Dynamic genomes, morphological stasis, and the origin of irreducible complexity

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Abstract

In spite of an enormous amount of genetic flux in plants and animals, the basic genetic processes and major molecular traits are believed to have persisted essentially unchanged for more than three-and-a-half billion years, and the molecular mechanisms of animal ontogenesis for more than one billion years. Moreover, systematics is based on virtually constant characters in space and time – otherwise this important branch of biology would not be possible. Additionally, the fossil record displays a regular pattern of abrupt appearances of new life forms (instead of their arrival by innumerable small steps in a

Darwinian manner), followed by the constancy of higher systematic characters often from the genus level upwards, in many cases succeeded by an equally abrupt disappearance of the major life forms, which have died out after different periods of time. As the doyen of the synthetic theory, Ernst Mayr of Harvard, has just recently admitted, this constancy (stasis) of life forms in the face of tremendously dynamic genomes is one of the greatest problems of contemporary evolutionary biology and demands an explanation. In agreement with several researchers, I refer to arguments and facts supporting the view that irreducible complexity (Behe) in combination with specified complexity (Dembski) characterize basic biological systems and that these hypothesesmight point to a non-gradualistic solution of the problem.

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Introduction

   Up to the 1950s the genome was imagined to consist of rather autonomous genes positioned on chromosomes like beads on a string specifying organismic development from their fixed locations. Moreover, by relatively infrequent mutations the genes could produce alleles thus providing the basis for evolution in Mendelian populations. Additional variation for evolution was guaranteed by equally rare gross and small chromosome mutations, which would rearrange the genes by duplications, inversions, and translocations (including varying position effects of gene functions) as well as by multiplications of single chromosomes (trisomy) or entire chromosome sets (polyploidy).
   In spite of the variation deemed to be necessary for evolution, the comprehensive message was that of rather constant genes in an overall fairly constant genome so much so that when Barbara McClintock proposed her first papers on the discovery of transposable elements (TEs) as parts of evidently much more dynamic genomes to a larger audience at the beginning of the 1950s, her work was either ignored, or met with "puzzlement", or, in some cases, even "hostility" (for further details, see [3, 4, 46, 69]).
   For the question of the origin of species and higher systematic categories including humans, the dominant genetic view of the 1950s meant a

pervasively slow, continuous and gradualistic mode of evolution in the sense defined by Darwin some 100 years earlier. He had proposed his theory in terms of selection of innumerable "small steps", "steps not greater than those separating fine varieties" "insensibly fine steps", "for natural selection can act only by taking advantage of slight successive variations; she can never take a leap, but must advance by the shortest and slowest steps" [16, 17]. This view has also become an integral part of the modern synthesis or synthetic theory of evolution, born in the late 1930s and early 1940s [24, 58], and is still dominating the theory to this very day [18, 36, 37, 53, 46, 65-67, 83]. However, according to the modern synthetic theory of evolution Darwin's insensibly fine steps are being caused by "mutations with slight or even invisible effects on the phenotype" [66], instead of Darwin's "changed habits" that he assumed to produce inherited effects.

A reversal of the previous ideas of the constancy of the genome only occurred in the 1960s when gene structure and gene regulation were more profoundly elucidated (Jacob-Monod model, bacterial insertion sequences and transposon-encoded antibiotic resistance). When molecular biology further advanced to clone and sequence eukaryotic genes, the disinterest, puzzlement, and hostility of the 1950s rapidly transformed into approval and recognition of McClintock's merits, culminating in the Nobel Prize for Physiology/Medicine in 1983 – a Nobel Prize, as it were, for the discovery of 'dynamic genomes'. Also, this constituted a fresh impetus for many research groups around the world to concentrate or expand their work not only on transposable elements but also on a range of further dynamical aspects of the genomes in the plant and animal kingdoms, most of which are briefly mentioned below.

As for the question whether this transformation of ideas from an overall rather constant genome to a strongly dynamic one was of any consequences for the theories regarding the origin of species, we will come back to this cardinal point under the subtitle of "new research topics (f)".

Dynamic genomes

The ensuing paragraphs present a brief reminder enumerating most of the different aspects of genomic changes so far known, followed by some simple illustrative explanations:

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1) Gene mutations; average rate 10^{-5} per gene per generation. For the Present generation of humans, this means that each gene has recurrently mutated more than 100,000 times (more than 6,2 billions individuals, some 30,000 to 40,000 genes).

2) Transposons – active and dormant (transpostion rate into functional genes up to 10 $^{-2}$ per generation); nearly 80% of the overall DNA mass of the maize genome appears to consist of transposon-derived sequences, 90% in Vicia faba, 45% in Homo sapiens (to mention just a few of the many further spectacular examples) [3, 4, 9, 40, 46, 50, 61-64, 79, 87]. At present there is a lively discussion among Biologists whether most of these sequences really constitute "junk" DNA and how much may be of functional value [34, 84].

