

## Advanced Track, Epoch 6

# Biological Evolution

*This Advanced Track provides a technical supplement to the introductory web site on cosmic evolution, produced by Eric Chaisson and based on courses taught mainly at Harvard University for the past few decades:*

[http://www.cfa.harvard.edu/~ejchaisson/cosmic\\_evolution/docs/splash.html](http://www.cfa.harvard.edu/~ejchaisson/cosmic_evolution/docs/splash.html)

*Currently, this Advanced Track is abbreviated while addressing mainly the concept of energy rate density—a numerical quantity proposed as a useful complexity metric for an underlying, unifying process that guides the origin, evolution, and destiny of all organized systems across the arrow of time, from big bang to humankind. In the summer of 2014, this supplement will grow dramatically, providing much more pertinent technical material at an advanced, quantitative level (suitable for colleague scientists and graduate students) well beyond that presented in the above-linked introductory web site (which is meant for non-scientists and beginning students).*

*A summary of this Advanced Track is here:*

[http://www.cfa.harvard.edu/~ejchaisson/advanced\\_track\\_sitesum.pdf](http://www.cfa.harvard.edu/~ejchaisson/advanced_track_sitesum.pdf)

*Further material related to the subject of cosmic evolution is available at:*

<http://www.cfa.harvard.edu/~ejchaisson>

*including a collection of recent research papers easily accessed and downloadable at:*

[http://www.cfa.harvard.edu/~ejchaisson/current\\_research.pdf](http://www.cfa.harvard.edu/~ejchaisson/current_research.pdf)

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## Cosmic Evolution

Biological evolution is an integral part of the grand scenario of cosmic evolution:

Cosmic evolution = physical evolution + **biological evolution** + cultural evolution.

During this sixth, biological epoch, the great number of diverse plants and animals known on planet Earth have intermediate values of energy rate density,  $\Phi_m = 10^{3-5}$  erg/s/g.

## Complexity Metric in Biology

Life depends critically upon energy usage; without a sustained flow of energy all life forms die. Organismal energetics are as fundamental as any process in biology, yet the bioscience community lacks a general consensus regarding the amount of complexity needed to specify life or a quantitative metric for the amount of energy needed to optimize life. The issue is exacerbated not only by the vast diversity of Nature's many varied, extant life forms, extending over nearly 20 orders of magnitude in mass from microbes to whales, but also by the inconsistent techniques, protocols, and units used in measuring energy-utilizing metabolisms.

Total genome size is often claimed as a possible measure of complexity among life forms (Szathmary and Maynard Smith, *Nature*, v374, p227, 1995), but most biologists no longer accept it since the latest data seem to rule it out. Generally, eukaryotes have larger coding genomes than prokaryotes, higher plants and invertebrates have larger genomes than protists, and vertebrates larger genomes than invertebrates. However, our human genes contain ~3G nucleotide base pairs, but the marbled lungfish has ~130G base pairs, and a rare Japanese flower (*Paris japonica*) a whopping ~149G base pairs, which is 50X that of our human genome—yet few researchers would claim that flowers or fish are more complex than the human species.

Genes per se aren't much better regarding complexity metrics among life forms, especially the

non-“junk” (ie, protein-coding) genes. Biologists greatly erred in their estimates of gene numbers before gene mapping techniques became widely available in the early 21<sup>st</sup> century; the human genome has now been mapped and found to have only ~22,000 genes, compared to roughly double that number for many clearly simpler species (eg, the water flea has ~31,000 genes, rice ~40,000, and an apple ~57,000!).

Likewise, the number of cell types in an organism has been suggested as an approximate indicator of its complexity (Kauffman, *Scientific American*, v265, p78, 1991), but this too suffers as a complexity metric. Compartmentalization and specialization were once thought to rise in proportion to the number of genes in an organism, from bacteria to humans, but now we know that our own gene number is remarkably small for our complex selves.

Variety of morphology and flexibility of behavior might provide other useful metrics of biological complexity (Bonner, *Evolution of Complexity*, Princeton U Pr, 1988), but these also seem untenable. Higher life forms display a rich spectrum of bodily structure and a wider diversity of actions. This implies that animals are more complex than plants, a proposition with which most researchers agree, but not one that provides a quantitative measure of complexity.

Physical sizes of organisms could conceivably estimate complexity (McMahon and Bonner, *On Size and Life*, WHFreeman, 1983). Cellular specialization is likely proportional to an organism's size, from microbes to whales, a conjecture that seems evident in the construction of all life forms. Yet it's unclear how this subjective impression can be made more objective.

It is indeed hard to quantify any of life's attributes and thus advance the discussion about complexity beyond the fluff of mere words, although most researchers do concur with the common-sense notion that complexity (with some exceptions) does rise along most biological lineages (McShea, v50, p477, *Evolution*, 1996; Carroll, v409, p1102, *Nature*, 2001). Accordingly, this Advanced Track for the BIOLOGICAL EPOCH will continue exploring the usefulness of energy rate density as a complexity metric—much as  $\Phi_m$  seems significant in characterizing physical systems that precede biology, as well as cultural systems that follow it along the arrow of time.

In terms both general (for there are qualitative exceptions; see Gould, *Full House*, Harmony, 1996) and specific to those used elsewhere in these Advanced Tracks (for we do want to push the envelope regarding

quantification of complexity), the more advanced a species, the greater the complexity of that species. Increased specialization surely allows an organism to process more energy (or information), and just as surely the adoption of multiple strategies to use it effectively likely promotes survival, factors that aid biological evolution's production of complex organisms.

To note just one prominent example regarding the case of animal respiration, the buildup of  $O_2$  in Earth's relatively early atmosphere permitted mitochondrial (eukaryotic) life to extract through respiration nearly 20X more energy from the sugars it uses as food (oxidation of a glucose molecule to  $CO_2$  and  $H_2O$  yields 36 ATP molecules) than did prokaryotic life via fermentation in the absence of  $O_2$  (which yields a mere 2 ATP molecules)—clearly an important step toward enhanced energy flow, increased  $\Phi_m$  values, and greater overall complexity.

**Energy Rate Density:** This Advanced Track for the BIOLOGICAL EPOCH treats energy flows in living systems in much the same way as for galaxies and stars in earlier Advanced Tracks of this web site—as open, non-equilibrium thermodynamic systems. My working hypothesis of energy rate density,  $\Phi_m$ , as a reasonable and consistent complexity metric is hereby extended to more organized systems that photosynthesize and respire among a large sample of plants and animals. The penultimate section also discusses specific metabolic rates for brains as well. The results show promise, not only revealing a correlation among complexity, evolution, and  $\Phi_m$  for major taxonomic groups, but also numerical values for the last of these falling appropriately between evolutionary systems that are physically simpler and of older origin and those that are culturally younger and more complex.

That the general trend of living systems increasing their  $\Phi_m$  values over generations is imperfect should not deter us, for no useful investigation can proceed if it must first scotch every ambiguity or explain every outlier. In the discussion, computations, and graphical presentation below, our earlier estimates of  $\Phi_m$  for living systems (cf, toward the end of Advanced Track for PARTICLE EPOCH) are refined and extended empirically, thereby connecting our previous views of thermodynamic physics with those of contemporary biology.

### Multicells

With the emergence ~1 Gya of multicellular organisms as a new type of structure—whether for

plants, animals, or microbes—a novel degree of complexity had evolved. Levels of organization higher than that would require interactions beyond individual life forms, indeed ample evidence exists that symbiosis occurred on our planet, and is perhaps continuing (Margulis, *Origin of Eukaryotic Cells*, Yale U Pr, 1970). Communities of living systems along with their immediate environments, or ecosystems, in turn coexisted and coevolved, once again aided and abetted by robust flows of energy and, as noted below, somewhat larger values of  $\Phi_m$ . Diverse species within such newly emerged ecosystems carved out their own niches, and different components of the ecosystem became increasingly coupled as competition, cooperation, and reproduction among populations played active roles in evolving communities (Lotka, *Elements of Mathematical Biology*, Dover, 1956). In some cases, energy optimization and efficient material cycles have become well established, as is the case today, for example, in the Amazon basin where as much as 75% of the  $H_2O$  is recycled.

The importance of the input and output of matter and energy in Earth's food networks has long been recognized as a vital step in the organization of any ecosystem (Odum, *Systems Ecology*, Wiley, 1983). The net effect of increasing biodiversity—yet another relation to the complexity of life forms en masse—within mature ecosystems is well documented (Wilson, *Diversity of Life*, Harvard U Pr, 1992). As with chemical evolution that led to primitive life and biological evolution that fashioned some of the first living ecosystems (or even stellar evolution within systems of mature stars, interstellar clouds, and supernova remnants), communities of life forms (such as plants, plankton, and fish in a lake) exploit energy in two ways: Available energy in the area helps to establish the enhanced complexity initially, and once matured, further energy flows helped maintain the ecosystem as a dynamic steady-state in geological, climatological, and biological settings. Such a dynamically balanced ecosystem is a good example of emergent behavior that cannot be explained without treating the entire process of which it consists.

## Plants

The most widespread, and probably most important, biological process occurring on Earth today is plant photosynthesis, which produces glucose ( $C_6H_{12}O_6$ ) for system structure and adenosine triphosphate (ATP) that acquires, stores, and expresses solar energy throughout the floral world. This biochemical activity,

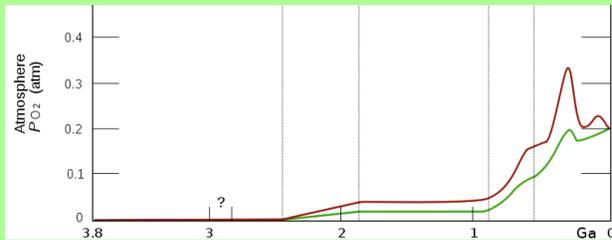
whose energy budget is well understood, provides a useful way to correlate the rise of complexity with biological evolution, especially since fossil records and molecular clocks provide robust data on plant origins well back in time.

By contrast (see next section below), animals' most prominent process is respiration, whereby oxygen ( $O_2$ ) converts consumed carbohydrates into the organics of tissue structure and synthesizes ATP in mitochondria, which can then release energy when needed for bodily activities. While it is often said that plants are producers and animals consumers, in fact both engage energy as an essential ingredient of life.

**Oxygen Buildup:** The roots of photosynthesis date back at least  $\sim 3$  Gy, when rocks of that age first trapped chemicals that facilitate this process in plants, algae, and some bacteria (but not archaea). The earliest practitioners likely used  $H_2S$  rather than  $H_2O$ , and some of them probably practiced chemosynthesis, a similar process that utilizes the chemical energy of inorganic compounds and is thus not dependent on the conversion of solar energy. Though still extant on Earth today, these primitive, non-oxygenic chemosynthesizers include some of the oldest known fossils.

Unicellular, aquatic, yet still prokaryotic cyanobacteria that do use  $H_2O$  appeared later, starting  $\sim 2.7$  Gya (late Archean, which formally ended 2.5 Gya), when traces of chlorophyll and oil biomarkers become evident in the geological record and when banded-iron formations (BIFs) are first seen in ancient sedimentary rocks as  $O_2$  began combining in Earth's oceans with dissolved Fe (having upwelled from the interior via hydrothermal vents and from erosion of surface layers) to precipitate minerals such as hematite ( $Fe_2O_3$ ) and magnetite ( $Fe_3O_4$ ) that drop to the seafloor; BIFs differ from the FeO-rich "red beds" that came later with the widespread appearance of rusty red rock strata beginning  $\sim 1.8$  Gya. Thereafter (probably when the seas became nearly saturated with it),  $O_2$  began accumulating in the atmosphere  $\sim 2.4$  Gya, heralding the so-called Great Oxidation Event, a gradual build-up of free  $O_2$  that was likely also aided by a decrease in atmospheric  $CH_4$ , which until then was a major (primordial) atmospheric gas.

The figure below is a graph of rising oxygen levels in Earth's atmosphere. A long and slow process, substantial amounts of  $O_2$  did not accumulate in the air until relatively recently.



*O<sub>2</sub> abundance in Earth's atmosphere has generally increased during the past few Gy. Although widely produced by early plants, O<sub>2</sub> was mostly absorbed by land and sea until ~2.4 Gya, and did not begin to seriously accumulate in the atmosphere until ~0.8 Gya. (The red and green curves represent upper and lower bounds of estimated O<sub>2</sub> concentration in units of % of total Earth atmospheric abundance, today's value being 21%; adapted from H. Holland)*

Early oxygenic, photosynthesizing plants were then, as now for blue-green algae (cyanobacteria), very simple organisms, having genomes of merely  $(1-9) \times 10^6$  nucleotide bases (*ie*,  $\sim 10^3 \times$  less than for humans). Even so, the enriched air eventually fostered the emergence of somewhat more complex life forms, most notably unicellular, eukaryotic protists; fossils imply that this momentous event likely occurred not more than  $\sim 1.7$  Gya by means of a mutually beneficial symbiotic relationship when an anaerobic prokaryote engulfed a respiring bacterium, thus initiating evolution of most, and perhaps all, eukaryotes (Margulis, *Symbiosis in Cell Evolution*, WH Freeman, 1983). In turn, yet only as recently as  $\sim 550$  Mya, one of those protists apparently experienced a second symbiosis (or "serial endosymbiosis") with a cyanobacterium. The result was a chloroplast—the specialized organelle comprising leaf cells rich in chlorophyll molecules where photosynthesis occurs in all plants—a key ancestral feature of all modern plants, which include such familiar organisms as trees, herbs, bushes, grasses, vines, ferns, and mosses.

