

Gene, Language, Number: The Particulate Principle in Nature

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ABSTRACT: Because blending constituents form combinations whose properties are averages which lie between those of the original constituents, systems that exhibit properties beyond those of their constituents are based on particles. Emergent properties of 'creative' systems ('self-diversifying' systems) are based on geometric associations that form among particles. The major self-diversifying systems, which also include a constituent of time, are the gene, language, and the number system, virtually structural triplets. All include (at the lowest level) a linear string of particulate constituents; (at the next level) a division of the string into sub-strings with a meaning attached; and (at the highest level) a re-organization of the meanings into a functional geometry. Human evolution was a matter of obtaining voluntary control of the above system, by behavioral insertion of (p)articulate, referential vocalizations into a formula already occupied by the gene and the number system.

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Introduction

In spite of our conviction that all sciences ought to be based on the same laws because all are based on physics, the several 'fields' of research remain isolated from one another. The separate vocabularies of chemistry, genetics, and linguistics, show that identical ideas have developed independently within each subject, even when important researchers knew one another personally. Thus, where chemistry experienced a controversy over 'atomism' vs. 'continuity' of matter beginning in 1805 (Greenaway 1966, pp. 4, 25), genetics experienced the same controversy a century later (Weismann 1893, pp. 19, 54; Fisher 1930, pp. 7-9), using the words 'granular' and 'particulate' vs. 'miscible', or 'blending' or 'swamping'. The vocabulary of 'discreteness' (Harris 1951; see index under 'discrete parts') was introduced into linguistics during the 1940's, in opposition to 'continuity' (Hockett 1963, p. 8). The phrase 'naturally-occurring' has the same meaning in chemistry or genetics that the phrase 'psychologically real' has in linguistics, i.e., both are opposed to 'artificially contrived'. The separate vocabularies and independent time-frames indicate that ideas have not transferred between scientific fields. The vocabulary of the 'particulate' gene, the 'discrete' phoneme, the 'integers' of arithmetic, (and the 'atom'), represents virtual synonyms in science.

I hope to show here, in abridged form, that emergent properties of creative systems (i.e., chemical molecules, genes, numbers, and sentences) are based on an emergent geometry of associations that form among particles. Further, gene, language, and number are sister particulate systems that share a common underlying natural source in the dimensional properties of matter.

The Particulate Principle

The stable, emergent geometry of 'creative' or 'self-diversifying' systems in nature (those that exhibit properties beyond those of their underlying constituents) is based on particles, because blending constituents (such as hot water and cold water) would combine to form a single, averaged mass with undifferentiated properties (Abler 1989; Studdert-Kennedy 1990, and in press).

Blending Systems

The model of a blending system is the mixing of water with ink, where any combination is possible, ranging from one drop of water in a bottle of ink to one drop of ink in a bottle of water. Since the combination of water and ink is a blending system, the result is an infinite variability that is limited to a one-dimensional scale of grey. The readings of a thermometer also exhibit infinite variation along a single dimension (of temperature).

Here, a clear distinction emerges between infinity and diversity. The two are routinely confused because both may involve large numbers, and because 'the infinite encompasses everything'. Infinity involves large numbers, but not necessarily anything else. Diversity is introduced when systems have properties that extend outside the properties of the constituents that compose them. Thus Humboldt's (1836, p. 70) 'infinite use of finite media', made famous by Noam

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Chomsky (1957, p. 27; 1965, pp. v, 8; 1966, p. 20), applies equally to blending as to particulate systems, and has only caused confusion.

Even though the weather is sometimes used as an example of a complex system, the weather is a blending system whose properties are strictly limited. Thus diversity of weather events is limited not to one dimension, but to just a few dimensions: hot or cold; wet or dry; sunny or cloudy; windy or calm. Rotating storms (Battan 1961, p. 81), and sun-dogs and rainbows (Bowditch 1977, pp. 881, 896 ff.) represent the limits to the circumscribed properties of the weather, i.e., storms do not form associations with other storms in the formation of something with properties beyond those of storms. Weather systems exhibit structure because they are so big that blending, or mixing, is not instantaneous.

Geology, too, represents a blending system whose properties are strictly limited. Mountains can be viewed as a slow isostatic fluid floating on the earth's molten interior (Wegener 1929, p. 41; Jones *et al.* 1996). When their properties reach an extreme, geologic structures flow. Thus geologic structures are limited to hills and valleys, mountains and plains, i.e., to just a few dimensions (high or low; level or steep; big or small; north-south-east-west). The actual description of any geologic structure is limited to specifying the precise values along just a few dimensions. Geologic systems exhibit structure because blending, or flow, is slow.

Particulate Systems

In contrast, great diversity is found in a system such as the chemical molecules, whose properties may be very different from those of the constituents (the chemical elements) that compose them. For example the properties of salt, in its transparency, its cubic shape, its thermal and electric conductivity, its flavor, its solubility, are nothing like the properties of sodium metal and chlorine gas. If sodium and chlorine acted as an averaging or blending system when they combined, the result would be silicon, not salt. Thus sodium and chlorine behave as particulate systems when they combine.

In this paper, we will be concerned with self-diversifying systems that (in addition to being particulate) also include a constituent of time in their construction or delivery: the gene, the number system, and the sentences of human language, which will emerge virtually as structural triplets.

As understood here, a particle is any entity that possesses a boundary defining an inside and an outside. Even if the boundary is vague, it guarantees that a particle will occupy some approximate place at some approximate time. No two particles can occupy the same place at the same time. Thus, if particles are, in addition, able to form stable associations with one another, the resulting emergent geometry, in itself, generates the emergent properties of creative systems. For example the emergent properties of the gene and other biological molecules are represented in their geometric shape. Entities that can be mapped onto known particles must also be treated as particles (perhaps as abstract particles). Particles retain their individual identities when they form combinations with one another.

Let us make a direct comparison between gene, language, and number, establishing, first, that they are all based on particulate constituents. The three systems have the same underlying structural design features for the same reasons; and statements which are obviously true of one system are also true of the others, even if less obviously so. See Figure 1.

Gene

If the genetic material were a blending system, individuals of modern populations would have features that were averaged over generations. The continuing variability of individuals in modern populations, in itself, shows that the genetic material is a particle.

Language

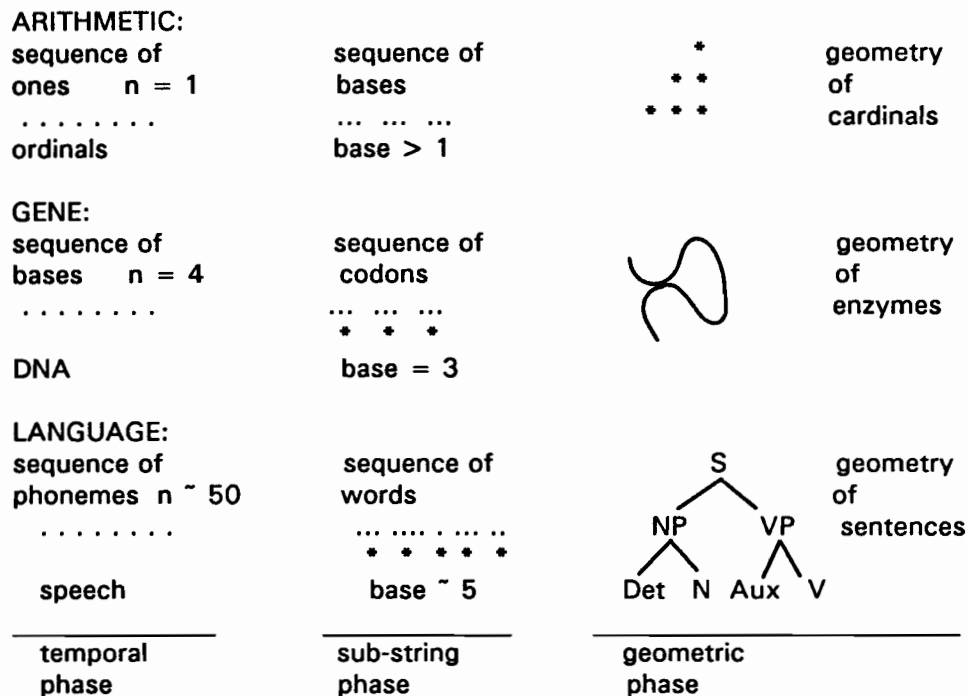
The vocabulary words of languages exhibit a diversity of meaning that extends far beyond the diversity found in the meaningless phonemes that represent them. If information concerning neighboring phonemes were blended or averaged together, the phonemes would lose their individual identities, and would no longer be able to form the basis of a large vocabulary. Phonemes are perceptual, or psychological, or cognitive, or abstract particles that can be mapped onto known physical particles (the alphabetic letters, which have a distinct boundary and a characteristic geometry). If information is shared between neighboring letters of a text, the letters blend together, lose their individual identities, and suffer the cost in illegibility.