3) Repetitive elements; detected in eukaryotes, their length varies from tens to thousands of bases. The highly repetitive fraction (5-100 bp) is repeated up to 10^6 times and consists of simple sequence DNA (constitutive heterochromatin, especially clustered close to chromosome ends and the centromere). The middle repetitive fraction consists of 100-500 bp, which occur ca. 100 to about 10,000 times in a genome (e.g. genes for coding for ribosomal RNA, transfer RNA, histones) [30, 45, 71].

4) Pseudogenes; a derivative of a functional eukaryotic gene thought to be produced by reverse transcription of messenger RNA and generally assumed to be non-functional due to rearrangements, disadvantageous point mutations (producing, for instance, stop codons), and absence of promoter-, intron-, and enhancer sequences. However, some functional exceptions have recently been detected [2, 34, 39, 43].

5) Gene duplication and amplification; thought to be up to 20 times more frequent than gene mutations [56]; up to 10% of the cells in animal and human tissue cultures can have gene amplifications [49, 50]

6) C-value-paradox; due to transposon-induced and further changes in DNA mass, the DNA amounts in the haploid genomes of closely related species, can differ enormously from each other (species of the genus Vicia, for example, vary between 1.8-13.3 pg [72, 73]. But even within the same non-polyploid plant species the C-value can vary notably even though some original examples for this phenomenon proved to be due to technical problems [8].

7) Gene- and genome amplification in ontogenetic development; rDNA-Amplification in Xenopus is one of the prime examples: in its oogenesis the 500 rDNA genes are replicated 4,000 times resulting in 2,000,000 copies; gene amplication is also found in some insects and protozoa [45]. On the other hand, genome amplification occurs regularly in special tissues of many organisms (e.g. in liver cells of mammals, in tapetum tissue of angiosperms).

8) Chromosome rearrangements: include any structural change of a Chromosome resulting in deletions, duplications, inversions, and

translocations. In addition to some morphological features, many closely related plant and animal species can also be distinguished by more or less small chromosome rearrangements [64].

9) Molecular clocks: nucleotide and amino acid substitutions were once believed to occur so regularly that a molecular clock measuring divergence time between different groups of plants and animals could be established. Although the clock seems to run often very irregularly, there is no question that many substitutions due to point mutations have occurred within and between species. In man the substitution rate was found to be faster in mitochondria than in the nucleus [32, 33].

10) Molecular drive: according to Gabriel Dover, a cohesive mode of 'species' evolution relevant for many gene families and noncoding sequences perhaps as a consequence of molecular mechanisms of turnover within the genome [25, 26].

11) Flax genotrophs: different forms of flax (Linum usitatissimum) generated by a process of environmentally induced changes in flax genomes, which "does not appear to be the generation of random variation". Cullis et al. assume that the heritable changes in this species are due to specific rearrangements at distinct positions of the genome. Highly repetitive, middle-repetitive, and low-copy-number sequences have all been shown to be involved in the polymorphisms detected, and sequence alterations of specific subsets of 5SrDNA have been identified [13, 14].

12) Methylation: methyl transferases can transfer a methyl group from a methyl donor to an acceptor molecule (DNA, RNA, protein). Could be important for the regulation of gene functions in natural populations [12].

13) Genomic shocks: extreme stress situations for genomes (artificially produced, for instance, by protoplast generation and tissue cultures in plant cells) are thought by B. McClintock to bring about accelerated species formation [69].

14) Exon shuffling: intron-mediated recombination of exons is assumed to produce new functional genes.

15) Gene expression: due to alternative splicing and alternative promoters thousands of protein isoforms can be generated from a few genes [70].

For further examples for dynamic aspects of the genome, see the present volume
(V(D)J   recombination, VNTR alleles, horizontal DNA-transmission and

others).

Genetic conservation

Becoming fully aware of the features specifying dynamic genomes as mentioned above, the overall impression most students of genetics inevitably have gained, could perhaps best be stated with the Greek philosopher Heraclitus of Ephesus (about 535 BC to ca. 475 BC), describing the essence of nature by his famous verdict: panta rhei kai ouden menei ("all things flow, nothing abides"). For almost 'everything' in the plant and animal genomes seems to be in a permanent process of flux so that in the long run one should hardly expect any constant genomic (and corresponding morphological) characters at all.

Thus, being cognizant of this background information presented on the overall genetic flux in most genetic papers, reviews and textbooks [e.g. 30, 40, 85], the following description of some further basic genetic facts appears to be absolutely astounding.

