

Predictive models for the “optimal” radius ratios in natural bi- and trifurcated vessels: beyond the Hess-Murray law

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Abstract

Bifurcated structures are ubiquitous in nature, both in living and non-living systems. The modern approach to their physical modelling starts from the recognition that in plants and animals the substitution of (a portion of) a straight vessel length with a branched one serves a biological “goal” that requires some energy and material “expenditure”. Such expenditure must be justified by a compensating gain for the resulting evolved structure. A great number of studies addressed this topic, mainly from a biomedical science perspective, but since all of them indicate a weak agreement with experimental data, it is useful to explore the matter in some more detail. The purpose of the vessels considered in this study is to “transport” material flows like sap, blood or air, and the striking geometrical similarity of the forked structures found in plants, circulatory systems, bronchial alveoli and river deltas suggests indeed the presence of a single underlying physical principle. Experimental evidence indicates that the topology of bifurcated blood, air and sap vessels (e.g., their “shape”) is amazingly similar under quite different external constraints, and this might imply that the shape of a bifurcation is at least to some extent independent of the boundary conditions. Furthermore, it is unclear if and to what measure the functional advantage obtained by repeated bifurcations decreases with the number of splitting levels. This paper presents a critical review of the most popular physical model formulated for the description of bifurcated structures, the so-called Hess-Murray law (“H-M” in the following). It is first shown that, under a very restrictive set of assumptions, the H-M law can be obtained by the assumption of constant wall stress in the parent and daughter branches. Then both Hess’ and Murray’s original derivations are discussed from a physical point of view, and the extension of the rule to the case of non-symmetrical bi- and trifurcations is presented.

It is then argued that in real branched networks the actual optimality criteria (i.e., in an evolutionary sense the “driving force”) may be quite different from the assumptions posited in the H-M law literature, which explains the weak predictive value of the law. Some adjustments to the model that include a resource-based cost/benefit of the formation of a bifurcation are presented and discussed.

Keywords: Bifurcated vessels; Branched Structures; Hess-Murray law; Entropy Generation Minimization; Constructal Theory

1. Introduction

1.1 The problem

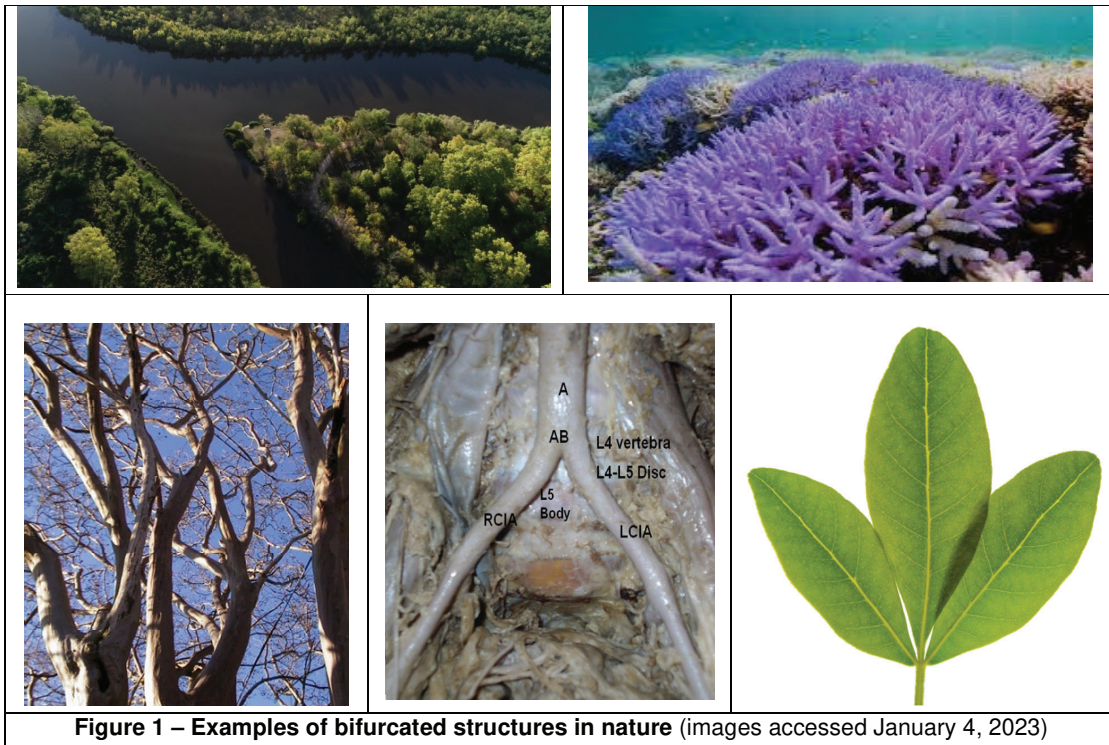
Bifurcated structures in fluid carrying channels and vessels appear in tree roots and branches, leaf veins, circulatory systems in animals, air vessels in the respiratory systems, corals, river deltas... (Figure 1). At first sight, such structures display an amazing degree of geometric similarity, and understanding the underlying physics is important for three reasons: first, if the existence of a unifying physical principle can be convincingly identified, this knowledge may lead to a better comprehension of natural evolution. Second, linking the “shape” of these structures to their “function” would allow for better aimed interventions in the case of malfunctions (overflow and flooding of rivers and channels, poor tree health, poor soil exploitation, circulatory diseases...). Third, a clearer insight on the physics of natural bifurcations may lead to the formulation of more accurate and efficient design guidelines of artificial (manufactured) branched structures, for example, in pipelines, heat exchangers, biological implants etc.