Number

The question of number presents special problems. Since equations are well-formed sentences that can be spoken out loud, mathematics has the appearance of being derived from language, and therefore of more recent origin. The real situation is very different.

Since we discover the properties of numbers rather than invent them, numbers are, in effect, naturally-occurring, found objects which have some manifestation apart from ourselves. For example, we can not invent the value of the number pi, but must instead discover the actual value (Beckmann 1971). Thus we are justified in asking, of what material substance are numbers composed? Numbers can be mapped onto the particulate digits that represent them, providing still further evidence that they are somehow material and particulate.

a)



b)

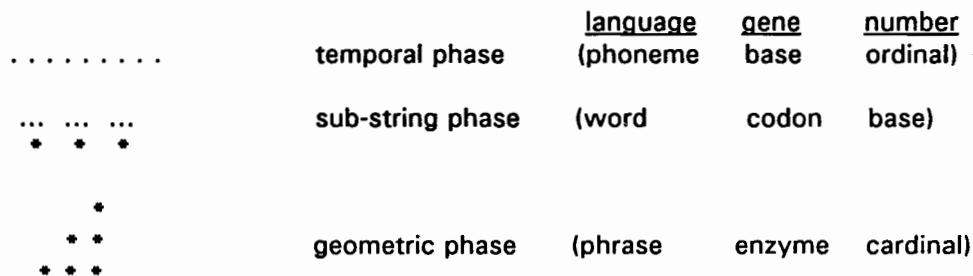


Fig. 1. The particulate principle of self-diversifying systems in its temporal aspect: gene, language, number. a) All three systems consist of: (Temporal phase) a small inventory of particulate units arranged or delivered in a linear order; (Sub-string phase) the string of units divided into sub-strings, each with an attached meaning, or referent; (Geometric phase) the sub-strings re-organized into a functional geometry. b) A more schematic representation of (a).

The nature of such material particles can be probed by attempting to construct an arithmetic based on blending constituents. If a blending arithmetic retains its self-diversifying, or creative, property, the particulate principle will be disproved by calculation. Using the blending of water and ink as a model, we see that blending numbers form averages when added together. Thus, under a blending system,

$$\begin{aligned} a + b & \text{ becomes } (a + b)/2; \\ a + b + c & \text{ becomes } (a + b + c)/3. \end{aligned}$$

If multiplication is a system of multiple additions, then $a \times b$ is represented by

$$a_1 + a_2 + a_3 + \dots + a_b$$

which becomes, under a blending system,

$$(a_1 + a_2 + a_3 + \dots + a_b)/b = a.$$

$a \times a$ (i.e., a^2) becomes

$$(a_1 + a_2 + a_3 + \dots + a_a)/a = a.$$

Under blending conditions, the Pythagorean theorem, $a^2 + b^2 = c^2$, which forms the basis for the 3-dimensional vector space which we inhabit, becomes $a + b = c$, i.e., all space is reduced to a single line.

Nor can blending arithmetic be dismissed as arbitrary or artificially contrived, since it represents the limiting case as velocities m and n approach c (the speed of light) in Einstein's (1905) expression

$$\frac{m + n}{1 + mn/c^2}$$

for the summation of velocities. Under the right conditions, blending arithmetic is naturally-occurring. Since the dimensional properties of 3-space collapse under blending arithmetic, the material substance of numbers is some dimensional property of nature.

Not only is a physical world ruled by a blending arithmetic incompatible with the evolution of living forms, but the same is true of a world ruled by an expanding arithmetic. Where, under blending conditions,

$$a + b \text{ becomes } (a + b)/2,$$

under an expanding arithmetic

$$\begin{aligned} a + b & \text{ becomes } (a + b) \times 2; \\ a + b + c & \text{ becomes } (a + b + c) \times 3. \end{aligned}$$

$a \times a$, (i.e., a^2) becomes

$$(a_1 + a_2 + a_3 + \dots + a_a) \times a = a^3.$$

But a^3 becomes

$$(a_1^2 + a_2^2 + a_3^2 + \dots + a_a^2) \times a = a^4.$$

Since, under an expanding arithmetic, the process of expansion can not be stopped, a^2 will expand without limit, to become an undefined expression.

The common particulate arithmetic of 'two and two is four' is not an arbitrary construction invented by mathematicians for their convenience, but reflects some real property of our particulate world, which teeters in the balance between a blending and an expanding condition. Physics as we know it, gravity, time, light, electromagnetism, length is incomplete, and will be solved only when the particulate principle of self-diversifying systems is included on an equal basis alongside the other properties of matter. It is the particulate property of numbers that is responsible for their properties of irrationality and transcendence.

The ubiquitous and ineluctable property of the particulate principle, together with the fact that it acts instantaneously,

GLN Theory

with no visible source or expenditure of energy, also suggests that it is dimensional in its nature, and represents some fundamental underlying property of matter.

The self-diversifying systems can be treated as axiomatic systems, with the properties of the underlying particles representing the starting conditions, or axioms. Gödel's proof (Nagel and Newman 1958) means, among other things, that emergent properties of axiomatic systems are real, and that we can never find out everything about an axiomatic system by looking just at that system alone. But by comparing the temporal self-diversifying systems, we can learn more about all three.

Gene-Language

We will begin by comparing the structures of the gene and language, since these are the best understood, and most obvious. At the lowest level of their organization, the gene and language are a linear sequence of particulate units. For the gene, these units are the genetic bases (adenine, guanine, cytosine, thymine); for language, these units are the perceptual phonemes.

Further, the inventory of such particulate units is small in both systems: a maximum of 100 and an average of about 50 phonemes in any language; exactly 4 genetic bases. The reason for such small numbers is that if there were, say, a million phonemes in some language, or a million different genetic bases, the difference between one and the next would be so small that they would approximate to a blending system. The reason for linear ordering, or one-at-a-time delivery, is that it maximizes reliable identification for each particle. A rosary represents the same principle manifested at our own scale. The gene is, in addition, a helix because a flat ribbon would be subject to crimping and folding. The discovery of any exotic organism with a linear gene would offer independent verification of the particulate principle.

Distinct levels of organization develop in self-diversifying systems because the associations that form among particles have, by their nature, a structural organization that is distinctly different from that of the particles that underlie them. Thus the underlying particles form the first layer or level of organization, while their simple combinations form the second.

At the second level in their organization, both the gene and language consist of short sequences composed of a few particulate units each, i.e., the linear ordering of the first level is divided into short sub-sections. The reason for dividing the linear string into sub-strings is that this is the simplest mechanism for generating a new sequence of new particulate units while still using the rosary principle. For the gene, the sub-strings are codons containing exactly 3 units each; for language, the sub-strings are words containing anywhere from one to a dozen (with an average of perhaps 5) phonemes each (for English).

The reason that each sub-string contains only a few particulate units is, again, the preservation of a self-diversifying system: If sub-strings contained, say, a million units each, differences between one and the next would be so small that they would approximate to a blending system.

To each sub-string, in both the gene and language, is appended a kind of referent. For the gene, the referent attached to each codon is a 'messenger' molecule and an amino acid (Day 1984, p. 142); for language, the referent attached to each word is a meaning (or a system of meanings).

At the last level in the organization of both the gene and language, the referents attached to the units of the second level are re-organized into a new, distinctive geometry. For the gene, the sequence of amino acids is re-organized into the two-armed geometry of enzymatic 'robots' (Day 1984, p. 185); for language, the sequence of word-meanings is re-organized into a geometry of syntactic relationships, now believed to have a tree-structure (Chomsky 1957, p. 27). I refer to the pioneering work because all current grammars will eventually be replaced, but the geometric property of syntax will remain.

Numbers

The properties of numbers continue to present special problems; but their fundamental organization can be understood by comparing the number system directly to the structure of the gene and language.

Numbers have a rich system of properties, although there is no obvious reason why they should. For example, if a keyring contains 9 keys, the number is a square; if 8, a cube; if 7, a prime. But the number of keys on a keyring should have no property other than its magnitude. Further, the distinction between the properties of ordinal numbers ('first', 'second', 'third') and cardinal numbers ('one', 'two', 'three') is much sharper than is usually realized. For example, 'square-root of 9' is a meaningful phrase, while 'square-root of ninth' is not. 'Five plus three' is meaningful, while 'fifth plus third' is not. Ordinals thus appear to have no property other than their magnitude, while cardinals have properties that are geometric (e.g., square, cube). Nevertheless, ordinal and cardinal interact on some common ground: For example, 'fifth plus three is eighth' is meaningful.

If we now compare the structure of the number system directly to the structure of the gene and language, we see that all three share the same underlying structural formula. Numbers consist of particulate units which, at the lowest level of their organization, are arranged into a linear sequence (the ordinal numbers) which has no property other than its magnitude. The number of kinds of units at the lowest level of the number system is small, i.e., exactly one, the unit.

At the next level of organization, the ordinal string is divided into substrings. In the language of the mathematicians, such sub-strings are called 'bases', e.g., base 2, base 10, base 12.