Lazcano and Miller report [48]:

"After the explosive metabolic that took place soon after the beginning Of life, the basic genetic processes and major molecular traits have persisted essentially unchanged for more than three-and-a-half billion years, perhaps owing to the linkages of the genes involved and the complex interactions between different metabolic routes. At a macroevolutionary level, this represents a case of conservation that is even more striking than the maintenance of the major body plans that appeared at the base of the Cambrian, and which have remained basically unchanged for 600 million years."

Moreover, at the beginning of the 1990s, a series of discoveries of utterly unforeseen constant or almost constant gene functions in developmental biology had led to a chain of comments describing the extraordinary amazement elicited by these findings. The following few examples may convey the extent of astonishment, which had seized most minds of the biological community at that time:

Shapiro concurs as follows [78]:

"I think it was a big surprise when a human cDNA clone was found to correct a cdc mutation in yeast. One has only to read News and Views in Nature to find many similar examples. This was really a surprise to people. The degree of conservation in function between proteins from different organisms is something that was totally unexpected."

He also mentioned the reason why this conservation was so totally unexpected:

> "The prevailing idea was that each particular gene is going to accumulate many changes over long periods of time and that this was how one organism turned into another."

In a similar vein De Robertis commented [20]:

> "[I]t is safe to say that no one would have predicted the degree of conservation in the molecular mechanisms that control development…. the molecular mechanisms that determine the antero-posterior (A-P) axis has been conserved in evolution to a degree beyond anyone's wildest expectations…"

Nüsslein-Volhard speaks of such facts thus [74]:

> "[O]ne great surprise of the past five years has been the discovery that very similar basic mechanisms, involving similar genes and transcription factors, operate in early development throughout the animal kingdom."

Lewin illustrated the problem by the example of the Hox loci [49]:

> "The most striking feature of organization of the Hox loci still defies explanation: why has the organization of the cluster, in which genomic position correlates with embryonic expression, been maintained in evolution?"

Subsequently he discussed several possibilities to answer the question, but thinks that no convincing solution could be given at present. Hultmark compared vertebrates with insects and commented on some molecular similarities as follows [42]:

> "Insects look nothing like vertebrates, and their organ systems seem to be built on entirely different principles. Nevertheless, as we get a better understanding of how these systems operate at the molecular level, unexpected similarities are emerging. Among them must must now be counted similarities in the respective immune defences, as reported in two recent papers."

Even more staggering were the discoveries of molecular similarities involved in the development of supposedly fully convergent anatomical features. After an account onnumerous molecular similarities within the vertebrates, Cohn and Tickle continue [11]:

"Even more remarkable is the conservation of molecules involved in patterning insect wings and vertebrate limbs. Signalling molecules common to vertebrates and Drosophila limbs include Shh (hh), Wn 7a (wg) and Bmp (dpp). The recent finding that chick LMX1 and the related apterous gene in Drosophila are expressed dorsally in wing buds and imaginal discs is striking."

No theorist in evolutionary biology will ever derive chicken and insects from a winged common ancestor, and yet, clearly related sequences are specifically expressed in wing buds and imaginal disks.

Thus, the "basic genetic processes and major molecular traits" are thought to have "persisted essentially unchanged for more than three-and-a-half billion years", and the molecular mechanisms of animal ontogenesis for more than a billion years. On the background of the prevailing idea of the synthetic theory from the 1940s well into the 1990s, that 'each particular gene is going to accumulate many changes over long periods of time and that this was how one organism turned into another' (Shapiro), as well as that of the many features of dynamical genetics as briefly summed up above (beginning in the 1960s and reaching its climax in the early 1990s), the discovery of the molecular conservation just documented was, indeed, 'totally unexpected' (Shapiro) and revealed, in fact, a constancy of gene functions 'to a degree beyond anyone's wildest expectations' (De Robertis).

Similar phenomenon have been described in plants, too [90].

Now, the fact that so many "old features" are molecularly still with us, nearly inevitably leads us to the basic biological question whether there are correspondingly constant morphological features in the plant and animal kingdoms – which point will be the topic of the next paragraphs.

Morphological stasis

The general constancy of systematically relevant features

Two of the great pioneers of general and systematic botany, Augustin Pyrame De Candolle, and Christian Konrad Sprengel emphasized a point nearly forgotten in our evolutionary world of today when they made the following comments on the cardinal characters distinguishing species and genera from each other [19] - and we would like to invite our readers to especially focus their attention on the use of the terms "invariable" (invariably), "invariableness" and "constant" in the ensuing paragraph:

"By Species (species), we understand a number of plants, which agree with one another in invariable marks. In this matter every thing depends upon the idea of invariableness. When an organ, or property of it is changed neither by difference of soil, of climate, or of treatment, nor by continued breeding, this

organ or property is said to be invariable. When, for instance, we have remarked for centuries, that Centifolia has always unarmed leaf-stalks, we say correctly, that this property of the Centifolia is invariable… What we know is, that from as early a time as the human race has left memorials of its existence upon the earth, the separate species of plants have maintained the same properties invariably…All properties of plants which are subject to change, form either a Subspecies (subspecies), or a variety (varietas)… By a Genus we understand the sum of the species which agree in certain constant properties of the essential parts… The generic character (character genericus) is the expression of the peculiar and invariable marks by which a genus of plants is distinguished from all others… every generic character must state shortly and distinctly the common marks which belong invariably to all species of the same genus… The generic character of the higher plants is borrowed solely from the organs of fructification."