**Plant Evolution:** Here is the briefest of summaries of plant biological evolution during post-Cambrian times (*cf*, Banks, *Evolution and Plants of the Past*, Wadsworth, 1970, with appropriate updates; Morton, *Eating the Sun*, HarperCollins, 2008). Modern plants likely evolved from protists, notably green algae, that have physical structures and metabolic functions closely resembling those of today's photosynthesizing organisms; calcified fossils of multicellular green algae, which were freshwater organisms yet were also capable of surviving on land, date back at least to the mid-Ordovician ( $\sim 470$  Mya), and possibly even earlier in

late-Cambrian times ( $\sim 500$  Mya); the oldest specimens found represent several genera and thus were already diversified. Mosses were among the first full-time inhabitants of the land, taking up residency early in the Paleozoic ( $\sim 450$  Mya). Vascular plants, having internal plumbing with leaves, stems, and roots akin to those of modern plants, originated during the late Silurian ( $\sim 420$  Mya, some fossils preserved) and by the mid-Devonian ( $\sim 380$  Mya, many fossil examples) had greatly multiplied and diversified while spreading into copious environments, thereby creating the first forests. Primitive seed plants emerged near the start of the Carboniferous ( $\sim 350$  Mya), though most such species perished during the Permian-Triassic mass extinction ( $\sim 250$  Mya). These earliest seed plants were the gymnosperms, whose "naked" seeds are not enclosed in protective structures and whose modern types include evergreen trees such as conifers and pinewoods. The angiosperms, by contrast, comprising the flowering plants with enclosed seeds as with most grasses and deciduous trees, were the last major group of plants to appear, evolving rather suddenly from among the gymnosperms during the early Cretaceous ( $\sim 125$  Mya) and then rapidly diversifying  $\sim 30$  My later. Although the gymnosperms dominated life for at least 250 My, angiosperms later crowded them out; today almost 90% of land plants are angiosperms, and a nearly continuous record of their fossils is preserved in rocks over the past 50 My.

These evolutionary steps did not likely happen because of dramatic environmental changes triggered by asteroids and the like. Rather, they probably occurred because of a variety of environmental stresses, including draught, salinity, and cold. Nor do we know if those changes were slow and gradual or fast and episodic; only new data can solve that.

**Photosynthesis Efficiency:** Living systems generally require larger values of  $\Phi_m$  than inanimate systems, not only to maintain their greater structural order (notably polymer cellulose for tissue and fiber) but also to fuel their complex functions of growth and reproduction. Plants, in particular and on average, need  $1.7 \times 10^{11}$  ergs for each gram of photosynthesizing biomass, and they get it directly from the Sun. Since from *SeaWiFS* satellite sensing, the global conversion of  $CO_2$  to biomass is  $\sim 2 \times 10^{17}$  g annually (*ie*, about twice 105 Gtons of C net primary production; Field *et al*, *Science*, v281, p237, 1998), Earth's entire biosphere uses energy at the rate of  $\sim 10^{21}$  erg/s (Lehninger, *Biochemistry*, Worth, 1975; Pessaraki, *Hdbk of Photosynthesis*, CRC,

2005). This is ~0.1% of the total solar power reaching Earth's surface (~90 PW), meaning that the electromagnetic energy of only ~1 in 1000 photons is converted into chemical energy of plants. Even at that low efficiency of energy conversion, photosynthesis represents the world's largest battery; it stores vast quantities of energy both in living plants as well as dead plants ("fossil fuels") as coal, oil, and gas. Expressed in units of the complexity metric preferred in these Advanced Tracks, given that the total mass of the terrestrial biosphere (*ie*, living component only, >99% of it in the form of uncultivated land biomass, and ~90% of that in forests) is  $\sim 1.2 \times 10^{18}$  g (or ~teraton, an average from many researchers, not including any potential "deep hot biosphere"; Potter, *BioScience*, v49, p769, 1999), the value of  $\Phi_m$  for the biogeochemical process of photosynthesis is, again globally averaged for the vast majority of Earth's plant life, ~900 erg/s/g. This is the value given in the table of preliminary calculations of  $\Phi_m$  toward the end of the Advanced Track for the PARTICLE EPOCH.

It is often said that photosynthesis is a highly efficient process that is not understood, whereas in reality it is a very inefficient process that is rather well understood. Photosynthesis is limited by a wide range of variables, including light intensity,  $CO_2$  abundance,  $H_2O$  availability, environmental T, and leaf morphology, all of which interact in complicated ways; the process also has optimal ranges for each of these variables, such as a minimum T below which and a maximum T above which photosynthesis will not operate (Galston, *Life Processes of Plants*, Sci. Amer. Lib., 1994). Photosynthesis is inherently inefficient for the complete metabolic process that converts sunlight into chemical energy stored in glucose molecules, *ie*, a ratio of output to input energies—not the higher rate (or effective absorptivity, which can reach as much as 65-90% depending on the species) of solar photons splitting  $H_2O$  and releasing  $e^-$ s. At the molecular level, the maximum quantum efficiency is ~28%. But only 45% of solar radiation is within the visible electromagnetic band (400-700 nm) where the light-harvesting pigment chlorophyll-a is active (trapping red and blue light, yet reflecting green), thereby reducing the actual molecular efficiency to only ~12%. (Another way of saying this is that 8  $\gamma$  are needed to fix 1  $CO_2$  molecule—*ie*, convert  $CO_2$  into organic compounds.) Furthermore,  $\sim 1/3$  of the absorbed energy is needed to power plant respiration, and  $\sim 1/5$  of sunlight is typically blocked by overlying canopy, leaving only ~6.5% as the

theoretical maximum efficiency of any plant (Zhu *et al*, *Current Opinion in Biotechnology*, v19, p153, 2008).

Operationally then, photosynthesis suffers high losses, converting into chemical energy only ~0.1% of the incoming solar energy falling onto a field of uncultivated plant life (Lehninger, *Biochemistry*, Worth, 1975); this very low efficiency is actually due more to limiting supplies of atmospheric  $CO_2$  than lack of energy (usually because leaves' pores, depending on weather conditions, only partially open and thus deprive some plants from adequate supplies of  $CO_2$ ). The value for  $\Phi_m$  (900 erg/s/g) computed two paragraphs prior, which is valid for the great majority of Earth's lower plant life, is sufficient to organize cellulose, the main carbohydrate polymer of plant tissue and fiber, for a field of wild plants, hence for the great bulk (>90%) of Earth's untended flora.

Any energy re-radiated as waste heat fundamentally causes an entropy rise in the surroundings, thereby adding to the natural thermal balance of Earth's atmosphere in accord with thermodynamics' 2<sup>nd</sup> law.

**Advanced Plants:** More organized fields of higher-order plants such as herbs and shrubs, and especially cultivated crops such as rice and wheat, can photosynthesize more than an order of magnitude more efficiently (1-2%) than the global average; their values of  $\Phi_m$  are typically in the range of 3000-18,000 erg/s/g. Abundant deciduous trees, with their larger absorbing leaves, capitalize on the short, hot summers by photosynthesizing fast, yet their leaves die young compared to evergreen trees that achieve slower, steadier growth year-round; averaged annually, net productivity and efficiency of the two types of trees are comparable, 0.5-1%, or 5000-10,000 erg/s/g.

Amongst the rarest of plants, the more advanced and complex  $C_4$ -type (that initially fix  $CO_2$  around the key enzyme RuBisCO (ribulose-1,5-bisphosphate carboxylase-oxygenase) to make 4-carbon sugars, such as for maize, sorghum, millet, amaranth and sugarcane, but also including some of the worst weeds such as crabgrass) have photosynthetic efficiencies ~twice (*ie*, 2-3.5%) that of the simpler, more widespread  $C_3$ -type plants (such as rice, wheat, barley, beans, potatoes, tomatoes, and sugar beets that have 3-carbon sugars). This is probably so because the  $C_4$  pathway—nonetheless practiced by ~7500 species of plants today, mostly grasses—uses less  $H_2O$  and  $CO_2$ , employs greater nutrient uptake, and displays longer growth cycles, although both use the Calvin-cycle to facilitate  $CO_2$  assimilation.

Empirical records imply that  $C_4$  plants evolved from their  $C_3$  ancestors only as recently as ~20 Mya (fossil dating) or ~30 Mya (molecular clock), in any case well after the K-T boundary and even long after the appearance of the first  $C_3$  grasses ~60 Mya. The  $C_4$  pathway likely arose as a competitive advantage either while coping with high-T draughts or reduced  $CO_2$  levels (atmospheric  $CO_2$  levels did decline rapidly from ~1000 to ~500 ppm between 25-30 Mya), or while adapting to open, tree-less environments, and maybe for a combination of all these reasons—yet did so independently on at least 45 separate occasions and therefore >45 separate lineages thereafter (Beerling, *The Emerald Planet*, Oxford U Pr, 2007). More recently, the  $C_4$  photosynthetic upgrade only rather recently caused grasses to transform the warm-climate subtropics, converting forests to grass-dominated savannahs between 3 and 8 Mya (Edwards, *et al*, *Science*, v328, p587, 2010). And even very much more recently, these grasses were additionally subjected to cultural evolution as our ancestors during the past 10 ky sought to breed crop production for agricultural purposes by making photosynthesis yet more efficient (alas, sometimes causing grocery-store tomatoes to look uniformly great but taste like tart cardboard). Some of these crop efficiencies will likely be bettered once again as ways of growing genetically modified crops become enhanced in today's technological society, such as current attempts to replace rice's inefficient  $C_3$  pathway with the  $C_4$  pathway found in maize and several other plant species able to produce a good deal more carbohydrates for a given energy/resource input—but this is mostly cultural, not biological evolution.

Cultivated plants do display higher values of  $\Phi_m$ , yet altogether produce <1% of the total yield of organic matter globally (Hall and Rao, *Photosynthesis*, Cambridge U Pr, 1999). The most highly cultivated  $C_4$  plants, such as maize and sugarcane that have been made more efficient (up to 3.5%) by advanced agricultural practices of recent times, probably cannot be fairly compared with fields of wild grasses and genetically unaltered trees and shrubs. Such well tended fields display higher energy rate densities, not only because the higher values of  $\Phi_m$  are consistent with increased metabolism of the more evolved tropical plants, but also because the enhanced organization of the field produced by modern agricultural techniques requires higher  $\Phi_m$  values to maintain that organization. Once again, this latter factor represents an energy contribution of a cultural, technological nature—corn and sugarcane, for example, have been made more

efficient by the agricultural practices of humankind—which is yet another phase of cosmic evolution discussed in the Advanced Track for the CULTURAL EPOCH.

Both corn and sugarcane have indeed been highly inbred by humans in recent times for agricultural purposes and probably cannot be realistically compared with fields of wild grasses or genetically unaltered trees and shrubs. By means of breeding and nutritional fertilization—another form of selection, namely cultural selection; *cf*, Advanced Track of the CULTURAL EPOCH—humanity has greatly increased agricultural productivity by accepting characteristics judged desirable and discarding those thought unnecessary or harmful, thereby permitting  $\Phi_m$  values aided by cultural evolution to reach much higher than those allowed by biological evolution alone. In particular, corn plants (modern maize, probably developed from the Mexican grass teosinte ~8 kya), with its many rows of grain on large ears and its numerous large leaves on tall stalks, is well advanced over its primitive grasslike ancestors whose earlier ears were smaller and disarrayed compared to their modern relatives.

Independent evidence suggests that energy use was likely a factor in the evolution of more advanced species of plants, especially the stunning diversification and rapid rise to ecological dominance of the angiosperms in the mid-to-late Cretaceous—an evolutionary event colloquially termed "Darwin's abominable mystery" (for there was nothing gradual about it). Angiosperms have higher growth rates and nutrient needs than gymnosperms; they sequester more  $^{14}N$  and  $^{31}P$  in their leaves, which then decompose quicker and thus, by positive feedback, create richer soil conditions for their own growth. Hence, the angiosperms probably utilized higher energy budgets than gymnosperms, allowing the former to out-compete the latter during one of the greatest terrestrial radiations in the history of life (Berendse & Scheffer, *Ecology Ltrs*, v12, p865, 2009). Furthermore and theoretically, hierarchies in energy density (if not energy rate density) have long been expected for organisms ascending the trophic ladder in ecosystems (Ulanowicz, *J Theoretical Biology*, v34, p239, 1972; May, *J Theoretical Biology*, v39, p155, 1973). By contrast, plants struggling under hot, arid conditions—such as the slow-growing succulents cacti and pineapple—photosynthesize mostly at night by means of a different process known as Crassulacean acid metabolism (CAM), which evolved to minimize  $H_2O$  losses, and these are among the least efficient in the living world.

