The aim of this book is to outline the contours of a newly emerging approach to the most complicated and finely regulated successions of events making possible our very existence: the development of organisms. Because of their ubiquity and spontaneity, our primary instinct would be to appreciate these events as given, and simply describe them one after another without asking why they take place at all. On the other hand, since ancient times human beings have not been satisfied by only apprehending any natural events, ranging from movements of celestial bodies to behavior of tiny particles of matter. Instead, people have invented some cognitive approaches, which created the basis for modern civilization, whether for good or evil. Our first aim will be to explore whether any of these approaches can help us to explain the development of organisms. We shall see that in spite of a prolonged history of the science about development (traditionally called embryology, but now named developmental biology) and many important discoveries in this field, this task has still not succeeded. Today, however, due to cooperation between several newly emerged branches of science, some new and unique possibilities allow substantial progress in these directions.

Among the approaches used by natural sciences, we start by outlining the two that have been often regarded as opposites. The first of them is oriented toward searching for components that are kept unchanged (invariant) among events looking quite different from each other. The second, on the opposite, is directed toward outlining reproducible differences between things that are at first glance hardly discernible. The first approach is directed toward formulation of as broad as possible \textit{invariable laws of nature}; this trend dominates in physical sciences since the times of Galileo and Newton. Its unique advantage is the predictive power. It is this approach that provided the tremendous technological progress achieved since then by mankind.

However, not all the sciences followed this path. The second approach, directed toward \textit{classification of events}, emphasizing their specificity and internal differences rather than any common laws that may join them, was long dominant in most of the natural sciences, and remained so in biology. If we are objective, we must admit that practically all the achievements of biology and related applied sciences
(medicine, agriculture, biotechnology) have been reached within the framework of this traditional approach, in the sense of remaining almost unconnected with any general laws. Accordingly, their results continue to be expressed in the form of specific receipts, instructions, drugs, etc. About a century ago, a German philosopher, Windelband defined this approach as ideographic while the law-oriented approach as nomothetic.

The contrast between nomothetic and ideographic approaches becomes most clear when they are applied to more or less prolonged successions of events. For clarifying this, let us use a simple allegory, or better to say, a kind of a caricature (Fig. 1). Frame A illustrates a nomothetic tendency directed toward embracing quite different successions of events by a common law. On the contrary, frame B depicts an old-fashioned postman whose pathway is determined by the addresses of the letters he has to hand. For making this allegory closer to conventional views on the development of organisms, let us assume that by coming to each next address, the postman receives the instructions of where to move further. Under these conditions, each next postman’s turn is determined by a specific instruction (which we may call a “cause”). This displays a principle of a so-called uniform determinism which, as related to embryology, will be discussed in the text. Frame C gives an example of a natural periodic process to which a priori any one of the above-mentioned approaches can be applied: it should be a matter of investigation to make a reasonable choice between them.

Fig. 1  Movements caused by invariable laws (a), by specific causes (b), or suggested to be caused by any of these components (c). a trajectories of the planets and of a falling apple are determined by the same law of gravity. b a complicated trajectory of a postman is determined by addresses written on the envelopes. c a record of a quasi-periodic movement. It is a matter of investigation to detect whether it may be embraced by a common law or the breaks of trajectories (some of them shown by arrows) should be ascribed to specific causes.
Initially both the approaches looked mutually exclusive. Since the second half of the previous century, however, a new version of the classificatory approach emerged, formalized within the framework of so-called systems theory (Bertalanffy 1968; Pattee 1973): it arranged the static events according to their characteristic dimensions, and the dynamic events according to their rates.

Briefly speaking, this approach invites us to distinguish small things from large ones and slow processes from fast ones. At first glance, this seems naïve, but is actually very deep. A use of this approach leads to nontrivial conclusions about the stratification of our world, both organic and nonorganic, into a restricted number of *discrete levels*, each of them populated with events of characteristic linear dimensions and characteristic times (i.e., reversed rates). As we shall see in Chap. 1, such stratification is indispensable for applying a law-centered approach to any complex system, whether organic or inorganic. Nevertheless, when taken in isolation, it is but a preparatory step for doing this.