At the next level of organization, the ordinal substrings are re-organized into an emergent geometry that is rich in unexpected (emergent) properties such as cube, square, prime, odd, even; Goldbach's conjecture, never proved or dis-proved, proposes that every even number is the sum of two primes. We can now see why Bertrand Russell numbers (based on sets, and sets of sets), and Giuseppe Peano numbers (based on the idea of succession) (Newman 1956, pp. 542, 1623) were only partly successful: They generate ordinals, not cardinals. See Figure 2.

The property of number presents further questions. If the number line contains an infinite number of points, and between any two points an infinite number, it should be impossible to find any integer. Yet we are surrounded in nature by the integer 'one' (and its compounds): exactly one zebra; exactly one bite; exactly one galaxy. The exponents of our most basic equations are integers. But we never have exactly one inch, or exactly one ounce. By what mechanism does nature generate exact integers?

Dimensional Mechanisms

Although it can be presented here only as an example, a single, simple natural mechanism is capable of generating the first two structural levels in the organization of gene, language, and number: Any resonating mechanism, such as a resonating string (Olive 1989), automatically generates exact integers, i.e., integral multiples of half-wavelengths. Such a mechanism generates the linear sequence of particulate units seen at the lowest level in the organization of temporal self-diversifying systems. If just one more resonant frequency is added to the first (with the right phase relationship), substrings of particulate units are automatically formed. See Figure 3.

Because everything is subject to arithmetic, the natural laws that determine the structure of the gene, language, and the number system, are older in cosmology than the atoms; and all three systems derive their shared properties independently from the same dimensional property of matter. If mathematics were derived from language, numbers would not be material; and their properties would be invented, not found. There is little prospect that computer technology, which contains only what we put into it, will soon duplicate a mechanism (language) based on the dimensional properties of the universe. Gene, language, and number may be viewed as 'transcendental' systems, in having no simple relationship to any simple schema.

Ordinarily, Albert Einstein receives credit for being first to ask the question, why do the properties of mathematics shadow, or mirror, the properties of the material world? Einstein's question can apparently be traced to an address entitled 'Geometry and Experience' that Einstein presented to the Prussian Academy of Sciences in Berlin, January 27, 1921. Einstein (p. 28) actually says that the question is one 'which in all ages has agitated inquiring minds'. In any case, the answer, under the particulate principle, is that numbers are material objects which share common properties with other material objects because all derive their properties from the same natural source.

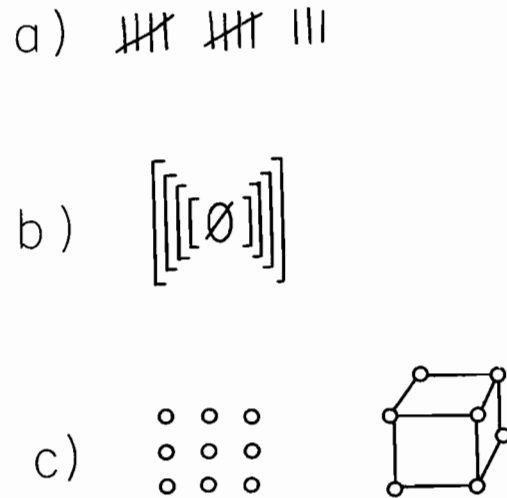


Fig. 2. Ordinal vs. cardinal. a) Peano numbers, based on the idea of succession. b) Russell numbers, based on the idea of sets, and sets of sets. Such numbers are ordinal because they have no property other than their magnitude, and because each has an identity only by reference to its predecessor, and therefore to its history. It is here that numbers exhibit their constituent of time. c) Cardinal numbers, with their geometric properties. Since cardinals can be 'ambiguous', e.g., 64 is both a square (of 8) and a cube (of 4), cardinals, too, have histories, and therefore contain a constituent of time.

Stability

Self-diversifying systems require some mechanism that will keep them stable at the higher levels of their organization, i.e., the distinctive, characteristic geometry of enzymes, phrase trees, and cardinal numbers, can not exist at all unless it is also stable. For biological molecules, the stabilizing mechanism is the quantum property of matter. For language, the stabilizing mechanism is what will be called here its property of abstractness.

Language's Place in Nature

Any complete theory of the organization of language must also include a theory of the evolution of language. But in order to understand the organization of language, we must first recognize the place of language in nature. While the precise steps in the origin of language are interesting in themselves, any search for them based on language alone, even if it is successful (e.g., Jespersen 1921, chapter XXI), will miss the main point: Ordinary evolution is a matter of historical accident, i.e., it represents the organism's adaptation to changing conditions, within the limits of existing anatomy and physiology. In the evolution of language, the outcome was fixed in advance (Figure 1); and the role of natural selection is unclear. Language can no longer be regarded as just one more biological marvel alongside the giraffe's neck, the elephant's trunk, the blue whale, and the hummingbird's wing.

Ever since Copernicus (1473-1543), discoveries in natural science have tended to push human beings away from the center of the universe. As a biological-behavioral system, language occupies a special place in nature, taking direct advantage of one of the most ancient and fundamental properties of matter. See Figure 4.

Evolution

Any theory of the origin of language must avoid what may be called the giraffe's-neck paradox, of which Charles Darwin was aware (Spingale 1968, p. 144). Often, it is supposed that giraffes have a long neck so that they can eat the leaves from the tallest trees during times of famine. But if we accept this idea, we find ourselves unable to explain why cows, deer, horses, sheep, goats, have short necks, since they live in regions where, from time to time, a long neck would be an advantage in reaching food. By the same token, if we suppose that language evolved purely under the stimulus of communicative fitness, we find ourselves unable to explain why parrots and mynah-birds can not speak (i.e., since they possess adequate organs of speech, and would presumably benefit from increased communicative power).

The critical step in human evolution and the origin of language was to obtain voluntary use of the particulate principle by obtaining 1) cognitive particulate units, and 2) a mechanism for keeping their associations stable.

The Abstractness Property of Language

Constructions at higher levels in the organization of language are not literally built out of constituents at lower levels in the way that a house is built out of bricks. This is the 'abstractness' property of language, and represents a generalized form of 'duality of patterning' (Hockett 1963, p.9). Under duality of patterning, language is separated from mood and

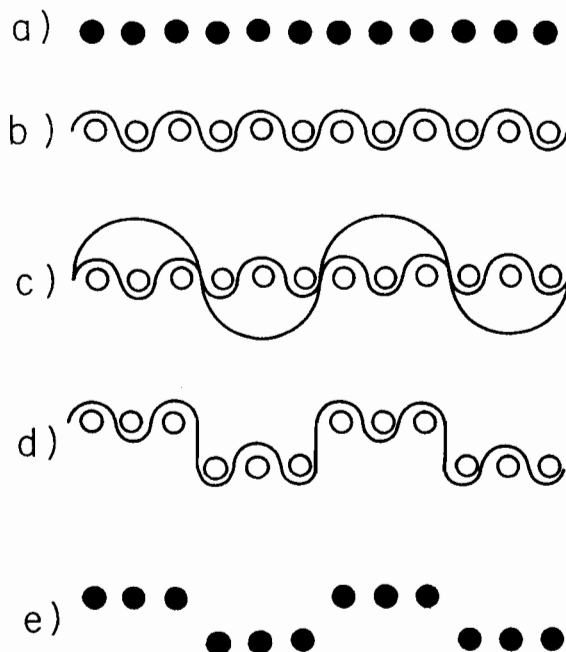


Fig. 3. A resonant mechanism capable of generating particles, and strings of particles. a) Linear string of particles, as seen at the lowest level of organization in gene, language, and number. b) String of integral particles generated by half-wavelengths of resonating dimensional element. c) A second resonant frequency added to first. d) The sum of resonant frequencies. e) String of particles divided into sub-strings by action of resonating dimensional elements. For higher organization, cf. 'oscillons' (Umbanhowar et al. 1996).

context, permitting the discussion of things not present either in time or space. It is duality of patterning that permits the making of plans, and the discussion of history and of ideas.

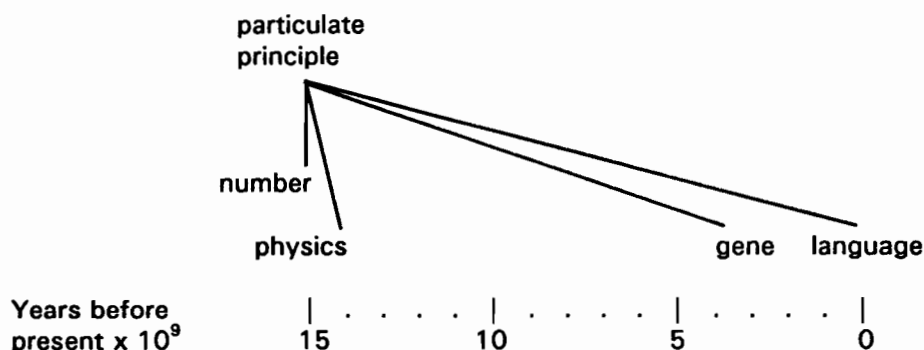


Fig. 4. Genealogy and cosmological ages of creative systems. Gene, language, and number derive their properties independently from the same underlying dimensional properties of matter. Adapted after Ablor (1989), with kind permission of Academic Press.