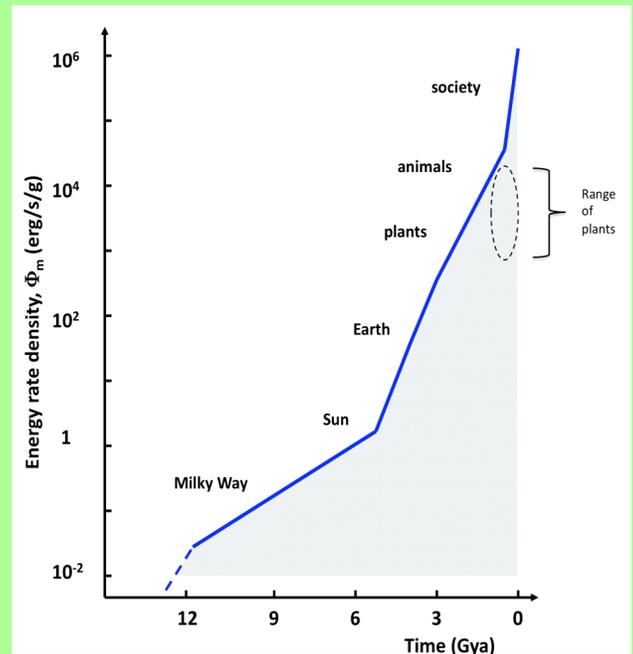
**Energy Rate Densities for Plants:** The table below summarizes various plant efficiencies,  $\epsilon$  (McDonald, *Photobiology of Higher Plants*, Wiley, 2003; Subbarao *et al*, *Hdbk of Photosynthesis*, Pessaraki, ed., CRC, 2005), noting that they and their associated  $\Phi_m$  values are averages for a wide spectrum of members within a given plant type. As with galaxies, stars, and all inanimate systems,  $\Phi_m$  values for animated life forms can range considerably, often over an order of magnitude or more—as in the case here for more organized, evolved plants. Variations occur among the plants because they do not equally absorb incoming sunlight and do not convert equally efficiently harvested energy into biomass. Given that photosynthesis is an inherently inefficient process, plants convert different amounts of light energy into chemical energy stored in its glucose molecules.

### Energy Rate Densities for Some Plants

Plant type	Time (Mya)	Example	$\epsilon$ (%)	$\Phi_m$ (erg/s/g)
tropical grasses ( $C_4$ )	30	maize, sugarcane	2.5	22,500
temperate herbs ( $C_3$ )	125	wheat, tomato	1.5	13,500
deciduous trees ( $C_3$ )	125	oak, beech	0.8	7200
evergreen trees ( $C_3$ )	350	pine, fir, larch	0.6	5500
protists	>470	phytoplankton, algae	~0.2	~1500

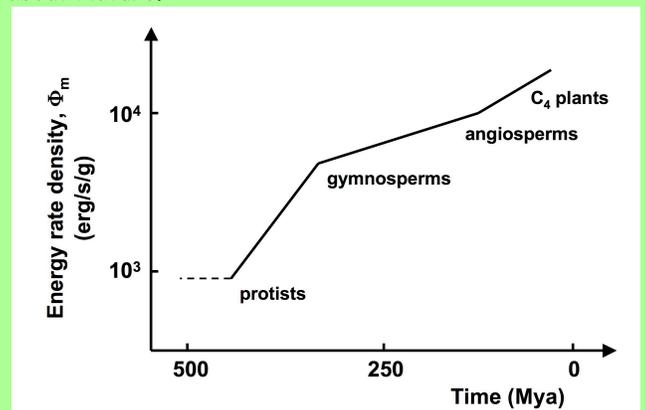
Values for  $\Phi_m$  listed in the right column of this table are relative to all plants in general with  $\epsilon = 0.1\%$  having  $\Phi_m \approx 900$  erg/s/g, as noted above. Those values clearly increase from bottom to top, where flowering angiosperms (topmost entries) are widely considered more botanically complex than the unprotected-seed gymnosperms (toward the bottom); the former have more specialized cell chemistry and more intricate reproductive structures. Taken together, the tabulated entries generally agree with this research hypothesis of these Advanced Tracks, namely that normalized energy flow, biological evolution, and increased complexity are reasonably well correlated.

The figure below places plants into the broader perspective of Nature's many varied complex systems by plotting a range of  $\Phi_m$  values for a variety of plants found on Earth. The dashed oval outlines the full range of changes in  $\Phi_m$  for plants as listed in the above table and then plotted in more detail in the following figure. The bracket at right spans the full range of  $\Phi_m$  for all known plants experiencing the biological-evolutionary phase of cosmic evolution.



*This graph repeats the essence of an earlier one (cf, end of Advanced Track for PARTICLE EPOCH), suggesting  $\Phi_m$  as a measure of rising complexity over all historical time. The dashed oval includes the range of increasingly ordered structures for a variety of living systems—in this case, for photosynthesizing plants at various stages of the biological-evolutionary phase of cosmic evolution.*

The next figure expands the above plot for a variety of plants during post-Cambrian times—but only those values of plant  $\Phi_m$  and their times of origin contained within the small dashed oval of the previous figure. Once again, energy rate density is a useful way to quantify the rise of complexity during biological evolution, much as done elsewhere in these Advanced Tracks for other open, complex systems scattered all about Nature.



The complexity of plants, expressed in terms of  $\Phi_m$ , is shown here for only the range of the previous figure outlined by the dashed oval. Note how flowering angiosperms have higher energy rate densities than gymnosperms or protists, and, in turn, more organized, cultivated  $C_4$  crops such as maize and sugarcane still higher values.

An alternative way of treating energy flow in plants, and thus acting a further numerical check on the  $\Phi_m$  complexity metric, is provided by measuring plants' energy yields when they or their fossil-fuel remnants are burned under controlled, laboratory conditions (Halacy, *Earth, Wind, Water and Sun*, Harper&Row, 1977; Davis, *Biomass Energy Data Book*, App B, US Dept of Energy, 2009). Chemical energy stored within plants' glucose bonds is then released as heat, fossil fuels being good examples of energy effectively stored (much like a battery) in organic matter trapped within rocks. The original energy input naturally comes from the Sun, is temporarily captured in the plants during photosynthesis, and is subsequently output as heat when fire frees up the energy stored in the plant, thus completing the flow through the system. More than 90% of the energy needed to power modern civilization currently derives from such decomposition products—coal, oil, natural gas—generated millions of years ago by photosynthetic organisms. The positive accumulation of free energy in these ancient deposits represents a decrease in entropy locally at the expense of the Sun; they are merely minor fluctuations in a general trend toward a state of higher global entropy.

For example, an acre (4047 m<sup>2</sup>) of softwood trees like white pine (a gymnosperm) annually produces  $\sim 4 \times 10^6$  g (4.5 tons) of biomass, which if burned yields  $\sim 2 \times 10^{10}$  erg/s (6500 Btu/lb, 20% moisture); and since an annual average of  $\sim 120$  W/m<sup>2</sup> (solar) realistically reaches Earth's surface in temperate latitudes where such trees grow,  $\epsilon \approx 0.4\%$  and  $\Phi_m \approx 3500$  erg/s/g, both of which approximate quoted values in the table above for evergreen trees. By contrast, hardwoods like red oak (an angiosperm) contain  $\sim 50\%$  more heat content, which is why they burn "hotter" and often longer in a fireplace, again in accord with values for deciduous trees in the above table. Such enhanced values of  $\Phi_m$  are not surprising given that a piece of fine, dense wood typically has a greater degree of organization than loose, uncultivated biomass. In turn, bituminous coal or refined gasoline ( $\sim 15,000$  Btu/lb), which of course are also mostly fossilized organic plant products, have  $\Phi_m$  values roughly twice that of raw wood; fossil fuels are

more concentrated, which is why their energy rate densities are higher. The same acre, if planted with sugarcane, would produce nearly 20 tons of biomass annually, and upon burning would make  $\Phi_m$  several times greater, again in reasonable agreement with the tabulated values above for the more evolved  $C_4$  crops.

**Phytoplankton et al.:** In contrast to many of the higher plants, the lower (non-vascular) plants have distinctly smaller values of  $\Phi_m$ . Among the simplest photosynthesizing life forms are the sea-based phytoplankton (some prokaryotic, others eukaryotic) that resemble early, single-celled microorganisms from which all plants arose, including microscopic eukaryotic algae and the even more primitive, prokaryotic cyanobacteria that made (as some still do today) the stromatolites; green algae, in particular, have ancestral links to land plants more than any other simple species. Globally,  $1/3$ - $1/2$  of net photosynthetic productivity worldwide is of marine origin (to oceanic depths  $\leq 100$  m), while the remainder is of mainly terrestrial land plants.

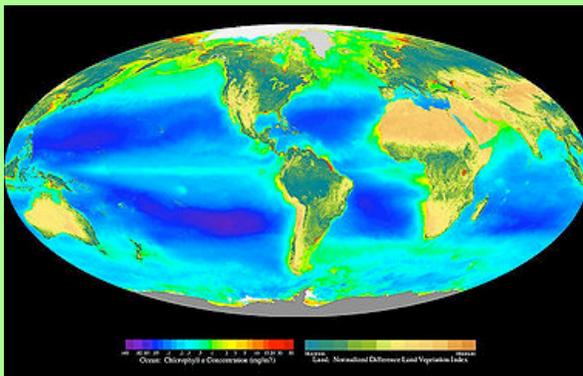
Photosynthetic efficiencies for naturally occurring microalgae are poorly documented, but satellite-sensor measurements of solar-energy utilization imply overall values averaging, respectively, 0.3% and at most 0.1% for plants on the continental landmasses and in the ice-free oceans (Field, *et al*, *Science*, v281, p237, 1998; see also Miyamoto, *et al*, *J Ferment Technol*, v57, p287, 1979). Such low efficiencies do approximate those computed above for the photosynthetic process operating today for the bulk of Earth's biomass, and thus likely include not only phytoplankton and a variety of protists but also green algae that have ancestral links to land plants more than any other simple species. These efficiency estimates are not biofuel production rates that can be higher for algae than for conventional crops owing largely to algae's short doubling time; nor are they laboratory idealized or commercially hyped values. The image below displays the global distribution of photosynthesis for both land and sea plants today.

The sea-based measures can be considered representative of energy utilization for some of the earliest protists—at least as far back as  $\sim 470$  Mya when the fossil record implies that algae became widely abundant, probably as much as  $\sim 1.7$  Gya when eukaryotic phytoplankton evolved in Proterozoic oceans (Falkowski, *et al*, *Science*, v305, p354, 2004), and possibly  $\sim 3$  Gya when rocks that old trapped traces of chlorophyll that probably facilitated photosynthesis in primitive algae and prokaryotic cyanobacteria (Lewis and McCourt,

*Amer J Botany*, v91, p1535, 2004). Aquaculture farming (including genetic modification, CO<sub>2</sub> enhancement, and active fertilization) under controlled conditions can better microalgae efficiencies, but that again is cultural evolution and not indicative of flora in the wild early on.

Remarkably, the tiny marine [cyano]bacterium *Prochlorococcus*, ~0.3 μ across and ubiquitous in non-coastal, non-polar waters, is the most common photosynthesizer on Earth today. These and other marine phytoplankton sequester atmospheric CO<sub>2</sub> at great ocean depths (>1 km), a downward flux of C that effectively removes it from surface layers solely due to gravitational settling; CO<sub>2</sub> eventually upwells to the surface in rifts, vents, and volcanoes as part of the "carbon cycle" (~10<sup>7-8</sup> y per cycle) in Earth's climasphere, an ongoing geophysiochemical "metabolic process" fundamentally driven by the Sun (*cf*, Advanced Track for PLANETARY EPOCH).

Measurements also show that larger, more advanced phytoplankton (>20 μ), such as diatoms (which comprise ~1000 species of unicellular algae having shapes from flat discs to thin rods and which probably emerged as recently as 100 Mya), display greater efficiency than smaller cells (<5 μ), somewhat contrary to expectations given their surface-to-volume ratios, yet perhaps in accord with plant physiology and the flow of energy through these earliest forms of life. All things considered, these many findings imply lower metabolisms, thus smaller Φ<sub>m</sub> values, for the smaller and simpler phytoplankton. Accordingly, we adopt an average value of Φ<sub>m</sub> of ~1500 erg/s/g for the protists that are generally considered forerunners of the algae and phytoplankton prevalent all across Earth.



*This false-color, composite image, based on data gathered by the SeaWiFS satellite, shows the global distribution of photosynthesis primary production in Earth's biosphere (actually of the concentration of*

*chlorophyll-a) for both terrestrial vegetation and oceanic phytoplankton (green and red colors maximum, respectively). Altogether, terrestrial and marine plants synthesize a staggering 2x10<sup>11</sup> tons of biomass each year (200 Pg/y) from CO<sub>2</sub> extracted from the atmosphere. (NASA)*

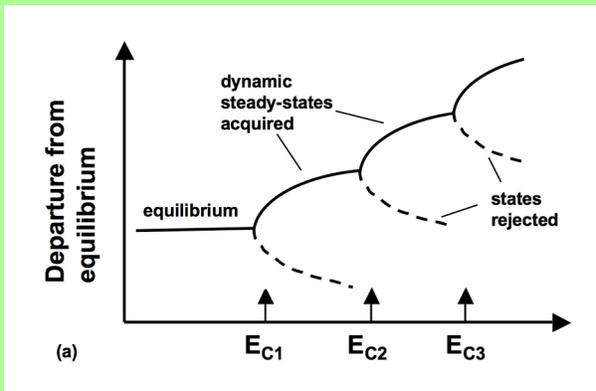
**Selection:** Plants are familiar examples of biological selection among a wide assortment of wondrous life forms adorning Nature. Here selection—genuine neo-Darwinism—is clearly at work, making use of energy rate densities well in excess of those for galaxies, stars, and planets.

Selection arguably works alongside the flow of resources into and out of all open systems, whether living or not. Moreover, systems of any degree of complexity seem selected partly for their ability to command energy. Energy flow and natural selection likely operate in tandem as systems evolve—the former utilized by those systems advantageously suited to their randomly changing environments, and the latter non-randomly eliminating those unable to do so. Conceivably, energy drives systems beyond equilibrium while selection aids the emergence of greater complexity for those systems able to manage the increased energy flow per unit mass. In other words, normalized energy flow rate may itself be a trait most often selected by successful systems of the same kind.

