The theory of increasing autonomy in evolution: a proposal for understanding macroevolutionary innovations

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Abstract Attempts to explain the origin of macroevolutionary innovations have been only partially successful. Here it is proposed that the patterns of major evolutionary transitions have to be understood first, before it is possible to further analyse the forces behind the process. The hypothesis is that major evolutionary innovations are characterized by an increase in organismal autonomy, in the sense of emancipation from the environment. After a brief overview of the literature on this subject, increasing autonomy is defined as the evolutionary shift in the individual system–environment relationship, such that the direct influences of the environment are gradually reduced and a stabilization of self-referential, intrinsic functions within the system is generated. This is described as relative autonomy because numerous interconnections with the environment and dependencies upon it are retained. Features of increasing autonomy are spatial separations, an increase in homeostatic functions and in body size, internalizations and an increase in physiological and behavioral flexibility. It is described how these features are present in different combinations in the major evolutionary transitions of metazoans and, consequently, how they should be taken into consideration when evolutionary innovations are studied. The hypothesis contributes to a reconsideration of the relationship between organisms and their environment.

Keywords Trends · Biological autonomy · Macroevolution · Evolutionary innovations · Major transitions · Robustness · Organismic biology

Recently several old questions in evolutionary biology have gained increasing attention: How are evolutionary innovations generated? What is the origin of new

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constructional principles and of new organs? What was at the beginning of the major evolutionary transitions: new structures, new genes, a new environment, a new behavior or new ontogenetic pathways? While the Synthetic Theory offered no solution to these questions, there have been increasingly tangible insights into some of these topics from recent research. These results, together with some new theoretical considerations, are beginning to trigger a new stage in the evolution of evolutionary biology itself (Carroll et al. 2005; Conway Morris 2003; Gerhart and Kirschner 1997; Jablonka and Lamb 2006; Kirschner and Gerhart 2005; Margulis and Sagan 2002; Schad 1993; Shubin and Marshall 2000; Wagner et al. 2000; West-Eberhard 2003).

Usually investigations are made into the origins of innovations and the mechanisms by which they were generated. However, a central aspect continues to be neglected. Are evolved organisms in some consistent aspect of their individual morphology, physiology and behavior different from more primitive ones in earlier times (McShea 1998)? There have been some attempts to tackle these questions, but they have not generated a great deal of interest.

Here it is proposed that a recurring central aspect of macroevolutionary innovations is an increase in individual organismal autonomy, in the sense of emancipation from the environment. After a brief look at the history of this notion a new definition will be given. Then some biological arguments and examples will be presented, followed by a discussion of its theoretical implications.

History

There have been recurring suggestions that there might have been increases in organismal autonomy during the course of animal evolution (for an overview see Rosslenbroich 2006). The considerations of Huxley (1948, 1957) are the most well known. Gerhart and Kirschner (1997) took this point up with respect to its significance in the origin of multicellularity and regretted that it was not discussed in evolutionary biology. In the physiological context, autonomization was regarded as emancipation from the vagaries of external conditions by the generation of an "internal milieu" and homeostatic abilities (Bernard 1859; Cannon 1932; Slobodkin 1964; Smith 1953). It has also been discussed in the context of constructional morphology (Gutmann 1981; Weingarten 1993), and there were also philosophical considerations on it (Jonas 1966; Spencer 1864; Steiner 1894).

However, comments on the principle of autonomy in evolutionary biology were rare and generally cursory. Authors usually gave some examples, but did not explore the implications in any depth. To date there has been neither systematic enquiry nor any definition of the principle. Such a systematic enquiry has been performed recently (Rosslenbroich 2007). The study showed that the relevance of the principle of autonomy for understanding macroevolutionary innovations was seriously underestimated in the past and that many major transitions in animal evolution lead to increased autonomous capacities. There is not a general continuos trend towards autonomy: many lineages exhibit this feature in different forms and independent of each other.

Many details are still unclear due to a lack of scientific endeavor on this topic. This holds true for questions on the systematic level at which increasing autonomy can be described and also whether there are autonomy-neutral and autonomy-destructive events. We, too, know little about the relation of autonomy to adaptation. Many of the underlying details are hidden in the physiological, morphological and palaeontological literature and need to be compiled from there under this aspect, while other questions may need to be addressed empirically.

There are two lines of argument in more recent literature, which also discusses the principle of autonomy. The first one is in both modern systems theory and autopoiesis theory (see Luisi 2003; Roth 1981; Varela 1979, 1981; for the origins of this discussion, and Barandiaran and Ruiz-Mirazo 2008; Bechtel 2007; Di Paolo 2004; Kauffman 2003; Moreno et al. 2008; Ruiz-Mirazo and Moreno 2004; Ruiz-Mirazo et al. 2008, for recent developments in the field). Systems biology attempts to understand whole organisms through an integrative view of all known regulatory and molecular processes whereas autopoiesis theory states that such systems are self-generated units by means of the production and transformation of networks. Within these considerations the discussion is mostly concerned about autonomy as an universal and defining feature of systems and life in general and about the question of how early life established it. It focuses on the principles of self-regulation, generation and regeneration of living systems and on their own functionality without a need for external control (Barandiaran and Ruiz-Mirazo 2008). Autopoiesis theory in particular is an ahistorical concept because it describes an organization emerging from the dynamics of components and not from evolution (Moreno et al. 2008).

The second line of argument does not use the term autonomy, but attempts to grasp the same principle from a different viewpoint, calling it "robustness" (Kitano 2007; Stelling et al. 2004; Wagner 2005). Robustness is understood as "the ability to maintain performance in the face of perturbations and uncertainty" (Stelling et al. 2004, p. 675). It mainly looks for the cellular and molecular processes such as feedback control, redundancy and modularity of functions, hierarchical organization of organisms and protocols which manage the relationships between parts or modules, thus enabling this stability. Robustness is a quite new concept in molecular biology and attempts to understand how organisms survive as invariant units within more or less threatening environments.