Under the abstractness property, all five levels in the organization of language (1- the acoustic signal; 2- the segmental phonemes; 3- the words, or morphemes; 4- grammatical structures; 5- meaning) remain separated from one another (cf. Chomsky 1957, p. 106). For example, pronunciation pairs such as "ehkenomics" and "eekenomics" ['economics'] could not exist if words were literally built of their phonemes, i.e., different phonemes would build different words (Chomsky 1957, p. 95). Further, ambiguous sentences (a single sentence with two interpretations) would not exist. For example, in a sentence such as 'Alvarez holds the entire scientific community in awe', 'Alvarez' can be either subject ('Alvarez is in awe of the entire scientific community') or object ('The entire scientific community is in awe of Alvarez'). If higher-level constructions were literally built of their constituents, the same words would build the same sentence.

Rhetorical figures illustrate abstractness at a higher level. For example, 'The joke with its punch-line' is described by Sigmund Freud (1960, p. 88) as resulting from 'the interesting process of condensation accompanied by the formation of a substitute'. Thus a joke such as, 'I feel like the atheist at his funeral: All dressed up and no place to go', is understood not by its syntax, but by the listener's profound understanding of theistic culture.

Under abstractness, not only does language as-a-whole enjoy duality of patterning, but each level in the organization of language enjoys duality of patterning with respect to its neighbors. Abstractness is ubiquitous, pervasive, and powerful in the organization of language. It permits each level of organization to have its own independent structure (Harris 1965), functioning at maximum efficiency in its own role, without being disrupted by the intrusion of structures from other levels. Abstractness breaks down under historical change.

Insertion: New Form of Evolution

Since the substantial material of language consists of two main types, (1) particulate constituents organized into a stable geometry permitted by (2) an abstractness mechanism, the origin of language was a matter of introducing these two systems. Studdert-Kennedy (in press) suggests that particulate structures were introduced into pre-human behavior when the vocal tract, with its mechanically semi-independent articulators (tongue, lips, velum, vocal cords) became capable of generating semi-independent gestures, each of which possessed some distinct, individual identity. The modern phonemes represent such discrete, or '(p)articulate' gestures, 'bleached' of their original meanings, i.e., the distinctly identifiable vocal gesture replaced meaning (cf. Cheney and Seyfarth 1992) as a referent for the associated sound. Such a process might be compared to the bleaching of meaning from the pictures that were the precursors of alphabetic letters, leaving only the sound of the original referent (Budge 1910, p. 28).

How did language evolve from vocalizations that were (p)articulate (in Studdert-Kennedy's terms), but non-linguistic? The direct action of natural selection upon communicative fitness (Pinker and Bloom 1990) seems to be the most promising theory. Natural selection is the only known mechanism of evolution, and is more powerful than has been thought. Thus, Nilsson and Pelger (1994) have shown that a spherical eye will develop from a few light-sensitive cells in the skin, after only 400,000 generations - less than half a million years in an animal (such as a fish) that has a new generation every year (Dawkins 1994). Nilsson & Pelger demonstrate the evolution not of a retina, the unique transparent humors, or an iris - but only of a sphere, arguably the simplest geometric shape in the universe. If language evolved in fewer generations than a sphere, then language had help.

Nevertheless, the natural-selection theory presents difficulties. As applied to evolution of behavior, natural selection is a kind of operant conditioning, or behavioral shaping, extended over a geologic time scale. Optimal behaviors, introduced by genetic variability, receive positive reinforcement (food and reproduction), while comparatively inefficient behaviors receive negative reinforcement (extinction). It is hard to believe that any form of operant conditioning, which is incapable of stimulating the development of language in the mind of organisms (human children) that already possess universal grammar (Chomsky 1959), could introduce universal grammar into the brain of organisms that did not possess it. Nevertheless, syntactic deep-structures and transformations might be introduced by genetic variability, i.e., better deep-structures would result in the production of better surface-structures, which would then be accessible to the senses, and to natural reinforcement. Yet the action of natural selection can be indirect (Gould and Lewontin 1979), i.e., anatomical and behavioral structures can arise as an indirect consequence of something else that was being selected.

More damaging to the direct natural-selection theory is the evolutionary history of the honey bee's communicative dance, which stands as a counterexample to any direct selection theory. In spite of profound differences between language and the communicative dance (which is based on continuity, not particulation), the bee's dance is the most sophisticated behavior known, apart from language. A natural-selection theory might easily be constructed: As a forager rushes into the hive from the field, bringing pollen and nectar, her movements attract the attention of other bees. The food that she carries stimulates them to rush out to find more. As a result of random genetic variation, some foragers would tend to run in a direction that was weakly correlated to the direction of the food source, while some bee recruits would tend to fly out in a direction correlated to the initial run of the returning forager. Natural selection would favor colonies in which such directional correlation became increasingly precise, and increasingly keyed to the direction of the sun (outside the hive) or the direction of gravity (inside).

Apart from more detailed information, the natural-selection theory is biologically impeccable. Reproductive fitness (Wilson 1971, p. 301) was indirectly involved in the evolution of the dance, by forcing increased socialization of all activities including foraging. But the precise details of the dance were determined in advance by the details of the social foraging flight, of which the communicative dance represents a point-for-point behavioral miniaturization (Lindauer 1971). The communicative dance of the honey bee is a distant evolutionary by-product (mediated through increasing social organization) of the queen's struggle to maintain genetic domination over her daughters.

Following a different formal template (the particulate principle in its temporal aspect), the evolution of language parallels that of the honey bee's communicative dance: Natural selection may have been involved, but only indirectly. Language is a third-tier consequence of bipedalism, its consequent social changes (Sheets-Johnstone 1989), the consequent introduction of a vocal tract and hand - the life of the whole animal - but its precise form was not the direct-object of natural selection. The three most basic systems known in biology (gene, language, number) follow the same underlying formula for the same reasons, indicating (1) that the similarities between the systems are neither superficial nor coincidental; and (2) that language developed when semantic 'bleaching', made possible by the introduction of (p)articulate vocalization, inserted the emerging proto-language into the pre-established, underlying schema of the particulate principle. The difference is that, where the bee's dance is a re-enactment of a previously-existing behavior, language represents behavioral invasion of a previously-existing formula (i.e., because the number system could not evolve by natural selection).

Universal Grammar

Since the properties of mathematical expressions must be discovered, not invented, mathematical expressions are, like numbers, naturally-occurring, found objects with some manifestation apart from ourselves. Since all material things are subject to the laws of mathematics, its properties are as ancient as matter. The schemas that determine the shape of mathematical expressions, and that determine the character of right and wrong mathematical statements, are more ancient than the sentences of language, and can not be modeled after sentences.

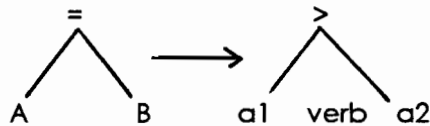
When we speak, we begin with the intention of using whole sentences (or something that, in context, can be interpreted as a whole sentence). Thus it is reasonable to represent the structure of a sentence as being organized under a single symbol. Because equations are sentences that can be recited aloud, the symbol that dominates the sentences of language corresponds somehow to the '=' symbol of algebra.

Equations become informative when they become asymmetrical, e.g., '4=4' is true; but '2+2=4' is informative. Syntax, on the other hand, distributes the gradient of asymmetry across the sentence as a whole. As a result, a phrase may be repeated to generate an informative sentence (e.g., 'A promise is a promise'; 'No means No'; 'When John plays the violin, he plays the violin'). (The structure of the word system is entrained by the meaning gradient that spans sentences: Words such as 'be' or 'to', which have their reference inside the system of language, have their source in the same matrix that produces operational symbols in algebra ['+', '-', '='], while words such as 'house' or 'idea', which have their reference

outside the system of language, have their source in the same matrix that produces numbers ['3'; '-3'; 'pi']. But in vocabulary there is no dividing line, only a gradient from more inward-looking to more outward-looking.)

Sentences, then, differ from equations largely in that the sentences of ordinary language are inequalities:

Here, the symbol 'verb' represents the '>' symbol in speech. This simple sentence formula, corresponding to the simplest equation, yields active sentences such as 'The boy ate the apple', 'The dog found a bone'. A large class of coordinate-compound sentences is formed by inserting a whole (or nearly whole) sentence at a1 and a2, and conjoining them by 'and', 'if . . . then', 'because', 'after', and numerous others (e.g., 'He came home early *because* it was raining').

