

Exergy cost analysis of bifurcated circular vessels with permeable walls: beyond the Hess-Murray law

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Abstract

Since bi- and trifurcated structures are ubiquitous in nature (from trees to rivers to bronchial alveoli to veins and arteries etc.), the idea that their striking topological similarity originates from a physical principle is appealing and stimulated a great number of theoretical and experimental investigations. The concepts of “nature’s economy” and of “goal-driven evolution” can be invoked to conjecture that there must be some “reward” for the effort placed by a biological system to build a bifurcated structure, in the sense that the evolutionary advantage gained by the system must more than compensate the additional resource consumption. The interest of engineers, botanists and biologists in this matter is justified by the expectation that linking the “shape” of these structures to their “function” would allow for better aimed interventions in the case of malfunctions (overflow of rivers and channels, tree roots rotting, poor soil exploitation, circulatory diseases...). Furthermore, provided the quite different boundary conditions are properly taken into account, such an insight may be translated into more accurate and efficient design guidelines of artificial (manufactured) branched structures like pipelines, heat exchangers, biological implants etc..

In the early XX century two physiologists, Walther R. Hess in 1903 and Cecil B. Murray in 1926, independently derived a general correlation between the successive radii of bi- and trifurcated vessels: since their derivation was based on a first-order “energy budget” of the operation of the bifurcated system, their result ($r_{i+1}/r_i=2^{-1/3}$) was seen as a confirmation of the evolutionary biology, then in its infancy. The Hess-Murray Law has undergone since a series of critical reviews both in biology and in engineering, and different researchers strived on the one side to reinforce its physical foundation and on the other side to justify the obvious disagreement of its predictions with experimental data.

In this paper, after a brief discussion of Hess’ and Murray’s original derivations, experimental evidence and physical considerations are used to argue that the “cubic root of 2” allometry cannot apply to the blood flow in arteries and veins. Its application to capillary flows must be corrected by introducing wall suction. On the same basis, it is argued that the law accurately represents the flow in sap-carrying vessels in leaves, but cannot be applied to tree branchings where the bifurcations are originated by a different sort of evolutionary trade-off.

It is then shown that an exergy cost analysis leads to a more credible quantification of the cost/benefit ratio of creating a bifurcation: an application to realistic models of permeable blood vessels indicate that a) the onset of a bi- or trifurcation always requires a larger use of resources w.r.t. the equivalent non-bifurcated configuration; b) the existence of an optimal radius ratio is not guaranteed; and c) the H-M optimal ratio can be seen as a limit value obtained by neglecting some of the relevant physical variables.

Keywords: Branched Fluid Structures; Hess-Murray law; Permeable wall vessels; Entropy Generation Minimization; Exergy cost

1- Introduction

1.1 - The problem

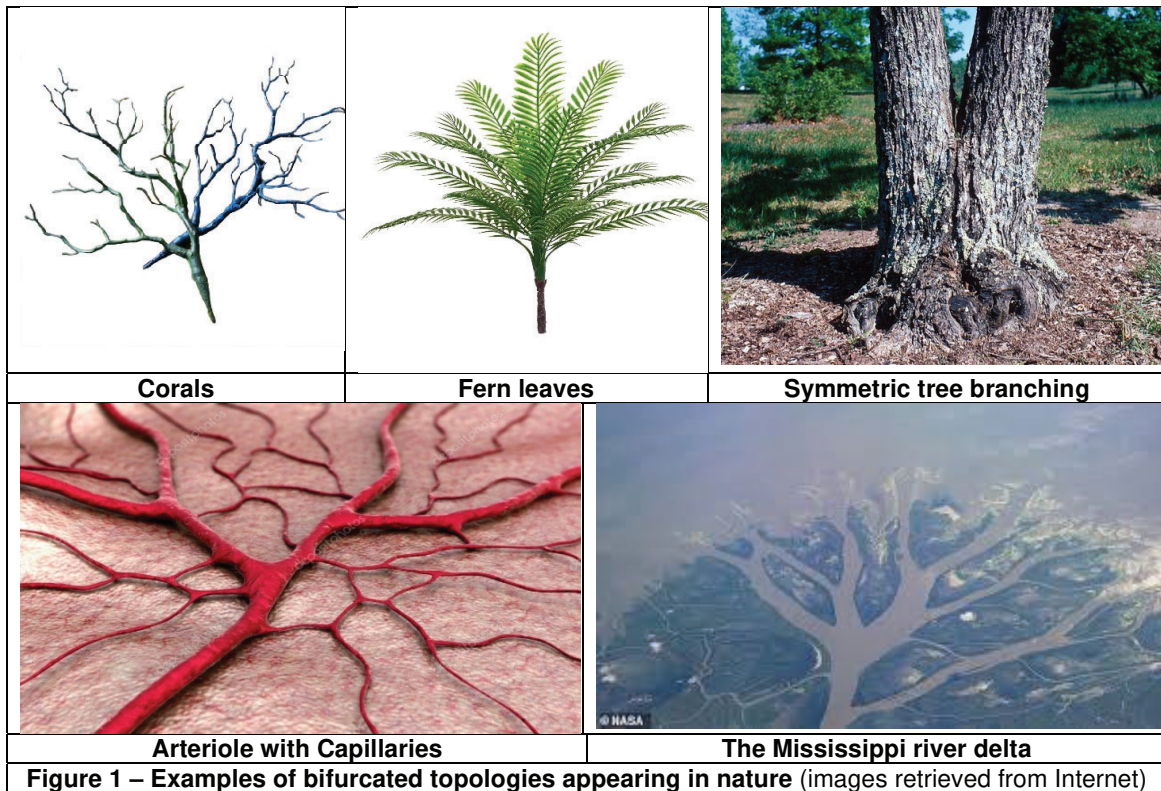
Bifurcated structures in fluid carrying channels and vessels are ubiquitous in nature: as shown in (Figure 1) the shape of tree roots and branches, leaf veins, circulatory systems in animals, air vessels in the respiratory systems, river deltas...display an amazing degree of geometric similarity, so pervasive to suggest the conjecture that their creation can be explained by some common evolutionary principle. Understanding the underlying physics might lead to a better comprehension of natural evolution and linking the “shape” of these structures to their “function” would allow for better aimed interventions in the case of malfunctions (overflow of rivers and channels, poor health of tree roots and tips, poor soil exploitation, circulatory diseases...). And a clearer insight on the physics of natural bifurcations may pave the way to the formulation of more accurate and efficient design guidelines of artificial (manufactured) branched structures (provided proper provision is made for the quite different boundary conditions).