Since these expositions on "invariableness" in systematics are almost 200 years old and were, indeed, first published 40 years before Darwin's Origin of Species in 1859, let us directly turn to some comments of modern systematics on the same questions. One hundred and thirty years later Stace comments in agreement with almost all contemporary authors [80]:

"Although flowers are no longer regarded as 'essential' and therefore taxonomically particularly important, they still provide the bulk of information contained in the diagnosis of angiosperm taxa. This is because in general the flowers appear to be more conservative than do most other organs."

In an earlier chapter Stace had already remarked that "This reliance on the flower is remarkable when one considers that most of the time the majority of angiosperms lack any flowers at all". This appears to be also true for seed- and fruit-structures. Concerning the conservative key systematic characters he further points out that "endomorphic vegetative characters are more conservative than exomorphic ones" and continues on p. 183 of his book [80]:

"Conservative characters are…most useful in delineating the higher taxa, where the emphasis is on the recognition of similarity between the members of a taxon."

Yet, for species and systematic categories below the species, he insists that the non-conservative characters seem to dominate.

Considering the general shift in systematics during the last 250 years, Stace is most probably correct in his analysis (Haeckel's verdict for zoology that "related species which had been united within a genus by Linné and within a family by Cuvier, now constitute an inclusive order with several families and many genera" [41] – implying that many of Linné's species have been elevated to the position of genera during the last centuries – is also valid for botany; for

further details, see [53]). Hence, one may conclude that the essentials have hardly changed in morphological systematics: The invariable characters delineating species and genera according to Linné, Cuvier, De Candolle, Sprengel and many other pioneers of systematics have become the conservative characters delineating higher taxa of modern systematics including the morphologically defined genera, tribus and families of today.

Stasis of systematic categories in time: Some examples

Taking the descriptions and definitions of the plant species produced by Linné some 250 years ago in his Species Plantarum (1753) or of the animal species in his Regnum Animale a few years later (Systema Naturae 1758), we have no difficulty in identifying the different species today on the basis of his descriptions [51, 52]. The same is true for the drawings and descriptions of plant species by Leonhard Fuchs (1542) [31], and Tabernaemontanus (1588/1590) [88] on maize and many other plants. Moreover, Cuvier had absolutely no difficulty in identifying the mummified animals of old Egypt being several thousand years old (Cuvier, 1833) [15]. Yet, the names of species and genera have often been excessively evolved, almost regularly including some or even many synonyms.

If some 250 to 500 or even several thousand years is simply nothing on an evolutionary time scale, what about the last 2.3 million years of European life history? This is characterized by "comparatively slow rates of evolution" [47], and Lang continues: "At the end of the tertiary the organisms consisted of species, almost all of which can be assigned to present genera, a large section even to living species. This applies not only for the European flora but also for its fauna" and appears to be true for other parts of the world, too. Moreover the environmental conditions for this time period have been characterized as excessively varying, temperatures rising and falling producing among other effects a series of ice ages – and spite of all these environmental variations there was hardly any evolution at all. The actualistic inferences and conclusions drawn from present ecological indicator values to quaternary paleontology are based on "this obviously far-reaching constancy of life forms down to the species".

Additionally, about half of the genera of flowering plants found in geological formations dated to be 37 million years old have been assigned to present genera [81], and many well-known present plant families and genera have even been identified in cretaceous formations (taxa sometimes dated to be older than 100 million years before present).
Or, to take a glimpse at another well-known plant group, the bryophytes. Agashe reports [1]:

"Members of both the major groups of bryophytes, i.e. Hepaticopsida (liverworts) and Bryopsida (mosses), are well represented in the known fossils. However, a detailed comparative study with modern bryophytes indicated that

the group has remained almost unchanged since the Paleozoic time. Hence the fossil bryophytes do not help us much in understanding evolution except for the fact that they formed a prominent part of the vegetation from the Paleozoic onwards."

Thus, bryophytes are assumed to have existed "almost unchanged" for some 400 million years on earth.