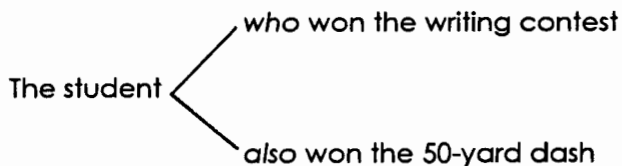


Doubling the verb to generate 'auxiliary-plus-verb', 'aux + V', produces the central core of English sentence types, and may represent the linguistic equivalent of re-writing an un-useable number (such as a prime) as the sum of two useable ones, e.g., 13 can be re-written as $2^2 + 3^2$. The doubled verb yields future ('will V'), progressive ('is V-ing'), modal ('would V'), negation ('didn't V'), among others. Movement of *aux* ('did') to the beginning of the sentence yields the question. The grammar derived here resembles most closely Chomsky's of 1957, except that the nodal *sentence* symbol is represented in the sentence itself.

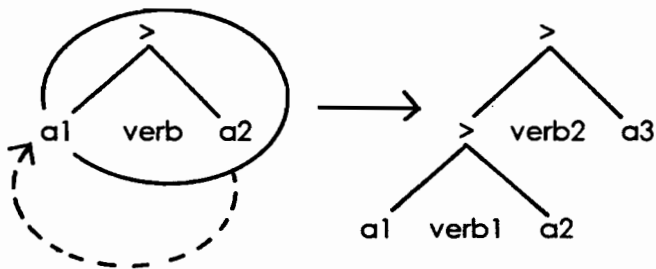


The grammar used here has the advantage of being referenced to a system, algebra, that is independently-occurring, and outside language. By transposition of a1 and a2, marked by alteration of *aux* to 'was V-en by', the same formula yields the passive construction. Intransitive verbs, adjectives, the comparative, and other constructions, are generated by the same mechanism.

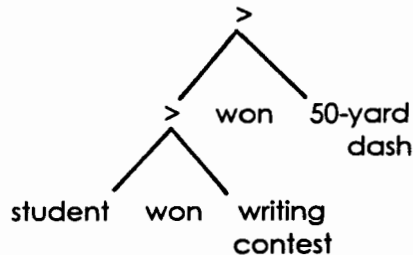
Parentheses in algebra amount to a parsing grammar, but discontinuous constituents in language (e.g., 'The student who *won the writing contest* also *won the 50-yard dash*') can not be characterized by a parsing grammar because no parsing can show that both clauses share the same subject. A diagramming grammar can show that much, but can not show how the sentence was formed.



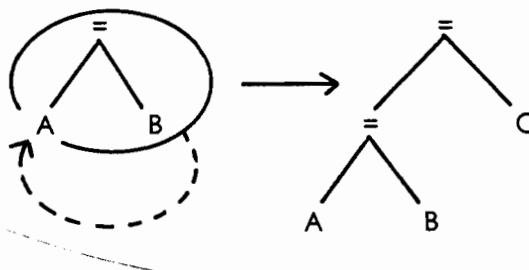
Under an algebraic syntax, discontinuous constituents arise by embedding the basic sentence formula into itself, i.e.,



e.g.,

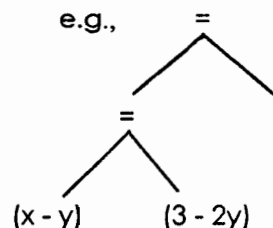


The basic formula for discontinuous constituents in language is the syntactic equivalent of the algebraic formula which states, in effect, that $A = B = C$, and is a solution to simultaneous equations such as $x + y = 3$; $x - y = 1$. To solve for x and y , we substitute, or 'embed', one equation into the other by setting both equal to the same quantity. Repeated, or 'recursive', embedding of constituents in language is thus a copy of a simple operation taken from algebra. Language is a



GLN Theory

subset of mathematics, not *vice versa*. It is not that language is subject to the consequences of mathematics, like the orbit of a planet, but that the two systems draw their formulas and operations from the same formal infrastructure. There is only one solution to the question of language. Grammar is universal but not innate: All that evolved is an ability and inclination to find it. Language created mind by introducing voluntary use of the formalisms of algebra.



Sources of Language

The standard theory of the origin of language is that language is a product of random variation and natural selection. Under the standard theory, mathematics becomes a by-product of language, because the two systems share a common formal basis (as shown above). The standard theory, then, presents mathematics as an eventual product of random variation. Such a theory is untenable, however, because the precise fit (described earlier) which holds between the consequences of mathematics and the properties of the material world could happen as a result of random process only if an infinite number of biological generations were possible (and such a fit being selected directly). These considerations, combined with the independent existence of mathematics (described earlier) indicate that mathematics preceded language, which borrows its properties directly from the dimensional properties of matter.

The properties of mathematics are more natural than axiomatic, but if mathematics is treated as being axiomatic, the particulate principle becomes its first axiom. Under Gödel's proof, which calls for an infinite number of axioms (apparently all different), the properties of mathematics are not somehow implicit, or contained, in the units. (Language borrows the same property, i.e., the properties of syntax are not implicit in the phonemes.) Higher-order properties are introduced, apparently from the outside. If we suppose that such properties are dimensional, language and mathematics acquire their properties by a process of accumulating them from already-existing dimensional sources. Such a view is compatible with the idea of a 'big bang' and the 'missing matter' of the universe, which become different manifestations of the same mechanism: The big bang represents the event during which matter accumulated its higher dimensional properties, while the 'missing matter' consists of dimensional elements which failed to accumulate such properties.

The original capture by the brain of the particulate principle, or the GLN principle, is an open question, i.e., it is not clear whether it was first represented by synaptic systems (which do not necessarily possess intrinsic organization), or by the interior of neurons, where GLN was already represented in the gene. In any case, language must be viewed as a kind of 'captive' or 'animated' algebra which functions as a kind of inorganic puppet held and manipulated by a biological 'glove'. Such arrangements are routine in biology, as when living bones or spicules take advantage of the properties of inorganic minerals (Inoue & Okazaki 1977). Syntax and language represent a tiny patch of order borrowed by our primate ancestors from a vast surrounding ocean of order. The questions of physics, language, and mind will be solved only when we understand the precise source of the properties of numbers.

The Underlying Matrix

Numbers and language are manifestations of a single underlying matrix whose properties can be deduced by interpreting its consequences, both in these and in other systems. The underlying matrix appears to have some property that allows numbers to be shifted from one side of the '=' to the other in an equation, creating a bilaterally symmetrical pattern, with neither side being primary. The same matrix represents the sentence in pre-language as 'Subject-Verb-Object: Object-Verb-Subject', with neither side being primary (cf. Greenberg 1963, p.88). Patterns within the individual wings of butterflies apparently proliferate by a comparable system of bilateral doubling (Nijhout 1991, p. 32) that occurs spontaneously. Mimicry is a matter not of copying line-for-line and spot-for-spot, but of finding a comparable underlying formula (Nijhout 1991, p.182). But now we are already deep within the mechanism of ordinary evolution. The orthogon, or rope-ladder plan of invertebrate nervous systems (Bullock & Horridge 1965, pp. 11, 666, 538 ff.) manifests the same lower-level serial organization seen in the genetic molecule and the backbone of vertebrates, and that is also borrowed in ordinal, or serial numbers. Evolution may proceed by a process of variation and selection, but the variation is not random. It is guided by patterns of translational (serial) and bilateral symmetry (Weyl 1952, pp. 1, 44) generated by resonant properties of the underlying dimensional matrix of matter, manifested at every scale (see also Physical Science Study Committee 1960, p.606).