The figure below helps visualize such an energy-selection process at work, depicting the general case of a system experiencing repeated opportunities to survive or terminate. Wherever and whenever optimum energy is available, systems capable of drawing power competitively, thereby building structures or functions needed to engage those energies, are favored; selection from among many energy-based choices rewards and nurtures dynamic steady-states that create pathways capable of utilizing power per unit mass. Those systems using energy either too much, too rapidly, too little, or too slowly or are rejected and destroyed—the former two cases because systems would burn, the latter two because they lack threshold energy.

Such energy-flow diagnostics display increased complexity for a variety of steady-states among plants that, following the solid curve in the figure below, evade locally and temporarily the usual entropy process. As noted above, photosynthesis operates more effectively in flowering angiosperms than in gymnosperms and, in turn, even more effectively in more organized, cultivated (C<sub>4</sub>) crops such as maize and sugarcane. Similar trends are also evident for animals

(*cf.* next section) yet with typically even higher energy rate densities along a broad evolutionary sequence spanning prokaryotes, ectotherms, and endotherms—as discussed below in the next section on animals. All this accords with recent arguments in ecology (*eg.* Vermeij, *Nature: An Economic History*, Princeton Univ Pr, 2004) that highly metabolizing opportunists enjoy advantages during periods of change.



Natural selection diagrams schematically illustrate how, at certain critical energies, labeled here variously  $E_C$ , systems can spontaneously change, or bifurcate (vertical arrows), into new, non-equilibrium, dynamic steady-states. Chance affects the opportunities that arise, but necessity determines which fork systems select, namely which structures and functions are acquired (solid, rising curve) and which become extinct (dashed curves), thus the result is inherently unpredictable as with all of evolution. Such energy-selection diagrams can be drawn for any physical, biological, or cultural system successfully able to adapt and take advantage of increased energy while further complexifying.

It is worth stressing two probable, general guidelines governing energy use, not only here for plants but also apparently for all open, complex structures: *Energy is likely a necessary, but not necessarily sufficient, condition for the growth, maintenance, and evolution of ordered systems*—much as, for example, in the case of plant growth,  $CO_2$  and  $H_2O$  are also needed. Furthermore, *optimum ranges of energy use exist for all ordered systems*—as here for plants for which not too much, yet not too little, energy is required for photosynthesis, just as plants enjoy optimal ranges in heating and watering, lest they either desiccate or drown. This differs from the pioneering work of Lotka (*Proc Nat Acad Sci*, v8, p147, 1922), who, albeit with great insight nearly a century ago,

speculated that biological evolution proceeds in order to maximize the total energy flux through systems; by contrast, the data imply no clear law of maximum (or minimum) production of power (or entropy), indeed no extremum principles of any kind.

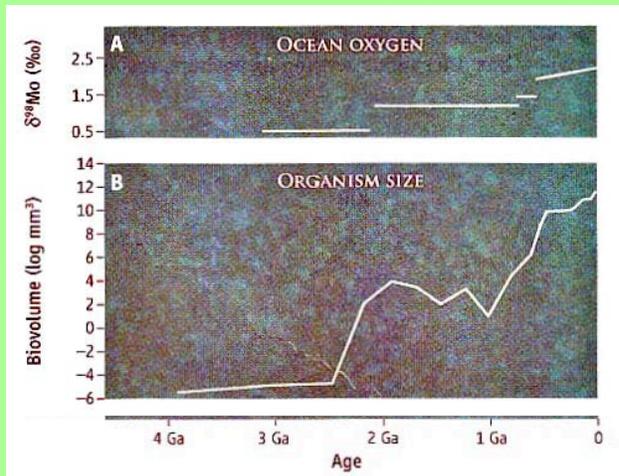
We need not dwell on the concept of selection operating throughout the bush of life, for the process is well accepted among biologists today. Yet, natural selection likely pertains to physical (*cf.* Advanced Track for STELLAR EPOCH) and cultural (*cf.* Advanced Track for CULTURAL EPOCH) events as well—for whether stars or humans among any ordered, complex systems, we encounter the same *general* trend found for plants: The greater the perceived complexity of the system, the greater the flow of energy density through that system—either to build it, or to maintain it, or both.

### Animals

It is often said that plants are producers and animals consumers, but in fact both engage energy as an essential process of life. For animals, the principal biological process is respiration, whereby oxygen ( $O_2$ ) converts consumed carbohydrates into the organics of tissue structure and synthesizes ATP in mitochondria, which can then release energy when needed for bodily activities. Energy flow in animals can be treated in much the same way as for plants above—indeed, our working hypothesis of energy rate density as a reasonable and consistent complexity metric can be extended to more organized systems by estimating specific (*i.e.*, mass-normalized) metabolic rates for whole bodies (this section) and wet brains (next section) among a large sample of animals.

Most animals aerobically respire to fuel minimal maintenance (basal metabolic rate) as well as to enhance more active lifestyles (field metabolic rate) when added  $O_2$  consumption rises to meet increased demand for ATP production during stress, growth, and thermoregulation (and beyond that, though rarely, catabolic anaerobic pathways, such as glycolytic production of lactic acid, can generate additional ATP during brief bursts of maximum activity like that experienced by darting lizards and marathon runners). The section above examined plants in some detail, suggesting how energy rate density might be judged as both a complexity metric and evolutionary driver; here, animals are likewise analyzed for their  $\Phi_m$  implications, treating animals in much the same way as for plants, indeed in a consistent manner as for all ordered structures observed in Nature.

Somewhat more technically, all the while seeking a connection to the discussion of plants above (for plants are the source of  $O_2$ ), the graphs in the next figure suggest how recent studies of molybdenum (Mo) isotopes in ocean sediments imply increased  $O_2$  levels beginning around the Cambrian period might have driven increased size among animals. Two growth spurts in animal biovolume are evident, one ~2.5 Gya (referred to earlier in this Advanced Track as the Great Oxygenation Event) when  $O_2$  first began accumulating on Earth (yet  $O_2$  was then still only ~1%, rising to ~10%, of its abundance today), and the second ~600 Mya when organisms emerged from their microscopic world and began developing skeletons and shells (yet  $O_2$  was then only ~10%, rising to several times that percentage, of its abundance today). These data might also imply a third stepwise oxygenation of the ocean (and by implication the atmosphere) in the Devonian ~400 Mya, when the development of plant ecosystems seem to correlate with the increasing size of fossil predatory fish. (Climate change, variable glaciation, and ozone [ $O_3$ ] buildup may have also contributed to animal growth.) Larger animals use more energy, that is require more  $O_2$ , and that can probably be met only in  $O_2$ -rich waters.



Increases in  $O_2$  in Earth's ocean and atmosphere probably gave rise to increased animal size twice, ~2.4 Gya and ~600 Mya. Graph (a) shows ocean  $O_2$  concentrations as inferred from  $^{98}\text{Mo}/^{95}\text{Mo}$  isotope ratios (a proxy for  $O_2$  abundance) preserved in sedimentary rock rich in organic matter. Graph (b) shows the size ( $\log \text{mm}^3$ ) of organisms recorded in the fossil record. (Adapted from Kump, *Science*, v330, 1490, 2010.)

**Evolution and Complexity:** A wealth of paleontological and genetic data available today imply that animals (multi-cellular eukaryotes) generally became increasingly complex with time—both in structure of individual organisms and in organization of ecological communities—and dramatically so in the Phanerozoic Eon since the Cambrian Period (McShea, *Evolution*, v50, p477, 1996; Carroll, *Nature*, v409, p1102, 2001; Wagner, *et al*, *Science*, v314, p1289, 2006). A clear yet rambling succession of life forms, broadly identifiable yet minus transitional details, is evident during the past ~0.54 Gy: invertebrates (>500 Mya), fish (~500 Mya), amphibians (~365 Mya), reptiles (~320 Mya), mammals (~200 Mya), and birds (~125 Mya). Much as suggested for plant evolution in the previous section of this Advanced Track for the BIOLOGICAL EPOCH, energy flow potentially affected animals, linking complexity growth and evolutionary pathways with increased energy usage, all of it likely in accord with Darwinian descent with modification guided by natural selection—from ectotherms in the hot, damp climates of the Palaeozoic Era, to increasingly diverse animals of intermediate metabolism that thrived in the warm and drier Mesozoic, and then to endotherms in the cooler, fluctuating climates of the Cenozoic.

Much of this change occurred by means of random evolutionary opportunities to secure food and escape predation, which initially required transport of  $O_2$  reserves from the open waters and thus elevated states of metabolic energy consumption, followed by the terrestrialization of the vertebrates that required yet more energy largely because reptiles moved on legs and pumped their chests; mammalian adaptation further aided the rising complexification of the animal world, resulting in not least the emergence of energy-hungry primates, including our high-energy human society, the last of these to be discussed in the next section of this Advanced Track (*cf* also, Advanced Track for CULTURAL EVOLUTION). While none of these energy additives was goal-directed, each arguably presented selective advantages for some species throughout a long and meandering evolutionary process during the most recent 10% of Earth's history.

**Ectotherms:** Ectothermic (also known as poikilothermic) animals control their body temperature  $T$  (~22°C) by means of external heat sources and include both invertebrates (all arthropods, including insects, worms, crustacea, and their relatives) as well as lower vertebrates (fish, amphibians, and reptiles). As a group, ectotherms have less active metabolisms

compared to endotherms that include mammals and birds and that self-regulate their core body T (37-42°C generally, which is higher than the normal T = 37°C = 98.6°F for most mammals, possibly to ward off fungi) by digesting food (Bennett, *Ann Rev Physiology*, v400, p447, 1978). In fact, low metabolic rates are notably characteristic of all extant reptilian taxa, which were the first fully terrestrial vertebrates and which later gave rise (probably along independent lines of descent during the early Mesozoic) to two major phylogenetic radiations of endothermic mammals and birds. Ectotherms also have lower specific metabolic rates, hence lower values of  $\Phi_m$ , than their warm-blooded cousins. Here, *in vitro* O<sub>2</sub> consumption rate effectively estimates metabolic rate, but caution is advised regarding wet and dry body mass, for it is wet (living) mass that counts when deriving values of  $\Phi_m$  in a consistent manner relative to other living creatures; furthermore, it is the basal rate (for fasting, resting, inactive states) that is most telling when making comparisons and not the more active rates experienced when contending with all the challenges of relying on the environment (ectotherms) or finding enough food (endotherms) to maintain body temperature (Bennett, *Adv Vet Sci and Comp Med*, 1994, v38B, p113, 1994). Added care is also required regarding incompatible units found throughout the bioscience literature; although the thermodynamic (cgs-metric) units used here may be unfamiliar to some readers, all the Advanced Tracks of this web site emphasize uniformity among physical, biological, and cultural systems; thus 1 liter O<sub>2</sub> consumption equals  $\sim 2 \times 10^{11}$  erg or  $\sim 4.8$  kcal (Scott, *et al*, *Nutrition and Metabolism*, v3, p1, 2006).

Current metabolic data display no clear evolutionary differences in  $\Phi_m$  values among the ectotherms (Makarieva, *et al*, *Proc Nat Acad Sci*, v105, p16994, 2008). Variations are statistically indistinguishable among the lower vertebrates, including fish, amphibians, and reptiles; most of their  $\Phi_m$  values range between  $2 \times 10^3$  and  $10^4$  erg/s/g, with a mean of  $\sim 4 \times 10^3$  erg/s/g. As expected from paleontology, aerobic capacities were not appreciably expanded as life made the transition to land; reptiles and amphibians have no more energy needs than fish of comparable size. Among invertebrates, which are also ectothermic and constitute >95% of all animal species,  $\Phi_m \approx 10^4$  erg/s/g  $\pm$   $\sim 30\%$ ; their slightly higher  $\Phi_m$  than for the lower vertebrates, if significant, may owe to some invertebrates being active flyers, including minute insects, which likely require more power per unit mass (as do birds, see below). That these mean values are

only slightly higher than for some photosynthesizing plants (*cf*, previous section) is not surprising. The resting rates for the least evolved respiring ectothermic animals are not likely much more complex than efficiently photosynthesizing land plants, the two processes having matured roughly contemporaneously in the Paleozoic. Occasional outliers and minor overlaps in  $\Phi_m$  values are evident throughout the evolutionary record for closely complex life forms, as acknowledged here and again below.

**Endotherms:** In contrast to the ectotherms, endotherms (also known as homeotherms) have distinctly higher levels of specific metabolism, hence higher values of  $\Phi_m$ . Many field studies and laboratory measurements of animals having comparable body M and T show basal metabolic rates 5-20 times greater in mammals than in reptiles (Makarieva, *et al*, *Proc Nat Acad Sci*, v105, p16994, 2008; Hulbert, in *Comparative Physiology: Primitive Mammals*. Schmidt-Nielsen (ed.), Cambridge U Pr, p129, 1980; Hulbert and Else, *Am J Physiology-Reg Integr Comp Physio*, v241, p350, 1981). Three-quarters of all known mammals display a range in  $\Phi_m$  value,  $10^4$ - $10^5$  erg/s/g, with a mean of  $\sim 4 \times 10^4$  erg/s/g. Variations in metabolic rates among mammals are apparent throughout these data; besides the most dominant influence of differing body mass, such variations likely reflect environmental conditions, ongoing adaptation, and numerous other factors that influence metabolism such as habits, habitat, climate, diet, and taxonomy (McNab, *Comp Biochem and Physio A*, v151, p5, 2008). To give a few examples: seals and whales have  $\Phi_m$  values about twice those of other animals of their size because they need to thermoregulate their bodies in cold water; small desert mammals have lower  $\Phi_m$  values than others of their size because they have adapted to a scarcity of food and water; and placental mammals have typically thrice the  $\Phi_m$  value of similarly sized marsupials because they are viviparous and have extra layers of energetically expensive brain mass.