A comprehensive survey about the phenomenon of constancy in the fossil record is beyond the scope of the present paper (for further details, see [10, 27-29, 35-38, 53, 58, 64, 68, 86]). The theory of punctuated equilibrium [27-29, 35-38], was developed to come to grips with the general phenomenon of abrupt appearance and stasis (constancy of the gestalt of organisms usually documented for millions of years) in the fossil record. The well-known "living fossils" in the restricted definition of the term ("They must today exhibit primitive morphological characters, having undergone little evolutionary change since dwindling to low diversity at some time in the past" [82]) are referring only to a very small minority of life forms also revealing that general phenomenon of abrupt appearance and constancy described by the theory of punctuated equilibrium as deduced from the paleontological documents [58]. Ernst Mayr, the doyen of the modern synthesis, has just recently called the phenomenon of morphological stasis (constancy) one of the basic unresolved problems of evolutionary theory specifying the problem in a recent interview as follows [67]:

"In evolutionary biology we have species like horseshoe crabs. The horseshoe crab goes back in the fossil record over two hundred million years without any major changes. So obviously they have a very invariant genome type, right? Wrong, they don't. Study the genotype of a series of horseshoe crabs and you'll find there's a great deal of genetic variation. How come, in spite of all this genetic variation, they haven't changed at all in over two hundred million years while other members of
their ecosystem in which they were living two hundred million years ago are either extinct or have developed into something totally different? Why did the horseshoe crabs not change? That's the kind of question that completely stumps us at the present time."

All the living fossils investigated so far also reveal most or all of the dynamics of genome reshuffling as pointed out to above – from transposable elements to multiple promoters and enhancers.

In this context the point should be emphasized again that examples like the horseshoe crab are by no means rare exceptions from the rule of gradually evolving life forms in Darwin's sense (see above). In fact, we are literally surrounded by "living fossils" in the present world of organisms when applying the term more inclusively as "an existing species whose similarity to ancient ancestral species indicates that very few morphological changes have occurred over a long period of geological time" [85]. Furthermore, Darwin's argument of the imperfection of the geological record has systematically been refuted for many animal and plant groups during the last 150 years: some 200 million

macrofossils have been accumulated and catalogued in museums worldwide and there are, indeed, billions of microfossils (for a series of references, see [64]).

Nor is the phenomenon of this quite unexpected yet generally detected abrupt appearance and stasis of forms a discovery of recent research. Darwin himself commented such facts already in 1852 as follows: "When I see that species even in a state of nature do vary little and seeing how much they vary when domesticated, I look with astonishment at a species which has existed since one of the earlier Tertiary periods. This fixity of character is marvellous" [76].

Including the observations and papers of Cuvier (1769-1832), who is generally known to be the founder of comparative anatomy as well as modern paleontology, this unsolved problem is at least 200 years old and hardly anybody denies that it demands a rational explanation.

Now, since all these "old features", morphologically as well as molecularly, are still with us, the basic genetical questions should be addressed in the face of all the dynamic features of ever reshuffling and rearranging, shifting genomes, (a) why are these characters stable at all and (b) how is it possible to derive stable features from any given plant or animal species by mutations in their genomes?

The significance and origin of irreducibly complex systems
in biology

A first hint for answering the questions raised in last paragraph is perhaps also provided by Charles Darwin himself when he suggested the following sufficiency test for his theory [16]: "If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down." Darwin, however, stated that he could "not find out such a case" – which would, in fact, have invalidated his theory. Biochemist Michael J. Behe [5] has refined Darwin's statement by introducing and defining his concept of "irreducibly complex systems", specifying: "By irreducibly complex I mean a single system composed of several well-matched, interacting parts that contribute to the basic function, wherein the removal of any one of the parts causes the system to effectively cease functioning."

Among the examples discussed by Behe are the origins of (1) the cilium, (2) the bacterial flagellum with filament, hook and motor embedded in the membranes and cell wall and (3) the biochemistry of blood clotting in humans. Moreover, the traps of Utricularia (and some other carnivorous plant genera) [59] as well as several furtherapparatus in the animal and plant world appear to pose similar problems for the modern synthesis (joints, echo location, deceptive flowers etc.).