W.L. Abler

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References

- Abler, W.L. 1989. On the particulate principle of self-diversifying systems. *Journal of Social and Biological Structures* 12:1-13.
- Battan, L.J. 1961. *The Nature of Violent Storms*. New York: Doubleday.
- Beckmann, P. 1971. *A History of Pi*. New York: St. Martin's Press.
- Bowditch, N. 1977. *American Practical Navigator*. Washington, D.C. 20390: Defense Mapping Agency Hydrographic Center. Publication No. 9. vol. 1.
- Budge, E.A.W. 1910. *Egyptian Language*. Re-published 1973. New York: Dover.
- Bullock, T.H. & Horridge, G.A. 1965. *Structure and Function in the Nervous Systems of Invertebrates*. San Francisco: W.H. Freeman.
- Cheney, D.L., & Seyfarth, R.M. 1992. The representation of social relations by monkeys. *Cognition* 37:167-196.
- Chomsky, N. 1957. *Syntactic Structures*. The Hague: Mouton & Co.
- Chomsky, N. 1959. Verbal behavior (review of B.F. Skinner). *Language* 35:26-58.
- Chomsky, N. 1965. *Aspects of the Theory of Syntax*. Cambridge: MIT Press.
- Chomsky, N. 1966. *Cartesian Linguistics*. New York: Harper & Row.
- Dawkins, R. 1994. The eye in a twinkling. *Nature* 368:690-691.
- Day, W. 1984. *Genesis on Planet Earth*, 2nd ed. New Haven: Yale.
- Ehrlich, P.R., and Ehrlich A.H. 1961. *How to Know the Butterflies*. Dubuque: W.C. Brown.
- Einstein, A. 1905. re-published (in English) as: On the electrodynamics of moving bodies. in Einstein, A. 1952. *The Principle of Relativity*. New York: Dover Publications.
- Einstein, A. 1922. Geometry and experience. in Einstein, A. *Sidelights on Relativity* (G.B. Jeffrey & W. Perrett, translators) London: Methuen.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford: The Clarendon Press. re-published 1958. New York: Dover.
- Freud, S. 1960. *Jokes and their Relation to the Unconscious*. New York: W.W. Norton & Company.
- Gould, S.J., and Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London*, B 205:581-598.
- Greenaway, F. 1966. *John Dalton and the Atom*. Ithaca: Cornell University Press.
- Greenberg, J.H. 1963. *Universals of Language*. Cambridge: MIT.
- Harris, Z.S. 1965. Transformational theory. *Language* 41:363-401.
- Harris, Z.S. 1951. *Methods in Structural Linguistics* (later changed to *Structural Linguistics*). Chicago: University of Chicago Press.
- Hockett, C.F. 1963. The problem of universals in language. Chapter 1 in: Greenberg, J.H. (ed.) *Universals of Language*. Cambridge: MIT Press.
- Humboldt, W.v. 1836. re-published 1971 (in English; G.C. Buck & F. Raven, translators) as: *Linguistic Variability & Intellectual Development*. Baltimore: University of Miami Press.
- Inoue, S., & Okazaki, K. 1977. Biocrystals. *Scientific American* 236(4):82-92.
- Jespersen, O. 1964 (1921). *Language*. New York: W.W. Norton.
- Jones, C.H., Unruh, J.R. and Sonder, L.J. 1996. The role of gravitational potential energy in active deformation in the southwestern United States. *Nature* 381:37-41.
- Liberman, A.M., Cooper, F.S., Shankweiler, D.P., and Studdert-Kennedy, M. 1967. Perception of the speech code. *Psychological Review* 74:431-461.
- Lindauer, M. 1961. *Communication among Social Bees*. Cambridge: Harvard University Press.
- Matisoff, J.A. 1973. Tonogenesis in Southeast Asia. pp. 71-95 in: Hyman, L.M. (ed.) *Consonant Types and Tone*. Southern California Occasional Papers in Linguistics S.C.O.P.I.L. no. 1. Los Angeles: University of Southern California 90007.
- Nagel, E., and Newman, J.R. 1958. *Gödel's Proof*. New York: New York University Press.
- Newman, J.R. 1956. *The World of Mathematics*. New York: Simon and Schuster.
- Nijhout, H.F. 1991. *The Development and Evolution of Butterfly Wing Patterns*. Washington: Smithsonian.
- Nilsson, D.-E., and Pelger, S. 1994. A pessimistic estimate of the time required for an eye to evolve. *Proceedings of the Royal Society of London*, B 256:53-58.
- Olive, D.I. 1989. Introduction to string theory: its structure and its uses. *Philosophical Transactions of the Royal Society of London*, A 329:319-328.
- Physical Science Study Committee 1960. *Physics*. Boston: D.C. Heath.
- Pinker, S. and Bloom, P. 1990. Natural language and natural selection. *Behavioral and Brain Sciences* 13:707-784.
- Romer 1966. *Vertebrate Paleontology*, 3rd ed. Chicago: University of Chicago Press.
- Spinage, C.A. 1968. *The Book of the Giraffe*. Boston: Houghton Mifflin Company.
- Sheets-Johnstone, M. 1989. Hominid bipedality and sexual-selection theory. *Evolutionary Theory* 9:57-70.
- Studdert-Kennedy, M. 1990. This view of language. (commentary) pp. 758-759 in Pinker and Bloom (q.v.).
- Studdert-Kennedy, M. (in press) The particulate origins of language generativity: from syllable to gesture. in: Hurford, J., Studdert-Kennedy, M., & Knight, C. (eds.) *Approaches to the Evolution of Language: Social and Cognitive Bases*. Cambridge: Cambridge University Press.
- Umbanhowar, P.B., Melo, F. and Swinney, H.L. 1996. Localized excitations in a vertically vibrated granular layer. *Nature* 382:793-796.
- Weismann, A. 1893. *The Germ Plasm*. New York: Scribner's.
- Wegener, A. 1929. re-published 1966 (in English; John Biram translator) as: *The Origin of Continents and Oceans*. New York: Dover.
- Weyl, H., 1952. *Symmetry*. Princeton: Princeton University Press.
- Wilson, E.O. 1971. *The Insect Societies*. Cambridge: Harvard University Press.

THE EVOLUTION OF BEAKS IN REPTILES: A PROPOSED EVOLUTIONARY CONSTRAINT

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ABSTRACT: It is proposed that, within tetrapods, "beaks" (keratinous rhamphothecae) have evolved by elaboration of the keratinous caruncle. The caruncle is transiently present on the snout of most tetrapods, and used to slit the extra embryonic membranes and crack the calcareous egg shell during hatching. It is an amniote synapomorphy secondarily lost in therians and squamates: thus, "amphibians", therians, and squamates are the only tetrapods that lack the caruncle. Significantly, "amphibians", therians and squamates are the only three very diverse groups of tetrapods that lack beaked taxa, even though they include representatives that occupy niches very similar to those occupied by beaked forms of other taxa. The proposed evolutionary model also explains why, in beaked taxa, caruncles and beaks develop from the same zone of epidermal hypoplasia and keratinisation, and why beaks almost always evolve initially on the tip of the snout, and only later spread to cover the rest of the jaws.

* * *

INTRODUCTION

Marginal teeth have been replaced by keratinous rhamphothecae (horny "beaks") in many tetrapods. "Beaks" have evolved within almost every major group of amniotes, and beaked taxa occupy an extremely varied range of habitats (terrestrial, fossorial, volant and aquatic) and exhibit a similarly diverse range of diets (carnivorous, herbivorous, and omnivorous). However, beaks are conspicuously absent in amphibian-grade tetrapods, and in two very diverse groups of amniotes, squamates (lizards and snakes) and therians (marsupials and placental mammals). All other major groups of tetrapods have beaked forms. Amphibians, squamates and therians have radiated extensively and in many cases occupy niches very similar to those occupied by beaked representatives of other groups. The total absence of beaked forms in these three groups is therefore surprising.

Here, I suggest that such beaks evolved through modification of the keratinous caruncle or "shell-breaker", a structure present transiently on the tips of the upper jaw of late embryos and neonates most amniotes. In beaked forms, the keratinous area spreads beyond the caruncle, and persists into adulthood, forming the beak. This explains why rhamphothecae almost always evolve initially on the tips of the upper jaws, and only later spread to other areas of the jaws. Amphibians, squamates, and therian mammals all lack caruncles. The total absence of beaked forms in these diverse groups is therefore explicable.

THE DISTRIBUTION OF THE CARUNCLE IN TETRAPODS

The late embryos and neonates of turtles, sphenodontids, crocodylians, and birds all possess a keratinous epidermal horn, the caruncle, on the tip of the snout (de Beer 1949; Fioroni 1962; Bellairs 1969; Ferguson 1985). Among mammals, monotremes possess a caruncle, but in these animals the structure contains a dermal bony core, the os carunculae. A vestigial caruncle has also been identified in marsupials (Hill and de Beer 1949). All other extant tetrapods - lissamphibians, squamates and eutherians - lack a caruncle (de Beer 1949; Fioroni 1962; Edmund 1969; Bellairs and Kamal 1981).

This distribution indicates that the caruncle is an amniote synapomorphy which was later lost, independently, in squamates and in eutherians (Gauthier et al. 1988; *contra* Lovtrup 1985; see Fig. 1). Its evolution was almost certainly correlated with the evolution of the amniote egg. The caruncle is used to slit the extra embryonic membranes and to break the calcareous egg shell during hatching, and is shed soon afterwards, usually within a month (e.g. Fioroni 1962; Moll and Legler 1971; Ferguson 1985). In squamates, the function of the caruncle is instead performed by modified premaxillary teeth (true egg teeth), while in therians the reduction (marsupials) and loss (eutherians) of the caruncle is presumably correlated with viviparity and absence of the calcareous egg shell.

* * *

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Bellairs (1969; Bellairs and Kamal 1981) has suggested that it is problematical that sphenodontids resemble crocodilians and turtles, rather than squamates, in possessing a caruncle. However, as a caruncle is primitive for amniotes, this resemblance is symplesiomorphic (a shared primitive feature) and therefore perfectly explicable. The morphology of the caruncle is taxonomically significant: a bifurcated caruncle (Ferguson 1985) appears to be diagnostic of crocodilians, a caruncle located on the dorsal surface rather than the tip of the snout (de Beer 1949) characterises birds, while (contrary to Gauthier et al. 1988) only monotremes possess an osseous core in the caruncle.