It is therefore not surprising that a multitude of studies have been -and still are being- published on the topic. In fact, engineers, botanists and biologists have devoted substantial time and resources to search for a general model of bi-, tri- and polyfurcated fluid carrying vessels. From a careful consultation of the archival literature [9,18,24,27,28] it is though apparent that there remain questions to be answered:

- 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?
- 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?

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:

- 1) Although different types of branchings display an amazing degree of large-scale geometric similarity, the specific details (radius- and length ratio of daughter and parent branches, branching angle, complanarity) depend on the type of fluid being transported (newtonian or non-newtonian, pure substance or particle laden), on the material of the channel walls (lignine, muscle fibers, gravel, sand...), and on the flow features (creeping, laminar or turbulent);
- 2) Although a branched network resembles a fractal structure, there is no indication that the fractal exponent remains constant over successive branching levels. Thus, Fractal models are not considered here;
- 3) While in plants the flow can be accurately modeled as stationary, 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.



1.2 – The currently most popular physical model: the Hess-Murray law

In 1903 the Swiss physiologist Walter Rudolf Hess formulated a model of blood flow in arteries and capillaries that results 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 1903, with expanded versions published in 1914 and 1917 [7,8]. The same correlation was "rediscovered" by the American physiologist Cecil Dunmore Murray in 1926 using a slightly different approach, and later refined and extended in the same year in two other papers [12,13,14]. Since the numerical result, i.e., the allometric rule, is the same, the law came to be referred to as "the Hess-Murray law".

The method proposed by Hess and Murray is described in detail in several review papers [4,20,24,28], and what is of interest here is to underline the novelty of their approach: they assumed that blood or lymph circulation in living organisms is governed by a "work minimization" principle. Although the legacy of the H-M law is considered to be the derivation of an "optimal branching ratio" $\delta = \frac{d_{i+1}}{d_i} = \frac{1}{\sqrt[3]{2}} = 0.7937$ between the daughter-to-parent diameters of symmetrical branchings, the real merit resides in the "energy cost" methods they adopted. As we shall see, their conjecture is in fact only a first approximation of the energy balance of bifurcated systems, but due to the simplicity of their "cubic root of 2" correlation and of its apparent universality, the "H-M radius ratio" is widely employed in biology and even in engineering as a modelling criterion. What goes often unmentioned is that extensive experimental assessments performed in the second half of the 20th century indicate that while the correlation is sufficiently accurate for the smallest vessels (capillaries), it fails for the larger ones (large veins and arteries); moreover, it can be extended to turbulent flows only by changing the exponent of the root [27]. Recent comparisons with numerical investigations of branched flows led to similar conclusions

[2,11,15,16]. It is argued in section 4 here below that this depends on intrinsic limitations of the H-M law and on some hitherto little explored restrictions to its theoretical foundation.

3 – A Brief description of Hess’ and Murray’s original derivations

3.1 – Hess’ problem position and solution

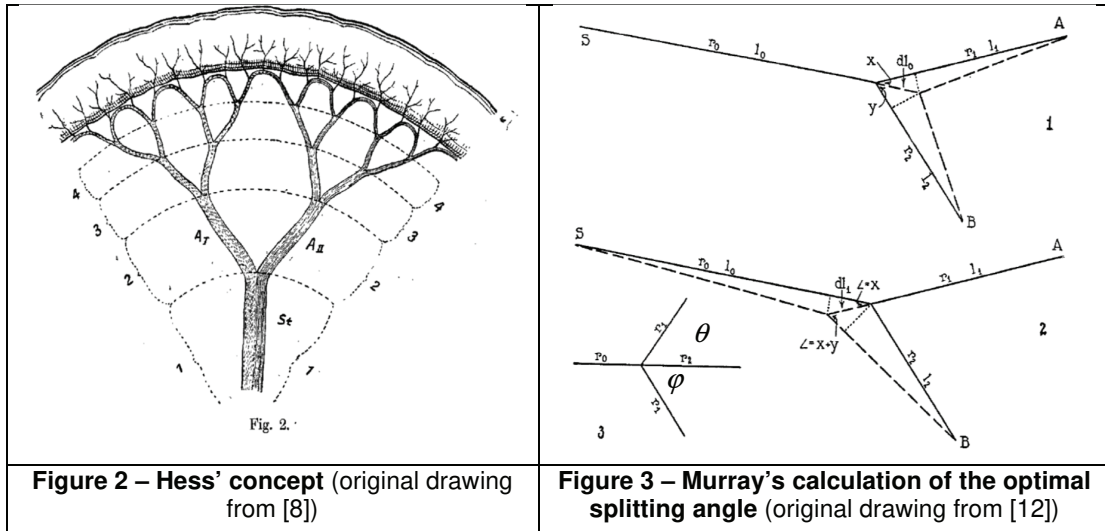
In 1903, in a preparatory paper for his M.D. thesis [7], the Swiss physiologist Walter Rudolf Hess proposed the existence of a physical “optimization criterion” that guides the branching of arterial vessels. This idea was also the topic of later work in his “Habilitation” thesis [8], but the 1903 work already contains a complete derivation of his “cubic root of 2” law. Hess’ interest was motivated by previous work by Roux [17] who postulated a “dynamic mechanical principle” to be the driver of vessel bifurcations in animal circulatory systems. To extract physical meaning from Roux’ experimental data, Hess suggested that nature would adopt a “minimum resource consumption” criterion to build the human circulatory system and proceeded to calculate how this task can be attained (*“Wie kann die Aufgabe des Blutes mit dem kleinsten Kraftverbrauch erledigt werden”* [7, p.5]). Hess’ idea is that 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 and the metabolic cost of the volume of the pumped blood. Since the former is inversely proportional to the fourth power of the radius and the latter to the square of the radius, an “optimal radius” exists and is proportional to the cubic root of the flowrate. Furthermore, if a vessel splits symmetrically and the mass flowrate in each of the branches is equal to the half of that in the mother vessel, imposing optimality on the daughter branches leads to the allometric law:

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

A detailed description of Hess’ derivation is provided in [20]: for the purpose of this paper, it suffices here to list the conditions under which the derivation is valid:

- a) The flow in arteries, arterioles, veins and capillaries can be described by Poiseuille’s law for steady laminar flow in circular vessels with rigid walls;
- b) Blood is a Newtonian fluid with constant viscosity;
- c) Blood has a metabolic cost proportional to the pumping work performed by the heart (neglecting its thermal content);
- d) Since flowrate and pumping power are directly proportional, a larger radius would decrease the pressure drop (and the pumping power) but increase the flowrate. The two effects are opposite, and the problem can be reformulated as a Lagrangian minimization:

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



Which results in:

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

Where the constant κ depends on the fluid properties and on the metabolic rate.