It is therefore not surprising that a large number of studies have been devoted to this topic. Leaving aside engineering applications, which require a separate discussion and are subject to quite different external constraints, botanists and biologists have dedicated substantial time and resources to the search for a general model of bi-, tri- and polyfurcated fluid carrying vessels. A brief list of the main questions to be answered can be extracted from a careful consultation of the archival literature¹:

- a) Why do bifurcated structures appear in nature?
- b) Why is the geometry of such structures apparently similar at all scales and in different instantiations?

¹ To the best of my knowledge, the first modern systematic inquiry into this matter was performed by Wilhelm Roux in his dissertation in 1878 [25]. The original text being not easily accessible, I had to rely on later citations.

- c) How and to what measure is the shape of a bifurcation independent of the prevailing boundary conditions?
 d) Does the functional advantage obtained by repeated bifurcations decrease with the number of splittings?



A final answer to the above questions is yet to be found, and one of the goals of this paper is to clarify the current state of affairs and suggest possible paths to a solution.

To place this study in the correct perspective, it is useful to begin by examining the available empirical evidence collected over decades of valuable experimental campaigns. A summary of the knowledge that can be inferred from the large set of available data is the following:

- 1) Different types of branchings display an amazing degree of geometric similarity at large scales, but the exact geometric details (radius- and length ratio of daughter-to-parent branches, branching angle, complanarity) depend on the type of fluid being transported (newtonian or non-newtonian, pure substance or particle laden) [39,41], on the material and/or state of the channel walls (lignine, muscle fibers, gravel, sand...) [13,14,24,28,39,], and on the flow features (creeping, laminar or turbulent) [2,13,22,23,40,42];
- 2) Although a branched network resembles a fractal structure, there is no indication that the fractal exponent remains constant over successive branching levels [35];
- 3) While in plants the sap flow can be accurately modeled as stationary², in blood and air systems as well as in rivers the non-stationarity of the flow has a substantial influence on the geometry of the bifurcations [39,40].

1.2 – A very popular physical model: the Hess-Murray law

Over a century ago, the Swiss physiologist Walter Rudolf Hess formulated a model of blood flow in arterioles and capillaries that resulted in an allometric correlation between the radii of successive branchings in bi/trifurcated vessels: the original concept is presented and discussed in Hess' doctoral thesis published in a little known 1903 paper, with two further extended versions published (in german) in 1914 and 1917 [10,11]. Using a similar approach, the American physiologist Cecil Dunmore Murray "rediscovered" the same correlation in a 1926 article, and later refined and extended it in two other papers [16,17,18]. Since the

² Here and in the following, a significant distinction in the nomenclature must be made: while in blood- and air circulation systems one refers in fact to individual vessels (capillaries, veins, arteries etc.), in plants the "vessels" are either the mesoscale ducts of leaves and roots (the "veins") or the large scale twigs and branches. At the smallest xylem scale there is no bifurcation.

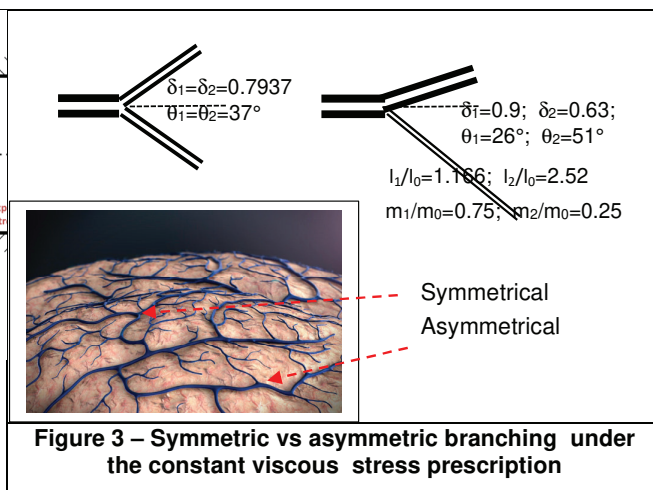
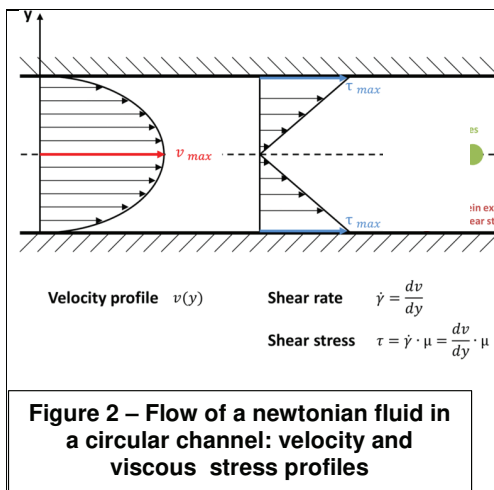
numerical result, i.e., the allometric rule, is the same, the law came to be referred to as “the Hess-Murray law”.

The methods proposed by Hess and Murray are described in detail in sections 3 and 4 below: it is important to underline the novelty of both approaches, based on the assumption that the circulation of blood, lymph and air in living organisms is governed by a “work minimization” principle. The popularity of the H-M law is though not due to the “energy cost” methods they adopted (for a documented critique, see sections 3 and 4 below), but rather to the derivation of an “optimal branching ratio” $\delta = \frac{d_{i+1}}{d_i} = \frac{1}{\sqrt[3]{2}} = 0.7937$ between the diameters of two successive symmetrical branches. This “cubic root of 2” correlation underwent extensive theoretical and experimental reassessment in the second half of the 20th century, and the results indicate that while it is sufficiently accurate for the smallest vessels (capillaries), it fails for the larger ones (large veins and arteries); moreover, it does not apply to turbulent flows [42]. Recent comparisons with numerical investigations of branched flows led to similar conclusions [22,24,39,40].