Curiously these two lines of discussion seem to have no connection to each other. However, neither attempt to describe changes in autonomy or robustness during evolutionary transitions. Thus, they are inclusive elements of the theory developed here, but only one part of the story.

Definition of autonomy

Increasing autonomy is defined here as an evolutionary shift in the system-environment relationship, so that the direct influences of the environment on the respective individual systems are gradually reduced and stability and flexibility of self-referential, intrinsic functions within the systems are generated and enhanced.
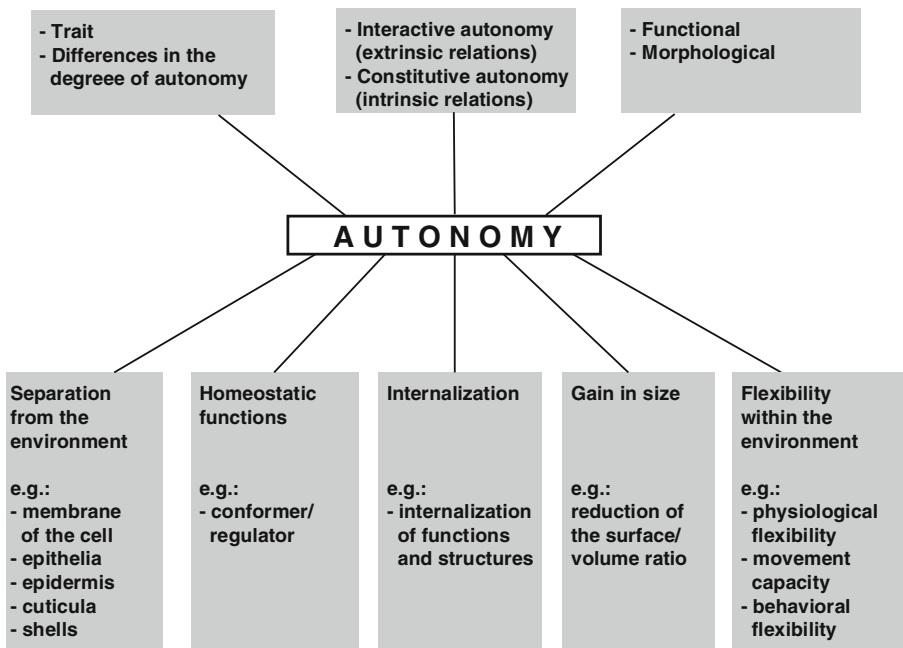
Fig. 1 Features and elements of biological autonomy

This is described as relative autonomy, while, at the same time, numerous interconnections with and dependencies upon the environment are retained. Thus, organisms undergo a relative emancipation from environmental fluctuations.

The definition contains several aspects (Fig. 1). The most general aspect is the *trait* of any organism in displaying relative operational closure and self-regulation. This aspect of the definition is identical with definitions in robustness theory as Stelling et al. (2004) formulates: "Biological systems maintain phenotypic stability in the face of diverse perturbations arising from environmental changes, stochastic events (or intracellular noise), and genetic variation" (p. 675). It is also covered by the definition of Ruiz-Mirazo and Moreno (2004), looking at the principle from the autopoietic perspective. They see "the conception of basic autonomy as the capacity of a system to manage the flow of matter and energy through it so that it can, at the same time, regulate, modify, and control (1) internal self-constructive processes and (2) processes of exchange with the environment. Thus, the system must be able to generate and regenerate all the constraints—including part of its boundary conditions—that define it as such, together with its own particular way of interacting with the environment" (p. 240).

Life processes within the system are not identical to those of the surrounding medium, but actively establish an internal compartment having physiological regulation opposed to the abiotic and biotic environment through energy consuming functions (Brooks et al. 1989; Luisi 2003). This form of autonomy distinguishes a living organism from non-living matter and makes all attempts to reduce biology to physics and chemistry suspect.

The internal compartment is established within a boundary which the system generates as a spatial separation from the environment. In its simplest form this principle is realized in a single-celled organism by means of a cell membrane. However, even the simple example of the cell membrane shows that in a biological system a complete separation is never obtained: instead we see the double function of a boundary and an exchange with the environment. Each cell membrane and each integument of an animal has to perform this double function. The same holds true for the general metabolic processes. Organisms have to balance these two requirements and each solution looks different. Thus, the term autonomy cannot be taken in an absolute manner, but always describes a *relative* autonomy. This distinguishes the definition used here from previous ones in evolutionary biology.

Furthermore an extrinsic-relation and an intrinsic-relation of autonomy can be distinguished. The extrinsic-relation describes the system-environment relation. The intrinsic-relation describes the self-referential, inner organization within the system (for example homeostatic stabilization of processes, intraorganismal signaling, connectivity within neuronal systems). This is basically identical with what has been called *interactive autonomy* (how autonomously a system behaves in interaction with its environment) and *constitutive autonomy* (within the context of the biological system itself) (Bertschinger et al. 2008; Moreno et al. 2008).

But this is only one aspect of the theory proposed here. A second aspect regards the process of changes in the degree of autonomy. The hypothesis is that organisms not only show autonomy as a general trait, but also that there are *differences in the degree of autonomy* within taxa. The evolutionary process generated organisms with distinguishable degrees of interactive and constitutive autonomy. Thus, there are organisms that are more subject to the direct physical, chemical and biological conditions of their surrounding and others that can act more on their own behalf, being more active, flexible and selective in their interaction with the environment.

To be more specific, this general feature is considered to be a complex of several biological elements which contribute in different degrees to the principle (Fig. 1). They are not general rules nor some sort of continuous trends. They rather function as a set of resources which can—singly or in combination with each other—increase autonomy.

These elements may not be complete. The various relations of the somewhat heterogeneous elements to each other will also need further thought in the future. But at least they can be identified within the major evolutionary transitions and changes in them can be described. Thus, they are obviously relevant.