Caution is needed to distinguish between basal (standard) and active (field) metabolic rates (Bennett and Ruben, *Science*, v206, p649, 1979; Nagy, Girard, and Brown, *Ann Rev Nutrition*, v19, p247, 1999) since the two can be as different as the fuel consumption of an automobile idling at a traffic light or speeding along a highway. For example, a horse expends  $\Phi_m \approx 5 \times 10^5$  erg/s/g at maximum exertion,  $\sim 3 \times 10^5$  during regular exercise, yet only  $\sim 8 \times 10^3$  at rest (Hodgson, *et al*, *Pflugers Arch European J Physio*, v417, p73, 1990).

Overall, laboratory studies of sustained (field) metabolic rates typical of all free-living animals in the wild display enhancements in  $\Phi_m$  by factors of 3-10 (and up to 50 for maximum exertion) over their basal rates, but still reveal that mammals outpace reptiles by nearly an order of magnitude (Nagy, Girard, and Brown, *Ann Rev Nutrition*, v19, p247, 1999; Hammond and Diamond, *Nature*, v386, p457, 1997). The different rates can nearly overlap for disparate life forms, much as noted two paragraphs above for simple animals (heterotrophic ectotherms) and efficient plants (advanced photoautotrophs). Likewise, endothermic vertebrates at rest and ectothermic insects in flight display comparable metabolic levels, as do maximum  $\Phi_m$  for darting reptiles when compared to many resting mammals. However, mixing rates creates unfair comparisons and bewildering confusion in the literature does not help. When level assessments are made for the same type of specific metabolic rate, relative  $\Phi_m$  values are clear and unambiguous: higher vertebrates (mammals and birds) have greater energy rate densities than any of the lower vertebrates or invertebrates.

**Birds:** Also endothermic, birds evolved from carnivorous, feathered dinosaurs during the late Mesozoic (~125 Mya), and among vertebrates have the highest values of  $\Phi_m \approx 10^5$  erg/s/g, which can sometimes reach an order of magnitude greater during sustained flight or while earnestly foraging for food for their nestlings. Such high  $\Phi_m$  might mean that birds' normal metabolisms are more energetic and akin to active (not basal) metabolisms among non-fliers; estimates of basal rates for birds resting at night, which afford even comparisons, are scarce and anecdotal. Many passerine (perching, frugivore) birds have  $\Phi_m \approx 5 \times 10^5$  erg/s/g, which is ~30% higher (McNab, *Nature*, v426, p620, 2003 claims this, but Nagy, Girard, and Brown, *Ann Rev Nutrition*, v19, p247, 1999 refutes it) than non-passerine fliers whose energy rate densities are comparable to mammals when active; however, uncertainties linger regarding whether reported avian rates are basal, active, or some sort of operational average. Hummingbirds, for example, when actively hovering can use as much as 8 times more energy than their resting rate, yet while sleeping (more than half of each day) when their body T drops to nearly that of the surrounding air their rates decrease to 3 times less than basal; the former state requires them to ingest nectar daily equal to ~50% of their body mass, while the latter subsides on minimal energy stores. Similar basal-active comparisons can be made

for mammals, such as for humans who maintain our basal rate by ingesting food daily equal to ~3% of our body mass; yet our active metabolisms also increase by more than an order of magnitude above our basal rates when swimming, jumping, or running, for which  $\Phi_m$  averages  $2 \times 10^5$  erg/s/g (Ainsworth, *Comp Phys Activity Tracking Guide*, [http://prevention.sph.sc.edu/tools/docs/documents\\_compendium.pdf](http://prevention.sph.sc.edu/tools/docs/documents_compendium.pdf)). For all active fliers <1 kg,  $\Phi_m$  is less than for comparably massive mammals while running. Furthermore, birds, much like human marathoners and cyclists who consume many times their normal food intake (~ $10^5$  erg/s/g), are fueled partly by rapid expression of bodily energy reserves (anaerobic glycolysis), not by sustained, concurrent energy intake; these enhanced metabolic rates are atypical physiologically, hence their overall rates are lower when averaged over time.

In addition to their habitually active states, birds might also have high values of  $\Phi_m$  partly because they are genuinely more complex than most other animals, including humans. After all, birds normally operate in 3-dimensional aerial environments, unlike much of the rest of animalia at the 2-dimensional ground level; thus avian *functions*, quite apart from structural issues, might be legitimately considered, somewhat and sometimes, more complex than those of the rest of us who can't fly. Brains aside (*cf.* discussion in a separate section below), the bodies of fliers can arguably be judged more complex than non-fliers, given the former's intricate lung sacs, pectoral muscles, and wing aerofoils that allow a constant, one-way flow of O<sub>2</sub>-rich air that helps birds maintain high metabolic rates to generate enough energy for flight. The European swift bird, for example, can fly non-stop up to 10<sup>3</sup> km during breeding season, performing many functions including sleeping on the way; foraging bees can fly several km/day from their hives, traveling up to 10 m/s (or ~30 km/hr). The act of flying does indeed demand great skill, more energy, and a higher cost of living in general, requiring birds to master (in effect) spatial geometry, materials science, aeronautical engineering, molecular biochemistry, and social stratification. Avian species are impressive by any measure; their speed, maneuverability, and endurance are outstanding among all known life forms, so perhaps they *should* have large values of  $\Phi_m$ ; in fact, any organism requiring an astonishing 160 flaps of its wings *per second*, as do big-bodied bumblebees during powered flight, would understandably have a large appetite.

Extraordinary avian physiology might well resemble enhancements in galactic ecology, each category of system—animals and galaxies—having members with

exceptionally high metabolisms. In-flight birds, which while temporarily aloft have among the highest animal complexity levels, typify the energetics of briefly erupting active galaxies; each tops the charts of metabolic rates, or L/M ratios (*cf.* Advanced Track for GALACTIC EPOCH), of their respective classes, with values of  $\Phi_m$  well higher than their basal, or normal rates. For relatively brief durations, such galaxies display values of  $\Phi_m$  up to ~100 times the usual value for normal galaxies.

Even high-endurance human athletes or those merely peddling mountains uphill require several tens of times their basal rate during short periods of maximum exertion when power expenditures can reach  $\Phi_m \approx 4 \times 10^5$  erg/s/g, an increase so dramatic as to be comparable to that of airborne birds. To be sure, as we shall see in the next section on humans, swimming, running, and flying (let alone periodic reproduction and even social behavior) all represent biological functions that raise metabolic rates among animals; more energy is needed to perform and coordinate their mechanical movements, in fact of order  $\Phi_m \approx 5 \times 10^5$  erg/s/g (or 3000 W per capita, compared to the nominal 130 W for humans) are used by typical Tour de France cyclists.

**Complexity Rising:** The challenge for zoology is to explain the truly vast diversity of animal species on Earth. In general, the trend is much the same for many of the major evolutionary stages of life: eukaryotic cells are more complex than prokaryotic ones, plants more complex than protists, animals more complex than plants, mammals more complex than reptiles, and so on. Whether stars, planets, or life, the salient point seems much the same: The basic differences, both within and among these categories, are of degree, not of kind. We have discerned a common basis upon which to compare all material structures, from the early Universe to the present Earth—again, from big bang to humankind inclusively.

Yet, can we become more specific and quantitative, presenting animals on a graph similar to those displayed earlier for galaxies, stars, planets, and plants? In general, the answer seems to be in the affirmative. Paralleling the brief description of plant evolution in the section above, here is a condensed, qualitative outline of the main zoological changes in post-Cambrian times that display increased energy-expenditure levels (based partly on Por, *Integrative Zoology*, vXX, pXX, 2009):

The mid-Cambrian (~520 Mya) was characterized by burrowing worms (especially the segmented marine

coeloms, compared to their soft-bodied flatworm precursors that moved only on the sediment surface) that developed hydrostatic skeletons and associated muscles to exert mechanical leverage—much of it probably an evolutionary advantage to escape from predation, yet which required transport of their own  $O_2$  reserve from the open waters and thus an elevated state of metabolic energy consumption. By the end of the Silurian (~420 Mya) and mainly into the Devonian (~380 Mya), several classes of fish-like vertebrates are found fossilized in brackish estuaries and fresh water deposits; for such organisms to adapt to changing salinity and chemical compositions, they likely required maintenance of a stable internal osmotic medium, and the energy cost of such osmoregulation is high—and only the mollusks, annelids, arthropods and vertebrates were able to invade the nutrient-rich estuaries, which in turn acted as evolutionary corridors leading to colonization of the continents. Specifically regarding numerical tables and figures below, reptiles and amphibians arose (or at least “exploded” in global diversity) as many new, fragmented habitats emerged after vast tracts of tropical forests died, ~305 Mya, probably owing to climate change that dried up those rainforests.

Throughout the Mesozoic (~250-65 Mya), the adaptation of the arthropods, predominantly the insects with their solar-aided metabolic activity, was very successful, yet all insects, which followed the plants onto the land, remained small as predator vertebrates in turn followed them to the land; yet further in turn, it was the feeding on ants and termites (myrmecophagy) that supplied the needs of primitive, insectivorous mammals, indeed still provides the large energy needs of modern shrew-like animals that feed constantly in order to maintain their endothermy. Of special import, the oldest mammals—mouse-sized and insecting-eating—evolved from reptiles (therapsids) ~200 Mya.

The terrestrialization of the vertebrates was more complicated, but it too required more energy; briefly and especially during the globally warm, 80-My-long Cretaceous (the longest geological period centered ~100 Mya), the ectothermic herbivores (including the dinosaurs) needed more energy if only because they were moving about on their legs and pumping their chests. Early endothermic mammals, greatly restricted during the Cretaceous, flourished as the world entered the Tertiary beginning ~65 Mya, and although initially far from modern mammals, energy requirements rose again; the high and constant body T as a mammalian

adaptation to the terrestrial environment also allowed sophisticated neural processing and complex learned behavior, namely two of the most prominent breakthroughs resulting from the thermodynamic evolution of the animal world—culminating (at least for now) in the rise of the great apes in the Miocene (~20 Mya), thence on to present high-energy-cost humans with their even higher-energy-utilizing brains. None of these energy enhancements were goal-directed, yet each seems to have presented selective advantages for some species at each and every step of the twisting, turning, ambling evolutionary process.

**Energy Rate Densities for Animals:** Consider once more some representative animals for which metabolic rates are known, recognizing that those rates can vary upwards under stress and exertion, their total energy budgets dependent largely on energetically expensive internal organs such as kidneys, hearts, brains, and livers. Laboratory studies of sustained metabolic rates for 50 vertebrate species (Hammond and Diamond, *Nature*, v386, p457, 1997) show that reptiles, mammals (including rodents, marsupials, and humans), and birds average  $\Phi_m \approx 9,000, 56,000,$  and  $78,000$  erg/s/g, respectively. These and other measurements noted above and below suggest that specific metabolic rates of ectotherms (cold-blooded organisms including all insects, fishes, amphibians, and reptiles) are only a fraction of those of similarly massive endotherms (warm-blooded organisms such as mammals and birds), much as we might expect on evolutionary grounds. This is hardly surprising since, for endotherms to carry with them portable, thermally regulated environments, there is an inevitable energy cost; such ability to thermoregulate likely confers a competitive, and even survival, evolutionary advantage, but more energy is required to attain it.

The order-of-magnitude difference in specific metabolic rates among birds, mammals and comparably sized reptiles can legitimately be cast in terms of relative complexity, since the need for the endotherms to homeostatically control body T (both heating and cooling) is surely a more complicated task that the ectotherms simply cannot manage—and it is the extra energy that allows for this added feature, or selective advantage, enjoyed by birds and mammals over the past few hundred million years. Even so, the ectotherms are much more abundant, both as species and as individuals, meaning that they, too, are quite successful in their own more limited realms.

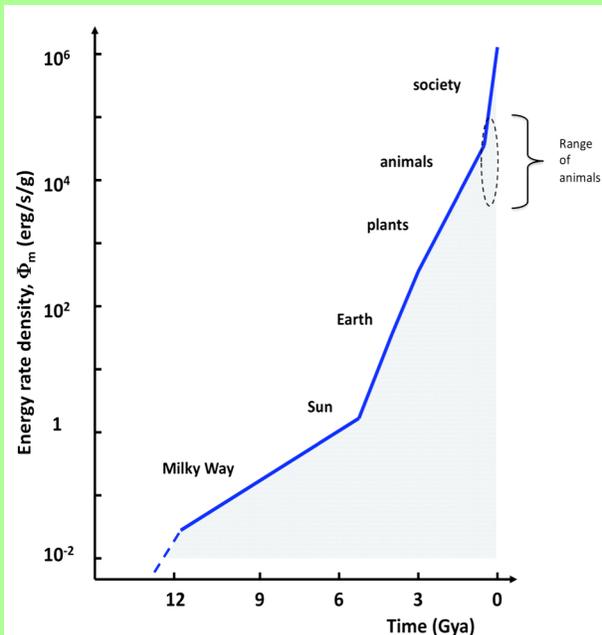
Among the eukarya (life's 3<sup>rd</sup> domain that includes all plants and animals), the cold-blooded ectotherms have  $\Phi_m$  values between  $2 \times 10^3$  and  $10^4$  erg/s/g, whereas the warm-blooded endotherms have not only a similarly wide range of values but also higher absolute values, namely  $10^4 - 10^5$  erg/s/g. The former are clearly among the earliest of biological evolution's animal creations, the latter widely considered more advanced, indeed among the most complex, of Nature's many varied life forms; with their portable microenvironments (shelter, fire, clothing, etc), the endotherms have enjoyed a strong competitive edge, enabling them to adaptively radiate to even the most inhospitable parts of the biosphere.