In 1997 Bejan [4] published a very ingenious generalization of the H-M law: he reasoned that, if the law holds, then every bifurcated stream that carries a material or immaterial flow from one point (the *source*) to two others (the *sinks* or *end-users*) should -in an evolutionary sense- develop along a global structure exactly specified by the “cubic root of 2” rule. This intuition forms the basis for his Constructal Theory (“CT”), which has since seen a great number of applications in the most diverse fields (see also [5,6,15] for the Authors’ own reassessment). Not by chance, the very name “constructal” was conceived to be an antonym of “fractal”, to signify that real structures follow from goals and physical laws, in line with Hess’ & Murray’s teleology, rather than from abstract “shape factors” or Lyapunov exponents (borrowing Bejan’s words: “*Nature is not fractal!*” [4]). The goals are in turn determined by external influences related, in nature, to evolutionary pressures [5], and in engineering, to design specifications. In this sense, CT represents a “closed” scientific paradigm, not only *qualitative* but *quantitative*: it proposes a novel interpretation and classification of natural (abiotic and biological) structures and leads to measurable and repeatable design procedures for engineered artefacts. The entire body of its results depends though on the applicability of the H-M law, and more precisely on the general validity of the “cubic root of 2” correlation (or any other correlation of the form 2^{-n}).

The real legacy of the H-M law is not its (doubtful) universal accuracy, but rather its conceptual foundations: it states that biological organisms can be described by means of an allometric scaling arising from an “energy costing” approach. As noted in [36] and later by [5,27,31], this in turn implies the existence of a similar allometry between different species: if the relative sizes of the respective blood or sap vessels scale according to a 2^{-n} rule then, whatever the value of n , the average physical dimensions of the individual organism depend on the radius of the main branch, which in turn depends on the metabolic rate of the species.

On the engineering side, in spite of Sherman [36] argument that -if the hydraulic diameter d_h is substituted for d - the H-M law should also hold with minimal corrections for human artefacts (pipelines, fluid carrying networks, porous media), the matter is more complex, because heat exchangers and fluid networks are designed under several “non-natural” constraints, some of which derive from purely technical requirements (entry length in a HE, material compatibility, vessel wall mechanical resistance, etc.) and others are cost-related (minimal material costs, optimal thermal insulation, minimum pumping work, etc.). The analysis of the applicability of the H-M law to engineered structures is outside of the scope of the present study.



2- Young's Constant Wall Stress Law

2.1 - Theoretical model

It is interesting to remark that, as reported by Thomas Young in its Croonian lecture 1809 [44], presented well before Hess' study, an exact form of the radius ratio in branched tubes was already known to hydraulic engineers. This formula also reads $\delta = \frac{d_{i+1}}{d_i} = \frac{1}{\sqrt[3]{2}} = 0.7937$, but its derivation does not depend on the approximations introduced by Hess on the "regulatory power of the blood flow" nor on the inaccurate "metabolic cost of blood volume" calculated by Murray.

2.2 - The mathematical derivation

Consider the steady laminar and isothermal flow of a Newtonian fluid in a symmetrically branched circular channel (Figure 3, top left). Assuming that the flow can be described by Poiseuille formula and remains laminar in the daughter branches (i.e., neglecting the possible onset of turbulence at the junction), the wall stress calculated in the parent (ℓ_0) and daughter (ℓ_1, ℓ_2) branches takes the form:

$$\tau_w = \frac{4vm_j}{\pi r_j^3} \quad (1)$$

with $j=0$ for the main and 1 and 2 for the splits. Let us impose the constancy of the wall stress throughout the bifurcation:

$$\tau_{w,0} = \frac{4vm_0}{\pi r_0^3} = \tau_{w,1} = \frac{4vm_1}{\pi r_1^3} = \tau_{w,2} = \frac{4vm_2}{\pi r_2^3} \quad (2)$$

If the split is symmetrical, then $m_1=m_2=m_0/2$, and we obtain:

$$\delta = \frac{r_1}{r_0} = \frac{r_2}{r_0} = \frac{1}{\sqrt[3]{2}} = 0.7937 \quad (3)$$

i.e., the same value prescribed by the H-M rule.

The validity of Eq. (3) rests of course upon the assumptions of steady Poiseuille flow, and therefore there is no reason for the exponent $n=-1/3$ to apply under turbulent- or non-stationary flow conditions. It is to be expected though that in leaf tubules, blood capillaries and in the smallest tubules of the respiratory tract, where diameters are well below 1 mm and the Reynolds number of the flow is very low, the above correlation should apply.

An interesting consequence of Eq. (3) can be derived if we prescribe the Δp in the main- and in the daughter branches to be the same. This implies:

$$\lambda = \frac{l_1}{l_0} = \frac{l_2}{l_0} = 2 \quad (4)$$

Eq. (4) would suggest that at each bifurcation the length of the daughter branches doubles, a condition not supported though by experimental evidence.

The above calculation can be adapted to non-symmetric branchings (Figure 3 top right). To close the calculation, we need to know the ratio of the mass flowrates through the daughter branches, $k_1=m_1/m_0=x$, $k_2=m_2/m_0=1-x$. We obtain:

$$\delta_1 = \frac{r_1}{r_0} = x^{1/3}$$

$$\delta_2 = \frac{r_2}{r_0} = (1-x)^{1/3} \quad (5)$$

In this case the pressure drops through the daughter branches are different, unless one selects a proper ℓ_1/ℓ_2 ratio:

$$\Delta p_1 = \Delta p_2 \quad \text{iff} \quad \frac{l_1}{l_2} = \left(\frac{1-x}{x}\right)^2 \left(\frac{\delta_1}{\delta_2}\right)^4 \quad (6)$$

3 – Hess' original model

3.1 - Problem position

In 1903, in a preparatory paper for his M.D. thesis [10], the Swiss physiologist Walter Rudolf Hess proposed the existence of a physical "optimization criterion" that guides the branching of arterial vessels. This idea was also the topic of later work in his "Habilitation" thesis [11], but the 1903 work already contains -albeit in a convolute way and with some debatable assumptions- a complete derivation of his "cubic root of 2" law. Hess was clearly inspired by previous work by Roux [25] who postulated a "dynamic mechanical principle" to be the driver of vessel bifurcations in animal circulatory systems. Trying to interpret the large mass of experimental data presented by Roux, Hess starts by assuming that nature would adopt a "minimum resource consumption" criterion to build the human circulatory system and proceeds to calculate how this task can be attained ("*Wie kann die Aufgabe des Blutes mit dem kleinsten Kraftverbrauch erledigt werden*" [10], p.5). In spite of his convolute writing style, Hess' approach emerges clearly: the optimal radius of a vessel carrying a given volumetric blood flowrate is the one that minimizes a cost function given by the sum of the pumping work (inversely proportional to the fourth power of the radius) and the metabolic cost of the volume of the pumped blood (proportional to the square of the radius).