- e) If a vessel bifurcates symmetrically (Figure 2), $m_1=m_2=m_0/2$, the optimality can be extended to the daughter branches:

$$r_0 = \kappa m_0^{1/3}; \quad r_1 = r_2 = \kappa \left(\frac{m_0}{2} \right)^{1/3} \quad (4)$$

Whence equation (1).

Throughout his papers Hess repeatedly states that his result depends on the assumption of validity of Poiseuille pressure drop formula and flow stationarity, and makes reference to selected contemporary literature to support his belief that *i*) a branching does not generate turbulence and *ii*) the low-frequency pulsations do not affect the flow in such a way as to invalidate Eq. (1).

3.2 – Murray's problem position and solution

Murray was aware of Hess' work, and makes his goal explicit in the first lines of his 1926 paper [12]: "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 maintained that his calculation of the blood cost was more accurate than Hess' and based on the latest experimental results. He also derived the "optimal angles" for a symmetric bifurcation using the principle of the minimum virtual work. Again, a detailed description of the mathematical steps is provided in [20]. Proceeding along the same path previously proposed by Hess, Murray obtained an expression for the power required to pump a given mass flowrate of blood in a straight vessel with rigid walls, $P_{pump} = K_1 \frac{m^2}{r^4}$, where K_1 is the same constant as in Hess' formulation. He then proceeded to calculate the metabolic cost of the pumped blood:

$$C_{blood} = bL\pi r^2 = K_3 r^2 \quad (5)$$

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 as per Murray’s estimates. 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:

$$\mathcal{L}_{Murray} = K_1 \frac{m^2}{r^4} + K_3 r^2 \quad (6)$$

Which results in:

$$r_{opt} = \left(\frac{2K_1}{K_3}\right)^{1/6} m^{1/3} = \xi m^{1/3} \quad (7)$$

Where the constant ξ depends on the fluid properties and on the power absorbed by the heart. If a vessel bifurcates symmetrically (Figure 2), 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 [13], Murray calculates the optimal branching angle by applying again the principle of minimum work: as shown in Figure 3, among the possible path lengths the one that minimizes the total work displays branching angles given by:

$$\cos\theta = \frac{r_0^4+r_1^4-r_2^4}{2r_0^2r_1^2}; \quad \cos\varphi = \frac{r_0^4+r_2^4-r_1^4}{2r_0^2r_2^2} \quad (8)$$

That is:

$$\theta = \arccos\left[\frac{r_0^4+r_1^4-(r_0^3-r_1^3)^{4/3}}{2r_0^2r_1^2}\right]; \quad \varphi = \arccos\left[\frac{r_0^4+r_2^4-(r_0^3-r_2^3)^{4/3}}{2r_0^2r_2^2}\right] \quad (9)$$

Introducing the optimal radius ratio δ (Eq. 1):

$$\theta = \varphi = \arccos\left[\frac{1+\delta^4-(1-\delta^3)^{4/3}}{2r_0^2\delta^2}\right] \sim 37.5^\circ \quad (10)$$

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 4, 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:

$$\psi = \arccos\left[\frac{r_0^2-(r_0^3-2r_1^3)^{2/3}}{2\gamma^2r_0^2}\right] \quad (11)$$

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

Although not mentioned by Murray, Eq. (8) leads to an interesting corollary: if $r_1=r_2$, it reduces to

$$\cos\theta = \frac{1}{2\delta^2} \quad (12)$$

Which implies that larger daughter branches ought to form higher angles with the parent vessel. For future record, consider that Murray’s angle formulae (8) and (12) retain their validity if applied to branching ratios different from the “canonical value” ($\delta = 0.7937$; $\theta = 37^\circ$): for example, a $\delta = \frac{1}{\sqrt{2}} = 0.707$ that ensures constant fluid velocity in the parent and daughter branches corresponds (Figure 7) to an angle $\theta=0^\circ$, i.e., to no splitting, while the $\delta=0.5$ derived from a constant Reynolds assumption in parent and daughter branches leads to impossible solutions of Eq. (12): this does though not agree with empirical evidence.

4 – SOME REFLECTIONS ON THE PHYSICS OF FLUID-CARRYING VESSELS

As certified by an impressive experimental database [9,18,23,24,25,27,28,30], the “cubic root of 2” correlation is reasonably accurate in small capillaries and in the small sap-carrying channels of leaves, but it fails in predicting branching ratios in human arteries (typical diameters 0.005-0.025 m) and veins (0.006-0.03 m), as well in smaller vessels in case of turbulent flow [27]. The discrepancies have been traditionally explained by considering that the blood flow is pulsatile, that the vessel walls are non-rigid, that blood is a non-Newtonian fluid with shear thinning characteristics, and that the junctions inevitably generate turbulence in the flow. In fact, in his original paper Hess made a point in stressing that his model was derived by neglecting all of the above.

