Available online at www.sciencedirect.com
SCIENCE DIRECT®

C. R. Palevol 5 (2006) 489–498

COMPTES RENDUS PALEVOL

http://france.elsevier.com/direct/PALEVO/

History of sciences / Histoire des sciences

Form, function, transformation

Jean-Pierre Gasc

USM 302, Muséum national d'histoire naturelle–CNRS FRE 2696, BP 55, 55, rue Buffon, 75005 Paris, France

Received 17 March 2005; accepted after revision 7 December 2005
Available online 23 March 2006
Written on invitation of the Editorial Board

Abstract

No transformational theory could have been proposed before clear definitions were derived for the concepts of form and function. The maturation of these concepts followed the slow discovery of the rules that underlie the structural and functional basis of living beings. This question raises apparent contradictions that were overcome, but still left some pitfalls for evolutionary biology. The main one is the remnants of teleology in the heart of the adaptation concept, necessary to recognize the effects of natural selection. Functional Morphology has the hard task to navigate through these difficulties. ***To cite this article: J.-P. Gasc, C. R. Palevol 5 (2006)***.

Résumé

Forme, fonction, transformation. Il n'a pas été possible de proposer une véritable théorie de la transformation des espèces vivantes, avant que des définitions claires des concepts de forme et de fonction aient été avancées. La maturation de ces concepts a suivi la découverte progressive des règles de l'organisation des êtres vivants. Ces questions ont soulevé plusieurs contradictions apparentes qui durent être surmontées, mais ont laissé des pièges, face à l'avancée de la biologie évolutive. Le plus important est représenté par le reste de téléologie qui subsiste au sein du concept d'adaptation, pourtant nécessaire à la reconnaissance des effets de la sélection naturelle. La morphologie fonctionnelle a le difficile devoir de naviguer au milieu de ces difficultés. ***Pour citer cet article : J.-P. Gasc, C. R. Palevol 5 (2006)***.

Keywords: History of Sciences; Morphology; Physiology; Evolution; Functional morphology; Biomechanics

Mots clés : Histoire des sciences ; Morphologie ; Physiologie ; Évolution ; Morphologie fonctionnelle ; Biomécanique

1. Introduction: historical background and definitions

The question addressed by the relations between form and function and their conflict with the transformational view of evolution lies at the heart of biology. As a first step, we can look at the way these terms were and are still understood. It is obvious from the common sense that the external world is populated by forms and that the way to know this world is to look at their diversity. However, the perception as well as the interpretation of any form is not neutral. The most ancient figures drawn on cave walls illustrated animals and humans in action. They show specific individuals that

E-mail address: gasc@mnhn.fr (J.-P. Gasc).

1631-0683/$ - see front matter © 2006 Académie des sciences. Published by Elsevier SAS. All rights reserved.
doi:10.1016/j.crpv.2005.12.010

can be recognized, but above all they describe situations that are most probably associated with a functional meaning at the social level that we can only infer through statistical and comparative analysis by archaeozoologists. Sometimes, stereotyped forms became objects that have lost most attributes of the original model. Then, their interpretation is more conjectural and requires analogical comparison with similar objects in recent cultures. This is the case of most anthropomorph figures from Palaeolithic ages (so-called 'Venus'), as well as the 'Zemis trigonoliths' of the Tainos Indians that were decimated during the conquest of the West Indies. History of pictographic writing exhibits a similar pathway that led from figurative representation of the real world to signs or even sounds. This process is well documented for Mesopotamian ancient cultures, because correspondence with languages still spoken in the region could be disclosed.

The ancient Greek texts, which came to us in the 11th century through Arabic translations, provide documents that surely have a more remote origin in the neighbouring cultures of Mesopotamia and Egypt. In them, form appears as a concept detached from any object. This is probably the result of the extensive use of geometry in those cultures based on the use of land. To measure cultivated fields, and to assess the amount of crops produced, mathematical tools were needed. The empirical practices of land survey and mapping lead us to think that forms may exist without any concrete support. We can play with those entities without any reference to the real outlines of a specified field geometry was thus born. This led to the idealistic concept of 'form–idea'. The real outlines, the shapes of things that we perceive, are only shadows cast on Plato's cave walls. The catalogue of the limited number of ideal forms is known only by the divinity; we can only perceive distorted images of these forms in our sensible world. All through history and even beyond the threshold of the rise of modern science, this conception has had a great influence.

In Aristotle's (385–322 BC) writings, which had a huge impact on occidental thought for more than twenty centuries, form takes a quite different meaning. Forms exist only because they serve aims (final causes). Forms are organisation of matter that is justified by their function. Form is pre-eminent face to matter, not because it reflects the world of ideas as thought Plato, but because the essence of form lies in its function, and within the whole body organs are instruments situated in relation to a specified aim: "*En effet, les animaux possèdent des caractères communs, tantôt selon l'analogie, tantôt selon le genre, tantôt selon l'espèce. Ainsi donc pour toutes les fonctions qui sont subordonnées à d'autres, il est évident que les organes auxquels correspondent ces fonctions sont dans le même rapport que ces fonctions elles-mêmes. De même, si certaines fonctions sont antérieures à d'autres et constituent, le cas échéant, leur fin, chacun des organes dont ces fonctions-là relèvent se trouvera dans le même rapport. Et, troisièmement, l'existence de certains organes est la conséquence nécessaire de l'existence d'autres organes*." [2]. Even though the translation of the Greek word here used (αι πράξεις) may not overlap the exact meaning of functions, this assertion contradicts the atomistic view of Democritus who claimed that forms as bodies consist only of elementary particles glued together.