3.2 - The mathematical derivation

In modern terms, Hess' procedure can be reformulated as follows:

- Assume the flow in arteries can be described by Poiseuille's law for steady laminar flow in circular vessels with rigid walls;
- Calculate the pumping power in W/(meter of vessel) required of the heart to process a flowrate m [kg/s]:

$$P_{pump} = K_1 \frac{m^2}{r^4} \quad (7)$$

where K_1 is a constant that depends on the fluid viscosity and density;

- Calculate the metabolic cost of the pumped blood, neglecting its thermal content:

$$C_{blood} = K_2 r^2 \quad (8)$$

Where C_{blood} is also in W/m of vessel and K_2 is a constant depending on the metabolic rate;

- Find the optimal radius by solving the corresponding Lagrangian³:

$$\mathcal{L}_{Hess} = P_{pump} + C_{blood} = K_1 \frac{m^2}{r^4} + K_2 r^2 \quad (9)$$

Which results in:

$$r_{opt} = \left(\frac{2K_1}{K_2} \right)^{1/6} m^{1/3} = \kappa m^{1/3} \quad (10)$$

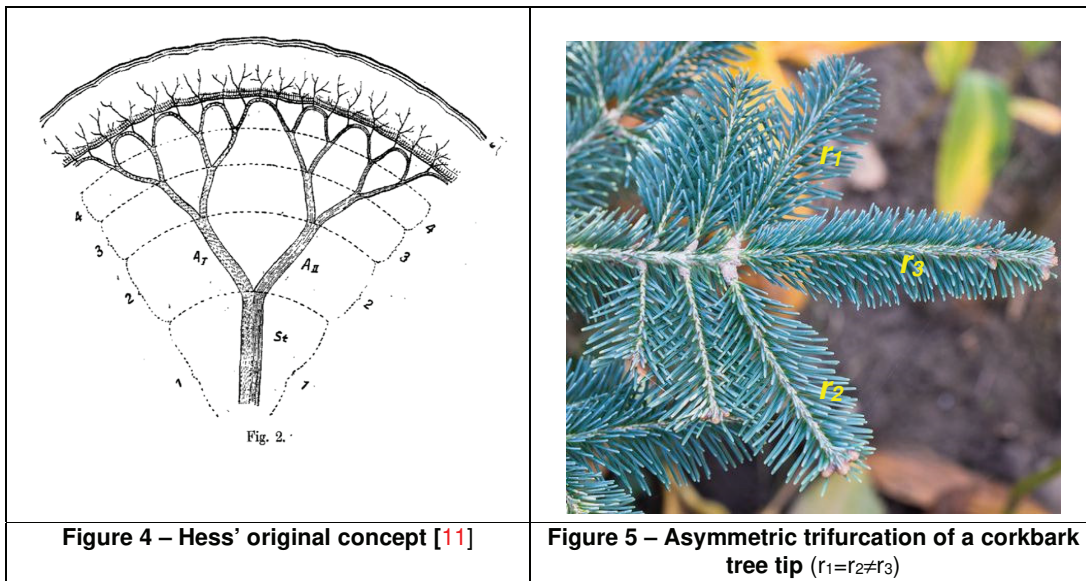
Where the constant κ depends on the fluid properties and on the metabolic rate. If a vessel bifurcates symmetrically (Figure 4), i.e., if $m_1 = m_2 = m_0/2$, the optimality can be extended to the daughter branches:

$$r_0 = \kappa m_0^{1/3}; \quad r_1 = r_2 = \kappa \left(\frac{m_0}{2} \right)^{1/3} \quad (11)$$

Whence

$$\delta = \frac{r_1}{r_0} = \frac{1}{\sqrt[3]{2}} \quad (12)$$

Throughout his papers Hess repeatedly stresses that he is aware that his result depends on two critical assumptions, namely Poiseuille flow and stationarity, and makes accurate reference to selected contemporary literature that reinforces his belief that a branching does not generate turbulence and that the low-frequency pulsations do not affect the flow in such a way as to invalidate Eq. (12).



4 – MURRAY'S model

4.1 - Problem position

Between 1926 and 1927, Cecil B. Murray, an American physiologist, published a set of papers aimed at the identification of the most "economic" oxygen supply to the human limbs via blood transport through the vessels. He demonstrated that such an optimal value can be derived by minimizing a cost function consisting of two terms: the power needed to overcome friction and the "metabolic cost" of the blood flowing through the vessel. The premises are similar to those posited by Hess, but the calculation of the blood cost function is different. He, too, arrived at a "cubic root of 2" formula. Murray -as Hess- assumed the blood flow to be

³ In fact, Hess only presents a graphical derivation, because the expression he derives for K_2 is not explicit in the variable "r", and thus he must use an approximation to make the dependence explicit

described by the stationary Poiseuille formula, and explicitly stated that his derivation ought to be considered a statistically valid theoretical guideline and that his model represents a “theoretical approximation” of the more complex physiology of blood transport. In his own words [16]: “If we examine the arterial system bearing in mind the question of economy, we find that there are two main antagonistic factors. If the vessels are too small, the work required to drive the blood through them becomes too great; if the volume of the vessels is too large, the volume of blood, being equally large, becomes a burden to the whole body”. Murray was aware of Hess’ previous work but maintained that his calculation of the blood cost was more accurate and based on the latest experimental results. Besides reformulating the theory, Murray also derived the “optimal angles” for a symmetric bifurcation using the minimum virtual work principle (Figures 6, 7).