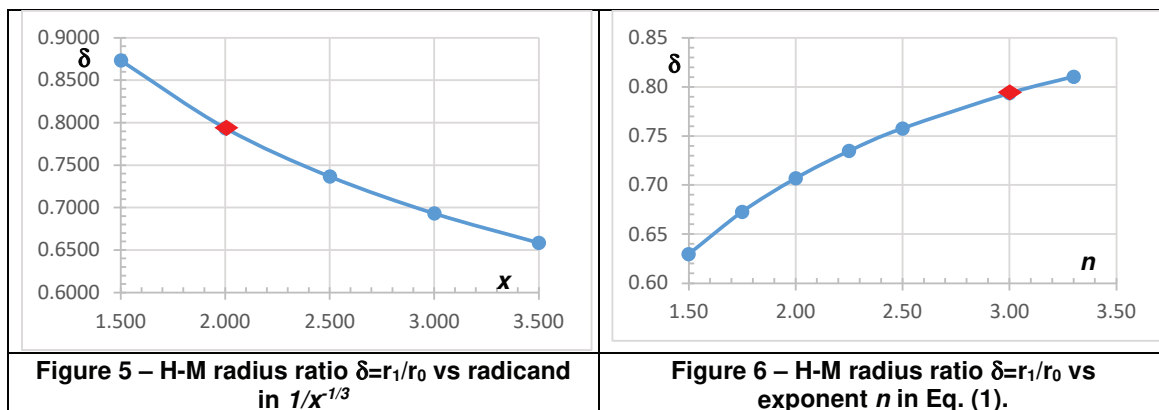
A possible explanation of the reason for the popularity of the H-M law in spite of its lack of generality may be found in its “robustness” with respect to both the radicand and the exponent of the root: as shown in Figures 5 and 6, changing the radicand from 1.5 to 3.5 results in a maximum difference of about 20% w.r.t. the H-M radius ratio, while changing the exponent $1/n$ of the root from 0.66 (=1/1.5) to 0.3 (=1/3.3) leads to a maximum derangement of about 17%. Translating these relative values into absolute measurement of the daughter branches, this means that the differences are of the order of fractions of a millimeter and can often be absorbed by the inevitable averaging over large series of *in vivo* measurements.

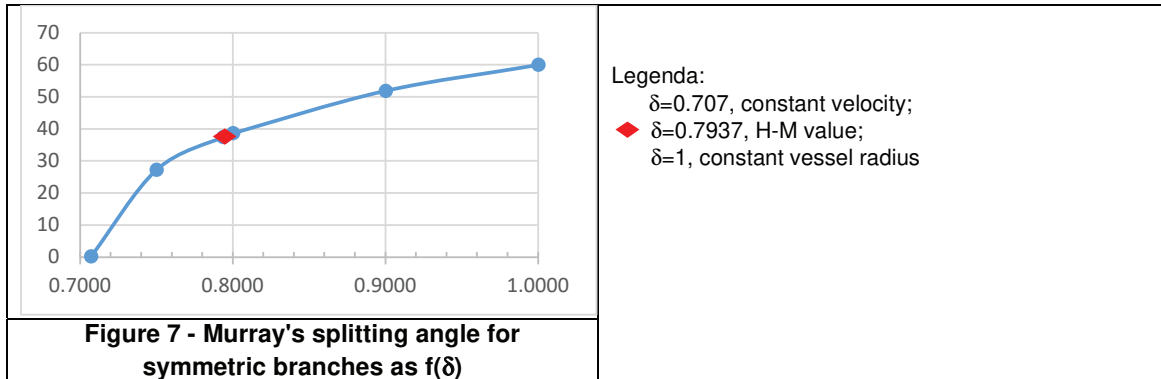
It is therefore legitimate to question the validity of the H-M model itself: is it missing some relevant variables? Or is its “universality” being overestimated? The remaining sections of this paper present a critical analysis of different physical instantiations.

5 – DIFFERENT TYPES OF BIFURCATED STRUCTURES IN NATURE

5.1 – River flows

The claim that the H-M law ought to apply to river flows appears at least as an arbitrary extrapolation of the principles on which the law is based. First, the flow in rivers is rarely laminar; second, it is an open channel flow rather than a genuinely internal flow; third, the flow characteristics are essentially determined by several factors not contemplated in the H-M derivation: hydraulic head, type of the river bed, structure of the banks, presence of obstacles on the water path; permeability of the terrain. In the absence of a physical model that includes all of the above effects, the similarity between a river delta and -for instance- tree roots is purely topological and the existence of an underlying common physical principle is not justifiable.





5.2 – Blood flow in arteries and veins

Experimental evidence demonstrates that we are dealing here with the unsteady turbulent flow of a non-newtonian fluid in vessels of variable diameter and with non-rigid walls. Again, the H-M model does not account for any of these characteristics. It is therefore legitimate to conclude that the apparent success of “semi-empirical exponent adjustment” of the H-M law is to be ascribed to its arithmetical “robustness” mentioned in section 4.

5.3 – Blood flow in arterioles, venules and capillaries

In these smaller vessels, the flow is with good approximation laminar, and the unsteadiness is strongly damped by the upstream circuit capacity (Figure 8). The H-M law ought to apply here, with a small modification to take into account the effects of permeable walls described in section 6 below.

5.4 – Sap flow in leaves capillary tubules

This is perhaps the most suitable instantiation of H-M flow: laminar, steady, very small flowrates and Reynolds numbers. As for the capillaries, a correction to the H-M model to account for the (significant) amount of wall permeability is in order: the treatment being the same as for blood capillaries, both the model and the results are shown in section 6.