In this mandatory search for finality, the whole form of organisms was not always clearly distinguished from the parts. This has been the role of anatomical works, which could not avoid the debate about form-function relationships. The Cetaceans, which are aquatic mammals, constitute a typical example: their fish-like shape contradicts their internal organization and mode of reproduction. Aristotle's thought was deeply imprinted upon Greco-Latin and then Arabic cultures. It was spread through the Christian world, although banned by the Roman Church. When in the beginning of the 19th century Georges Cuvier founded comparative anatomy, and even promoted the comparative approach in biology, he recognized the debt he owed to Aristotle in the maturation of his principle of organic correlations: "*Tout être organisé forme un ensemble, un système unique et clos, dont les parties correspondent mutuellement et concourent à la même action définitive par une réaction réciproque. Aucune de ces parties ne peut changer sans que les autres changent aussi ; et par conséquent, chacune d'elles prises séparément indique et donne toutes les autres*." [15]. Cuvier broke the circular reasoning about 'organization' and the definition of living beings that was debated during the 18th century (life is characterized by the faculty of organization and so living beings are 'organized beings', but what is 'organization'?). The comparative method of Cuvier combines Aristotelian functionalism and the hierarchic view of organismal composition that the botanist Antoine-Laurent de Jussieu offered in 1789. "*C'est dans cette dépendance mutuelle des fonctions, et ce secours qu'elles se prêtent réciproquement, que sont fondées les lois qui déterminent les rapports de leurs organes, et qui sont d'une nécessité égale à celle des lois métaphysiques ou mathématiques : car il est* *évident que l'harmonie convenable entre les organes qui agissent les uns sur les autres, est une condition nécessaire de l'existence de l'être auquel ils appartiennent, et que si une de ses fonctions étoit modifiée d'une manière incompatible avec les modifications des autres, cet être ne pourroit pas exister*." [14]. The Cuvieran method became a powerful tool to decipher the rules of organismal construction, and brought to light a domain of predictability previously unknown in natural history. Everybody knows the famous history of the fragment of fossil skeleton found in the caves of Montmartre, which Cuvier recognized as belonging to an opossum, a now tropical animal. However, this tool became in the hands of too powerful a person a real obstacle to understanding a possible change in the relations among constituent parts of the organism.

2. The transformational perspective and its difficulty

Since the middle of the 18th century, several attempts have been made to promote the idea that living forms could have been transmuted during their history. Buffon, Diderot and, in a more provocative way, Maupertuis and Bonnet went far in their speculations about a transformational process. The starting point of this idea was the apparent contradiction revealed by the fact that the extreme diversity of forms can be reduced to a few models. It was the value of incipient comparative anatomy, beginning with Daubenton and Vicq d'Azir, to have emphasized this contradiction.

"*Et si les parties qui différent le plus en apparence se ressemblaient au fond, ne pourroit-on pas en conclure avec plus de certitude qu'il n'y a qu'un ensemble, qu'une forme essentielle, et que l'on reconnoît partout cette fécondité de la nature qui semble avoir imprimé à tous les êtres deux caractères nullement contradictoires, celui de la constance dans le type et de la variété dans les modifications ?*" [48].

The philosopher Denis Diderot (1713–1784) was aware of anatomical works that were undertaken at this period, and wrote in 1753 this surprising text [18]: "*Il semble que la nature se soit plu à varier le même mécanisme d'une infinité de manières différentes. Elle n'abandonne un genre de productions qu'après en avoir multiplié les individus sous toutes les faces possibles. Quand on considère le règne animal, et qu'on s'aperçoit que, parmi les quadrupèdes, il n'y en pas un qui n'ait les fonctions et les parties surtout intérieures, entièrement semblables à un autre quadrupède, ne croirait-on pas volontiers qu'il n'y a jamais eu qu'un premier animal prototype de tous les animaux dont la nature n'a fait qu'allonger, raccourcir, transformer, multiplier, oblitérer certains organes, quand on voit les métamorphoses successives de l'enveloppe du prototype, quel qu'il ait été, approcher un règne d'un autre règne par des degrés insensibles, et peupler les confins des deux règnes (s'il est permis de se servir du terme de confins où il n'y a aucune division réelle) ; et peupler, dis-je, les confins des deux règnes, d'êtres incertains, ambigus, dépouillés en grande partie des formes, des qualités, des fonctions de l'un, et revêtus des formes, des qualités, des fonctions de l'autre, qui ne se sentirait porté à croire qu'il n'y a jamais eu qu'un premier être prototype de tous les êtres ?*".

Such a view, which is focused on the continuity in nature ("*s'il est permis de se servir du terme de confins où il n'y a aucune division réelle*"), is the direct account of the debates that occurred in the famous Baron d'Holbach's 'salon', where the *Encyclopédie* project was first designed. Leibniz's claim that nature does not make leaps and that the power of nature has no limit, was the heart of these debates. Of course, this thought was in complete contradiction with the efforts made by the taxonomists to replace the criteria of arbitrary systems by a 'natural order', which for most of them was supposed to reflect the Creator's will. In contrast, any classification is based on a discontinuous conception of the world, and at the same period Linnaeus founded at once a principle of classification and a rule for naming species that is deeply rooted in an idealistic philosophy. The 10th edition of his *Systema Naturae*, in 1758, is still recognized as the birth for scientific nomenclature, and even Buffon, who was a critic of Linnaeus, recognized the practical use of a discontinuous system [17].