One such element is *spatial separation from the environment* as with cell membranes, cell walls, integuments of metazoans with cuticles, shells, hairs or feathers. In different degrees they all serve to keep the environment outside the organism and to regulate and direct exchange with it. *Homeostatic functions* are means to establish internal functional stability. Another element is the displacement of morphological structures or functions from an external position into an internal position within the organism, here summarized as *internalization*. Multiple processes of internalization are involved in building up the inner anatomy of organisms, ontogenetically as well as phylogenetically. During ontogeny, gastrulation and neurulation are typical internalizations. During phylogeny, for example

the transition from prokaryotes to eukaryotes obviously included the internalization of some organisms within others (endosymbiosis). A *gain in size* in many transitions leads to a reduction of the surface to volume ratio. This means that in larger animals there is less direct contact to the immediate environment relative to the existing body mass. The smallest cells we know, bacteria, have a large surface for environmental exchange. In larger bodies this direct exchange capacity is reduced relative to the body mass. The rates of change of state internally are much slower, giving them an 'inertia'-effect which smoothes out the fluctuations and gives time for regulatory functions to operate. They may have better opportunities for storage of energy and substances and they may have room for more complex internal regulatory structures. It is well known in physiology that larger animals are more likely to be regulators, who stabilize their internal conditions also under fluctuating environmental circumstances (Willmer et al. 2000). Although there are no linear increases in size, evolution obviously deals with it, so that size matters and is not random.

These elements are prerequisites for establishing a certain amount of physiological flexibility within a given environment, i.e. a capability of organisms to generate *flexible functional answers* to conditions and changes in their environment. Finally, this principle can be widened to include all forms of *behavioral flexibility*, emancipating organisms from mere short-term reactions to environmental factors.

In the following text some of the major evolutionary transitions are described and it is shown that these elements can be identified in many of them. Thereby their significance will be outlined further.

However, autonomy only describes morphological and physiological characteristics. The theory attempts to recognize macroevolutionary patterns, it is not a theory on the driving forces of evolution.

The prokaryotic cell

Autonomy is a feature of life in general, as every organism differs fundamentally from the surrounding processes of the inorganic environment (Barandiaran and Ruiz-Mirazo 2008; Bechtel 2007; Luisi 2003; Moreno et al. 2008). In a basic manner this is already established within prokaryotes. They are surrounded at the very least by a membrane that functions as a boundary, enclosing a compartment within which metabolism and genetic information are internalized and protected from destructive external influences. However, at the same time there is a relative openness towards the environment, so autonomy can always be questioned, pointing at the flux of environmental components through the organism. But this "openness" is as relative as autonomy. Thus, the usual definitions of an organism either as an "open" or as a "closed" system are both one-sided. Every organism is both, however, with shifting emphasis.

It is likely that during early evolution different layers of surrounding material were involved. Cavalier-Smith (2006) assumes that primordial cells had an envelope of two distinct lipid bilayer membranes. This was followed by a loss of the outer membrane and changes in the murein wall. In a subsequent transition cell surfaces

became "potentially more flexible by replacing the rigid eubacterial corset of cross-linked murein peptidoglycan by separate glycoproteins" (p. 970), closely followed by the origin of the eukaryote cell. If this model of early transitions is correct, it shows a conflict that obviously occurs often during evolution: the conflict between a more rigid and enclosing surface structure on the one side and a less rigid structure, allowing more flexibility, on the other side. According to my definition, both are elements of autonomy. A good deal of evolution may include the requirements for organisms to find a balance between these possibilities.

In addition, the biochemical networks establish a disequilibrium towards the environment, concentrating specialized metabolites with organically utilizable energy. In opposition to the destructive influences of the outer inorganic environment the intracellular, energy-rich bonds are kept stable. Through self-regulation energy is used in small amounts rather than in fast bursts.

The information of the genome enables the cell to generate order, thus acting against the general tendency of the inorganic world towards an increase in entropy. It establishes the identity of the individual as well as of the species. Thus, the genetic information provides a basis for autonomy. As the metabolism, the flow of energy and the usage and transmission of the genetic information are regulated in time, there is also autonomy of processes in time, which are described by chronobiology.

Although there are these elements of autonomy, prokaryotes are still basically very open and dependent on their environment. Being small they have a large surface area relative to their volume and perform extensive molecular exchanges.

The eukaryotic cell

Although many details of early eukaryotic evolution are still a matter of discussion, some corner stones of contemporary theories, as well as obvious differences between prokaryotes and eukaryotes can be used to show that also during this transition the elements of an increasing autonomy are involved.

Generally, the appearance of eukaryotic cells widened the capacity of physiological self-regulation. More complex cells gradually reduce the openness and increase the relative isolation from the environment. Increase in size reduced the surface area being in direct contact with the surrounding medium. During this transition new methods of substance transport were generated. The cytoskeleton offered the opportunity for stronger and more effective movements within the environment, including the drive by flagella and cilia. This widens the capacity to move and to reach new environments. Some single-celled algae for example perform migrations which go many meters deep within their lakes.

Several internalizations took place. Intracellular organelles and the compartmentalization of the cytoplasm enabled the internalization of many functions such as respiration and photosynthesis, which in prokaryotes are still associated with the outer membrane surfaces. It is believed that organelles such as mitochondria and chloroplasts arose by the internalization of other prokaryotes, which then functioned as endosymbionts. The nucleus also may be a product of an internalization process

(López-García and Moreira 2004). While much chemical exchange in prokaryotes takes place directly through transporter molecules on the cell surface and digesting enzymes are released to the outside to prepare uptake, in eukaryotes substances tend to be internalized through endocytosis. DeDuve (2007) suggests "that the highly advantageous conversion from extracellular to intracellular digestion, associated with membrane internalization, acted as the evolutionary driving force of the process…This heralded…the beginning of cellular emancipation. Henceforth, heterotrophic cells were no longer obliged to reside within their food supply; they were free to pursue their prey actively, living on endocytized bacteria and other engulfed materials, which they digested intracellularly within their lysosomes" (p. 397). In eukaryotes the genome is internalized into an additional compartment, the nucleus.