Much like the above table of  $\Phi_m$  values for plants, the table below summarizes values of  $\Phi_m$  for the bodies of a spectrum of mature, adult animals. These are mean values for a wide range of diverse taxonomic groups that are resting (basal) and at normal body T, excerpted and averaged from many of the references noted above. Evolutionary times approximate those at which listed animal types emerged in natural history.

**Energy rate densities for some animals**

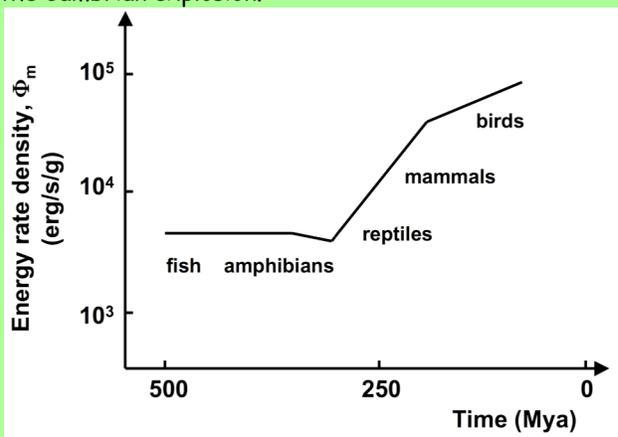
Animal	Time (Mya)	Examples	Body $\Phi_m$ (erg/s/g)
birds	125	jays, parrots	$9 \times 10^4$
mammals	200	mice, elephants	$4 \times 10^4$
reptiles	320	lizards, snakes	$3 \times 10^3$
amphibians	365	frogs, toads	$4 \times 10^3$
fish	500	carp, goldfish	$4 \times 10^3$

The figure below places the tabulated range of  $\Phi_m$  values for animals into the larger perspective of energy rate densities for all known complex systems. This plot resembles similar graphs presented in earlier *Advanced Tracks* for galaxies, stars, planets, and plants at various evolutionary stages in the natural world. As is abundantly clear, we are continuing to move up the curve of rising complexity with the march of time.



This graph repeats the essence of an earlier one (cf, end of Advanced Track for PARTICLE EPOCH), suggesting  $\Phi_m$  as a measure of rising complexity over all historical time. The dashed oval includes the range of increasingly ordered structures for a variety of living systems—in this case, for respiring animals at various stages of the biological-evolutionary phase of cosmic evolution.

And here is an expanded plot of  $\Phi_m$  values for specifically those types of animals contained within the small dashed oval of the previous figure and taken from the previous table. It shows in greater detail the general rise in  $\Phi_m$ , and hence animal complexity, since the Cambrian explosion.



The complexity of animals, expressed in terms of  $F_m$ , is shown here rising in more detail in order to highlight some of the increasingly intricate structures for a variety of bodies at various stages of the biological-

evolutionary phase of cosmic evolution. Note how, within broad categories of animals, endotherms (including mammals and birds) have higher energy rate densities than ectotherms (including invertebrates as well as lower vertebrates such as fish, amphibians and reptiles) among all taxonomic groups found on Earth.

**Evolutionary Advancement:** No strong distinctions between  $\Phi_m$  values and biological evolutionary are made for members of the animal kingdom. Energy rate density may well qualify as a broad complexity metric for life, but current data preclude strong  $\Phi_m$ -related statements about specific evolutionary paths for individual species within major taxonomic groups of the animal kingdom. Suffice it to say that nearly all zoological  $\Phi_m$  values are tightly confined to within hardly more than an order of magnitude of one another, nestled midway between smaller botanical values for photosynthesizing plants (see above) and higher neurological ones for central nervous systems (see below). Further, correlations do link evolution, complexity, and  $\Phi_m$  for major animal categories, notably those separating reptiles, mammals, and birds. For example, endothermy is surely one of the most striking animal adaptations, requiring extensive restructuring of many parts (including lung, heart, and skeletal muscle) of vertebrate bodies. The greater aerobic heat production in the endotherms is, of course, the basis of their homeothermic condition that grants them independence from environmental thermal fluctuations, and this arguably makes them more complex. Endothermy likely evolved in mammals from reptiles in the early Mesozoic as mitochondrial volume density gradually increased in their respective tissues, causing microscopic metabolisms to accumulate and with them total organismal specific metabolic rates to rise (Else and Hulbert, *J Comp Physio B*, v156, p3, 1985). The original vertebrates (possibly ostracoderms) were active, predatory carnivores with metabolic patterns similar to most modern fish; the transition of vertebrates from aquatic to terrestrial habitats eventually would have enabled greater  $O_2$  use, since  $O_2$  in the aerial environment is more easily accessible owing to its increased diffusivity and concentration. However, most traits related to  $O_2$  consumption do not fossilize and other factors have also been implicated as having granted major selective advantages (Bennett, *J Exp Bio*, v160, p1, 1991). Thermoregulation itself allows body temperature of mammals and birds to remain both higher and more constant than those of most ectothermic vertebrates, and this alone might enhance

prospects for survival; endothermy, with its constant portable microenvironment, surely conferred competitive evolutionary advantages in benign environments and allowed those species so endowed to adaptively radiate into hostile parts of the biosphere. Higher levels of  $O_2$  consumption also likely expanded the range of sustainable exertion and long-distance endurance, granting opportunities for greater complexity to parallel the rise in  $\Phi_m$  values for mammalian and avian lineages. Regardless of how it emerged, a clear prerequisite underlies endothermy: more energy is required to attain it.

Energy flow was likely only partly responsible for evolutionary advancement of rising complexity. Non-evolutionary effects also surely contributed to the observed range in  $\Phi_m$  values, for stressful environments thermodynamically drive some organisms to extremes. For example, aquatic mammals have specific metabolic rates that are necessarily higher (by factors of 2-3) than those of similarly sized land mammals (since, much as for birds, the former operate in a 3-dimensional world, in this case where water conducts heat 20X faster than air). An opposite extreme is found in desert mammals, whose anomalously low specific metabolic rates reflect food shortages, though they can rehydrate rapidly by drinking the equivalent of a third of their body weight in 15 minutes. Dietary, water, behavioral, and habitat factors will all likely cause variations in  $\Phi_m$  values in addition to evolution per se, resulting in rare outliers in such diverse samples of animals. Body mass itself is the biggest cause of variation among metabolic rates for mammals; much the same is true for birds, as body mass alone accounts for >90% of their variation in  $\Phi_m$  (McNab, *Nature*, v426, p620, 2003). All things considered, macroscopic life forms display clear and abiding, yet general, trends between evolution-associated complexity and energy rate density.

**Allometry:** Quantitative assertions in this section are independent of the ongoing debate about allometric scaling of metabolism among mammals from mice to elephants (spanning 6 orders of magnitude in body mass), nor is it important here whether their mass-dependent,  $M^n$ , metabolic exponent is  $n = 2/3$  as expected for surface-to-volume principles, as for any spherical body dissipating heat from its surface, (Rubner, *Zeitschrift Biologie*, v19, p535, 1883), or  $n = 3/4$  based on laboratory measures (Kleiber, *The Fire of Life*, Wiley, NY, 1961) and fractal theory of nutrient supply networks, as might any elastic machines having

muscular systems and skeletal loads subject to gravity (West, Brown and Enquist, *Science*, v276, p122, 1997; Brown and West, eds, *Scaling in Biology*, Oxford U Pr, 2000); it may, in fact, be neither (Kolokotronis, *et al*, *Nature*, v464, p753, 2010), as metabolic-rate dependence on body mass likely differs with activity level (Darveau, *et al*, *Nature*, 417, 166, 2002), during lifetime development (Zotin and Zotina, *J Theory Bio*, 17, 57, 1967), and among evolutionary lineage (White, Blackburn and Seymour, *Evolution*, v63, p2658, 2009). In any case, claims of a universal law of bioenergetics for all life forms from bacteria to elephants (Smil, *Nature*, v403, p597, 2000) are mathematically (Dodds, *Phys Rev Lett*, 104, 048702-1-4, 2010) and empirically (Makarieva, *et al*, *Proc Nat Acad Sci*, v105, p16994, 2008) dubious.

Of central import to the present study is the fact that all animals, and not just mammals, but including the whole range of known heterotrophic species, have specific metabolic rates within a relatively narrow range of  $\Phi_m$  extending over a factor of only ~30. The far majority of specific metabolic rates for animals vary between  $3 \times 10^3$  and  $10^5$  erg/s/g, despite their masses ranging over ~11 orders of magnitude from fairy flies to blue whales (Makarieva, *et al*, *op cit*). Among mammals alone, specific metabolic rates do vary inversely yet weakly with body mass,  $\sim M^{-0.2}$ . Indeed, in cosmic evolution, as the present work contends, it is the *specific* metabolic rates that are most telling, namely those normalized to mass and which therefore for many life forms vary weakly with mass, namely as  $M^{3/4}/M = M^{-1/4}$ . This quarter-power scaling law is pervasive in biology, probably the result of physical constraints on the circulatory system that distributes resources and removes wastes in bodies, whether it is the geometrical pattern of blood vessels branching through animals or the vascular network nourishing plants. Natural selection seems to have optimized fitness by maximizing surface areas that exchange nutrients while minimizing transport distances and times of those nutrients (West *et al*, *Science*, v284, p1677, 1999). That the smallest animals have somewhat higher  $\Phi_m$  values probably owes to their frequent eating habits, high pulse rates, robust activity levels, and relatively short life spans; they live fast and die young. By contrast, the largest animals have slightly lower  $\Phi_m$  owing to their more specialized cells, each of which has only limited tasks to perform and energy needed, thus granting greater efficiency and a longer life.

Naturally, those species whose individuals enjoy longevity are also likely to experience more extreme

environmental stress and therefore be exposed during their lifetimes to enhanced opportunities for adjustment and adaptation, and thus for evolution toward greater complexity (as well as toward extinction should the stresses be too large). The result with the passage of time, as a general statement for bodies of similar mass, is a feedback process whereby those successful systems able to assimilate greater energy flow live longer, evolve faster, and typically complexify, which, often in turn, leads to higher metabolic rates, and so on.

Deep into discussions of biological metabolism, we once again encounter a widespread astronomical factor—the mass-based gravitational force so integral to our earlier discussion of the underlying agents that established the conditions for increasing complexity among, for example, stars (*cf.* Advanced Track for STELLAR EPOCH). Astrophysics and biochemistry are not uncoupled parts of the cosmic-evolutionary scenario, as allometric scaling makes clear.

### Humans

Humans deserve more than a passing note in any zoological discussion, not because we are special but because we are them. Each adult individual, globally averaged, normally consumes ~2800 kcal/day (or ~130 W) in the form of food to drive our metabolism. (In the affluent U.S. society, the Dept of Agriculture reports that in 1909 the daily per capita consumption was ~3500 kcal, and in 1994 it was ~3800 kcal.) This energy, gained directly from that stored in other (plant and animal) organisms and only indirectly from the Sun, is sufficient to maintain our body structure and T (37°C) as well as to fuel our physiological functions and tetrapodal movements during our daily tasks. (To avoid confusion, note that the thermodynamical definition of a calorie, 1 cal = 4.2x10<sup>7</sup> erg—the amount of heat needed to raise 1 g of H<sub>2</sub>O by 1°C—does not equal a dietician's large Calorie with a capital "C," which is 10<sup>3</sup> times more energetic than a physicist's calorie.)

Metabolism is a genuinely dissipative mechanism, thus making a connection with previous thermodynamic arguments that some researchers might have considered applicable only to physical systems. Heat is generated continuously owing to the work done by the tissues among the internal organs of the body, including contracting muscles that run the heart, diaphragm and limbs, ion pumps that maintain the electrical properties of nerves, and biochemical reactions that break down food and synthesize new tissues. Here is a breakdown

of the flow of energy in our human bodies, and a further subdivision of metabolic activity:

movement (muscles)	15 W		
labor (muscles)	20		
metabolism	95	}	
	130 W	}	
		}	brain 20 W
		}	gastrointestinal 20
		}	heart 15
		}	kidneys 8
		}	muscles (internal) 15
		}	other internal 17

Therefore, with an average body mass of 70 kg, a typical adult man or woman maintains  $\Phi_m \approx 2 \times 10^4$  erg/s/g while in good health. Humans have mid-range mammalian metabolic values because our bodies house average complexity among endothermic mammals, all of which harbor comparable intricacy, including hearts, livers, kidneys, lungs, brains, muscles, and guts. Despite our manifest egos, our bodily selves do not have the highest energy rate density among animals, nor are we likely demonstrably more complex than many other mammalian species.