Another eminent figure of the Enlightenment was Paul-Louis Moreau de Maupertuis (1698–1759), who held the illustrious position of president of the Berlin Academy. He put into circulation the Latin text of a *Dissertatio* by a so-called Dr Baumann, which was printed in French under the title *Essai sur la formation des corps organisés* in Berlin and Paris in 1754 (in [42]). Nobody was fooled by the actual authorship of this sulphurous booklet, which was later included in the complete works of Maupertuis and published in 1756 under the title *Système de la Nature* [42]. In order to fight the preformationist conception of individual development, Maupertuis called attention to the rather rare case of the occurrence of six digits (polydactyly) in human beings. After an accurate inquiry in Germany, and the help of his skill in mathematics, he demonstrated that this character does not occur in the germ but is transmitted as well by maternal as paternal ways, thus founding the statistical analysis of heredity. Furthermore, he tried to find the material basis of this hereditary transmission, and in parallel to Buffon's theory of 'molécules organiques', he proposed his view of the organism as an aggregation of elementary particles, triggered by forces analogous to the Newtonian attraction. Such a conception of 'organisation', which recalls Democritus's atomism, led directly to materialism and even atheism on philosophical ground, but also to a possible transformation of species.

"*De deux seuls individus, la multiplication des espèces les plus dissemblables aurait pu s'ensuivre : elles n'auraient dû leur première origine qu'à quelques productions fortuites, dans lesquelles les particules élémentaires n'auraient pas retenu l'ordre qu'elles tenaient dans les animaux pères et mères : chaque degré d'erreur fait une nouvelle espèce ; et à force d'écarts répétés serait venue la diversité infinie des animaux que nous voyons aujourd'hui, qui s'accroîtra peut-être encore avec le temps, mais à laquelle peut-être la suite des siècles n'apporte que des accroissements imperceptibles.*" (Système de la Nature, *XLIV*).

The relation between form and function took on a peculiar aspect in the works of Julien Offray de La Mettrie (1709–1751), who was a medical physician. His *Traité de l'âme* (1745) [32] and *Homme-machine* (1748) [33] are devoted to a vigorous demonstration of the material basis of what the dualistic views formalized by Descartes called 'soul'. "*Mais ces philosophes s'en tenant ainsi à l'écorce des choses, auraient bien peu examiné la parfaite ressemblance qui frappe les connaisseurs, entre l'homme et la bête : car il n'est ici question que de la similitude des organes des sens, lesquels, à quelques modifications près, sont absolument les mêmes, et accusent évidemment les mêmes usages. Si ce parallèle n'a pas été saisi par Descartes, ni par ses sectateurs, il n'a pas échappé aux autres Philosophes, et surtout à ceux qui se sont curieusement appliqués à l'Anatomie comparée*" (*Traité de l'âme*). Thought, instinct, and even moral sense are products of a special organ, the brain: "*Comme, posées certaines lois physiques, il n'était pas possible que la mer n'eût son flux et son reflux, de même certaines lois du mouvement ayant existé, elles ont formé des yeux qui ont vu, des oreilles qui ont entendu, des nerfs qui ont senti, une langue tantôt capable et tantôt incapable de parler, suivant son organisation ; enfin elles ont fabriqué le viscère de la pensée. La nature a fait dans la machine de l'homme, une autre machine qui s'est trouvé propre à retenir les idées et à en faire de nouvelles* […] *Ayant fait, sans voir, des yeux qui voient, elle a fait sans penser, une machine qui pense.*" (*Traité de l'âme*). More than any philosopher of his time, La Mettrie associated Materialism with the rejection of teleology in nature.

"*Concluons donc hardiment que l'Homme est une Machine, et qu'il n'y a dans tout l'Univers qu'une seule substance diversement modifiée*" (L'Homme-Machine).

The prospect for transformationism to explain the diversity of life was thus of the minds in the Enlightenment period. However, the explanatory mechanisms called for were diverse and based only on speculation.

3. From 'physiology' to 'biology'

The rise of new concepts yields the need for new words, or at least the use of words in a new sense. This was the case with 'Physiology', which lost the initial meaning of general description of natural phenomena, when 'Histoire naturelle' was promoted by Buffon, to be restricted to the study of functional aspects of life. This was already the sense used in medical sciences by Fernel in the 16th century and for Albrecht von Haller (1708–1777), there was a place for what he called 'anatomia animata' [43]. However, there was no clear definition of the concept concealed in the word 'function'. Xavier Bichat (1771–1802) in his *Recherches physiologiques sur la vie et la mort* [6] introduced the distinction between 'animal' and 'organic' functions, all of them resisting death in a peculiar balance between the action of the external world and the reaction of living matter ("*la vie est l'ensemble des fonctions qui résistent à la mort*"). Georges Cuvier began the *Leçons d'anatomie comparée* [14] by a general description of the diverse functions that characterize the phenomenon of life. Then his lessons reviewed the diverse organs that perform these functions. Such an order emphasizes the choice of a functionally based analysis of the organism, following Aristotle's principle. However, Cuvier's view of physiology is quite narrow. The letter to Jean-Claude Mertrud that precedes the first lesson contains a comparison between the physical sciences and life sciences, which are supposed to be faced with the impossible task of reducing problems to simple quantified elements, in contrast to physics and chemistry (the possible influence of Kant's views on Newtonian supremacy). "*Toutes les parties d'un corps vivant sont liées ; elles ne peuvent agir qu'autant qu'elles agissent toutes ensemble : vouloir en séparer une de la masse, c'est la reporter dans l'ordre des substances mortes, c'est en changer entièrement l'essence. Les machines qui font l'objet de nos recherches ne peuvent être démontées* *sans être détruites ; nous ne pouvons connoître ce qui résulteroît de l'absence d'un ou de plusieurs de leurs rouages, et par conséquent nous ne pouvons savoir quelle est la part que chacun de ces rouages prend à l'effet total.*" The comparison of the diverse associations of organs disclosed by comparative anatomy is the only way for physiology to proceed. Such a reduction of physiology to an ancillary role was sharply criticized by Claude Bernard (1813–1878) : "…*pour savoir quelque chose des fonctions de la vie, il faut les étudier sur le vivant. L'anatomie ne donne que des caractères pour reconnaître les tissus, mais elle n'apprend rien par elle-même sur leurs propriétés vitales. Comment, en effet, la forme d'un élément nerveux nous indiquerait-elle les propriétés nerveuses qu'il transmet ? Comment la forme d'une cellule du foie nous montrerait-elle qu'il s'y fait du sucre ; comment la forme d'un élément musculaire nous ferait-elle connaître la contraction musculaire ?*" [5]. The unfortunate fate of Antoine-Laurent de Lavoisier (1743–1794), who could not participate in the rise of modern sciences that occurred at the beginning of the 19th century, had probably created a time lag in the expansion of experimental biology.