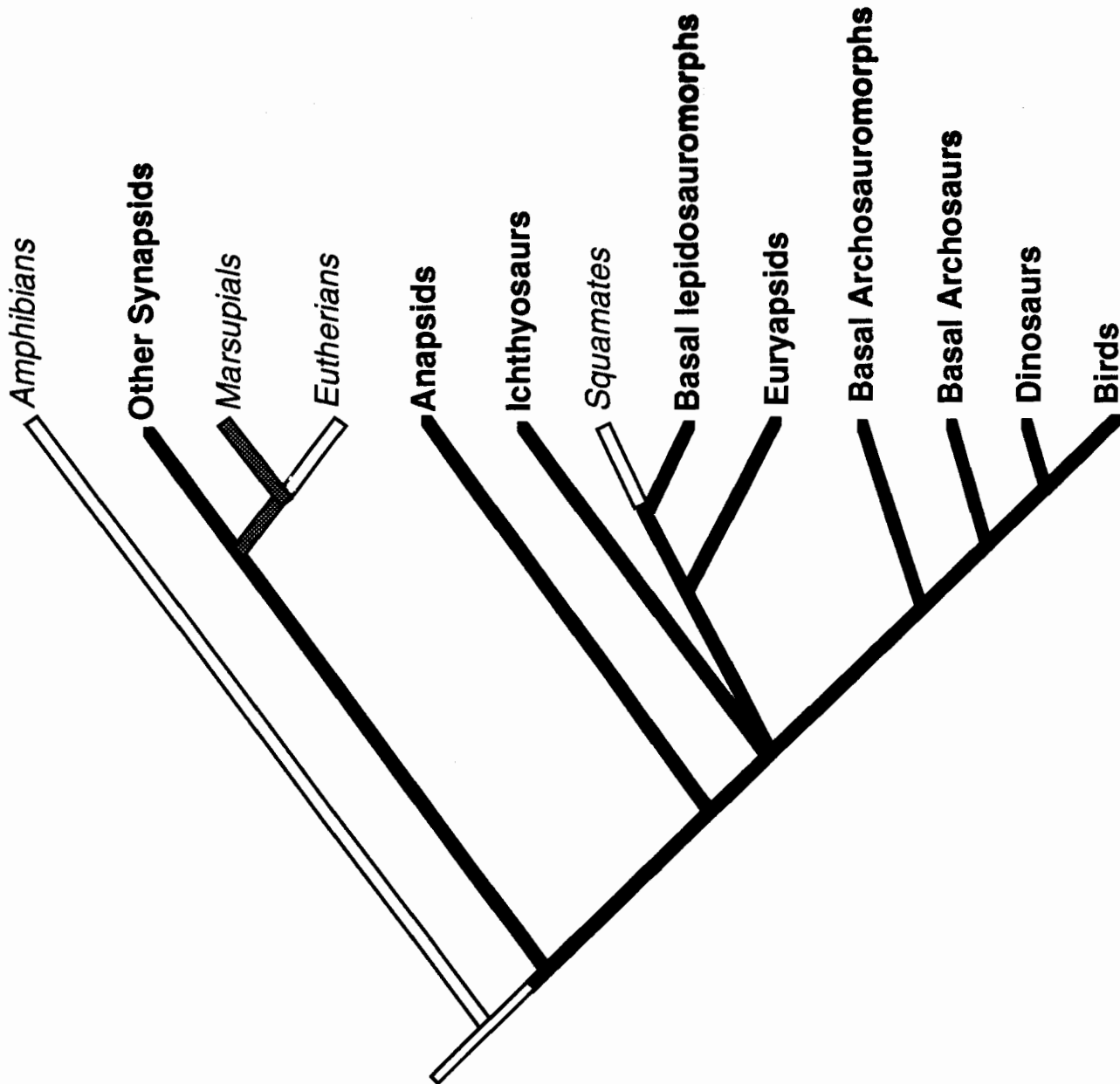


FIGURE 1. Simplified phylogeny of the major groups of tetrapods (after Gauthier et al. 1988; position of Euryapsids after Rieppel 1995), showing the concordant evolution of the caruncle and the presence of beaked taxa. Solid lines indicate presence of caruncle, shaded lines, a vestigial caruncle, unshaded lines, absence of a caruncle. The caruncle is absent in amphibian-grade taxa, and is an amniote synapomorphy convergently reduced (marsupials) or lost (eutherians) in therians, and also lost in squamates. Taxa shown in normal typeface contain beaked forms, taxa shown in *italics* lack any beaked forms. The only diverse groups of tetrapods that lack beaked taxa are amphibians, marsupials, eutherians and squamates.

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THE DEVELOPMENT OF THE CARUNCLE AND THE EVOLUTION OF BEAKS

The caruncle forms from epidermal cells which become hyperplastic and keratinous (Fioroni 1962; Ferguson 1985), just like the rhamphothecae ("beaks") of extant birds and turtles (de Beer 1949; Bellairs 1969). The development of the caruncle and rhamphothecae in extinct forms obviously cannot be ascertained. Thus, an obvious proposal is that beaks in various groups of amniotes evolved when hyperplasia and keratinisation, initially confined to the caruncle in late embryos and neonates (hatchlings), spread outwards along the jaws, and persisted into adulthood. This hypothesis makes several predictions, and these are evaluated below.

1. Rhamphothecae should only evolve in taxa which possess caruncles during their ontogeny.

This prediction appears to hold. Figure 1 is a simplified representation of tetrapod phylogeny, showing the concordant distributions of beaks and caruncles. As shown in Fig. 1, apart from amphibians, squamates, marsupials and eutherians, all diverse tetrapod groups contain representatives with beaks (Fig. 1). Here, a "diverse" group is arbitrarily considered to be one which contains more than twenty genera as listed in Carroll (1988).

Beaks have evolved convergently at least sixteen times within amniotes (Romer 1956, 1966; Carroll 1988): in anomodonts (non-mammalian Synapsida), turtles ("Anapsida"), placodonts (Euryapsida), sphenodontids (Lepidosauromorpha), huphesuchids (Ichthyosauria: M. Caldwell, unpublished data 1996), rhynchosaurs, *Trilophosaurus*, stagonolepids (Archosauromorpha), *Lotosaurus*, pterosaurs, (Archosauria) ornithischians, prosauropods, ornithomimosaur, oviraptorosaurs, segnosaur (Dinosauria), and modern birds (Aves). The number of times beaks have evolved in archosauromorphs and included clades is particularly striking. However, beaks have never evolved in amphibians, which lack the caruncle. Beaks have also never evolved in marsupials, eutherians or squamates, which are also (significantly) the only three diverse amniote groups which have lost (or, in marsupials, greatly reduced) the caruncle (Fig. 1). Together, amphibians, marsupials, eutherians and squamates account for much of the known morphological and taxonomic diversity of tetrapods, and occupy just about every conceivable ecological niche open to tetrapods. Yet beaks have never appeared in these groups, but have appeared at least sixteen times in other tetrapods, at least once in every other diverse group shown in Fig. 1. For instance, many squamates (e.g. iguanids) occupy niches similar to those occupied by beaked (non-squamate) taxa (e.g. rhynchosaurs). Similarly, many therians occupy niches similar to beaked, non-therian taxa; for instance, elephants and prosauropod dinosaurs, bats and birds or pterosaurs.

Maynard Smith et al. (1985 p.277) suggested that developmental constraints are best identified by "comparative studies of two different taxa whose members have been exposed to a similar range of ecological conditions. Should one taxon show variants of a kind not shown by the other, it would be likely that the latter taxon was subject to some degree of developmental constraint". The distribution of beaked forms within tetrapods constitutes strong evidence for the hypothesis presented here.

It is theoretically possible to statistically test the hypothesis that this distribution is significantly different from random. This could be done using the concentrated changes test (Maddison 1990) or the contingent states test (Sillén-Tullberg 1993). It would involve mapping the origins of beaks onto a species-level phylogeny of tetrapods (!), observing that they evolve sixteen times along branches with functional caruncles, and never along the large numbers of branches where the caruncle is greatly reduced or absent (i.e. on branches within amphibians, therians, and squamates). It could then be determined whether this distribution is significantly different from that expected under the null hypothesis of beaks being equally likely to evolve along any branch.

This test is of course currently impractical, and a much cruder test will have to suffice. A 2x2 contingency table was constructed, using the taxa in Fig. 1, to test the significance of the association between presence of caruncles, and presence of beaked taxa (Table 1). H_0 is that taxa would be randomly distributed across the four cells, H_1 is that taxa would be distributed in two cells, beaked and with caruncles, no beaks and no caruncles. The correlation is almost perfect, and is significant at $P < 0.05$ ($X^2 = 5.06$ with continuity correction, $P = 0.0245$). The only exception to this pattern are marsupials. They represent the only diverse tetrapod group with

caruncles that has failed to evolve beaked representatives. However, the caruncle in marsupials is vestigial and apparently non-functional (Hill and de Beer 1949), which might be the reason why it has never been elaborated into a beak in any group. As emphasised above, however, this test is crude since the number of taxa recognised (i.e. "replicates" in the contingency table) depends on how the phylogeny is subdivided.