While within prokaryotes there is still an extensive exchange of genetic material between individuals (horizontal gene transfer) it is severely restricted in eukaryotes (Doolittle 1999), stabilizing the genomic self-assertion of the individual as well as that of the species.

Multicellularity

The generation of multicellular animals, sometime in the Precambrian Era, can be understood from the perspective of an increased capacity of self-assertion of the individual organism within its environment. The central feature here is that the cells of the multicellular organism are organized into a compartment which is more or less regulated by themselves (Fig. 2). Through the generation of a common extracellular matrix, a buffer zone is established, which is an intrinsic and constitutive part of the organism (Bonner 1998; Gerhart and Kirschner 1997; Rieger 1994; Waggoner 2001). In addition, the cells build up epithelia and integuments surrounding them as boundaries towards the environment. Thus, cells and organs are integrated into a matrix of a considerable homeostatic potential. Transitions to multicellularity occurred independently several times (Waggoner
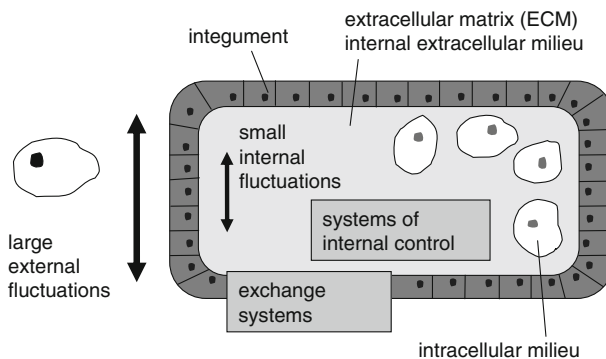

Fig. 2 The principle of the stabilized extracellular milieu. Systems of control regulate the exchange with the environment (e.g. epidermis, gills) and the composition of body fluids (e.g. nephridia)

2001), showing again that the process discussed is not a linear one. On this basis the large evolutionary radiation of animals at the beginning of the Cambrian period occurred.

The study of the volvocine algae provides a model to explore some details of an evolutionary pathway leading from a unicellular ancestor to multicellular organisms (Kirk 2005). At the same time it provides a model for the generation of autonomy during this transition (Rosslenbroich 2007). This includes the internalization of cells into a common matrix, the internalization of germ-cells and reproduction, the reduction of relative surface area, increased motility, increased metabolic autonomy and emancipation from the amount of nutrients in the immediate environment.

Within animals, the potential which multicellularity provides was realized in very different ways with differences in the capacity of closure, regulation and flexibility. Using possible elements of autonomy, feasible animal body plans seem to have been explored. The generation of the different, more or less enclosing integuments was one of the functions involved (Bereiter-Hahn et al. 1984; Lillywhite and Maderson 1988; Rieger 1984; Willmer 1990). A host of different organs, appendages and functions was generated, which stabilized the animals in different ways against the fluctuations of their environment. Each group generated its own combination of elements of autonomy. While, for example, bivalves built up a massive boundary, other organisms developed a high manoeuverability, thus becoming more independent from the immediate conditions. The capacity for movement was increased with the evolution of lever-based appendages, as in marine arthropods. During the Palaeozoic motility was developed further by inland arthropods, such that fast running on land and flight became possible. The combination of the chitinous cuticle as an effective boundary and structural substance, together with the huge flexibility of movement through lever action was the basis of the high autonomy within many arthropods and may have been the basis of their phylogenetic success, as they expanded their environmental access.

The cohesion of numerous cells into compartments created the potential for large increases in size (Bonner 1988), which further reduced the relative surface area. Exchange surfaces were concentrated on specialized tissues, which became more effective and were internalized into the body (Willmer et al. 2000). For example, gaseous exchange in primitive and small animals can take place through the general body wall, but in more developed and larger animals internalized gills, trachea or lungs were generated. The gut is another example, where tissues, which absorb food substances from the environment and break them up, are taken into the inside of the body. Circulatory systems made possible the isolation of tissues from an outside fluid medium, which was previously necessary for oxygenation and feeding, as is predominantly still the case in sponges, which are not enclosed by real epithelia but are rather open to the environment. In different forms, self-produced fluids—like blood or hemolymph, selectively isolated from the surrounding medium, fulfill this task (Fig. 3).

In animals which conquered land, these circulatory systems had to gain enough independence to enable them to maintain the fluid surroundings that each cell needs within a dry environment. Increasingly efficient renal organs maintained homeostasis of body fluids (Smith 1953). The emancipation from water is one of the most
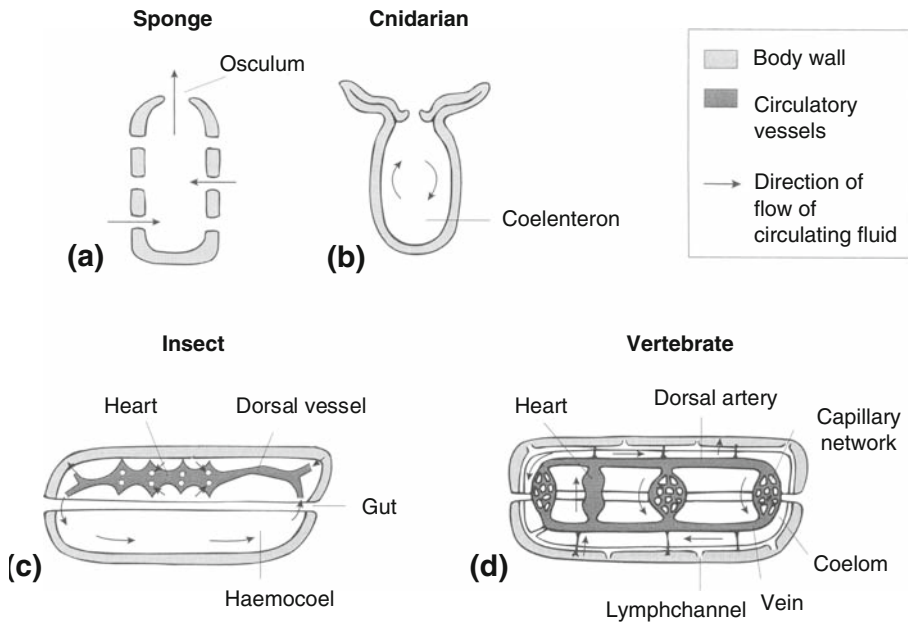
Fig. 3 Some circulatory systems. **a** and **b** Circulation of the external medium through a sponge and a cnidarian. **c** Circulation of hemolymph within the open system of an insect. **d** Circulation of blood within the closed system of a vertebrate. (Modified from Willmer et al. 2000)