One point is clear: granted that there are indeed many systems and/or

correlated subsystems in biology, which have to be classified as irreducibly complex and that such systems are essentially involved in the formation of morphological characters of organisms, this would explain both, the regular abrupt appearance of new forms in the fossil record as well as their constancy over enormous periods of time. For, if "several well-matched, interacting parts that contribute to the basic function" are necessary for biochemical and/or anatomical systems to exist as functioning systems at all (because "the removal of any one of the parts causes the system to effectively cease functioning") such systems have to (1) originate in a non-gradual manner and (2) must remain constant as long as they are reproduced and exist. And this could mean no less than the enormous time periods mentioned for all the living fossils hinted at above. Moreover, an additional phenomenon would also be explained: (3) the equally abrupt disappearance of so many life forms in earth history. In a strict gradualistic scenario of the origin and evolution of life forms one would expect that – except in catastrophic events (also long denied in uniformitarian geology) like the Permian or Tertiary impacts – most species would continually adapt to varying environmental conditions. So most forms would not simply die out but continue to evolve gradually. However, this is not what has been found inpaleontolgy. Instead, most life forms appear abruptly, remain constant, and disappear equally abrupty from the world's scene (for the details, see [10, 27-29, 35-38, 53, 58, 64, 68, 86]. The reason why irreducibly complex systems would also behave in accord with point (3) is also nearly self-evident: if environmental conditions deteriorate so much for certain life forms (defined and specified by systems and/or subsystems of irreducible complexity), so that their very existence be in question, they could only adapt byintegrating further correspondingly specified and useful parts into their overall organization, which prima facie could be an improbably process – or perish.

Thus, it appears to be entirely clear that irreducible complexity of biological systemsand/or correlated subsystems could explain the typical features of the fossil record and the foundations of systematics (morphological stasis – the basic constancy of characters distinguishing higher systematic categories) and the "basic genetic processes and major molecular traits", which are thought to have "persisted essentially unchanged for more than three-and-a-half billion years", and the perseverance of the molecular mechanisms of animal ontogenesis for more than a billion years equally well.

According to Behe and several other authors [5-7, 21-23, 53-60, 68, 86] the only adequate hypothesis so far known for the origin of irreducibly complex systems is intelligent design (ID), a hypothesis, whose scientific basis will be further discussed in the following paragraphs in connection with Dembski's criterion of specified complexity.

Dembski's definition of specified complexity as a scientific
tool explaining the origin of irreducible complexity

In three monographs about the scientific criteria to testably distinguish between necessity, chance, and intelligent design (ID), Dembski [21-23]. has proposed and elaborated the term "specified complexity" by incorporating five main factors to guarantee its applicability not only to diverse human branches of research (e.g. forensic science, cryptography, intellectual property law, random number generation, insurance claim investigation, archaeology, SETI), but also to the origin of species and higher systematic categories [22, 23]. To identify design, an event has to display the following five features, for whose mathematical formulation and exemplary composition the interested reader is referred to Dembski's monographs (in the ensuing paragraphs again a few unsophisticated but illustrative examples, mostly following Dembski, may besufficient for our present purposes):

(a) high probabilistic complexity (e.g. a combination lock with ten billion possible combinations has less probability to be opened by just a few chance trials than one with only 64,000).

(b) conditionally independent patterns (e.g. in coin tossing all the billions Of the possible sequences of a series of say flipping a fair coin 100 times are equally unlikely (about 1 in 10^{30}). However, if a certain series is specified before (or independently of) the event and the event is found to be identical with the series, the inference to ID is already practiced in everyday life).

(c) the probabilistic resources have to be low compared to the probabilistic complexity (refers to the number of opportunies for an event to occur, e.g. with ten billion possibilities one will open a combination lock with 4,000 possible combinations about 156,250 times; vice versa, however, with 64,000 accidental combinations, the probablity to open the combination lock with 10 billion possible combinations is only 1 in 156,250 serial trials).

(d) low specificational complexity (not to be confused with specified complexity): although pure chaos has a high probabilistic complexity, it displays no meaningful patterns and thus is uninteresting. "Rather, it's at the edge of chaos, neatly ensconsed between order and chaos, that interesting things happen. That's where specified complexity sits" [23].

(e) universal probability bound of 1 in 10^{150} – the most conservative of several others (Borel: 1 in 10^{50}, National Research Councel: 1 in 10^{94}; Loyd: 1 in 10^{120} – for the details see again [23])

"For something to exhibit specified complexity therefore means that it matches a conditionally independent pattern (i.e., specification) of low specificational complexity, but where the event corresponding to that pattern has a

probability less than the universal probability bound and therefore high probabilistic complexity" [23]. For instance, regarding the origin of the bacterial flagellum, Dembski calculated a probability of 10^{-234} [22] (for further points, see below).

Yet, if we assume with the Dembski and Behe that organisms in general display signs of specified and often also irreducible complexities, this does not mean that the extant 100,000,000 or so morphological species of plants and animals [53] have directly been originated by ID. On the contrary, usually a combination of several of the factors specifying the dynamics of the organism's genomes as enumerated above, appears to be sufficient to have generated more than 99.99% of such species, albeit not necessarily in a gradualistic manner [53, 55, 56], nor due to the input of new complex information [53, 63, 64]. Or, to state one essential aspect of the question in Ohno's pointed words on dispensable genes, which appear to be especially relevant for neutral and regressive evolution: "...the notion that all the still functioning genes in the genome ought to be indispensable for the well being of the host should be abandoned once and for all" [75]. However, as further explicated below, the hypothesis of a link between the genetic potential of a primary species and ID should also be considered.