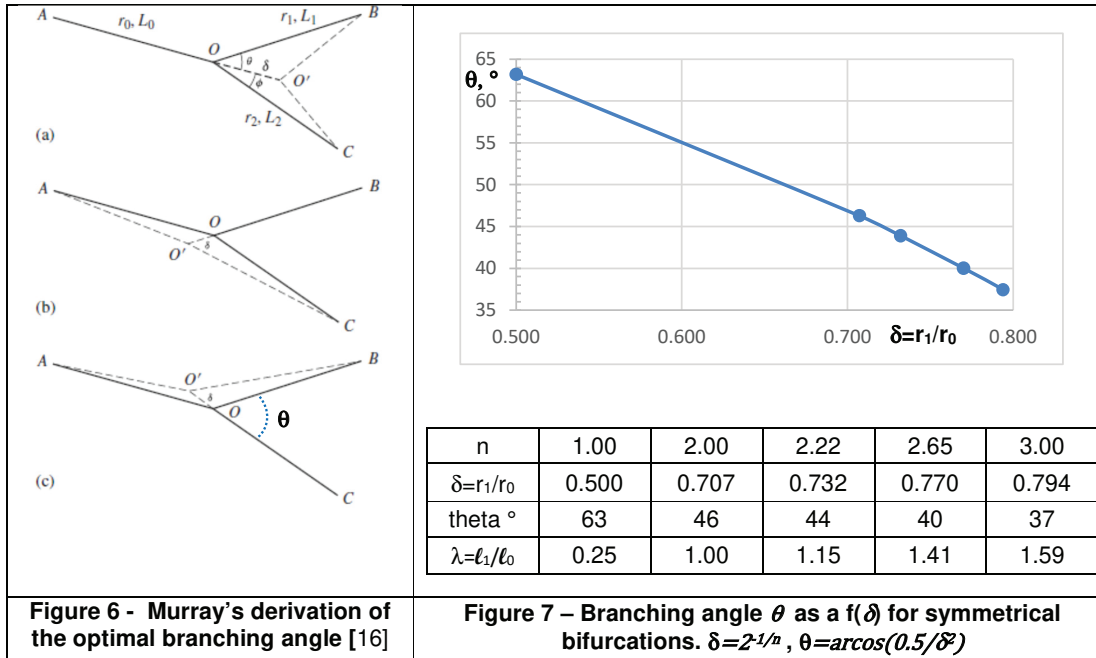


Figure 6 - Murray’s derivation of the optimal branching angle [16]

Figure 7 – Branching angle θ as a $f(\delta)$ for symmetrical bifurcations. $\delta=2^{1/n}$, $\theta=\arccos(0.5/\delta^2)$

4.2 - The mathematical derivation

Proceeding along the same path previously proposed by Hess, Murray obtained an expression identical to Hess’ for the power required to pump a given mass flowrate of blood in a straight vessel with rigid walls, Eq.

$$(7): P_{pump} = K_1 \frac{m^2}{r^4},$$

where K_1 is the same constant as in Hess’ formulation.

He then proceeded to calculate the metabolic cost of the pumped blood:

$$C_{blood} = b \rho l \pi r^2 = K_3 r^2 \quad (13)$$

Where b is the “cost of blood” calculated on the basis of the then available data on heart rates, and varies between 980 and 1980 W/m³ according to the adopted calculation method. For the purpose of this paper, the accuracy of the value of b is though irrelevant.

The optimal radius is again obtained by solving the corresponding Lagrangian:

$$\mathcal{L}_{Hess} = P_{pump} + C_{blood} = K_1 \frac{m^2}{r^4} + K_3 r^2 \quad (14)$$

Which results in:

$$r_{opt} = \left(\frac{4K_1}{K_3} \right)^{1/6} m^{1/3} = \xi m^{1/3} \quad (15)$$

Where the constant ξ depends on the fluid properties and on the power absorbed by the heart. If a vessel bifurcates symmetrically (Figure 3, top left), i.e., if $m_1=m_2=m_0/2$, the optimality can be extended to the daughter branches and the “cubic root of 2” law $\delta = \frac{r_1}{r_0} = \frac{1}{\sqrt[3]{2}}$ is recovered.

In a second paper [17], Murray calculates the optimal branching angle by applying again the principle of minimum work: as shown in Figure 6, among the possible paths the branching angles that minimize the total work are given by:

$$\cos \theta = \frac{r_0^4 + r_1^4 - r_2^4}{2r_0^2 r_1^2}; \quad \cos \varphi = \frac{r_0^4 + r_2^4 - r_1^4}{2r_0^2 r_2^2} \quad (16)$$

Now Murray argued that, since according to Eq. 10 the mass flow rate at optimal configuration is proportional to the cube of the radius, the correlation between the radii of the main- and the daughter branches is:

$$r_0^3 = r_1^3 + r_2^3 \quad (17)$$

So that the final relationship between the splitting angles becomes:

$$\theta = \arccos \left[\frac{r_0^4 + r_1^4 - (r_0^3 - r_1^3)^{4/3}}{2r_0^2 r_1^2} \right]; \quad \varphi = \arccos \left[\frac{r_0^4 + r_2^4 - (r_0^3 - r_2^3)^{4/3}}{2r_0^2 r_2^2} \right] \quad (18)$$

Introducing the optimal radius ratio δ (Eq. 12):

$$\theta = \varphi = \arccos \left[\frac{1 + \delta^4 - (1 - \delta^3)^{4/3}}{2\delta^2} \right] \sim 37^\circ \quad (19)$$

The above result predicts that symmetrical branches should have a total branching angle ($\theta + \varphi$) of about 75° . If the vessel trifurcates as shown in Figure 5, with two side daughter branches being symmetrical with equal radii $r_1 = \gamma r_0$ and the third coaxial with the main and also of radius $r_2 = r_1$, the optimal value of the radius ratio is $\gamma = \frac{1}{\sqrt[3]{3}} = 0.6934$ and Murray's optimization procedure provides:

$$\psi = \arccos \left[\frac{r_0^2 - (r_0^3 - 2r_1^3)^{2/3}}{2\gamma^2 r_0^2} \right] \quad (20)$$

with the splitting angle $\psi = 57^\circ$.