often mentioned examples for an emancipation of organisms from the environment. But it has been criticized that the dependence on a water environment was merely exchanged for a dependence on the terrestrial environment, and that on the whole there was no increase in general independence (Dobzhansky et al. 1977; Simpson 1971). However, it is now clearer that land-based animals have a greater degree of emancipation in the following way: through circulatory systems organisms can carry their own "pond" within them and take it into surroundings that are basically hostile and life-threatening to cells. The cells remain different from their immediate environment within their own, self-regulated milieu. This is the true emancipation in the transition to life on land.

The stabilization of homeostasis

Physiology distinguishes three general patterns which animals show in dealing with environmental changes (Willmer et al. 2000). They may avoid them by behavior, or they may tolerate them either as conformers or regulators. Conformers allow their own internal conditions to follow those of the outside world, while regulators maintain internal conditions that are predominantly independent from the environment. This can be observed in different functions like osmoregulation, temperature control and many more. Often homeostasis can only be maintained within certain limits in what may be for example "limited regulators".

It is not easy to give generalizations about patterns of avoidance, tolerance and regulation across the animal taxa, but smaller and soft-bodied animals are more likely to be avoiders or conformers. Large- and medium-sized animals with hard outer layers (exoskeletons) have better options for regulation and a greater independence (Willmer et al. 2000). Arthropods are more likely to show partial regulation, while large animals are much more likely to be regulators in all environments. Regulation is especially refined within vertebrates whereby birds and mammals reach a high degree of regulation in every habitat. This is a clear phylogenetic stabilization of homeostasis.

The ability to maintain stable inner conditions (1) at a level typical for the species and different from the environment and/or (2) to maintain constant levels within fluctuating environments are elements in the evolution of physiological autonomy.

Chordates

I argued that autonomy was realized in different ways and combinations within the different phyla. One starting point during the Cambrian explosion was an effective basic organization of the locomotor apparatus of chordates. According to the reconstruction of an archaic fishlike vertebrate by Carroll (1988) it is likely that it had segmented muscles on each side of the body, which were attached to the chorda dorsalis. The chorda served as an axle, which stabilized the length of the body, without deforming it, while at the same time it was elastic and flexible. The muscular antagonism and the concentration of forces on one single axis, which transforms the forces to the medium, made the system effective and economic. The elasticity of the axis leads to continuous thrust.

This chorda-myomere-system was the basis for the development of a high capacity for movement with fast swimming and powerful sprints. This system was largely refined by the generation of the vertebral column and further development and reconstruction of the attached muscular system. The potential for highly autonomous movements within the environment formed the basis of vertebrate evolution. In addition, the vertebral column could serve as the central constructional stabilization for movement on land (Ahlberg and Clark 2006; Ahlberg et al. 2005). High movement capacity emancipates from the conditions of the direct environment as larger areas can be reached and more flexible reactions to special situations are possible.

Numerous examples of increases in autonomy can be described in some detail within vertebrate evolution. Thus, amphibians emancipate from water to some extent, but are still dependent upon moist surroundings especially for reproduction. During the transition from fishes to amphibians, a central innovation emerged, which would again form the basis for an extended capacity of movement on land: the evolution of limbs (Ahlberg and Clark 2006; Ahlberg et al. 2005). As within arthropods, but using different building materials, an effective system of the use of lever action was again developed, but this time working internally within the endoskeleton. This led to fast runners, such as the cheetah and high-performance flyers, such as terns and swifts. Especially within mammals a high divergence of

possible movements evolved such as running, climbing, digging, flying, swimming and many more.

Reptiles increased their independence from moist surroundings by building a hard water-resistant skin and making changes in their circulatory system (Sumida and Martin 1997). However, the most important innovation was the generation of the amniotic egg, which effectively emancipated reproduction from water. Further steps leading to the internalization of reproductive processes followed, especially within mammals. In eutherian mammals embryonic development has been completely internalized into the body.

Endothermy in mammals and birds

A central element during the transition to mammals and birds was the conversion from ectothermy to endothermy. The origin and generation of these differences are still a challenge for evolutionary biology, as it remains unclear which forces initiated and selected this "wasteful strategy of energy use" (Koteja 2000, p. 479). Figure 4 summarizes the main evolutionary changes occurring during this transition, presented as a system of interrelated and interdependent features.