5.5 – Tree branchings, including roots

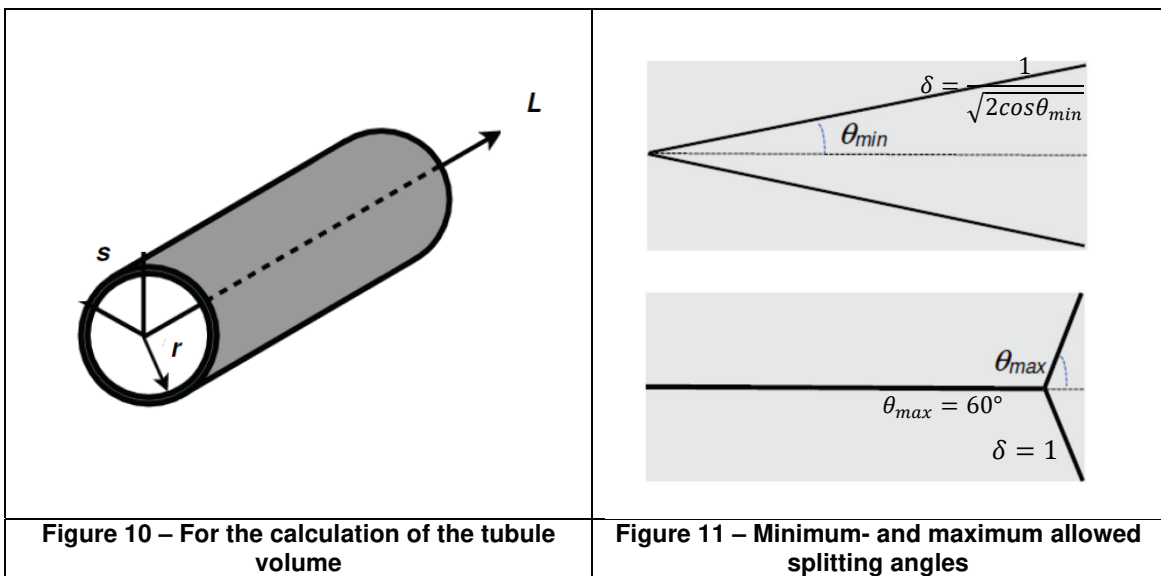
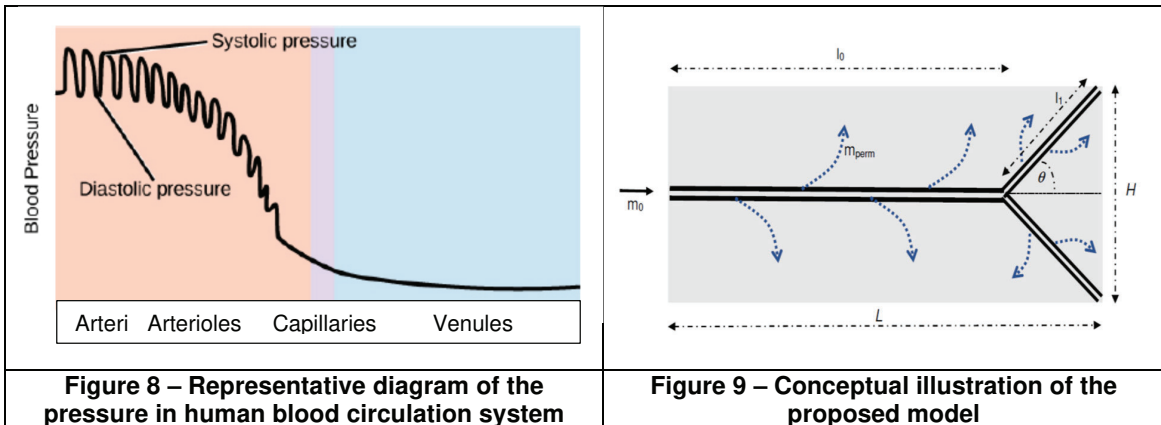
The attempt to apply the H-M law to these systems is based on wrong premises. To begin with, there is no “fluid branch splitting” here, because the carrying vessels (xylems and phloems) do not bifurcate. The splitting of the woody structure seems to obey some sort of reproducible rule, probably linked to the advantage the plant obtains from a larger crown, that depends in turn on the number of branchings, since the final twigs carry the most leaves. A possible non H-M model is described in [21].

6 – A MODEL BASED ON THE EXERGY COST OF A BIFURCATION

6.1 – Theoretical justification

As stated in the Introduction, the major merit of the Hess-Murray approach is the idea of the existence of an “energy cost” principle that guides the creation of a branching: in essence, a vessel bifurcates in such a way that the energy budget of the main- and of the daughter branches is “optimal”. There are two energy cost items in the H-M budget: the energy rate required to overcome friction (pumping power) and that needed to “create” the blood (its metabolic cost). This is a very reasonable physical principle and in fact leads to accurate predictions for the class of flows it has been originally derived for.

It is likely that in capillary flows the permeability of the walls has some influence on the shape of the structure, and in this section we shall examine a model that accounts for these effects. Before doing that though, it is important to consider that when we deal with problems in which different forms of energy are involved (in this case, material energy and pumping work) the proper thermodynamic quantifier is exergy. The model discussed in the next sections is in fact based on a comparison of the exergy cost [26] of a bifurcated structure w.r.t. to its non-bifurcated counterpart. The results presented here apply to capillary blood flow and sap flow in leaf tubules and -most likely with lesser accuracy- to blood flow in arterioles and venules.



Consider a straight portion of vessel of length L and uniform radius r_0 : it will “feed” a domain $H \times L$ as shown in Figure 9. Under steady state conditions, the amount of fluid mass permeated through the wall is proportional to the vessel external surface:

$$m_{perm} = 2\pi r_0 L \xi \quad (13)$$

where ξ [kg/(m²s)] is the wall permeability coefficient.

This mass flowrate must be equal to the difference between the inlet and outlet mass flowrates: for ease of calculation, let us assume that the length L is a “terminal” portion and the outlet flowrate is zero:

$$m_{metab} = \gamma H L s \quad (14)$$

where γ [kg/(m³s)] is the local metabolic rate and s is the thickness of the surrounding tissue, assumed constant over the domain $H \times L$.

The inlet mass will be thus equal to:

$$m_0 = m_{metab} = \gamma H L s \quad (15)$$

There are three terms in the exergetic cost of the structure: the first is equal to the pumping power required to propel the fluid through the length L :

$$\dot{E}_p = \frac{f m_0^3 L}{4\pi^2 \rho^2 r_0^5} \quad (16)$$

where f is the friction factor (in the following calculations the value $f=64/Re$ has been assumed throughout). The second cost is the amount of exergy required of the main system (the body, the tree...) to generate the blood or the sap:

$$\dot{E}_f = e_{fluid} m_0 \quad (17)$$

where e_{fluid} [J/kg] is the specific exergy of the blood or sap. The third cost term is the exergy embodied into the walls of the vessel (Figure 10):

$$\dot{E}_{mat} = \frac{e_{fluid} \phi \pi L r_0^2 (\sigma^2 + 2)}{\tau} \quad (18)$$

where τ [s] is the assumed operational life of the vessel, ϕ is a coefficient that accounts for the ratio of the “vessel construction time” to τ and $\sigma = s_0/r_0$ is the ratio of the wall thickness to the radius. Thus the total exergy cost (in W) of the “linear vessel segment” of length L is:

$$\dot{E}_L = \frac{f m_0^3 L}{4\pi^2 \rho^2 r_0^5} + e_{fluid} m_0 + \frac{e_{fluid} \phi \pi L r_0^2 (\sigma^2 + 2)}{\tau} \quad (19)$$

For a symmetrically branched structure the above calculations can be repeated separately for the unsplit length l_0 and for the two branches l_1 . The result is:

$$\dot{E}_{BIF} = \frac{f m_0^3 L}{4\pi^2 \rho^2 r_0^5} \left(\lambda_0 + \frac{\lambda_1^4 \cos^3(\theta)}{4\delta^5} \right) + e_{fluid} m_0 + \frac{e_{fluid} \phi \pi L r_0^2 (\sigma^2 + 2)}{\tau} (\lambda_0 + 2\lambda_1 \delta^2) \quad (20)$$

where $\lambda_0 = l_0/L = 1 - a/(2\tan\theta)$; $\lambda_1 = l_1/L = a/(2\sin\theta)$, $\delta = r_1/r_0$ and $a = H/L$ is the domain aspect ratio.