Murray did not elaborate on the fact that Eqs. (16) & (20) retain their validity under any law of the type 2^{-n} . Figure 7 displays the branching angle θ as a function of the radius ratio δ for $n=1, 2, 3$ and two experimentally & numerically validated values, namely 2.22 and 2.45 [13,26,34,41,42].

Another consequence of the H-M law (or of any similar allometric correlation) is that the length of the branches may also be derived as a function of n : for example, imposing a constant pressure drop across all branches (i.e., $\Delta p_0 = \Delta p_1 = \Delta p_2$, not necessarily an "optimal" choice) one obtains

$$\lambda_1 = \frac{\ell_1}{\ell_0} = 2 \left(2^{\frac{n-2}{n}} \right) \quad (21)$$

The λ_1 are also shown in Figure 7: in spite of their not being optimal in any sense, these values can be used as a yardstick for assessing field-measured values. In fact, the largest majority of field data report ℓ_1 values lower than 1, which indicates that the "constant Δp " is not a preferred configuration in nature.

5 – Limitations of the Hess-Murray Law

5.1 - Theoretical analysis

The applicability of the H-M law depends on several assumptions, the more stringent being:

a) *Validity of the Poiseuille flow*

While in plants the sap flow is so slow that it can be modelled as a creeping flow, in animals laminarity is the exception rather than the rule. Notice though that this fact *per se* does not affect the value of the branching ratio: the necessary condition for the H-M law to apply is that a phenomenon can be modeled as emerging from the combined influence of two competing "forces", one proportional to the square of the mass flowrate and to the inverse fourth power of the radius, and the other to the square of the radius.

b) *Validity of the steady state flow conditions*

This is a major simplification, and both experimental [12,20,21,34,45] and numerical [2,13,22,23,24,33,34,40] studies demonstrated that the inherent unsteadiness in blood vessels has a major impact on the exponent of the allometric correlation.

c) *Independence on the type of fluid*

Both sap and blood are non-Newtonian fluids, and experimental and numerical studies demonstrate that releasing the newtonianity condition results in a different value of the exponent n in Eq. (15).

d) *Validity of the assumption of rigid walls*

On this point one must differentiate between application of the law to plants and animals: in the former case, the lignino-cellulosic walls are for all practical purposes rigid, while in the latter the compliant muscle-structure of arteries and veins may even invalidate the non-slip condition.

Allometric branching models exist that are not derived from a Hess-Murray perspective (for details see [7,43]), but their treatment is outside of the scope of this paper.

5.2 – Comparison with experimental results

Given the convenience of a simple correlation like the H-M law, several experimental campaigns have been conducted over the years to verify its applicability, especially in biology. The verified experimental evidence may be summarized as follows:

a) As anticipated by Murray, both *in vitro* and *in vivo* tests convincingly demonstrate the validity of a H-M-like allometry in capillaries and arterioles, with exponent values in the range $2^{-0.16}$ through $2^{-0.43}$ [2,23,26,36,41]. In larger vessels (veins, arteries) a $2^{-0.47}$ value is more appropriate [26,41].

b) More importantly, several independent experiments on animal circulatory systems [12,45] conclude that radius-dependent *slenderness factors* appear to be correlated by a power law of the type $\ell/(2r) = \alpha r^n$, with $0.47 < n < 1.1$ and α a case-dependent function of r_0 : this implies that the dimensionless splitting length $\lambda_0 = \ell_0/L$ (see Figure 7) is also a relevant parameter.

c) Although, for the reasons discussed in the previous sections, the agreement is expected to be better in plants, independent studies report vessels ratios between 0.47 and 0.85 for both leaves and soft twigs [1,25]. Following Murray [19] and in spite of a critique by Savage [27], some Authors assume bough-to-trunk and twig-to-bough radius ratios to follow the “cubic root of 2” rule: as we shall see in section 6.4, it is possible to formulate a physical model for such a case also by assuming a volume conserving law that leads to an exponent $n=2$. Some Authors prefer to use a log/log fit for the branch lengths and the radius [12,20].

Referring the reader to [29,31] for a more detailed discussion, it is fair to conclude this analysis by saying that the Hess-Murray's law:

- a) Has the great merit of introducing the idea that the growth of branches in a tree or in epithelial tissue is dictated by a “balance” of material and metabolic energy cost;
- b) It is valid in a first approximation for all processes in which the two contrasting “forces” are friction and fluid volume;
- c) Displays an acceptable agreement for small, rigid-walled vessels and laminar flow, but fails significantly to describe branching ratios observed in real structures for any other condition (larger vessels, compliant walls, non-newtonian fluid, turbulent flow).

6 - Models based on a different “cost” structure

All of the hitherto formulated alternative models maintain the physical approach suggested by Hess and Murray: the formation and operation of a branched configuration must serve some physiological goal and therefore it ought to “minimize” in some sense the resources invested by the system in generating the bifurcation. Adam [1] proposes some alternative cost functions, all of them confirming the “cubic root of 2” correlation but having different values for the constant ξ in the solution of the “optimal” radius (Eq. 15). The unsatisfactory agreement of the H-M law has stimulated further research in the topic, and it is instructive to examine some other Lagrangians that have been explicitly or implicitly proposed in relatively recent archival publications. In this section we shall discuss three alternative models based on the consideration that a bifurcation must be created with an investment of both material and energy.