The systematic stasis referred to above is generally valid only for higher systematic categories from (many) genera upwards (i.e. genera, families, orders, classes, phyla). Presently we count only about 18,750 extant plant genera and altogether some 7,000 animal families (for the details on this differentiation for plants and animals as well as the numbers given, see [53]). Thus, as to the origin and constancy (stasis) so regularly found in systematics and paleontology, it is essentially the constancy of the defining features of higher systematic categories that have to be explained genetically (not to mention the contribution to stasis by cell organelles, membranes, and cell walls).

New research topics

On the strictly scientific level the combination of stasis and ID does not mean the end of enquiry (as is sometimes objected), but the very beginning of entirely new research programmes. For several questions have to be thoroughly investigated before valid scientific inferences can be suggested. To name but a few:

> a)   The hypothetical irreducible complexity of biological systems and/or correlated subsystems has first to be fully established on the different functional levels, i.e. genetically, anatomically, and physiologically. Since there are hardly any entirely non-redundant systems in biology, the irreducibly complex core systems have to be discovered and

scientifically be defined and analyzed on the levels just mentioned. Closely associated with that task is the problem of developing realistic models for the initial/primary biological boundary conditions for the origin of new putative irreducibly complex systems, i.e. for thoroughly delineating the gap between them and hypothetical evolutionary precursors. Dembski's improbability calculation of of 10^{-234} for the origin of the bacterial flagellum quoted above constitutes nothing but a first potentially falsifiable hypothesis in that research programme [7, 64].

b)   Granted that such systems can be established, the correlation between the organism/species and its different environmental conditions have to carefully studied pertaining the question, to what extent a species can relinquish certain subsystems without selective disadvantages under special circumstances. Although a subsystem could be irreducibly complex as such, some organisms might florish without it (the topic of regressive evolution holds a large series of instructive examples for this question) [46, 53, 63]. Problem (b) is intimately connected with the question for the boundaries of morphological variation of functional phenotypes [53, 55, 56]. In simple terms, a part of the ID research programme could thus be put: find the boundaries of functional phenotypic and physiological variation under different realistic environmental conditions.

c)   Specified complexity is not necessarily irreducible. So, what could be the molecular connection/relation between specified complexity 'only' and the phenotypic constancy found in most of the higher systematic categories of living organisms? Although it seems that many gene functions specifying constant generic and higher systematic characters are somehow (and this 'somehow' is a research programme of its own) integrated in a correlated web of interdependent cascades in Behe`s sense, nevertheless some parts appear to be reducible in the sense given in paragraphs (b) and (e), and yet might display marks of specified complexity.

d)   There appear to be many ornamental and even luxurious structures in the plant and animal kingdoms, structures that – from a purely functional point of view – do not seem to be absolutely necessary, to say the least. For instance, in terms of population density, reproductive success, and geographical distribution, the house sparrow (Passer domesticus) is much more successful than the

peacock (Pavo cristatus), whose males display the ingenious beauty of its fanned tail to perform courtship display and mate with a female – yet often also inviting a tiger for an easy prey and meal. In the plant kingdom the orchid family is one of several groups providing a range of further intricate ornamental as well as functional structures (e.g. the extreme examples of the reproductive organs of Coryanthes and Catasetum, which have posed enormous problems for gradualism [57]), whilst most plant species survive – again often much more successfully in the terms just mentioned above – by much simpler devices. Even independently of the fact that the often quoted answer of sexual selection for the origin of the peacock's tail (and similar examples) in itself poses a series of further unsolved problems [53] and, what is more, can hardly be applied to plants, the ensuing questions have to be investigated: to what extend can specified and irreducible complexity be detected on the genetic, anatomical, and physiological levels of such more or less selectionally 'neutral' or even hypertrophic organismic structures, too, and can this research programme provide scientifically more realistic answers than those given so far?

e)   Also, there exist many constant features delineating morphological speciesand genera from each other that are probably due to further factors than specified and irreducible complexity. For example, features due to losses of more or less redundant gene functions [63] affecting morphological features, but with a very low probability to revert or being counteracted by compensating mutations in other genes (modifiers), can be constant for all the time a species survives. Let's have a look at an event, which has repeatetly occurred in wild as well as in cultivated species: originally red flowering plant species have irreversibly lost their ability to generate anthocyanin – and these species might produce white flowers almost forever. Other possibilities to generate rather stable features by mutations include buffering gene functions by gene duplications and polyploidy. On the other hand, mutations in essential gene functions involved in the formation of species- or genera-specific structures, – functions, which were originally buffered by accessory redundant genes – could become regularly lethal after mutational loss of that redundancy.

f)   There are some indications that at least a part of biodiversity is, so to speak, predestined by the constitution of the genome and its mechanisms, possibilities, and limits to generate functional DNA-variations, including preferential insertions of transposons of an initial line or species [64].