The difference $\dot{E}_L - \dot{E}_{BIF}$ represents the additional resource cost the main system incurs into when developing a bifurcation in the domain $H \times L$. It is convenient to use Eq. (12) to eliminate the radius ratio δ and obtain an expression in the angle θ :

$$\Delta \dot{E}_{BIF} = \dot{E}_L - \dot{E}_{BIF} = K_P \left(\frac{a^3 \cos^{1.5}(\theta)}{2^{0.5} \tan^4(\theta)} - \frac{1}{\tan(\theta)} \right) + K_M \left(\frac{1}{\sin(\theta) \cos(\theta)} - \frac{1}{\tan(\theta)} \right) \quad (21)$$

With

$$K_P = \frac{a f m_0^3 L}{8\pi^2 \rho^2 r_0^5}; \quad K_M = \frac{a e_{fluid} \phi \pi L r_0^2 (\sigma^2 + 2)}{2\tau} \quad (22)$$

Plots of $\Delta \dot{E}_{BIF}$ as a function of θ for different aspect ratios are shown in Figures 12 and 13: only the graphs for $a=0.25$ and $a=1$ are shown, since the general shape remains similar for the intermediate aspect ratios. As expected, the results are somewhat different for blood and sap:

I. Blood flow

- a) The $\Delta \dot{E}_{BIF}$ is always positive, i.e., the construction of a bifurcation always leads to a reduction of the exergy cost born by the system;
- b) The cost reduction is of the order of few percentage points for each single bifurcation (see Table 2), with the absolute exergy savings in the range 10^{-7} W/bifurcation: it is clear that the

savings at system level make sense only if the number of branchings is sufficiently high (an estimate of the number of bifurcations in the human blood circulation system is of the order of billions [25]);

- c) The aspect ratio of the domain has a direct influence on the resource savings because it sets a limit to the possible splitting lengths: $\theta_{min} = \arctan(\frac{a}{2})$ and $\theta_{max} = \arccos(0.5)$ as shown in Figure 11;
- d) The curve of the saved resource is rather flat and it shows an optimal value (i.e., maximum resource savings) towards the lowest allowed splitting angles;
- e) The optimal radius ratio δ lies between 0.715 (narrowest domain, $a=0.25$) and 0.759 (square domain, $a=1$): it is interesting that not only these values are consistently lower than the Hess-Murray 0.7937 value, but also that they do not reproduce either the constant Re value (0.5) or the constant velocity (0.707);
- f) The value of the ratio K_P/K_M has an important influence on the numerical results (i.e., on the percentage savings), but since all physical quantities in both K_P and K_M are rather rigidly determined for blood and sap (Table 1), this value has a reasonably small variability.

II. Sap flow

- a) The $\Delta\dot{E}_{BIF}$ is three orders of magnitude higher than in blood capillaries, with the average value being about $10^{-2}W$;
- b) Here, too, the aspect ratio plays a significant role in determining the range of θ ;
- c) The curve of the saved exergy resource is clearly skewed towards the lowest allowed splitting angles;
- d) The value of the ratio K_P/K_M has an important influence on the numerical results, but it is rather rigidly determined for the known physical properties of sap and has a small variability.

The above results are somewhat less “deterministic” as those of previously published allometric models [3,4,18,24,28], and lead to an interesting interpretation:

- i- The advantage of a single bifurcation is very small, and it becomes relevant at system level only if a sufficiently high number of branchings exist;
- ii- While every angle between θ_{min} and θ_{max} leads to exergy savings that differ by few percent points- Blood and sap display different savings for different splitting angles, but the optimal values in both cases are skewed towards the lowest allowable angles (daughter branch length ℓ_1 as long as possible);
- iii- For each aspect ratio, the radius ratio δ has a lower limit set by the domain shape and grows with the splitting angle to an upper limit $\delta=1$ (established by experimental evidence) that corresponds to $\theta_{max}=60^\circ$;
- iv- Within θ_{min} and θ_{max} thus, solutions are in practice almost equivalent (see Table 2), and different values of the radius ratio are acceptable, possibly influenced by the external boundary condition. For comparison with previous works [1,3,4,19,24,28,29], the H-M solution $\delta = \frac{1}{\sqrt[3]{2}}$ with $\theta_{max}=35.5^\circ$ is also shown on the graphs;
- v- There is no general allometric rule that governs the branching in ALL blood and sap carrying vessels! The solutions displayed here apply only to capillaries and small leaf tubules. The balance of larger vessels (arteries, veins, large sap tubes) is much more complicated, due to several other relevant variables that enter the game.

Parameter	Value	Parameter	Value
a=H/L, aspect ratio	model parameter	$\delta=r_1/r_0$, radius ratio	calculated
b, kcal/m ³ , Murray's "blood cost"	0.39	γ , kg/(m ³ s), metabolic rate	calculated
e, kJ/kg, specific exergy	e _b =1.7; e _s =25.	θ , rad, splitting angle	model parameter
\dot{E} , kW, exergy rate	calculated	χ , rad, generic angle	n.a.
f, Moody friction factor	64/(Reynolds #)	$\lambda_j=\lambda_j/L$, length ratio	model parameter
H, m, domain width	model parameter	μ , kg/(ms), dynamic viscosity	$\mu_b=0.08$; $\mu_s=0.08$
ℓ_0 , m, 1 st splitting length	model parameter	ν , m ² /s, kinematic viscosity*10 ⁵	$\nu_b=8.05$; $\nu_s=8$
ℓ_1 , m, 2 nd splitting length	model parameter	φ , s, time	$\varphi_b=0.015$; $\varphi_s=0.02$
L, m, domain length	L _b =0.01; L _s =0.01	ψ , rad, generic angle	n.a.
m, kg/s, mass flowrate	calculated	ρ , kg/m ³ , density	$\rho_b=105$; $\rho_s=994$
n, Hess-Murray exponent	model parameter	$\sigma=s/r$, wall thickness ratio	$\sigma_b=0.125$; $\sigma_s=0.125$
r ₀ , m, parent radius ⁶	r _{0b} =8*10 ⁻⁶ ; r _{0s} =0.001	τ , s, lifetime*10 ⁻⁷	$\tau_b=250$; $\tau_s=3$
r ₁ , m, daughter radius	= $\delta*r_0$	ξ , kg/(m ² s), wall permeability	calculated
s, m, tissue thickness	s _b =0.005; s _s =0.0005	ζ , numerical coefficient	n.a.
v, m/s, fluid velocity	v _b =3*10 ⁻⁴ ; v _s =1*10 ⁻⁴		

