and its effects will be local and regional – more energy trapped in the

atmosphere produces more intense weather systems, which in turn accelerates desertification in arid regions, increased intensity and frequency of storms in other regions, and the warming of Arctic and cold weather regions. It is axiomatic that the emergent behaviour of the climate ‘metasystem’ is not entirely predictable. So, too, the emergent behaviour of economies and cultures, now connected and interlinked globally, are in the process of substantial reconfiguration, with uncertain outcomes. The significant recent changes to culture, climate and energy economies have destabilised the equilibrium of the cultural and physical ecology in which architecture lives. The ecological opportunity that has arisen is part of the growing cultural fascination with fluidity and dynamics, with networks and new topologies, and with soft boundaries between private and public domains, and between interior and exterior space. The experience of being in spaces that flow one into one another, where differentiation between spaces is achieved less by rigid walls than by extended thresholds of graduated topographical and phenomenological



Branching network of pulmonary arteries and bronchi. Resin cast of the system supplying blood and air to the lung, viewed from the front. Clear resin was used to fill the airways, red in the case of the pulmonary arteries. The trachea branches into the left and right principal bronchi: the large pulmonary trunk divides into the right and left pulmonary arteries in front of the left principal bronchus. On the left of the image, the branch of the right pulmonary artery to the upper lobe of the lung is evident.

character, and in which connectivity and integration are enhanced, is central to contemporary existence.

The emerging architecture that relates pattern and process, form and behaviour, with spatial and cultural parameters, has a symbiotic relationship with the natural world. The study of metabolisms suggests the means of developing an architecture that is strongly correlated to the organisations and systems of the natural world. The logic of photosynthetic and ectothermic metabolisms can be extended to develop metabolic morphologies and material systems for buildings and cities. New concepts and geometries of building surface arrays, of metabolic networks for individual, and groups of, environmentally intelligent buildings can be explored through the development of 'process' models and simulations, in design explorations that begin within the relationships of metabolism and morphology. The proliferation of 'metabolic morphologies', of a symbiotic architecture that will invade and colonise towns and cities, has barely begun. Yet it is clear that the intellectual history of these ideas is very long, and that the climatic, cultural and economic pressures that are changing the world are very great. Architecture is within the horizon of a systemic change. **▷**

Notes

1. D'Arcy Wentworth Thompson, Prologue to *On Growth and Form*, first published 1917, Cambridge University Press (Cambridge), 1961.
2. M Kleiber, 'Body size and metabolism', *Hilgardia* 6, 1932.
3. $6\text{CO}_2 + 12\text{H}_2\text{O} + \text{light energy} = \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2 + 6\text{H}_2\text{O}$
4. Referred to as C_3 photosynthesis, as the first metabolic product has three carbon atoms.
5. Referred to as C_4 photosynthesis, as the first metabolic product has four carbon atoms.
6. Referred to as CAM photosynthesis, Crassulacean Acid Metabolism, after the plant it was first discovered in.
7. Werger Poorter, 'Light environment, sapling architecture, and leaf display in six rain forest species', *American Journal of Botany* 86, 1999, pp 1464-73.
8. HS Horn, *The Adaptive Geometry of Trees*, Princeton University Press (Princeton, NJ), 1971.
9. Fibonacci number series begins: 0, 1, 1, 2, 3, 5, 8, 13, 21, 34, 55 and so on.
10. KJ Niklas, 'The role of phyllotactic pattern as a "developmental constraint" on the interception of light by leaf surfaces', *Evolution* 42, 1988.
11. L Sack and NM Holbrook, 'Leaf hydraulics', *Annual Review of Plant Biology* 57, 2006, pp 361-81.
12. CA Price and BJ Enquist, 'Scaling mass and morphology in leaves: An extension of the WBE Model', *Ecology*, May 2007, pp 1132-41.
13. RE Horton, 'Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology', *Geological Society of America Bulletin*, Vol 56, No 3, 1945, pp 275-370; and LB Leopold and T Maddock, 'The hydraulic geometry of stream channels and some physiographic implications', *US Geological Survey Professional Paper 252*, Reston, Virginia, 1953.
14. KJ Niklas, 'Branching patterns and mechanical design in palaeozoic plants: A theoretic assessment', *Annals of Botany* 42, 1978, pp 33-9.
15. H Honda and JB Fisher, 'Tree branch angle: Maximizing effective leaf area', *Science* 199, February 1978. pp 888-90.
16. LB Leopold, 'Trees and streams: The efficiency of branching patterns', *Journal of Theoretical Biology* 31, 1971, pp 339-54.
17. The weight, or mass, of an organism is a function of its size and is directly proportional to the organism's volume. Living forms are composed mainly of water, and as 1 cubic centimetre of water has a mass of one gram, living tissues are a little more than one gram per cubic centimetre.
18. N Marbà, CM Duarte and S Agustí, 'Allometric scaling of plant life history', *Proceedings of the National Academy of Sciences* 104, October 2007, pp 15,777-80.
19. C Loehle, 'Tree life history strategies', *Canadian Journal of Forest Research* 18(2), 1987, pp 209-22.
20. CA Price, BJ Enquist and VM Savage, 'A general model for allometric covariation in botanical form and function', *Proceedings of the National Academy of Sciences* 104, 2007, pp 13,204-09.
21. The term 'allometry' was introduced by English biologist Julian S Huxley in his 1932 book *Problems of Relative Growth*, Methuen (London), 1932.
22. PL Else and AJ Hulbert, 'Comparison of the "mammal machine" and the "reptile machine": Energy production', *American Journal of Physiology* 240, 1981; and PL Else and AJ Hulbert, 'Evolution of mammalian endothermic metabolism: "leaky" membranes as a source of heat', *American Journal of Physiology* 253, 1987.
23. L Demetrius, 'Directionality theory and the evolution of body size', *Proceedings of the Royal Society London B*, December 2000, pp 2385-91.
24. BJ Enquist, 'Allometric scaling of plant energetics and population density', letters to *Nature*, September 1998; and GB West et al, 'A general model for the origin of allometric scaling laws in biology', *Science* 276: 122-6, 1997; and DL Turcotte et al, 'Networks with side branching in biology', *Journal of Theoretical Biology* 193: 577-92, August 1998.

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