A tradition now disputed by historiography tells us that the word 'biology' itself was simultaneously forged in 1802 by Treviranus in Germany and by Lamarck in France. Notwithstanding, it responded to the need to replace "physiology" and to designate the integrative view of the life sciences among the sciences that deal with all natural phenomena [13,43].

4. Experimental biology and the new physiology

The new physiology, devoted to the study of the 'functioning' of living beings, had its origin within the works of chemists trained in the analytic approach. This was in contrast to the holistic view of Cuvier and even Lamarck, and was the beginning of a divorce between naturalistic and experimental life sciences. Inferring function from form, Cuvier was responsible for some long-held errors. His refusal to accept an auditory source of the night navigation of the bats is exemplary. Lazare Spallanzani (1729–1799) performed a series of remarkable experiments in 1794 to prove that bats could travel in complete darkness through a net of threads, even though they were blinded. However, Cuvier rejected the hypothesis of an auditory source of information and proposed a tactile hypothesis, supported only by the high density of nervous endings in the wing membranes. The authority of Cuvier was such that this inference was universally accepted even after two naturalists, Raymond Rollinat and André Trouessart, repeated the Spallanzani experiments in 1900. The theory of ultrasonic sensory apparatus was elaborated only after 1920 and demonstrated later.

The birth of modern physiology was narrowly linked to the rise of modern chemistry, which took place in France. Around Lavoisier and after him, persons such as Antoine-François de Fourcroy (1755–1809) Jean-Antoine Chaptal (1756–1832) and Nicolas-Louis Vauquelin (1763–1829) brought out the basis for understanding life activities such as respiration, fermentation and excretion. To study the heat production of living processes, the astronomer Pierre-Simon de Laplace (1749–1827) helped Lavoisier to conceive the ice calorimeter, which was one of the main instruments used by physiologists in the 19th century. Contrary to Cuvier's assumption, life sciences also needed quantification. A coming back to Galileo's thinking and to the Cartesian concept of the machine occurred, especially in Germany where vitalism and *Naturphilosophie* dominated the first quarter of the century. In reaction, as declared defenders of materialism, the German physiologists were also influenced by the works of René Joachim Dutrochet (1776–1847), who showed that many chemical and physical phenomena have a peculiar behaviour whenever they are produced within organised beings. This was the motivation to conceive a wonderful set of apparatuses especially adapted to demonstrate and record diverse living actions. Most of the research undertaken was then applied to agriculture or human health. Justus Liebig (1803–1873), Emil Du Bois Reymond (1818–1896), the inventor of electrophysiology, and Hermann von Helmholtz (1821–1894), who studied the motion of the eyes, colour vision, and acoustics, extensively applied chemistry and physics to analyse biological properties. Furthermore, they tried to conciliate the analysis that needs to separate phenomena, with the generally accepted Cuvieran organic correlations. This constraint led to the production of non-invasive experimental procedures largely inspired by the instruments used in physics. This was the case especially for the studies concerning the diverse movements that occur in the living body. The same measurements as for physical phenomena were applied to animal systems and more than ever the term 'animal–machine' was appropriated. Space, time, and their derivatives, velocity, acceleration, force and energy, were then recorded and calculated. Étienne-Jules Marey (1830–1904) may be placed in the same progression as the German physiologists. During his whole life, he searched for a universal language able to describe accurately any movement, without any disturbance introduced by the observer [40]. This prospect led him to devise remarkable sets of instruments that, although technology was then still limited, gave surprisingly precise results, as for instance the curve tracing the ground force reaction on the human foot during walking [41]. Marey was a physician and he always relied on his anatomical knowledge, or collaborated on works on animal physiology with Chauveau, a veterinarian and professor in the Paris Muséum. Of course, his best-known contributions dealt with locomotion, which led him to invent diverse kinds of image recorders based on photography, from the superimposed chronophotograms to the evident ancestors of the cinematograph. However, Marey was not alone; he was on the contrary a part of an interdisciplinary current, comprising physicists, civil engineers, physiologists, physicians, zoologists, and veterinary surgeons. In his *leçons* at the 'Collège de France', he declared on 23 March 1867: « *Plus on approfondit un point de la science, plus on lui trouve de connexions avec tous les autres. Faut-il rappeler les services que la zoologie et la botanique ont rendus à la géologie, l'utilité de la chimie et de la physique pour ceux qui cultivent l'anatomie ou la physiologie* ? ». This active collaboration led in 1901 to the publication of the singular volume called *Physique biologique*. Modern Biomechanics and ergonomy, comprising metabolic aspects, is in great part explained in this work, which unfortunately was later ignored. When biomechanical approach began to yield scientific productions, it was only in the medical domain, to support clinical aspects of surgery and orthopaedics, without any evolutionary or even comparative considerations. When James Gray treated animal movements in the 1940s, it had only little morphological basis. *Animal Mechanic*s, by McNeill Alexander, whose first edition was published in 1968 [1], did not refer to the French school exemplified by Marey, although Alexander book is exactly in its tradition; it began a renewal of the comparative approach.