The energy budget derived here for humans assumes today's average, sedentary citizen, who consumes ~65% more than the basal metabolic rate of 1680 kcal/day (or  $\Phi_m \approx 1.2 \times 10^4$  erg/s/g) for an adult fasting while lying motionless all day and night. By contrast, our metabolic rates increase substantially when performing occupational tasks or recreational events—again, that's function, not structure. And once again,  $\Phi_m$  scales with the degree of complexity of the task or activity. For example, fishing leisurely, playing a violin, cutting a tree, and riding a bicycle require about  $3 \times 10^4$ ,  $5 \times 10^4$ ,  $8 \times 10^4$ , and  $2 \times 10^5$  erg/s/g, respectively (Ainsworth, *Compendium of Physical Activities Tracking Guide* [http://prevention.sph.sc.edu/tools/docs/documents\\_compendium.pdf](http://prevention.sph.sc.edu/tools/docs/documents_compendium.pdf) ). Clearly, jamming a musical instrument or balancing a moving bicycle are complicated functions, and therefore more energetically demanding activities, than waiting patiently for fish to bite. Thus, in the biological realm, the value-added quality of functionality does indeed count, in fact quantitatively so. Complex tasks actively performed by humans on a daily basis are typified by values of  $\Phi_m$  that are often larger than those of even the metabolically imposing birds, in part because birds cannot operate instruments or ride bicycles!

Here are some relevant comparisons of human-related  $\Phi_m$  values that do rise with task difficulty, noting that walking is a more complex activity than

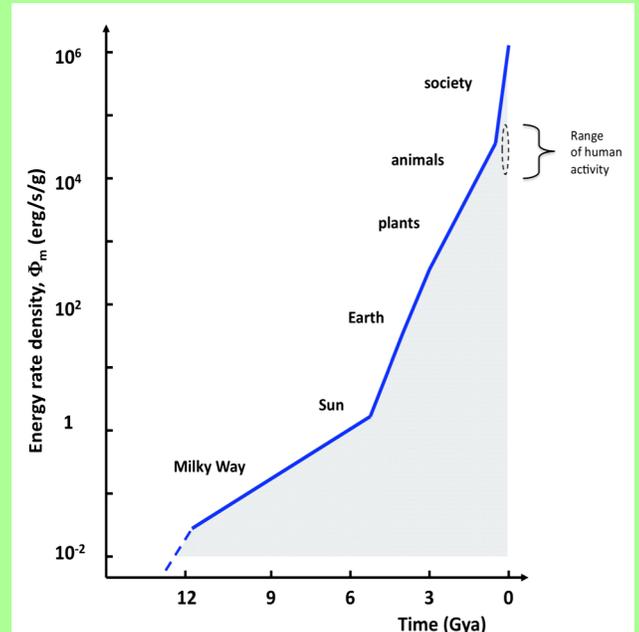
sleeping, and sewing and bicycling still more complex than any stationary task.

### Energy rate densities for some human activities

Human activity	Duration (hrs)	Rate (kcal/min)	$\Phi_m$ (erg/s/g)	Total (kcal)
sleeping/lying (basal)	8	1.1	11,000	540
sitting (reading, eating)	6	1.5	15,000	540
standing (at ease, indoors)	6	2.4	23,800	860
walking (steady, outdoors)	2	2.8	27,800	320
other (sports, exercise)	2	4.5	44,700	540
Total $\approx$ 2800 kcal/day				

This, then, is how humankind, like all of the animal world, contributes to the rise of entropy in the Universe: We consume high-quality energy in the form of ordered foodstuffs, and then radiate away as body heat (largely by circulating blood near the surface of the skin, by exhaling warm, humidified air, and by evaporating sweat) an equivalent amount of energy as low-quality, disorganized infrared photons. Like the stars and galaxies, we too among all other life forms are dissipative structures, thereby making a connection with previous thermodynamic arguments that some researchers might (wrongly) think pertinent only to inanimate systems.

The figure below shows the range of human-specific metabolic rates along our standard curve of rising complexity throughout all of natural history. The lower bound (basal rate) is midway for most mammals; the upper bound (active rate) typical of most birds in flight. Later, in the Advanced Track for the CULTURAL EPOCH, we shall encounter even higher energy rate densities for humans collectively, that is, for society as an integrated system. Indeed, humankind advancing, along with its artificially invented technological gadgets, are most evident near the (current) top of this iconic graph of  $\Phi_m$  throughout all of historical time.



*This graph repeats the essence of an earlier one (cf, end of Advanced Track for PARTICLE EPOCH), suggesting  $\Phi_m$  as a measure of rising complexity over all historical time. The dashed oval includes the range of energy-using metabolisms for humans specifically. It is within this small range along this large plot that the many varied complex activities of individual humans are expressed, noting that bicycling and running, for example, have higher energy rate densities than sewing or walking, whereas sleeping has the lowest of all.*

### Brains

Regarding brains, which nuclear magnetic resonance (fMRI) imaging shows are always electrically active regardless of the behavioral posture (even while resting) of their parent animal bodies, they too derive nearly all their energy from the aerobic oxidation of glucose in blood; thus, for brains, basal and active rates are comparable. Similar trends in rising complexity noted above for bodies are also evident for brains, though with higher  $\Phi_m$  brain values for each and every animal type—much as expected since cerebral structure and function are widely considered among the most complex attributes of life forms (Allman, *Evolving Brains*, Sci Amer Bks, New York, 1999; Jerison, *Evolution of the Brain and Intelligence*, Academic Pr, NY, 1973). Here, some quantitative details are compiled from many sources, again treating brains as open, non-equilibrium, thermodynamic systems, and once more casting the analysis of energy flow through them in terms of energy rate density. (While acknowledging several other potentially useful neural metrics—cortical

neuron numbers, encephalization quotients, brain/body ratios (Roth, and Dicke, *Trds Cog Sci*, v9, p250, 2005)—I specifically examine brains here for their  $\Phi_m$  values in order to be scrupulously consistent with my proposed complexity metric of energy rate density for all complex systems.) However, brain metabolic values culled from the literature often suffer, as noted above for bodies, from a lack of standard laboratory methods and operational units; many reported brain masses need to be corrected for wet (live) values (by multiplying measured *in vitro* dry masses by a factor of 5 since *in vivo* life forms, including brains, are ~80% H<sub>2</sub>O). Note also that the ratio of brain mass to body mass (used by some neuroscientists as a sign of intelligence) differs from the ratio of brain power to brain mass (which equals  $\Phi_m$ ), nor is "brain power" the same as that term used in colloquial conversation, rather here it literally equals the rate of energy flowing through the cranium.

This section makes no attempt to survey brains comprehensively, rather to synthesize them broadly, so representative mean values of brain  $\Phi_m$  will suffice for a spectrum of extant animals. Comparing mammals and reptiles,  $\Phi_m \approx 10^5$  erg/s/g for mice brains (in contrast to  $\sim 4 \times 10^4$  for their whole bodies) exceeds  $\sim 5 \times 10^4$  erg/s/g for lizard brains ( $\sim 3 \times 10^3$  for their bodies; Hulbert and Else, *Am J Physio-Reg. Integr. Comp. Physio*, v241, p350, 1981); this is generally the case for all such animal taxa as  $\Phi_m$  values are somewhat greater for mammal brains than those for reptile brains by factors of 2-4, and those for mammal bodies by roughly an order of magnitude (Hofman, *Quar Rev Bio*, v58, p495, 1983). The great majority of vertebrate fish and amphibians show much the same 5-10 times increase in brain over body  $\Phi_m$  values (Freeman, *Bio. Bull.*, v99, p416, 1950 Itazawa and Oikawa, *Cell & Mol Life*, v39, p160, 2005) with, as often the case in biology, some outliers (Nilsson, *J Exp Bio*, v199, p603, 1996). Even many invertebrate insects show several factors increase in  $\Phi_m$  values for their brains ( $\sim 5 \times 10^4$ ) compared to their bodies ( $\sim 10^4$ ), most notably the flying insects (Kern, *Comp Biochem & Physio*, v81A, p501, 1985). However, for brains in particular, ectotherms generally have only slightly lower values of  $\Phi_m$  than endotherms, the reason being that on a cellular level brains function in essentially the same way for both warm- and cold-blooded creatures and heat production plays a relatively minor role in brain energy expenditure (Soengas and Aldegunde, *Comp Biochem & Physio Pt B*, v131, p271).

Among mammals alone, primates, which evolved from tree-dwelling, insect-eating ancestors ~65 Mya, have

not only high brain/body mass ratios but also relatively high  $\Phi_m$  values ( $\sim 2 \times 10^5$  erg/s/g) for those brains. Although primates allocate for their brains a larger portion (8-12%) of their total bodily (resting) energy budget than do non-primate vertebrates (2-8%) (Hofman, *Quar Rev Bio*, v58, p495, 1983; Armstrong, *Science*, v220, p1302, 1983; Leonard and Robertson, *Amer J Human Bio*, v4, p179, 1992), average primate brains'  $\Phi_m$  values tend to be comparable to those of brains of non-primates; brain mass-specific, allometric scaling is even slighter— $M^{-0.15}$ —than noted for bodies in the previous section on animals, causing  $\Phi_m$  brain values to remain approximately constant across 3 orders of magnitude in mammalian brain size (Karbowski, *BMC Biology*, v5, p18, 2007). As with bodies above, brains do not necessarily confer much human uniqueness; brains are special, but all animals have them, and our neural qualities seem hardly more than linearly scaled-up versions of those of other primates (Azevedo, et al, *J Comp Neuro*, v513(5), p532, 2009).

Brains of birds are also revealing, although the derisive term "birdbrain" is quite unfair to some avian species that demonstrate remarkable cognition (Isler and van Schaik, *Bio Lett*, v5, p125, 2009). On average, brains of birds are an order of magnitude larger than those of equivalently massive reptiles. Brain/body mass ratios for the cleverest birds, such as crows and ravens that display much intraspecies cooperation and social cunning, are comparable to those of some primates. Brain  $\Phi_m$  values are also comparable, again because less energy of a bird's total body metabolism is devoted to its brain, probably owing to the formidable energetic requirements of bodily flight. As noted in the next paragraph below, the most evolved primates (especially humans) direct to their brains as much as a quarter of their total body metabolisms, whereas birds, like all other animals, allocate much less. This then illustrates a subtle difference between brain/body ratios and relative  $\Phi_m$  brain comparisons, the latter a potentially better sign of intelligence—if only data were available.

**Human Brain:** The adult human brain—surely, and without anthropocentrism implied, among the most exquisite clumps of matter in the known Universe—has a cranial capacity of typically 1350 g and requires ~400 kcal/day (or 20 W) to function properly. Our brains therefore have  $\Phi_m \approx 1.5 \times 10^5$  erg/s/g, most of it apparently to support the unceasing electrical activity of myriad neurons. Such brain power per unit mass flowing through our heads is larger than for any living

primate—not merely ~10X higher  $\Phi_m$  than for our bodies, but also slightly higher than for the brains of our closest, comparably massive, ape relatives, including chimpanzees. This substantial energy-density demand testifies to the disproportionate amount of worth Nature has invested in evolved brains; occupying only ~2% of our total body mass yet accounting for 20-25% of the body's total energy intake (*ie*, total  $O_2$  consumption; Clarke and Sokoloff, in *Basic Neurochemistry*, 6<sup>th</sup> ed, Siegel, G.J. (ed.), Lippincott-Raven, NY, p637, 1999), our cranium is striking evidence of the superiority, in evolutionary terms, of brain over brawn. Thus, to keep thinking, our heads glow (in the far-IR) with as much energy as a small lightbulb; when the "light" goes out, we die.

Incidentally, our central nervous system's share of our total (basal) metabolic budget—the just mentioned ~20% of our total daily bodily energy intake—means that we devote 2-10X greater percentage of our body metabolism to our brain than any other anthropoids: the great apes (anthropoid primates) devote only 7-12% typically, other mammals (vertebrates such as rats, cats, and dogs, but excluding humans and primates) use 2-6%, and reptiles even less. Still, by all accounts, brains everywhere are energy-hungry organisms.

As with other structures, animate or inanimate, human brains have  $\Phi_m$  values that vary somewhat depending on level of development. The above paragraph pertains to a mature adult brain, which typically consumes ~20% of the body's total energy consumption. By contrast, the brain of a newborn child utilizes ~60% of the energy acquired, a not surprising result given that a human's lump of neural matter doubles in size during the first year of life and synapse formation is most dramatic in the pre-school years. Thus,  $\Phi_m$  can average several times larger for an infant brain than for an adult brain. This pattern is evident throughout cosmic evolution: For planets, for example, substantially more energy was needed during formative development, but less is now needed to maintain them (*cf*, Advanced Track for PLANETARY EPOCH). Much the same pertains to stars, too, since their formative, protostellar stages have high energy rates (*cf*, Advanced Track for STELLAR EPOCH). Likewise, as noted above in the section on animals, during ontological development many organisms change from a higher to lower metabolic rate.

**High  $\Phi_m$ —High Complexity:** The tendency for complex brains to have high  $\Phi_m$  values, much as for complex whole animal bodies above, can be tentatively

correlated with the evolution of those brains among major taxonomic groups (Allman, *Evolving Brains*, Sci Amer Bks, NY, 1999). Further, more evolved brains tend to be larger relative to their parent bodies, which is why brain-to-body-mass ratios also increase with evolution generally—mammals more than reptiles, primates notable among mammals, and humans foremost among the great apes (Roth and Dicke, *Trds Cog Sci*, v9, p250, 2005; Hofman, *Quar Rev Bio*, v58, p495, 1983).