6.1 – Minimal pumping power in a target volume

The simplest cost function considers only the “system operation cost”, i.e., the pumping power required to overcome friction losses. Simply imposing minimum P_{pump} (Eq. 7) leads of course to the trivial and unphysical result $r \rightarrow \infty$. It is though interesting to investigate the existence of geometrically constrained values for the radius ratio and for the branching angle. Consider Figure 8: in real instantiations a branching takes place within a “volume” (here, area) defined by the origin “O” and the final points A and B, and if the splitting point moves along the parent branch, l_0 varies and so does $l_1=l_2$ (if the branching is symmetrical). The Poiseuille pressure loss along the three vessels is:

$$\Delta p_0 = \frac{8vl_0m_0}{\pi r_0^4}; \quad \Delta p_1 = \Delta p_2 = \frac{4vl_1m_0}{\pi r_1^4} \quad (22)$$

The corresponding pumping powers:

$$P_{pump,0} = q_0\Delta p_0 = \frac{8vl_0m_0^2}{\pi\rho r_0^4}; \quad P_{pump,1} = P_{pump,2} = q_1\Delta p_1 = \frac{2vl_1m_0^2}{\pi\rho r_1^4} \quad (23)$$

The lengths l_0 and l_1 are subject to the constraints:

$$L = l_0 + l_1\cos\theta; \text{ or } \quad \lambda_0 = 1 - \lambda_1\cos\theta \quad (24)$$

The ratio P_{bit}/P_0 is less than unity (i.e., it brings an advantage in terms of pumping power) only above a certain splitting angle of about 61° , i.e. for an exponent $n \neq 2$ and a radius ratio very close to $\frac{1}{\sqrt{2}} = 0.707$ (Figure 9). There is no minimum.

Notice that the application of Eq. (23) results in an implicit correlation between the radius ratio and the aspect ratio $a=H/L$ of the 2D domain defined by the branching, because the splitting lengths l_0 and l_1 depend on the aspect ratio and θ as per Eq. (24). This is a useful outcome, and shows that different values of the exponent n may accommodate more closely the deviations from the H-M law in real plants and blood vessels.

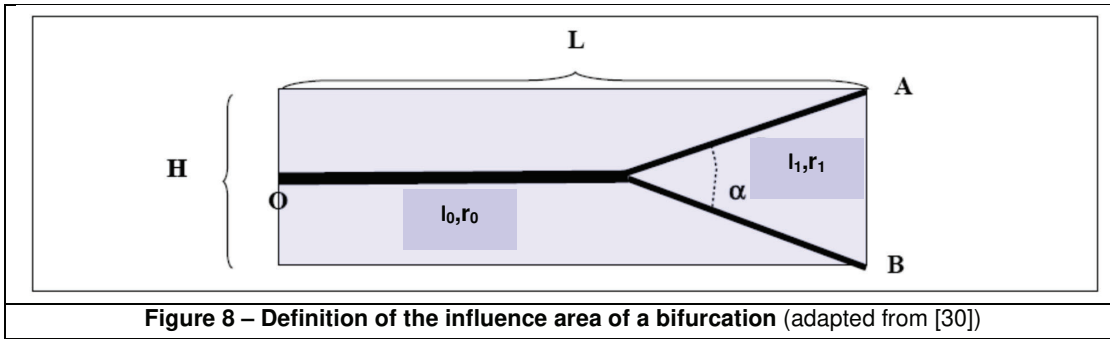


Figure 8 – Definition of the influence area of a bifurcation (adapted from [30])

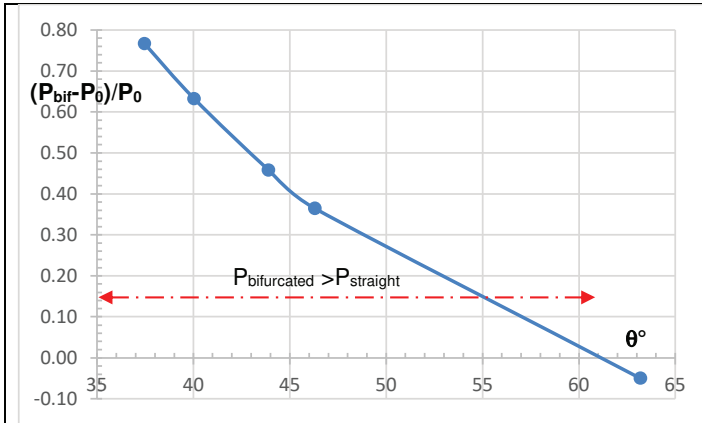


Figure 9 – Symmetric bifurcation: dimensionless pumping power vs. splitting angle θ

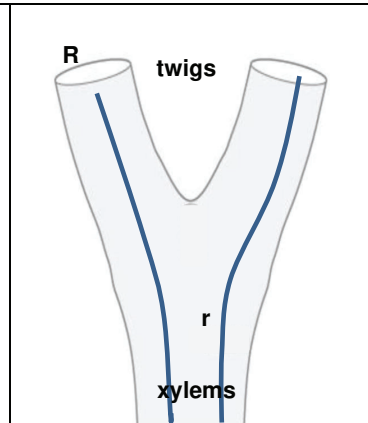


Figure 10 – Vessel vs. twig radius in a tree bifurcation

6.2 - Minimal entropy generation

Another very useful paradigm used to optimize bifurcated structures, pioneered by Bejan [3], is the Entropy Generation Minimization (EGM). True to its name, EGM is based on the idea that the “optimal” shape of a branched fluid-carrying conduit ought to minimize the total irreversibility occurring during its operational window (the lifetime of the vessel). EGM was formulated earlier than CT, is undoubtedly more comprehensive than the latter and -more important- it generates richer insight. Contrary to common belief, it can be proven that the two approaches do not consistently lead to the same results [30,31]. Since the flow of sap and blood can be assumed as isothermal and single phase, the only entropy generation is caused by friction, and the Lagrangian becomes:

$$\mathcal{L}_s = K_s \dot{s}_{visc} \quad (25)$$

It turns out that, since the rate of viscous entropy generation is directly proportional to the lost work due to friction, the solution to Eq. (25) leads to the same results as in section 6.1 [29].