Reptiles have a limited capacity for aerobically supported movements. At higher levels of activity most of the energy comes from anaerobic metabolism, leading to fast exhaustion, long recovery periods and limited movement capacities (Ruben 1995; Pough 1980). One evolutionary innovation of endotherms was an increase in
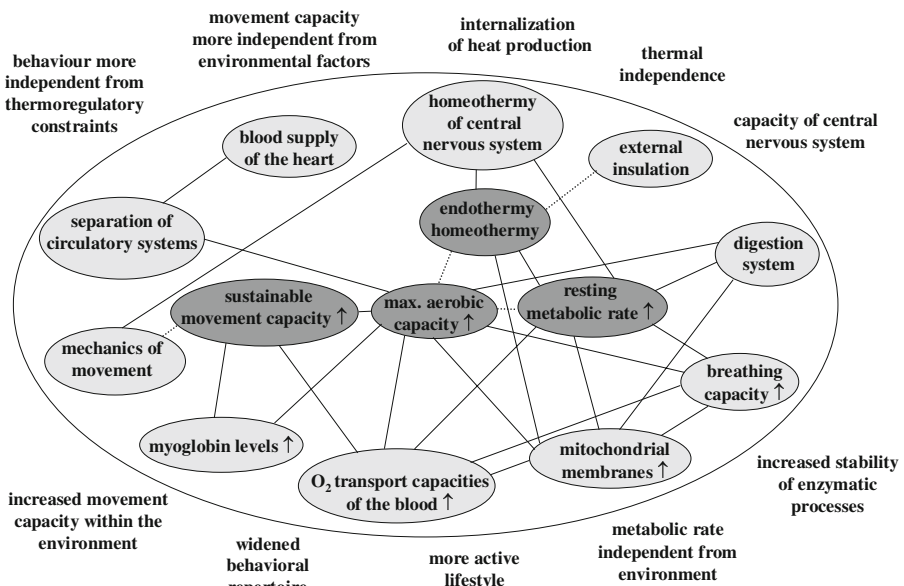

Fig. 4 Graphic representation of the functional complexity of endothermy. The *lines* indicate interrelationships as usually described in comparative physiology. The related features of autonomy are indicated at the *outside* of the *larger oval line*

the capacity for aerobically supported movements. This resulted in substantially increased routine activity levels, stamina and endurance (Bennett 1991; Ruben 1995). The increased oxygen demand is achieved through increased lung ventilation rates, expanded vascularizations of the lung, integration of a diaphragm, increased pulmonary surface area and diffusion capacities as well as increased abilities of oxygen transport (Bennett 1991; Ruben 1995; Ruben et al. 2003; Pough 1980). The complete structural separation of the cardiac ventricles occurred in this transition and maximal cardiac output has been greatly increased. The high arterial pressure which was established requires an efficient and powerful heart muscle, with a blood supply completely arranged by a coronary circulation. General rearrangements of skeletal elements lead to two different solutions for movement characteristics in the avian and the mammalian lineage.

In the sum the thermal and metabolic independence from temporal fluctuations increased. Many reptiles can raise their body temperatures above ambient levels so as to carry on some of their biological activities. Nonetheless they generally obtain the necessary energy from external sources. In contrast, birds and mammals internalized their energy generation so that the potential for movement within the environment is in principle always available. Endothermy allows the animal to be "instantly" ready for additional high-rate activity.

The substantial increase in sustainable movement capacities gives a much larger potential for and range of activities, including migrations, and leads to a much more active life-style with expanded degrees of freedom and enhanced ecological possibilities. The more or less continuously available capacity for activity allows for more complex behavioral and social repertoires.

However, there are costs and novel dependencies associated with it like the need for a large and constant food supply. One could argue that the ecological effect is only a change from one type of niche to another. But the main point is that a new flexibility for the individual and a much greater physiological and behavioral plasticity are gained. This flexibility is obviously so central that during evolution the shift to a dependency on high resource expenditure as well as the extensive conversions took place. The gain in flexibility is greater and compensates for what has been lost.

Nervous systems

Nervous systems appear in their simplest forms as distributed nets and in more complex forms they have concentrations of neurons. They mediate the reactions to the environment, so that an organism does not react like a billiard ball to a push, but rather in a more or less self-determined way. They process incoming signals, so that the resulting reaction is indirect and has an active component detached from the environmental signal. This modulation produces the capacity for flexible, self-determined reactions of different degrees to environmental stimuli and is thus a feature of autonomy. With the concentration of nervous systems within complex brains, this detachment and self-determination was extensively widened. Especially impressive is the behavioral flexibility of the octopus. A comparison of different

degrees of centralisation and of the different paths, by which they were reached, shows again the non-linearity of the process. However, the feature is obvious in several lines, often independent from one another (Conway Morris 2003).

The concentration of nervous systems is well known within the vertebrate lineage (Butler and Hodos 1996; Roth and Wullimann 2001). However, it is generally overlooked that this is part of a more universal evolutionary process and that it correlates with other elements of autonomy.

For example, the flexibility of movements is largely enhanced within vertebrates. In evolutionary primitive cyclostomes the spinal cord works on its own, with little control from the brain. Central pattern generators along their spinal cord induce the bending of the body to both sides for swimming movements in a fairly monotonous way. Evolutionary changes lead to an increasing plasticity of neuronal motor control. In more evolved vertebrates, neural processes of locomotion are uncoupled from one another so that each of them controls only restricted parts of the motor apparatus. These parts can act in more differentiated and partly independent ways. Dubbeldam (2001) assumes that this differentiation into units of activation gave birth to new degrees of flexibility and versatility.

In addition, the whole motor system is increasingly supplemented by motor control through the developing forebrain and by capacities for voluntary movements. This not only supports fast movements of many mammals and birds, but also other skills like the use of the forehand in hunting prey, digging, climbing or the use of prehensile forelegs etc., often fulfilling several of these activities. The telencephalon introduced the capacity to generate new combinations of movements—in coordination with the increasingly sophisticated sensory system.

The development of the corticospinal tract appears to be associated with the acquisition of dexterous motor skills. In birds, a sensorimotor circuit is present which is related to skilful "handling" of food. In humans the forelimbs are completely freed from movement tasks and develop a nearly endless potential for dexterous abilities.

Again there is no linear and direct evolution towards one of these capabilities and the diversity of different combinations of neuronal and motor flexibility is considerable (Butler and Hodos 1996).

These principles of flexibility, independence and self-determination are at least in part an answer to the important questions repeatedly posed by Bullock (1993, 1995). He asked for an analysis of the qualitative differences between brains of animals belonging to different major grades of brain complexity and cognitive capacities, their relevance to behavioral differences and the consequences for the understanding of evolution.