Assuming an original vast genetic potential for functional morphologic deviations – to what extend is specified and irreducible complexity relevant for that originally purely potential part of genetic variation realized in time and space of the history of a genus? [53] Moreover, several transposon specialists have, in fact, postulated rapid species formations by transposable elements (thus we are coming back to the question posed at the end of the introduction): concurring with McClintock [69], Syvanen [87] stated: "I believe that transposons have the potential to induce highly complex changes in a single event". Also, Shapiro [79] is convinced that "there must exist mechanisms for large-scale, rapid reorganisations of diverse sequence elements into new configurations" for the integrated mosaic genome to make evolutionary sense. However, to date hardly any positive experimental evidence can be cited for this view [46, 53, 64]. A research project testing the possibilities and limits of species formation by TEs could also include the issue of the evidence for specified and irreducible complexity on the DNA- and morphological levels, e.g. can TEs be key factors in releasing a dormant genetical potential possibly displaying the marks of ID – say a master regulator with a set of corresponding target genes – for abrupt morpho-species formations?

g)   Another question that should be investigated is, to what extent the correlations between the genome and its cellular surroundings (cell organelles, membranes, cell walls, physiological cascades and their interrelationships) can be lighted up and explained by a research programme addressing particularly specified and irreducible complexities in this area. For the first steps into such a research programme, see Behe [5] and Lönnig [53].

Some basic objections

Nevertheless, in the face of all the different dynamic genetic mechanisms generating enormous masses of quantitatively and qualitatively different DNA sequence variations as shown above – the question may be raised whether is it really necessary to postulate ID for the origin of basic structures and processes of living organisms.

In the following paragraphs, we will discuss a few of the points that could be relevant for this question:

A fait accompli is that during the last few hundred years at least 680 animal species have died out (and presently at least 5,438 are critically endangered/endangered or vulnerable) and at least 449 plant species have become extinct (37,969 plant species are threatened) [44, 89]. As far as these

species are concerned, all the impressive possibilities and quantities of DNA sequence variations known so far have indisputably not been sufficient to avoid the extinction of these species.

However, it could be objected that most of these extinctions are due to environmental shifts in the wake of human activities, which happened too fast for nature to follow, and that there is, in fact, evidence for the hypothesis that there has existed an enormous genetic potential for a wide range of environmental adaptations in many plant and animal genera and/or families, yet within certain physiological, anatomical and morphological boundaries, producing altogether the some 100,000,000 morpho-species mentioned above (for a detailed discussion, see again [53]).

On the other hand, as to the candidates of irreducibly complex systems mentioned above (the cilium, bacterial flagellum, blood clotting, traps of Utricularia and some other carnivorous plant genera, joints, echo location, deceptive flowers as Coryanthes and Catasetum etc.), it can be confidently stated that up to now, none of these synorganized systems has been satisfactorily explained by the modern synthesis or any other evolutionary theory. Nor has a testable naturalistic theory been advanced for the basic features of the fossil record (abrupt appearance of most life forms, stasis, and later often also abrupt disappearance). Whether the totality of factors contributing to the genomic dynamism with all the above named mutagenic consequences can solve the questions posed remains doubtful – in several cases the systems to be explained have been well-known for more than a hundred years: Utricularia, Coryanthes, Catasetum and others have already been investigated by Darwin. Additionally, natural selection itself may not have the stringency and power usually ascribed to it (for details, see [54, 59, 60, 77, 86]).

Last not least, it should perhaps be pointed out that research on irreducible and/or specified complexities in biology definitely do not constitute metaphysical research programmes, but is at least as scientifically valid as the SETI (search for extraterrestrial intelligence), which is presently supported by thousands of scientists worldwide, not to mention the affiliated network of more than 4 million computers in over 200 countries around the globe (for an exhaustive discussion of further basic questions, see the contributions of Behe, Dembski, Lönnig, Meyer, and others [5-7, 21-23, 53-58, 68, 86]). Irreducible and specified complexity are inspiring tools that can and should be emperically investigated. Also, the concepts are potentially falsifiable in actual research (Popper) and thus clearly belong to the realm of science.

Note: It should be stated that the hypotheses of Behe and Dembski and my applications of them to the further biological phenomena as decribed above have been formulated in an intellectual climate of enormous tensions between different world views, often so much so that it seems to be necessary to point out that an author supporting ID is speaking not in the name of an institution, but gives his personal opinion. However, I am fully convinced that there are a range of cogent scientific arguments (of which some have been discussed above) encouraging open-minded researchers to carefully consider and investigate the topic within their different biological disciplines.

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