Relatively big brains are energetically expensive. Neurons use energy as much as 10X faster than average body tissue to maintain their (structural) neuroanatomy and to support their (functional) consciousness; the amount of brain devoted to network connections increases disproportionately with brain size and so does the clustering and layering of cells within the higher-processing neocortex of recently evolved vertebrates (Jarvis, *et al*, *Nature Rev Neurosci*, v6, p151, 2005; Stevens, *Nature*, v411, p193, 2001). Much of this accords with the "expensive-brain hypothesis" (Aiello and Wheeler, *Current Anthro*, v36, p199, 1995; Isler and van Schaik, *Bio Lett*, v2, p557, 2006), which posits that high brain/body ratios are indeed more energetically costly, at least for mammals and many birds, that energy flow through brains is central to the maintenance of relatively large brains, especially for primates, and that relatively large brains evolve only when either brain energy input increases or energy allocation shifts to the brain from some other bodily organ or function. Although the human brain's metabolic rate is not much greater than for selected organs, such as the stressed heart or active kidneys, regional energy flux densities within the brain greatly exceed (often by an order of magnitude) most other organs at rest.

The pressures of social groups and social networking might also direct growth in brain size, cognitive function, and neurophysiological complexity along insect, bird, and primate lineages (Dunbar, *Ann Rev Anthro*, v32, p163, 2003; Smith, *et al*, *Proc Roy Soc London, Series B*, 2010, in press). Human brain size has increased dramatically during the past few My, in contrast to those of our great ape relatives. Much field work has been devoted to understanding how the challenges of living in changing environments or even in stable social groups might have beneficially enhanced cognitive abilities among primates, especially humans, during this time. However, in the spirit of the present research program outlined in these Advanced Tracks that emphasizes energetics writ large throughout natural history, the use of energy by brains may well be

a contributing factor, and perhaps even a prerequisite, in the evolution of brains and of their increased brain-to-body-mass ratios (*cf.*, Advanced Track for BIOLOGICAL EPOCH). Indeed, the above-mentioned expensive-brain hypothesis predicts that relatively larger brains can evolve only when either energy input increases from the environment or when there is a reallocation from another expensive body function, such as energy-expensive tissues like the digestive tract in primates and the pectoral muscles in birds.

Throughout biology generally, brain tissue is known to be energetically expensive, requiring nearly an order of magnitude more energy per unit mass than several other body tissues at rest. This high energy cost on the brain might therefore constrain natural selection's effect on an animal's survival and/or reproductive success. Recent data on a large sample of basal metabolic rates and brain sizes among vertebrates do suggest that energy flow through the brain is key in maintaining relatively large brains, especially for non-human primates. Furthermore, among ~550 species of mammals, the brain-to-body-mass ratio displays a positive correlation with metabolic rate, and even among ~400 species of birds the expensive-brain hypothesis holds (Isler & vanSchaik, *Biol Lett*, v5, p125, 2009).

Throughout the biosphere, the high-energy cost of brains might reasonably limit brain size and constrain natural selection's effect on an animal's survival or reproductive success; indeed, the brain is the first organ to be damaged by any reduction in O<sub>2</sub>. This, then, is the observed, *general* trend for active brains *in vivo*: Not only are brains voracious energy users and demonstrably complex entities, but evolutionary adaptation also seems to have favored for the brain progressively larger allocations of the body's total energy resources.

Among more recent prehistoric societies of special relevance to humankind, the genus *Homo's* growing encephalization during the past ~2 My may be further evidence of natural selection acting on those individuals capable of exploiting energy- and protein-rich resources as their habitats expanded (Foley and Lee, *Phil Trans Roy Soc London, Series B*, v334, p223, 1991). By deriving more calories from existing foods and reducing the energetic cost of digestion, cooking was likely central among cultural innovations that allowed humans to support big brains (Wrangham, *Catching Fire: How Cooking Made Us Human*, Basic Books, NY, 2009). Energy-based selection would have naturally favored

those hominids who could cook, freeing up more time and energy to devote to other things—such as fueling even bigger brains, forming social relationships, and creating divisions of labor, all of which arguably advanced culture. As with many estimates of human intelligence, it's not absolute brain size that apparently counts most; rather, brain size normalized by body mass is more significant, just as the proposed  $\Phi_m$  complexity metric is normalized by mass, here for brains as for all complex systems at each and every stage along the arrow of time, from big bang to humankind.

The net finding for brains, broadly stated though no less true for the vast majority of animals, is that their  $\Phi_m$  values are systematically higher than for the bodies that house them, nearly all of their brain values falling within a rather narrow range between  $\Phi_m$  values for lower biological systems (such as plants) and higher cultural ones (such as societies). Although absolute brain masses span ~6 orders of magnitude, from insects to whales, their  $\Phi_m$  brain values cluster within a few factors, more or less depending upon their mass and evolutionary provenance, of ~10<sup>5</sup> erg/s/g.

## Ecosystems

The past ~0.5 Gy of evolution has caused our biosphere to become populated with a multitude of ecosystems, each exquisitely adapted to different environmental conditions and each having the means to sustain ongoing "traffic patterns" of incoming resources, outgoing wastes, and distributed energy—all so intricate and so optimized that a human-made replica of any one such system still eludes us. Day in and day out, these mostly ancient ecological systems continue on quietly, efficiently, and cleanly, each self-controlled by the steady flow of energy through Earthly environs. With occasional stress to their surroundings, ecosystems manage to transform and regenerate, to respond to the checks and balances of Nature, to organize and reorganized yet again as did less complex systems before them. What the untrained eye sees as disorder and randomness in an overgrown woodlot, a dense rain forest, or a backyard stream are actually splendidly ordered and impressively complex ecosystems. More than that, these are the life-support systems essential to humankind's survival.

We are indeed entering the Life Era and the resulting landscape might be as new to us, and the ecosystems surrounding us, as it was to the newly formed atoms that changed the early Radiation Era into

the Matter Era >10 Gya (cf, Advanced Track for PARTICLE EPOCH).

On a larger and more complex scale than individual ecosystems is the global biosphere itself, arguably the integrated sum of all Earth-based ecosystems. Others suggest it is more than that, namely, that the whole biosphere is greater than the sum of its parts, the essence of emergence and holism once again. Modern-day Gaians—disciples of the Gaia hypothesis (Lovelock, *Gaia*, Oxford U Pr, 1979) and descendants of worshippers of the terrestrial Greek goddess—go even further, claiming planet Earth to be a single, vast superorganism, indeed one that is itself alive (“strong Gaia”), a view not inconsistent with our expansive definition of life:

*Life is an open, coherent, spacetime structure kept far from equilibrium by a flow of energy through it—a C-based system operating in a H<sub>2</sub>O-based medium with higher forms metabolizing O<sub>2</sub>.*

Reality or metaphor, the idea of Gaia contends that living creatures affect the composition of Earth's atmosphere (and not just the other way around), both environment and life acting in a coupled way so as to regulate the former for the benefit of the latter (“weak Gaia”)—actually an old notion dating back well more than a century and one that need not be at odds with neo-Darwinism. Microorganisms, for sure, excrete metabolic products that modify their environmental conditions, a property that has clearly enhanced their own species' survival, which not coincidentally extends, and most impressively so, over billions of years. Accordingly, living things have seemingly prevented drastic climatic changes throughout much of Earth's history, as evolution has endowed organisms with improved ability to keep surface conditions favorable for themselves.

For example, as our Sun ages, thus becoming more luminous and sending more heat toward Earth, life responds by modifying Earth's atmosphere and surface geology to keep the climate fairly constant—a kind of “geophysiological thermostat” that basically adjusts CO<sub>2</sub> levels down by preferentially getting wrapped up in calcium carbonate (CaCO<sub>3</sub>) under high T, thereby cooling the atmosphere; if those T go too low, the reaction to form carbonate decreases and the amount of CO<sub>2</sub> and the atmospheric T both rise, the whole CO<sub>2</sub> cycle acting as positive feedback that keeps H<sub>2</sub>O liquid and Earth habitable. And if the biosphere can be considered at least as a self-regulating and perhaps even self-reproducing system, then might not the concept of Gaia extend to the stars and galaxies

beyond? By thinking broadly enough, one could conceivably reason that stars, too are reproductive; as noted in the Advanced Track for the STELLAR EPOCH, from the demise of some stars come the origins of other stars—a cyclical, generative (and not just developmental) change from galactic clouds to nascent stars to exploded supernovae, and so on through many generations, the whole process repeating endlessly in a kind of cosmic reincarnation. If this further blurs the distinction between animate and inanimate systems, then we have achieved another of our stated objectives for this research program; they differ not in kind, rather only in degree of complexity.

### In Sum

The thermal gradients needed for an energy flow in Earth's biosphere could not be maintained without the Sun's conversion of gravitational and nuclear energies into radiation that emanates outward into unsaturable space. Were outer space ever to become saturated with radiation, all T gradients would necessarily vanish, and life among many other ordered structures would cease to exist; this is essentially a version of Olber's paradox, a 19<sup>th</sup>-century puzzle inquiring, in view of the myriad stars in the heavens, why the nighttime sky is not brightly aglow. That space is not now saturated (or the nighttime sky fully illuminated) can be attributed to the expansion of the Universe, thus bolstering the suggestion that the dynamic evolution of the cosmos is an essential condition for the order and maintenance of all organized things, including not only Earth, but also life itself. All the more reason to welcome life within our cosmic-evolutionary cosmology, for the observer in the small and the Universe in the large are not disconnected.

Plants and animals among biological systems regularly exhibit intermediate values of  $\Phi_m = 10^{3-5}$  erg/s/g—and human bodies rightfully are not the most complex among them. So much for human uniqueness; all animals are outstanding in their own ways, and although we do have special traits, so do bees, giraffes, and other large vertebrates.

For plant life on Earth, energy rate densities are well higher than those for galaxies, stars, and planets, as perhaps best illustrated by the evolution of the most dominant process in Earth's biosphere—photosynthesis:

- from microscopic protists >470 Mya ( $\Phi_m \approx 10^3$  erg/s/g)
- to gymnosperms ~350 Mya (~ $5 \times 10^3$ )
- to angiosperms ~125 Mya (~ $7 \times 10^3$ )

- to highly efficient  $C_4$  plants ~30 Mya ( $\sim 10^4$ ).

Onward across the bush of life (or the arrow of time)—cells, tissues, organs, organisms—much the same metric holds for animals while evolving and complexifying. For adult bodies (much as for brains, which have order of magnitude larger  $\Phi_m$ ), the temporal trend of rising  $\Phi_m$  continues:

- from fish and amphibians 370-500 Mya ( $\Phi_m \approx 4 \times 10^3$  erg/s/g)
- to cold-blooded reptiles ~320 Mya ( $\sim 3 \times 10^3$ )
- to warm-blooded mammals ~200 Mya ( $\sim 4 \times 10^4$ )
- to birds in flight ~125 Mya ( $\sim 9 \times 10^4$ ).

Here, system functionality and genetic inheritance, two factors above and beyond mere system structure, help to enhance complexity among animate systems that are clearly living compared to inanimate systems that are clearly not. In either case, energy is fuel for change, apparently (and partly) selecting systems able to utilize increased power densities, while driving others to destruction and extinction—all in accord with neo-Darwinism's widely accepted modern synthesis. Energy flow and natural selection likely operate in tandem as systems evolve—the former utilized by those systems advantageously suited to their randomly changing environments, and the latter non-randomly eliminating those unable to do so.

Life does seem to operate optimally within certain limits and not surprisingly also has an optimal range of normalized energy flow; the vast majority of  $\Phi_m$  values for both plants and animals generally fit neatly (again with some exceptions and overlaps) between inanimate physical systems having lower  $\Phi_m$  and more advanced cultural systems having higher  $\Phi_m$ . That the trend of living systems increasing their  $\Phi_m$  values with evolution over generations is imperfect should not deter us, for the great diversity of animals will always disclose wide physiological adaptations to extreme environments, and in any case no useful investigation can proceed if it must justify every exception or outlier. The challenge for zoology is to explain the vast diversity of animal species on Earth and if it can do so, even approximately, by means of a single metric, then all the more insightful.

The rise of  $\Phi_m$  *generally* parallels the emergence of many of the major evolutionary stages of life: eukaryotic cells are more complex than prokaryotic ones, plants more complex than protists, animals more complex than plants, mammals more complex than reptiles, and so on. Claims regarding the role of  $\Phi_m$  in evolutionary advances are broad and general, not

specific and detailed along individual lineages; the objective in this research program is to identify how well life forms fit quantitatively within the larger scenario of cosmic evolution. Indeed, similarities between galaxies and animals (as briefly noted earlier) are amply evident, including variation within category types, adaptation to changing conditions, and possibly even natural selection among early, interacting galaxies (Volonteri and Rees, *Astrophys J*, v650, p669, 2006), much as argued for stars and plants, respectively, in the Advanced Track for the STELLAR EPOCH and earlier in this Advanced Track for the BIOLOGICAL EPOCH. All these systems are open to their environments, with matter and energy flowing in while wastes flow out, indeed all resemble metabolisms at work on many scales. Our Milky Way Galaxy is as much a metabolic system, albeit simpler, as any life form—transacting energy while forming new stars, cannibalizing dwarf galaxies, and dissolving older components. Whether stars, galaxies, or life itself, the salient point seems much the same: The basic differences, both within and among all of Nature's many varied systems, are of degree, not of kind. We have discerned a common basis upon which to compare all material structures, from the early Universe to the present Earth—again, from big bang to humankind inclusively.