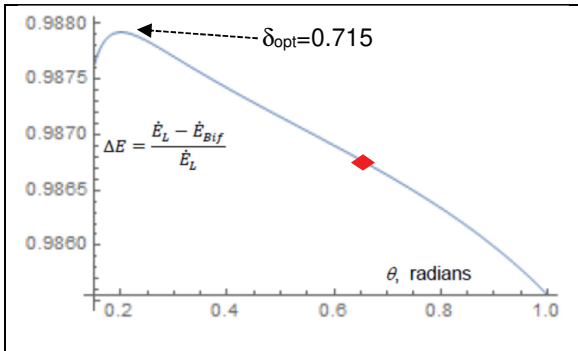


Figure 11a – Blood capillary, a=0.25: ratio of Exergy rate gain to unsplit geometry, $\Delta\dot{E}_{BIF}/\dot{E}_L$

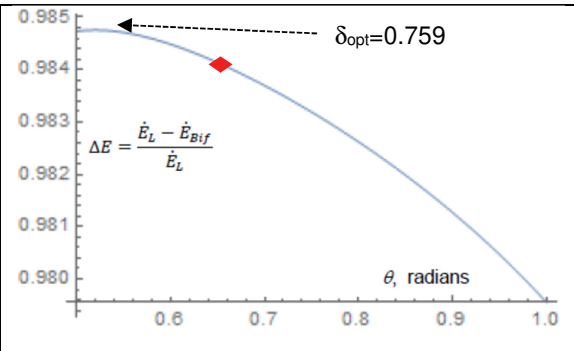


Figure 11b – Blood capillary, a=1: ratio of Exergy rate gain to unsplit geometry, $\Delta\dot{E}_{BIF}/\dot{E}_L$

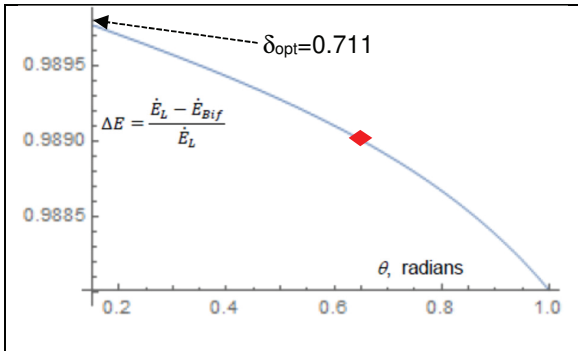


Figure 12a – Sap tubule, a=0.25: ratio of Exergy rate gain to unsplit geometry, $\Delta\dot{E}_{BIF}/\dot{E}_L$

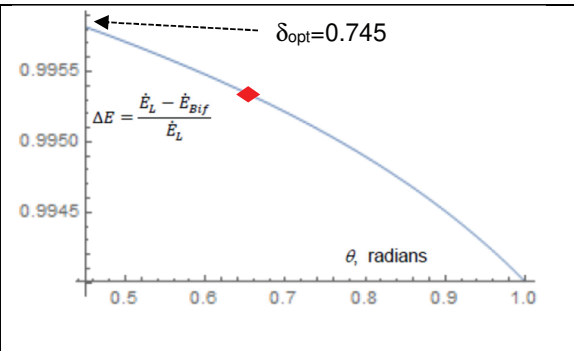


Figure 12b – Sap tubule, a=1: ratio of Exergy rate gain to unsplit geometry, $\Delta\dot{E}_{BIF}/\dot{E}_L$

Legenda: ◆ $\delta=0.7937$, H-M value

Aspect ratio a=H/L	Blood capillary			Sap tubule		
	$\Delta\dot{E}_{BIF}/\dot{E}_L$ max	δ_{opt} , Eq. (12)	θ_{opt}	$\Delta\dot{E}_{BIF}/\dot{E}_L$ max	δ_{opt} , Eq. (12)	θ_{opt}

0.25	1.2%	0.715	0.22 rad, 12.60°	1.04%	0.711	0.15 rad, 8.59°
0.5	1.28%	0.730	0.35 rad, 20.05°	0.36%	0.718	0.25 rad, 14.32°
0.75	1.4%	0.745	0.45 rad, 25.78°	0.36%	0.730	0.35 rad, 20.05°
1.	1.52%	0.759	0.52 rad, 29.79°	0.44%	0.745	0.45 rad, 25.78°

7 - CONCLUSIONS

The paper presents a new model to predict the splitting angle and the radius ratio of a single, symmetric bifurcation in small blood vessels and sap tubules. The model consists in the calculation of the exergy cost difference between an unsplit vessel of length L in a domain HxL and the bifurcated configurations in the same domain. The balance is obtained by imposing that the fluid mass flowrate at the inlet is completely permeated to feed the surrounding tissue with the metabolically necessary nutrients. Three “cost terms” are identified: the pumping exergy rate, the exergy rate of the transported fluid and the exergy rate equivalent to the amount embodied in the construction of the vessel structure. The concept is clearly borrowed from the 20th century seminal works of Hess and Murray, but the use of exergy instead of energy and the inclusion of the permeation lead to substantially different results. In conclusion, it can be said that the creation of a bifurcation is -under the boundary conditions specified here- always convenient for the system, in the sense that a bifurcated structure reduces the overall exergy consumption. Furthermore, the resource savings depend on the aspect ratio of the domain, i.e., on the extension of the surrounding tissue the vessels deliver nutrients to. Finally, the concept of “optimal splitting radius ratio” does not apply, because there is a rather wide range of legitimate splitting angles all of which are “convenient” for the system and each one of which corresponds to a different radius ratio. The H-M value falls within the range of allowable angles, but is not optimal in any sense. The advantage for sap vessels is of 3 orders of magnitude higher than for blood capillaries, and this is compensated by a much larger number of capillary junctions w.r.t. those experimentally detectable on leaves and other sap carrying vessels. It must be stressed however that the model does not apply to xylems and phloems that do not bifurcate.