Behavioral flexibility

Within the vertebrate lineage brain evolution led to a domination of the telencephalon, which allowed new and more complex behavioral capabilities to evolve. However, within ethology there is a longstanding debate over what these capabilities are, how differences can be described and what animal intelligence is.

Some ethologists who prefer adaptational interpretations hold that there might be no general difference in these features in animals on different evolutionary levels, but only different forms of adaptation, yielding a divergence of brain forms. In contrast, other ethologists try to describe the qualitative differences in behavioral abilities.

One among several characteristics of behavior is flexibility. Animals have different capabilities of flexible behavior, which allow for novel, individual and non-determined solutions to problems and tasks. Thus they are another expression of autonomy and stand in contrast to fixed action patterns (FAP). Although most of animal behavior is characterized by FAPs, flexible components can also be found in animals on very different evolutionary levels. The most widespread of these is learning, which means that more or less restricted parts of their behavior can be modified by experience. Many mammals and birds have broad learning dispositions. Well known examples for animals with pronounced learning abilities are the octopus, dolphins, great apes, parrots and ravens.

Another behavior, which is characterized by high flexibility, is play. Play is observed in some birds and in most mammals (Bekoff and Byers 1998). It has been difficult to understand animal play from the perspective of adaptation and thus it remained an enigma. However, it is a consequence of the evolutionary patterns which lead to increasingly autonomously acting animals. Behavioral elements can occur in new and changing combinations, detached from life-supporting necessities. Sometimes during play new movements and combinations of movements can be invented. Thus, play expresses a certain degree of freedom, which is only possible within a "relaxed field" (Eibl-Eibesfeldt 1999; Hassenstein 1969).

There are many more examples for behavioral flexibility. Some primates are able to imitate behavior, which is completely outside the range of their normal repertoire. Some have been demonstrated to have insight into simple physical relationships. This also applies to some ravens and it includes some capabilities for planning and thinking ahead (Byrne 1995; Heinrich 2004). Further skills can include insight into social relationships within a group of apes and also some simple forms of empathy have been demonstrated. A high flexibility is especially demonstrated in experiments with signals as communicative tools in dolphins, chimpanzees and some parrots.

In song-birds different degrees of flexibility and degrees of freedom from innate song repertoires such as song learning, imitation, duet singing and counter singing can be described (Streffer 2009).

Any complex behavior emancipates organisms from the environment to some degree, as they not only *react* upon environmental influences, but *act* actively within their environment. Beyond this, flexible behavior introduce further levels of independence from environmental restrictions and from FAPs. Flexible behavior is typically described in animals with large and complex brains (Roth and Wullimann 2001). Although it is not easy to give a clear-cut answer to what the biological and behavioral effects of sophisticated brains are in each single case of the broad divergence of animals (Butler and Hodos 1996) the recurring principle is obviously a feature of autonomy.

Discussion

Some general characteristics of the evolutionary pattern identified here have to be considered. First it is important to mention again that this is obviously not a linear process. There is rather a broad range of forms with different combinations and different features of autonomy at very different levels. Within arthropods there are forms with sophisticated possibilities of independence, physiological stability and movement capacities. Also within vertebrates there is rather a divergence of different forms of autonomy within the classes. However, in certain evolutionary lineages and especially in the major transitions crucial innovations appeared, leading to new possibilities of action and reaction towards the environment. Further studies must analyse the diversity of the pattern to draw a more complete picture.

Such studies would have to regard the many cases of evolutionary convergence, which Conway Morris (2003) carved out of the evolutionary "trajectories" of animal evolution. Many of his examples are features of autonomy as defined here. Thus, the topic of autonomy is an essential part of his proposal to explore how evolution "navigates" and it develops the basis for a more general theory of biology, describing the "ground rules" of life and its evolution.

In the same sense such studies presumably would identify lines with decreasing autonomy. Possible cases would be parasites, which use the autonomy of their host organism and thereby lose some of their own homeostatic abilities. If the parasites are harmful they even may reduce some of the autonomous capacities of their hosts. Another case could be when an organism gets extremely well adapted to a very specific environment, losing the capacity to deal with other ones. Then, one question could be to find out whether these lines can have some evolutionary potential or whether they are side lines. Some birds gave up their capacity of flying. Did they reduce their movement capacity in order to adapt to special environments, to increase size or to gain metabolic stability rather than to invest into high level energy expenditure during flight? Did they change to other features of autonomy (the ostrich to running, the penguin to rapid swimming and diving)?

Symbiosis may often increase the autonomy of the whole system while the symbiotic partners give up some of their autonomy as individuals, especially when the partnerships become obligatory. An obvious example for this is the formation of the eucaryotic cell, as discussed before. Changes in organism-environment relations may also be an important component of eusociality. Large insect states like those of the honey bee are able to establish some homeostasis in their colony, even gaining homeothermic possibilities for the whole system.

The general impression is that major evolutionary transitions lead to new basic capacities of autonomy and within the following radiations organisms explored the available possibilities. Within these possibilities different requirements of autonomy may come into conflict or tension. Is it perhaps possible that large dinosaurs attempted to gain thermal autonomy through an increase in size, referred to as "mass endothermy" and the consequent cost was restrictions in movement capacity? To elevate metabolic productivity was the solution in mammals and birds. In total that solution gave more flexibility and therefore was more successful.

Increase in autonomy is an observable pattern. The intention here is "first to define and to describe the perceivable pattern in order to help to detect and identify underlying structure and cause", as was proposed as the appropriate way to study patterns, processes and directions in the history of life during a Dahlem workshop (Wake 1986, p. 47). Presumably this principle should be studied in its relation to other possible patterns in macroevolution like complexity, size, entropy and so on (McShea 1998; Rosslenbroich 2006). Second, it demonstrates the heuristic potential of the concept of autonomy for learning more about "how evolution navigates".