The approach of Claude Bernard was different, as exhibited by his definition of physiology: "*la connaissance des causes des phénomènes de la vie à l'état normal, c'est-à-dire la physiologie, nous apprendra à maintenir les conditions normales de la vie et à conserver la santé*" [4]. He was the instigator of analytical and directly invasive experiments based on the concept of 'milieu intérieur'. In contrast to German physiologists and Marey, Bernard's work could be described as a continuation of the humoral medical school; he opened the reductionist perspective in life sciences. To his eyes, living forms and their diversity are anecdotic. What is of interest is the unity of basic functioning. He missed the evolutionary explanation of diversity, which was later completely left aside by most medical scientists.

5. Descent with modification, a possible unifying theory

Indeed, everything should have been different after the publication in 1859 of Charles Darwin's *Origin of Species*. Darwin placed morphology, the study of form, at the heart of the biological sciences, although he was not himself a morphologist. The theory of 'descent with modification' through natural selection might have reconciled the observed fact that forms correspond to functions with the hypothesis of a gradual transformation over geologic time. He did not notice any contradiction between organized function (adaptation) and species transformation, writing in 1862:

"*Although an organ may not have been originally formed for some special purpose, if it now serves for this end, we are justified in saying that it is especially adapted for it. On the same principle, if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for its present purpose. Thus throughout nature, almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms*" [16].

The possible uncoupling of form and function was more explicitly emphasized by Anton Dohrn in 1875 with the idea of functional substitution, a slow gliding of an organ from one specified role to another [20]. Several examples of such phenomena when a more accurate knowledge of invertebrate development emerged in the second half of the 19th century. However, even before Genetics made its first steps among life sciences, the processes of natural selection were discarded from evolutionary mechanisms. Far from the Darwinian current, some experimental works tried to place the generation of form in the context of a direct result of mechanical constraints. Raoul Anthony (1874–1941), who began his career in the 'Station physiologique' created by Marey, demonstrated that the dog's skull shape is greatly modified if temporal muscles are extirpated in puppies. In Germany, W. Roux emphasized the physical (mechanical) factors in the construction of the organism [13]. In his unique 1917 work, *On Growth and Form*, D'Arcy Thompson wrote :

"*The form, then, of any portion of matter, whether it be living or dead, and the changes of form which are apparent in its movements and in its growth, may in all cases alike be described as due to the action of force. In short, the form of an object is a 'diagram of forces', in the sense, at least, that from it we can judge of or deduce the forces that are acting or have acted upon it*" [47]. Living forms are not distinct from any physical body, and there is no integration within a functional net in relation to survival.

On the other hand, morphologists and palaeontologists who supported evolutionary theory were often floating between neo-Lamarkian and neo-Darwinian views, and focused all their interpretations of form in terms of adaptive features. This trend unfortunately continued, often lowering studies to an anecdotical level, as Étienne Rabaud (1942) denounced: « *Négligeant le principe essentiel de la recherche scientifique, qui est de rassembler tous les faits, d'envisager un problème sous toutes ses faces, diverses conceptions transformistes reposent avant tout, sur l'interprétation des formes. Elles admettent que l'organisme entier se résume dans sa morphologie ; elles croient que la morphologie donne une vision claire du passé, qu'elle détermine le mode d'activité, qu'elle s'harmonise au mieux avec l'habitat, avec les moyens d'existence créés par l'environnement.* […] *Attribuer pareille importance à un seul des aspects des organismes vivants est sans conteste, une erreur fondamentale. Avant d'affirmer certains rapports, la prudence élémentaire commande de s'assurer que ces rapports existent.* ».

This is particularly visible in the public galleries of museums conceived at this time in the United States under the influence of Henry Fairfield Osborn (1857–1935). Until around 1940, there was a period of theoretical confusion, and Darwinism was a word used (as it is unfortunately still in journalistic language) in a sense that is largely contradictory to Darwin's thought.

Natural selection was reintroduced as a causal factor when Dobzhansky (Theodosius, 1900–1975) and Wright (Sewall, 1889–1988) demonstrated that natural selection could have significant effects in natural populations [43]. With population genetics, the formulation of Darwinian theory in terms of population spread through the life sciences, and a 'synthetic theory' could be framed, uniting zoologists (E. Mayr, J. Huxley), palaeontologists (G. G. Simpson), theoretical population geneticists (L.S.B. Haldane, R.A. Fisher), and experimental population geneticists (T. Dobzhansky, G. Teissier). In the 1950s, the demonstration of the molecular basis of genetic information stressed the 'fully genetic' solution for any evolutionary question, and molecular technology cast a strong shadow on all former biological disciplines. Organismal study was discarded from evolutionary topics, in its adult stage as well as in its developmental aspects [26]. Comparison of morphological patterns was regarded as useless in the search for hypothetical evolutionary processes at the molecular level. Adaptation was viewed as the effect of natural selection which alters genes frequencies in populations. The fact that adaptation was automatically derived from the selection paradigm was however sharply criticized in 1966 by G.C. Williams [50]. If evolution only involves populations, what is being adapted? What is the selective unit: individual organisms, species, populations? Is adaptation a source of innovation or on the contrary a means to keep what has been acquired? Furthermore, there was often confusion between adaptation as a state and adaptation as an evolutionary process [25]. Is every structural feature adaptive in the organism? A considerable storm arose following Kimura's demonstration (1968) that at the molecular level most modifications have no selective value [30], and in 1979, the aggressive paper of Gould and Lewontin showing that features considered adaptive may be the simple results of structural necessity [28]. The word adaptation itself was banned from some evolutionary biology papers for a while! In such a debate, what could be the place for form–function studies?