		Beaks	
		Present	Absent
Caruncles	Present	9	1
	Absent	0	3

TABLE 1. A 2X2 contingency table showing the association between presence of caruncles and presence of beaked taxa. $X^2=5.06$, $P=0.0245$.

2. In embryos and neonates, the caruncle and rhamphothecae should be initially continuous, both structures developing from a single region of epidermal hyperplasia and keratinisation.

This prediction can obviously only be evaluated in extant beaked taxa (birds and turtles). In both groups, the caruncle and rhamphothecae are initially a single, continuous structure (e.g. de Beer 1949; Bellairs 1969; see Fig. 2). Soon after hatching, however, a zone of weakness develops and the caruncle is shed, leaving a raised scar on the rhamphotheca (e.g. Legler 1960). This prediction, of course, cannot be verified in the numerous extinct tetrapod groups with rhamphothecae (see above).

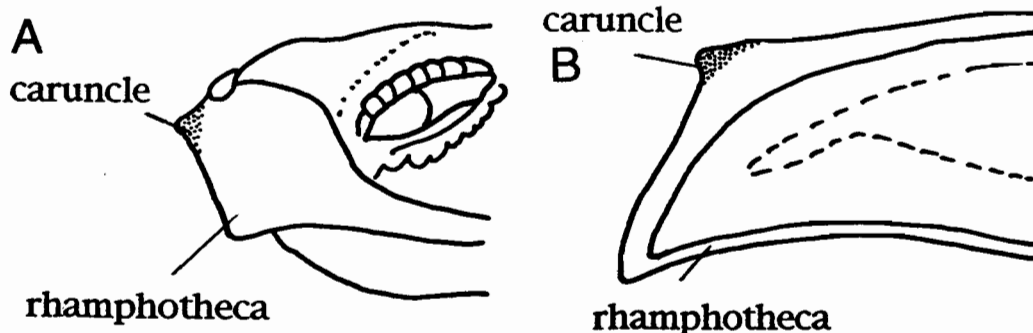


FIGURE 2. (A) Snout of neonate turtle, showing continuity of caruncle and rhamphotheca (After Legler 1960) (B) Sagittal section of beak of a chick, again showing continuity of caruncle and rhamphotheca (after de Beer 1949).

3. Rhamphothecae should evolve first in the region of the caruncle, and only later spread to the posterior regions of the jaws.

This is indeed almost always the case. Many extinct amniotes have evolved beaks that are confined to the anterior regions of the jaws: rhynchosaurs, *Trilophosaurus*, stagonolepids, ornithischians, prosauropods, segnosaurians and sphenodontids (e.g. Romer 1956, 1966; Weishampel et al. 1990). In four groups, the horny beak initially occupied the tip of the snout in primitive, basal forms and later came to line the entire jaw in derived forms. This happens within pterosaurs (Wellnhofer 1991), anomodonts (King 1983, 1990), placodonts (Romer 1966), and birds (Feduccia 1980). I only know of only one possible exception to this pattern: in ornithomimosaur a toothless keratinous beak appears to evolve initially in the rear of the jaw and later spreads to the front (Perez-Moreno et al. 1994). In the remaining beaked taxa, turtles (Gaffney 1990; Lee 1993), *Lotosaurus* (Sun 1989), oviraptorosaurs (Barsbold et al. 1990) and huphesuchids (Carroll and Dong 1991), rhamphothecae line the entire jaws in all known representatives, and the initial stages in the evolution of the beak cannot be determined. Thus, the prediction that beaks should appear initially in the snout, and only

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later may spread elsewhere, holds in eleven out of twelve instances. However, the sole exception deserves further study and necessitates an *ad hoc* explanation. The above hypothesis provides an alternative to the obvious functional explanation for the usual appearance of beaks in the anterior region of the jaws: that a continuously growing keratinous sheath is useful in herbivorous forms since this part of the jaw is exposed to the greatest wear. This explanation, of course, cannot explain the initial appearance of beaks in this region in many carnivorous taxa.

The three predictions of the hypothesis presented here are therefore largely satisfied. Any good theory in evolutionary biology should not only explain what can happen, but also specify what won't happen (e.g. see Maynard Smith et al. 1985). The hypothesis that beaks evolve by elaboration of the region of keratinisation originally meant for the caruncle not only helps explain why beaks evolve in the snout region first. It also suggests reasons why there are no beaked amphibians, therians and squamates.

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REFERENCES

- Barsbold, R., Maryańska, T. and Osmólska, H. 1990. Oviraptorosauria. In Weishampel, D. B., Dodson, P. and Osmólska, H. 1990 (eds.) *The Dinosauria*. pp. 249-258. University of California Press, Berkeley.
- Bellairs, A. d'A. 1969. *The Life of Reptiles*. Weidenfeld and Nicolson, London.
- Bellairs, A. d'A., and A. M. Kamal. 1981. The chondrocranium and development of the skull in recent reptiles. In Gans C. and Parsons, T. S. (eds.) *Biology of the Reptilia. Volume 11*. pp. 1-263. London, Academic Press.
- Carroll, R. L. 1988. *Vertebrate Paleontology and Evolution*. W. H. Freeman, New York.
- Carroll, R. L., and Dong, Z.-M. 1991. *Huphesuchus*, an enigmatic aquatic reptile from the Triassic of China, and the problem of establishing relationships. *Philosophical Transactions of the Royal Society of London, Series B* 331: 131-153.
- de Beer, G. R. 1949. Caruncles and egg teeth: some aspects of the concept of homology. *Proceedings of the Linnean Society of London* 161 (2): 218-224.
- Edmund, A. G. 1969. Dentition. In Gans, C., Bellairs, A. d'A. and Parsons, T. S. (eds.) *Biology of the Reptilia. Volume 1*. pp. 117-200. Academic Press, New York.
- Feduccia, A. 1980. *The Age of Birds*. Harvard University Press: Cambridge MA.
- Ferguson, M. W. J. 1985. Reproductive biology and embryology of the crocodylians. In Gans, C., Billet, F. and Maderson P. F. A. (eds.) *Biology of the Reptilia. Volume 14. Development A*. pp.329-492. Academic Press, New York.
- Fioroni, P. 1962. Der Eizahn und die Eischwiele der Reptilien. *Acta Anatomica* 49: 328-366.
- Gaffney, E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History* 194: 1-263.
- Gauthier, J. A., Kluge, A. G. and Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4: 105-209.
- Hill, J. P., and de Beer, G. R. 1949. Development of the Monotremata. Part VII. *Transactions of the Zoological Society of London* 26: 503-544.
- King, G. M. 1988. *Anomodontia. Handbuch der Paläoherpetologie, Teil 17C*. Gustav Fischer Verlag, Stuttgart.
- King, G. M. 1990. *The Dicynodonts: A Study in Palaeobiology*. Chapman and Hall, London.
- Lee, M. S. Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science* 261: 1716-1720.
- Legler, J. M. 1960. Natural history of the ornate box turtle, *Terrapene ornata ornata* Agassiz. *University of Kansas Publications Museum of Natural History* 11: 527-669.
- Lovtrup, S. 1985. On the classification of the taxon Tetrapoda. *Systematic Zoology* 34: 463-470.
- Maddison, W. P. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree. *Evolution* 44: 539-557.

- Maynard Smith, J., Burian, R., Kauffman, S., Alberch, P., Campbell, J., Goodwin, B., Lande, R., Raup, D., Wolpert, L. 1985. Developmental constraints and evolution. *Quarterly Review of Biology* 60: 265-287.
- Moll, E. O., and Legler, J. M. 1971. The life history of a Neotropical slider turtle, *Pseudemys scripta* (Schoepff) in Panama. *Bulletin of the Los Angeles County Museum of Natural History* 11: 1-102.
- Perez-Moreno, B. P., Sanz, J. L., Buscalionia, A. D., Moratalla, J., Ortega, F., and Rasskin-Gutman, D. 1994. A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature* 370: 363-366.
- Rieppel, O. 1995. Studies on skeleton formation in reptiles: implications for turtle relationships. *Zoology: Analysis of Complex Systems* 98: 298-308.
- Romer, A. S. 1956. *Osteology of the Reptiles*. Chicago: University of Chicago Press.
- Romer, A. S. 1966. *Vertebrate Paleontology*. 3rd ed. Chicago: Chicago University Press.
- Sillén-Tullberg, B. The effect of biased inclusion of taxa on the correlation between discrete characters in phylogenetic trees. *Evolution* 47: 1182-1191.
- Sun, A.-L. 1989. *Before Dinosaurs: Land Vertebrates of China 200 Million Years Ago*. China Ocean Press, Beijing.
- Weishampel, D. B., Dodson, P. and Osmólska, H. 1990 (eds.) *The Dinosauria*. University of California Press: Berkeley.
- Wellnhofer, P. 1991. *The Illustrated Encyclopedia of Pterosaurs*. London: Salamander.