Another heuristically interesting sideline is the overlap in the notion of autonomy with autopoiesis theories, although it lacks the evolutionary dimension, as indicated earlier. Getting autonomy more into focus also from this point of view may allow us to get closer to a definition of life in general. Moreno et al. (2008) may be correct in their opinion that "autonomy is the main feature of life, the key notion for any attempt to define it" (p. 310). This is especially interesting for all of us who are looking for an organismic biology, rather than a biology that claims that all phenomena of life can be completely reduced to physical and chemical processes. Moreno et al. (2008, p. 311) deliver some elementary formulations for this. They see as essential for autonomy "…a recursive net of component production that builds up its own physical border. The global net of component relations establishes a self-maintaining dynamics, whose action brings about the constitution of the system as an operational unit." They see autonomy as a condition of subordinating all changes to the maintenance of the organization and self-asserting capacity of the system. Here the term "subordinating" is a central one, as this distinguishes living systems from non-living ones. Purely physical phenomena like tornadoes and candle flames in which self-organizing properties appear, are not autonomous in the sense of living systems: "… the autonomy of the system depends on the existence of internal constraints able to channel its process dynamics in one of the possible directions. This amounts to some form of additional causality with respect to law-governed dynamics, exerted by the system itself" (p. 311). They stress that work is needed to build these constraints, whereby work is seen as the coordinated, coherent and constrained release of energy. They call this the "work-constraint cycle".

Autonomy and adaptation

At first glance the principle of autonomy might contradict the concept of adaptation, perhaps in the sense of some form of "anti-adaptation". However, it may also be a necessary, but neglected, element of adaptation. In a first approximation it can be stated as follows: if adaptation is used as a term for the characters or traits observed in animals, which are the result of selection or as a process that reveals characters leading to fitness (Willmer et al. 2000), there is no reason why an increase in autonomy should not be part of the fitness of an organism and thus adaptive. On the contrary, the stabilization of self-regulated functions and the autonomous buffering against influences from the environment may well be a means leading to fitness.

The question may also be approached in a further sense. Mahner and Bunge (1997) identified eight different meanings of the term "adaptation" in the context in

which it is used today. In all these variants one fundamental point is neglected. Adaptation describes an organism-environment relationship, which means that there is on the one side the organism and on the other side the environment. In any case the organism maintains its specific life-functions within an established boundary, something which is true also for the simplest forms of life. Thus, adaptation contains these two elements: (1) the biological integrity of the organism, (2) which is maintained by dealing with the conditions of the environment, leading to cohesion between many morphological, functional and behavioral properties of the living being with its environmental circumstances. The theory of autonomy describes how element (1) changes during evolution, using element (2) as one of several means to stabilize and maintain the integrity of the organism.

If adaptation is only understood as a remodeling of the properties of the organism to the specific requirements of the environment, organisms only seem to be passive results of extrinsic factors. This neglects the intrinsic competence of the organism itself (McNamara 1990). The components of biological integrity of the individual, mutual interconnections between organism and environment and the modifications within these systems have to be considered differentially in order to come to an understanding of evolution which matches reality.

Lewontin (2000) regards it as necessary to revise the notion of adaptation through a broader understanding of the relations between organism and environment. He shows that this relation is much more complicated and may not be reduced to a passive principle. He states that the environment of an organism is not a given physical world outside, to which it has to fit, but that there are rather complex interactions between both sides. Organisms determine which elements of the external world are relevant to them to form their environment and they smooth out the temporally and spatially varying external conditions. Moreover organisms actively construct a world around themselves and are in a constant process of altering this environment. "The time has come when further progress in our understanding of nature requires that we reconsider the relationship between the outside and the inside, between organism and environment" (p. 47).

Launching off from Lewontin, niche construction has been discussed as a relevant factor of evolution (Odling-Smee et al. 2003; Laland et al. 2005). It refers to the capacity of organisms to construct, modify, and select important components of their local environments such as nests, burrows, cocoons, chemicals and nutrients. However, niche construction may also be a further resource for organisms to make themselves more autonomous from vagaries of the environment. Beaver's dams, for example, smooth out changes in the amount of water in a certain surrounding with all the positive effects they can use for their needs. Ants need a temperature not below 20°C for their activity, but can survive in different temperature zones by regulating the temperature of their nests. They plug entrances to their nests at night or when it is cold and adjust the height or slope of the mound to optimize intake of heat from the sun. The plugging of nest entrances is also characteristic of many burrowing mammals in arid or cold regions. Turner (2007) studied termite mounds and described how they are constructed not only to capture wind to power ventilation but especially to regulate the ventilation altogether. "Think for a moment just how remarkable that is. The mound captures wind energy

at a particular rate that is matched to the colony's metabolism, which makes it an organ of homeostasis." (p. 25).

Turner proposes to focus more upon the dynamic interaction between living organisms and their environment, and the building of homeostatic units within this relation, referred to as "Bernard machines". Homeostatic units can either be organs, organisms or organisms together with their environment. They are relevant for evolution, not only the genes which are imagined by an atomistic doctrine as the only important entity of evolution. Thus, function has an evolutionary capacity on its own and seems not to be reducible to purely genetic processes, although the genetic text is important, of course, as a part of the whole assembly.

Turner formulates that "a more robust homeostasis will ensure a system's persistence over a wider range of perturbations and further into the future than will a less robustly regulated system." (p. 219). This is basically the same as what autonomy describes. However, while autonomy, as presented here, focuses more on the individual animal, Turner's perspective is somewhat broader. It integrates the environment and the organism into a whole correlative system. This is a relevant point of view which supplements the individualistic one. Then, the next questions can be posed concerning the relation of more or less evolved (more or less autonomous) organisms within these systems, giving the whole topic a more evolutionary perspective.

Questions of this sort will not only widen our understanding of the effects of evolutionary innovations but also of the organism-environment relations and that of intrinsic and extrinsic factors in evolution. It will contribute to overcome the one-sided "adaptationist paradigm", criticized by Gould (1983, 2002) see also Barker 2008.

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