6. Functional morphology and evolution

We have to return to 1935, when Hans Böker published two volumes of his *Anatomical Biology* [9]. This work exhibits a wide survey of the morphological features that can be related to the daily life of vertebrates; for instance the shapes of fins, wings, claws, and bills in relation to feeding and locomotion were catalogued. This is a direct continuation of Darwin's famous observations of the finches in Galapagos Islands. The return of organismal biology, which operates on phenotypic features (sensu lato), was based on the view that some of these features could contribute to final fitness. Notwithstanding what occurs at the genetic level, natural selection operates on the individual organism. Bock and von Walhert [8] forged the term 'biological role' to replace 'action' and to anchor functional studies in the evolutionary thought. Other morphologists proposed to recognize functional units within the organism. This view was specially applied to studies dealing with cranial components involved in feeding of mammals (J. Van Der Klaauw), reptiles (P. Dullemeijer), birds (R. Zusi, W.J. Bock,), and fishes (K. Liem, J. Osse). Again, the objective was to reconcile the use, from structural elements, of mechanical analytic concepts and the engineering experimental approach with the Darwinian selective process [21]. Musculoskeletal systems seemed to provide particularly good models for such studies, because jaws could be seen as directly involved in chewing and food processing, every action of which could be assigned to the means of organismal survival. The postorbital ligament of birds interpreted in relation to bill mechanics and food processing was an illuminating example [7,19]. The same reasoning may be applied to the limbs and vertebral column in relation to locomotion. Furthermore, these systems exhibit evident mechanical analogies to which they can be reduced, as already shown by Leonardo Da Vinci, Claude Perrault, and Giovanni Borelli [10]. However, there is no guarantee that such functional units represent actual selective units. Such studies led to ecological considerations. They need data from the field to specify the exact use of structures in the daily life of individuals [3]. However, although the term was created by Haeckel, as a discipline ecology has not been much concerned with evolution since its beginnings. Dealing with relations between living species and their biotic and physical surrounding, most of the methods and concepts used by ecologists do not incorporate the long time scale of evolution and the diachronic processes involved in species transformation, but on the contrary are focused on the search for static equilibrium conditions. Even the central concept of the ecosystem does not involve the evolution of species. This is in contrast with the fact that such ecological factors as predation, resource levels, and reproductive potentials are evident components of the selective forces. A huge leap was achieved when R.H. MacArthur and E.O. Wilson published in 1967 their *Theory of Island Biogeography* [39]. This book had an influence beyond the community of ecologists. Although the approach is limited to the mathematical model applied to a study case, it opens ecology to microevolutionary processes disclosed with population fragmentation and biogeography to historical geological events. Using one of the means explored by Darwin (geographical distribution of species), especially based on the natural experiments offered by islands, these authors created the basis for 'evolutionary' ecology. The diverse levels of integration and historical factors were now included into population dynamics and its genetic basis to understand observed diversity of life forms. *Evolutionary Ecology*, the classic book that Eric Pianka published a little later, includes a chapter on 'ecological physiology', showing that there were no more obstacles to integrating the daily performance of essential functions into the frame of transformational thinking [45]. In 1986, Harry W. Greeene wrote: "*Behavior thus serves as a functional couple between the structural features of an organism and its environment, and must be a component in the complete evolutionary analysis of form.*" [29]. The concept of design was introduced to specify a structural element that performs one or more mechanical functions [27,49]. This is partly a non-historical concept, because it does not refer to the selective effect of features, otherwise difficult to test in long life time organisms as vertebrates [34]. However, it has the merit of indicating that the first step in the analysis of biological phenomena consists of an accurate use of physical rules. To reach evolutionary meaning, functional approaches need to be tested by independently obtained phylogenetic data [44]. There were of course dangerous and recurrent pitfalls on the way. The first one is Aristotle's ghost: teleology, when organs or characters are considered as the result of an obligatory trend toward the recent biological role, for instance feathers considered as strictly designed for flight. The second one is the frequent occurrence of convergent transformation due to the limited solutions offered by physical laws to functional questions. 'Functional morphology' was introduced to specify that this new approach within the frame of evolutionary biology is not the peripheral field of amateurs coming from ecology or palaeontology. Functional morphology is a distinct interdisciplinary science that needs to be practiced with accuracy, using a large range of techniques, some of them borrowed from physiology or engineering, but dealing with evolutionary questions that are also addressed by other biological approaches [22,23,31]. When a new edition of Russell's classic *Form and Function* [46] was published in 1982, George Lauder wrote an *Introduction* that constitutes one neo-adaptationist program for functional morphology, and a clear balance to the anti-adaptationist dogmatism that followed the 'San Marco' paper. With the authority of his own works bearing on food acquisition and locomotion in fishes, he demonstrated how a new insight into the evolutionary pathways taken by an organ's system could be obtained by a thoroughly conducted study within a monophyletic line [35,36]. Thus, although functional studies do not have the objective of producing phylogeny, they can participate in the debate by providing the physical limits for any transformation, and the polarity of characters, their redundancy or their homoplasic nature. In some case, experimental study of function may disclose unsuspected characters to be taken into account in a phylogenetic context [37].