Which of these approaches—or combination of them—has dominated conventional embryology? Because developmental events lie at the very heart of biology, it is in no way surprising that the traditional classification approach dominated throughout the entire history of developmental biology and retained until now the leading positions. This is true not only for so-called descriptive embryology, dealing with normal course of development, but also for experimental research, performing “causal analysis” of developmental mechanisms: this is because the results of such analysis are usually presented as a set of “specific causes,” having as a rule nothing in common with each other. Such an approach, seeming at first glance quite safe, will be shown to involve us into a series of principal uncertainties and contradictions.

On the other hand, a classification of developmental events according to their space temporal scale has also been used intuitively for a long time. Already a century or so ago, embryologists actively disputed the relations between a developing “whole” and its parts, thus intuitively using what we call today the interlevel approach. As we shall see later, some of their ideas criticized by contemporaries as being too vague and even nonscientific previewed in fact some firmly accepted notions of the present-day knowledge. However, it remains still uncertain whether it would be reasonable and constructive to transform embryology into a law-centered science. On the one hand, by referring to a classical Maxwell’s definition of physics [“Physical science is that department of knowledge which relates to the order of nature, or, in other words, to the regular succession of events” (Maxwell 1871, 1991)], one should immediately regard embryology as but a part of physics: nothing in nature better represents “the regular succession of events” than the development of organisms. However, the successions of events which are really taking place during development of organisms are completely unparalleled in any nonliving systems, both in their duration and complexity. It is not surprising therefore, that in spite of isolated, remarkable attempts by certain authors (to be discussed later), the law-oriented approach in embryology remained marginal, while the majority of researchers could not believe such complicated chains of events to proceed without any specific “instructions.”
We suggest that such a situation can be due to a premature use of the law-oriented approach, rather than by its inherent nonadequacy. Until recently, this approach was used in the so-called linear approximation, which did not permit to reproduce unusual dynamic properties of complex multilevel systems; nonlinear approaches (see Chap. 1) emerged much later.

Before coming to these, it would be desirable to find a common category of physical events participating in the main, if not all the activities of developing systems. At first glance, such enterprise looks hopeless. Fortunately, this is not the case. Both superficial observation of the developmental processes and their refined analysis up to the molecular level shows that practically all of them are associated with regular and repeatable deformations of material units ranging roughly from $10^{-3}$ to $10^{-9}$ m, that is, from cell collectives to single molecules. What is called morphogenesis is actually a succession of such deformations observed at the cellular and supracellular levels. It is but natural to extend this same term to the lower structural levels as well.

By considering the deformations taking place at any structural level to be the leading component of development, we take a crucial step toward what we call morphomechanics. Although nobody can deny that organized deformations are essential parts of development, most researchers of even a recent past believed them to be no more than epiphenomena of independent deeply hidden regulatory mechanisms, nonaffected by deformations themselves. Such views are explicable as extrapolations from traditional constructions of common man-made devices, implying a sharp segregation of a macroscopic executive domain from a miniature regulatory mechanism. We shall see however that in living systems this is not the case: executive and regulatory mechanisms are mutually dependent. In other words, we must be ready to accept that morphogenesis can be self-regulated.

Meanwhile before doing this, we would like to see at what point the morphomechanics deviates from the ordinary mechanics. Such fundamental notions as the deformations and mechanical stresses (MS) are common for both. A basic difference occurs at the next step of our reasoning and is as follows. The ordinary mechanic does not ask, as a rule, what is the origin of the force(s) producing MS, taking it as given (under the name of “initial conditions”): its only concern is in calculating MS as precisely as possible. On the contrary, for morphomechanics the problem of MS origin is central. Moreover, by dealing with such prolonged successions of deformations as those constituting morphogenesis, we cannot be satisfied by discovering the origin of a single force: rather, we must operate with the chains of forces, each of them creating a basis for the next one to appear. But for doing this, we have to introduce a distinction between the passive and active forces. The passive force is that acting to a material element of a biological tissue from outside, while the active one is that generated as a response within this element, certainly by spending some of its internal energy. In these terms, we shall consider morphogenesis as a relay of passive–active forces and corresponding deformations and shall try to construct an embracing law for this relay.