6.3- Minimal pumping power and material formation cost

This model, formulated by researchers investigating tree growth, [8,9], is based on the premise that the growth of a bifurcation carries a cost equal to the biological production expenditure required of the tree to produce the volume of the material (lignine) of the new sap carrying vessels. This cost is assumed to be proportional to the Net Primary Production of the plant (NPP), a measure of the efficiency of the tree to transform its global resource input into “new wood” [20,21,37,38]. This expenditure must be added to that required to pump the sap. It is readily seen that the new volume is proportional to the square of the vessel radius, and thus the Lagrangian takes the same form as Hess' one, although with a different value for the constant K_s .

$$\mathcal{L}_{material} = K_1 \frac{m^2}{r^4} + K_5 r^2 \quad (26)$$

Thus, while the optimal radius that carries a given mass flow rate of sap is of course different than that predicted by the H-M law, still the radius ratio of the daughter branches to the parent one follows the cubic root of 2 rule, because the solution of (28) is again $r_{opt}^3 = \left(\frac{K_1}{K_5}\right)^{1/2} m$.

6.4- Minimal pumping power, material formation and fluid cost

It is useful to address the problem from a different viewpoint: it is correct that the system “resource expenditure” is proportional to the pumping power and to the material cost required for building the vessel’s envelope, one ought to consider that the scope of circulating the nutrients is to allow the system to “grow”. Therefore, there is another expense required, namely that of the generation and maintenance of the material that surrounds the vessel: in a tree, the twig, and in an animal system, the surrounding tissue. The additional cost is proportional to the metabolic rate required by this “growth”, and it dictates the mass flowrate⁴. Denoting as R the radius of the twig or bough (or of the organic tissue surrounding a blood vessel), the mass flow of sap or blood depends on the growth rate, and at steady state can be expressed as:

$$m = K_3 R^2 \quad (27)$$

Where K_3 is a function of the metabolic rate of nutrients needed to build a cylinder of radius R and unit length. The Lagrangian becomes:

$$\mathcal{L}_{ex} = K_4 \frac{R^4}{r^4} + K_5 r^2 \quad (28)$$

With $K_4 = K_1 * K_3$. Experimental evidence shows that the volume per unit length of the two splits is equal to that of the root trunk⁵:

$$V_{root} = V_{b1} + V_{b2} \quad (29)$$

i.e., that (Figure 10):

$$R_{root}^2 = R_{b1}^2 + R_{b2}^2 \quad (30)$$

And in a symmetric bifurcation:

$$\frac{R_{b1}}{R_{root}} = \frac{1}{\sqrt{2}} \quad (31)$$

The radius R of the twig or epithelial system is obviously much larger than the radius r of the xylems or of the capillaries, and thus the constant K_5 must also contain the number N of the vessels participating to the feeding of R , a constant not affected by the differentiation. Minimizing the Lagrangian leads to:

$$\delta = \frac{r_1}{r_0} = 2^{-2/3} = 0.63 \quad (32)$$

Since the correlation between θ and δ is derived on the basis of the minimization of virtual work, Murray’s formula still applies, and for a symmetric bifurcation we obtain:

$$\theta = \arccos\left(\frac{1}{2\delta^2}\right) = \arccos\left(2^{-1/3}\right) = 37.5^\circ \quad (33)$$

i.e., a value almost equal to that prescribed for a symmetric bifurcation before introducing the cubic correlation between the vessel radius and the mass flowrate (Eq. 19). Notice that in this type of model it is necessary to take into account the permeability of the vessel walls: a more detailed description is provided in [32].

7 - Conclusions

In spite of its being overcelebrated -especially in biosciences- the Hess-Murray law does not display a satisfactory agreement with experimental results. Furthermore, most of the assumptions on which the $n=3$ exponent has been derived are far from being realized in nature. Nevertheless, its fruitful legacy is the concept that the *creation and maintenance of a bifurcation serves an evolutionary criterion of minimal energy cost*. The idea underlying the study discussed in this paper is that it is not the allometry itself, but the “cost/benefit” evaluation that is worthy of further analysis. In fact, a different model based on a different form of the Lagrangian “cost function” leads to a different “optimum” (or to no optimum altogether).

This suggests to extend the horizon of the investigation: in line of principle, it would be very satisfactory if the “construction” of a bifurcation could be derived by a single principle of minimization of the amount of resources needed to create and maintain the branched structure so that it serves the scope for which it was generated. The mass- and energy balances of a living system (be it a plant or an animal) depend on the amount of resources the system can avail itself of, and these “costs” include “nutrients”, thermal and chemical flows, water and solar radiation. It is likely that the benefits could be expressed in terms of “more effective access to resources” or “higher productivity”, and in such a perspective the most convenient quantification of both resource cost and evolutionary benefit is the equivalent amount of primary exergy resources consumed for each given “task”. The resulting models become somewhat more involved and are left for a future study.

8 - References

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⁴ The nutrients required by the maintenance and growth of the “surrounding tissue” diffuse through the selectively permeable blood vessel walls. In plants, leaf tubules display a sufficiently high permeability to distribute sap through the leaf body.

⁵ This is called the “Da Vinci rule”, because it was apparently stated for the first time in one of Leonardo’s notebooks.

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