Probably owing to anthropocentrism, most morphofunctional studies have been carried out on vertebrates, first in the human being, horse and domestic animals close to man, then on general questions involving a comparative survey, for instance, the feeding processes of fishes, the bill shape of birds and modes of locomotion [12]. The huge world of arthropods did not receive much consideration, nor did soft-bodied animals possessing hydrostatic skeletons. In comparison, plants are neglected, especially those that produce no wood. However, vertebrates are not the best candidates for evolutionary morphofunctional studies. How can the effect of a peculiar functional feature on fitness (differential reproductive success) be measured in species that have generally a so long life span relative to our own? What is heritable in a functional complex? Unfortunately there is no vertebrate comparable to the fruit fly which has been so precious to geneticists. Among some tests, we may quote Lande and Arnold [34], who applied quantitative genetics to evaluate the fitness of snakes, and Losos [38], who tested biomechanical predictions about morphological proportions in a set of lizard species, within the *Anolis* radiation in the Western Indies, using statistical analysis of jumping and running performance related to body segment proportions, removing the effect of size. In any case, the conclusion stressed the fact that results concern only the clade in which the study was carried out, revealing the danger of inductive generalization [24]. This is also the proof that phylogeny, that is historical transformation, introduces many other factors than simple form-function relationships, such as for instance contingency.

7. Conclusion

There is no further need to demonstrate that organisms cannot escape physical rules, either in their process of construction (morphogenesis) or in their actions (life history). However, their structural organization has recorded past states of their lineage, including the 'blueprint' of their most remote ancestors. Sometimes evolutionary 'innovations' are only tinkering using the pre-existing material through a shift in function. Compromises are mandatory between what has been called structural and historical constraints [11]. The present state of any extant organism is an overall adaptation, that is to say the capability to produce a new generation (to transmit its genes). This state consists of a fragile balance that was called 'optimisation', a concept that must be taken in a relative sense [27]. For all the reasons given above, any morphofunctional study has to specify the levels of integration checked (molecular, cellular, organismic), the phylogenetic hypothesis taken as reference, the life history traits that constitute the selective regime (*sensu* Baum and Larson) [4].

The task of functional morphology is not so easy in regard to the strong reluctance of some phylogeneticists to support the idea that functional features could be of interest in building evolutionary classifications. Considering recent trends in phylogenetic research, one could even ask if form in living beings is still taken into account. The use of computerized matrix of characters taken all over literature necessitates the control of disparate data and finally the return to a whole organism view. Due to the usual habit of putting everything into labelled boxes, functional morphology has had little success in the institutional framework. This has been especially true in France, although some research groups have operated in this domain, generally known more at the international than the national level.

Furthermore, the practice of this way of research needs at once great skill in morphology, some knowledge of physics, and an up-to-date view in evolutionary biology, which are nowadays rarely associated in academic training. However, the huge expansion of developmental biology, of evolutionary ecology, and even of molecular genetics has revealed the need to return to a more accurate knowledge of all the phenotypic features of the individual life, a view of the organism seen from its diverse levels of integration and along its lifespan. Experimental results obtained from a limited number of species models (selected laboratory animals) now have to be questioned in the perspective of the diversity of biological forms, requiring accurate comparative studies of wild related species, within a well-known phylogenetic framework. The demand for morphofunctional data is more and more visible from diverse domains, as fundamental as palaeontology, or as applied as robotics or human medicine.

References

[1] R. Mc, N. Alexander, Animal Mechanics, Sidwick and Jackson, London, 1968.

[2] Aristote, Les parties des animaux, Livre I, 20, Transl. P. Louis, Les belles Lettres, Paris, 1956.

[3] S.J. Arnold, Morphology, performance, and fitness, Am. Zool. 23 (1983) 347–361.

[4] D.A. Baum, A. Larson, Adaptation reviewed: a phylogenetic methodology for studying character macroevolution, Syst. Zool. 40 (1991) 1–18.