By focusing itself onto this task, morphomechanics follows a way unusual for classical mechanics. True, the gap between both trends of mechanics should not be
considered as impassable: the responses of some nonbiological systems to mechanical forces can be also rather complicated and treated as active ones. However, what takes place in developing organisms has at least two major features going far beyond what can be observed in nonbiological systems. The first of them is the multilevel organization and, the second, a very high diversity and specificity of the morphological structures. Can these properties be adequately and usefully treated within the framework of morphomechanics? These are the questions to be discussed in this book.

The structure of the book is as follows:

In Chap. 1 we start from reviewing the main concepts related to morphogenesis. After doing this, we reformulate developmental events in the language of symmetry theory, so effectively used in physical sciences. This step is necessary for coming toward the realm of the self-organization theory (SOT). We hope to demonstrate that SOT creates an adequate basis for interpreting development but is itself too general for being applied to concrete processes.

Chapter 2 deals with morphomechanical processes related to lower structural levels, ranging from single macromolecules to entire cells. In recent years, this research area has been developed in a really explosive way permitting to reach much more integrated views upon the relations between mechanical events and those treated traditionally as chemical ones. The dynamic processes belonging to these levels are treated in terms of symmetry and mechanically based feedbacks.

In Chap. 3 we pass toward a supracellular level and review the main modes of collective cell behavior separately from each other.

The aim of Chap. 4 is to integrate these modes into natural developmental successions, based on morphomechanical feedbacks.

Chapter 5 comprises a review of plant morphomechanics, written by Dr. Andrei Lipchinsky from the Department of Plant Physiology, St. Petersburg University.

The aim of the “Concluding Remarks” is to generalize the beforehand accounted matters and to outline most important still unsolved problems: the relations between developmental nomothetics and ideography are here discussed again.

One of the main author’s problems was to trace a border line between the information to be accounted for reaching the main goal of this book and one that could be left aside. This task was mostly difficult for the adequate solution as related to Chap. 2, due to enormous amount of closely interrelated data; we are far from sure that the optimal balance was achieved. In any case, this monograph in no way can be regarded as a substitution for regular textbooks on the molecular, cell, and developmental biology, which are recommended for the interested reader to be studied beforehand.

To some extent, this book can be considered as an elaborated version of that published almost two decades ago (Belousov 1998), but the differences between them are substantial. To a considerable part they may be ascribed to existing research progress in related areas, especially in molecular biology of the cell. However, even most important were not always visible, but in fact quite profound recent shifts in scientific paradigms. Among these, the first to be mentioned is extensive penetration of a self-organizing approach in biology accompanied by
increased understanding that so-called “genetic information” is an integral part of more extensive feedbacks rather than a sole master of development.

There are too many people to which the senior author of this book (LB) is obliged by everything. The first part of LB’s scientific life which was spent almost without any contacts with the Western authors provided nevertheless a unique possibility to assimilate the traditions of the Russian school of “rational morphology,” with its attitude to the rejuvenated idea of the primacy of organic forms. The main person to be mentioned here is Alexander Gurwitsch (1874–1954), who brought toward the midst of the last century a living spiritual memory of Wilhelm Roux and Hans Driesch—his teachers and personal friends—but whose ideology he finally rejected (giving a kind of excuse for making the same with Gurwitsch’s “cell field” theory). Remembered should be also other bright persons from the same team: Vladimir Beklemishev, Alexander Liubischev, Sergey Meyen, Pavel Svetlov. His restricted knowledge of SOT and the related parts of physics LB is owed to Prof. Chernavskii and his seminar members from Lebedev Physical Institute. More recently, when a worldwide free exchange became possible, LB got a possibility to establish contacts with many outstanding persons among whom most influential were the talks and a real friendship with Albert Harris and Brian Goodwin. The idea of hyper-restoration emerged in discussions with Jay Mittenthal from Illinois University.

LB had also the privilege to work together with outstanding representatives of the next generation—Boris Belintzev, Vladimir Cherdantzev, Vladimir Mescheryakov, Alexander Stein, and several others. Much of what was taken from them is incorporated in this book. And last but not least—a view of even younger population of researchers, now filling our Lab of Developmental Biophysics—gives the hope that in spite of all the surrounding troubles the great traditions of a fundamental science about development of organisms will never be broken. LB thanks a member of this team, Ilya Volodyaev, for critically reading the manuscript and making valuable remarks.

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