The analysis is performed under rather stringent specifications: laminar flow, rigid permeable walls with constant diameter and constant wall thickness, and an exact balance of the inlet mass flowrate with the permeated one. The inclusion of different levels would imply a major complication in the modelling effort.

8 - REFERENCES

- [1] J.A.Adam, 2011: *Blood Vessel Branching: Beyond the Standard Calculus Problem*, Math. Magazine, 84,196–207
- [2] A.A.Al-Shammari, E.A.Gaffney, S.Egginton, 2014: *Modelling capillary oxygen supply capacity in mixed muscles: capillary domains revisited*, J. Theor.Biology, 356, 47–61.
- [3] A.Bejan, 1997: *Constructal-theory network of conducting paths for cooling a heat generating volume*, Int. J. Heat Mass Transf., 40, 799–816.
- [4] A.Bejan, S.Lorente, 2011: *The constructal law and the evolution of design in nature*, Physics of Life Reviews, 8, n.3, 209-240
- [5] J.A.Borgert, L.M.Moura, 2013: *Exergetic analysis of glucose metabolism*, Int. J. Exergy, v.12, n.1, 31-53
- [6] E.M.Cherry, J.K.Eaton, 2013: *Shear thinning effects on blood flow in straight and curved tubes*, Phys. Fluids v.25, 073104
- [7] W.R.Hess, 1903: *Eine mechanisch bedingte Gesetzmäßigkeit im Bau des Blutgefäßsystems*, (A mechanical rule for the construction of the blood circulatory system), Arch. Entwicklungsmech. Org.,16, 632–641

- [8] W.R.Hess, 1914: *Das Prinzip des kleinsten Kraftverbrauches im Dienste hämodynamischer Forschung* [Habilitation], (The principle of minimum power applied to blood dynamics studies). Veit. Arch. Anat. Physiol., Leipzig, 1–62
- [9] W.Huang, R.T.Yen, M.Mclaurine, G.Bledsoe, 1985: *Morphometry of the human pulmonary vasculature*, J. Al. Physiology, 81, n.5, 2123–2133
- [10] N.Kunert, L.Schwendenmann, D.Hölscher, 2010: *Seasonal dynamics of tree sap flux and water use in nine species in Panamanian forest plantations*, Agricultural & Forest Meteorology 15, 411–419
- [11] M.Massoudi, T.X.Phuoc, 2008: *Pulsatile flow of blood using a modified second-grade fluid model*, Computers and Mathematics with Applications 56, 199–211
- [12] C.D.Murray, 1926a: *The physiological principle of minimum work applied to the angle of branching of arteries*, J. General Physiol., 20 July, 9, n.6, .835–841.
- [13] C.D.Murray, 1926b: *The physiological principle of minimum work – I: the vascular system and the cost of blood volume*, Proc. Nat. Acad. Sci., 12, 207–214.
- [14] C.D.Murray, 1926c: *The physiological principle of minimum work – II: oxygen exchange in capillaries*, Proc. Nat. Acad. Sci., 12, 299–304.
- [15] M.S.Olufsen, C.S.Peskin, W-Y.Kim, E.M.Pedersen, A.Nadim, J.Larsen, 2000: *Numerical Simulation and Experimental Validation of Blood Flow in Arteries with Structured-Tree Outflow Conditions*, Annals Biomedical Engineering, 28, 1281–1299
- [16] M.U.Qureshi, G.D.A.Vaughan, C.Sainsbury, M.Johnson, C.S.Peskin, M.S.Olufsen, N.A.Hill, 2014: *Numerical simulation of blood flow and pressure drop in the pulmonary arterial and venous circulation*, Biomech. Model Mechanobiol., n.13, 1137–1154.
- [17] W.Roux, 1878: *Über die Verzweigungen der Blutgefäße der Menschen: eine morphologische Studie*, (On the branching of blood vessels in humans: a morphological study), Doctoral thesis, Jena; 1878. in W.Roux *Gesammelte Abhandlungen über Entwicklungsmechanik der Organismen*. V.1, I-XII, 1-76. Wilhelm Engelmann Verlag Leipzig, 1895
- [18] A.G.Roy, M.J.Woldenberg, 1982: *A generalization of the optimal models of arterial branching*, Bull. Math. Biology, 44, n.3, 349–360.
- [19] E.Sciubba, 2011: *Entropy Generation Minimization as a Design Tool. Part 1: Analysis of Different Configurations of Branched and Non-branched Laminar Isothermal Flow Through a Circular Pipe*, IJoT 14, 1, 11-20
- [20] E.Sciubba, 2016: *A Critical Reassessment of the Hess–Murray Law*, Entropy, 13, 283-300
- [21] E.Sciubba, 2023: *A model for bifurcation formation in plants based on a comparative exergy cost analysis*, submitted to Plants, march 2023
- [22] E.Sciubba, F.Zullo, 2013: *Stable and periodic solutions of an exergy-based model of population dynamics*, Energy, 58, 202–209
- [23] R.S.Seymour, Q-H.Hu, E.P.Snelling, 2020: *Blood flow rate and wall shear stress in seven major cephalic arteries of humans*, J. Anat. 236,522--530
- [24] T.F.Sherman, 1981: *On Connecting Large Vessels to Small: The Meaning of Murray's Law*, J. General. Physiol., 78, 431-453
- [25] D.F.J. Tees, P.Sundd, D.J. Goetz, 2006: *A flow chamber for capillary networks: leukocyte adhesion in capillary-sized, ligand-coated micropipettes*, Chapter 10 in Principles of Cellular Engineering, 213-231, Acad. Press
- [26] C.Torres, A.Valero, 2021: *The Exergy Cost Theory Revisited*, Energies 14 (1594)
- [27] H.B.M.Uylings, 1977: *Optimization of diameters and bifurcation angles in lung and vascular tree structures*, Bull. Math. Bio, 39, 509–520.
- [28] G.B.West, J.H.Brown, 2005: *The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization*, J. Exp. Biology, 208, 1575–1592.
- [29] T.Young, 1809: *The Croonian Lecture: On the Functions of the Heart and Arteries*, Phil. Trans. R. Soc. London, 99, 1-31
- [30] M.Zamir, S.M.Wrigley, B.L.Langille, 1983: *Arterial bifurcations in the cardiovascular system of a rat*, J. General Phys., 81, 325–335