[5] C. Bernard, Introduction à l'étude de la médecine expérimentale, Baillière et fils, Paris, 1865.
[6] X. Bichat, Recherches physiologiques sur la vie et la mort, Paris, 1880.
[7] W.J. Bock, Kinetics of the avian skull, J. Morphol. 114 (1964) 1–42.
[8] W.J. Bock, G. von Wahlert, Adaptation and the form-function complex, Evolution Int. J. Org. Evolution 19 (1965) 269–299.
[9] H. Böker, Einführung in die vergleichende biologische Anatomie der Wirbeltiere, G. Fischer, Jena, Germany, 1935.
[10] G.A. Borelli, D.M. Animalium, Leyde, The Netherlands, 1680.
[11] D.R. Carrier, Conflict in the hypaxial musculo-skeletal system: documenting an evolutionary constraint, Am. Zool. 31 (1991) 644–654.
[12] A. Casinos, J.-P. Gasc, V. Bels, Biomechanics: a tool for understanding the evolution of vertebrates, in: V.L. Bels, J.-P. Gasc, A. Casinos (Eds.), Vertebrate Biomechanics and Evolution, Bios Scientific Publishers, Oxford, 2003, pp. 3–10.
[13] W. Coleman, Biology in the Nineteenth Century, Cambridge University Press, 1971.
[14] G. Cuvier, Leçons d'anatomie comparée, Baudouin et fils, Paris, 1805.
[15] G. Cuvier, Discours sur les révolutions du globe, Paris, 1824.
[16] C. Darwin, The various contrivance by which British and foreign orchids are fertilized by insects, and on the good effects of intercrossing, John Murray, London, 1862.
[17] P.H.D. d'Holbach, Système de la nature ou des lois du monde physique et du monde moral, Y. Belaval, Hildersheim, Georg Olms, Paris, 1965.
[18] D. Diderot, De l'interprétation de la nature (pensées sur l'interprétation de la Nature), 1753, in: Diderot, textes choisis, tome II, Éditions Sociales, Paris, 1971.
[19] F.J. Dzerzhinsky, Biomechanical Analysis of Bill Apparatus in Birds, Moscow University Press, 1972 (in Russian).
[20] A. Dohrn, Der Ursprung der Wirbelthiere und das Princip des Functionswechsels, W. Engelmann, Leipzig, Germany, 1875.
[21] P. Dullemeijer, Concepts and approach in animal morphology, Van Gorum, Assen, The Netherlands, 1974.
[22] C. Gans, Adaptation and the form-function relation, Am. Zool. 28 (1988) 681–697.
[23] C. Gans, J.-P. Gasc, Functional morphology: requirements and uses, Ann. Sci. Nat., Zool. Paris, 13e sér. 2 (1992) 83–96.
[24] T. Garland Jr., J.B. Losos, Ecological morphology of locomotor performance in squamate reptiles, in: P.C. Wainwright, S.M. Reilly (Eds.), Ecological Morphology: integrative organismal biology, Chicago University Press, Chicago, IL, USA, 1994, pp. 240–302.
[25] J.-P. Gasc, À propos du concept d'adaptation, Information sur les sciences sociales, Paris 16 (5) (1977) 567–580.
[26] J.-P. Gasc, Évolution des organismes, in: P. Tort (Ed.), Dictionnaire du Darwinisme et de l'évolution, Presses universitaires de France, Paris, 1996, pp. 1506–1529.
[27] J.-P. Gasc, Analyse d'ouvrage, in: E.R. Weibel, C.R. Taylor, L. Bolis (Eds), Principles of animal design. The optimization and symmorphosis debate, Rev. Écol. (La Terre et la Vie) 54 (1) (1999) 92–96.
[28] S.J. Gould, R.C. Lewontin, The spandrels of San Marco and the panglossian paradigm: a critique of the adaptationist programme, Proc. R. Soc. Lond. B, Biol. Sci. 205 (1979) 581–598.
[29] H.W. Greene, Natural history and evolutionary biology, in: M.E. Feder, G.V. Lauder (Eds.), Predator–prey relationships. Perspectives and approaches from the study of lower Vertebrates, The University of Chicago Press, Chicago, 1986, pp. 99–108.
[30] M. Kimura, The neutral theory of molecular evolution, Cambridge, Cambridge University Press, 1968.
[31] L.P. Korzun, C. Erard, J.-P. Gasc, F.J. Dzerzhinsky, Biomechanical features of the bill and jaw apparatus of cuckoos, turacos and hoatzin in relation to food acquisition and processing, Ostrich 74 (2003) 48–57.
[32] J.O. de la Mettrie, Histoire naturelle de l'âme ou Traité de l'âme, 1745.
[33] J.O. de la Mettrie, L'Homme-machine, Leiden, 1745.
[34] R. Lande, S.J. Arnold, The measurement of selection on correlated characters, Evolution Int. J. Org. Evolution 37 (1983) 1210–1226.
[35] G.V. Lauder, Functional and morphological bases of trophic specialization in sunfishes, J. Morphol. 178 (1983) 1–21.
[36] G.V. Lauder, Biomechanics and evolution: integrating physical and historical biology in the study of complex systems, in: J.M.V. Rayner, R.J. Wooton (Eds.), Biomechanics and Evolution, Cambridge University Press, Cambridge, 1991, pp. 1–19.
[37] R.E. Lombard, Experiment and comprehending the evolution of function, Am. Zool. 3 (1991) 743–756.
[38] J.B. Losos, The evolution of form and function : morphology and locomotor performance in West Indian *Anolis* lizards, Evolution Int. J. Org. Evolution 44 (5) (1990) 1189–1203.
[39] R.H. McArthur, E.O. Wilson, The Theory of Island Biogeography, Princeton University Press, Princeton, NJ, USA, 1967.
[40] É.-J. Marey, Du mouvement dans les fonctions de la vie, 1868.
[41] É.-J. Marey, La Machine animale, Felix Alcan, Paris, 1891 (2e éd.).
[42] P.-L.-M. de Maupertuis, Système de la Nature (paru en 1754 sous le titre Essai sur les corps organisés, sous le pseudonyme de Baumann), in: P.-L.-M. de Maupertuis, Œuvres, Paris, 1756.
[43] E. Mayr, The growth of biological thought, The Belknap Press of Harvard University Press, Cambridge, MA, USA, 1982.
[44] K. Padian, Cross-testing adaptive hypotheses: phylogenetic analysis and the origin of birds flight. 1, Am. Zool. 41 (3) (2001) 598–607.
[45] E.R. Pianka, Evolutionary Ecology, Harpers and Row, New York, 1978.
[46] E.S. Russell, Form and Function, John Murray, London, 1916.
[47] D.W. Thomson, On Growth and Form, The University Press, Cambridge, 1917.
[48] F. Vicq d'Azir, Mémoires sur les rapports qui se retrouvent entre les usages et la structure des quatre extrémités dans l'homme et les quadrupèdes, Œuvres, vol. 4, 1787.
[49] S.A. Wainwright, W.D. Biggs, J.D. Currey, J.M. Gosline, Mechanical Design in Organisms, Princeton University Press, Princeton, NJ, USA, 1976.
[50] G.C. Williams, Adaptation and natural selection, Princeton University Press, Princeton, NJ, USA, 1966.