

Morphological Evolution: Estimation Principles, Patterns, and Mechanisms

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Abstract—Directions, modes, specializations, and coordination systems of morphofunctional changes are discussed based on modern data. Phylogenetic heterochronies (pedomorphoses and outstripping), which provide the basis for parallel, mosaic, and saltation development and different rates of morphological evolution, are regarded as important events of morphological diversification. The analysis of specificity and relationships of structural levels of organization (including genetic and epigenetic) and the elaboration of evolutionary principles of their dynamic stability are thought to be the most promising fields of modern research.

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INTRODUCTION

One of the most topical problems of evolutionary biology in the past 30 years has been the relationships of *gene–morphogenesis–morphological character*, which provide the basis for the understanding of relationships of molecular genetic and epigenetic levels of structural organization. However, the adherents of different concepts differ considerably in highlighting key points in these questions. Thus, from the positions of the synthetic theory of evolution (STE), the leading role belongs to the microevolutionary level and, hence, to the study of population variations of morphological characters in adult phenotypes as a result of micro- and macromutations and the action of natural selection (Yablokov, 1982; Altukhov et al., 1997; Korochkin, 2002). Researchers in the field of developmental biology and evolutionary embryology criticize STE for ignoring the molecular and morphogenic mechanisms, which remained “a missed chapter” in STE and an essential gap in studies of morphological macroevolution (Alberch, 1982a, 1982b; Belousov, 1986; Hall, 1999). Structuralists clamor against the functional approach, i.e., recognition of natural selection as the primary factor of evolution, and attach the major importance to the intrinsic causes of development and to the analysis of transformation of the shape in the course of evolution (Goodwin, 1982). At the same time, in the studies devoted to the patterns of morphological evolution, the majority of morphologists and paleontologists traditionally use the method of Haeckel’s Triad, which is based on the concordance between comparative morphological, embryological, and paleontological data. The most significant achievements of this method in the 1930s and 1940s were the theory of phyl-embryogenesis and the concept of morphophysiological

and biological progress proposed by A.N. Severtsov (1939), the concept of the evolution of ontogeny, the concept of the organism as a whole in individual and historical development (Schmalhausen, 1982), and, since the 1970s, the hypothesis of the leading role of heterochronies in morphological evolution (Gould, 1977).

In the 1980s, researchers in the fields of experimental and molecular biology were engaged in studies of morphological evolution, making attempts at creating evolutionary models of morphological processes to explain their causal essence. A successful example is the model for the ontogenetic establishment of tetrapod limbs (Shubin and Alberch, 1986), which has influenced the vision of many researchers studying evolutionary transformations of fins of Devonian fishes into limbs of terrestrial vertebrates, with reference to the revision of principles of homology of their skeletal elements (Shubin, 1995; Vorobyeva and Hinchliffe, 1996; Hinchliffe, 2002; etc.).

CONCEPT OF MORPHOLOGICAL EVOLUTION

The foundation of ideas concerning morphological evolution from the viewpoint of the Darwinian theory about the unity of the origin of species is provided by the historical approach, which implies the construction of gradualistic evolutionarily morphological and paleontological series of forms. This approach is in general retained to the present day. However, methodological discussions arise concerning the extension or restriction of the area of application of this method and concerning the concept of morphological evolution. In particular, whether evolutionarily morphological studies should be limited to the macroanatomical level, or

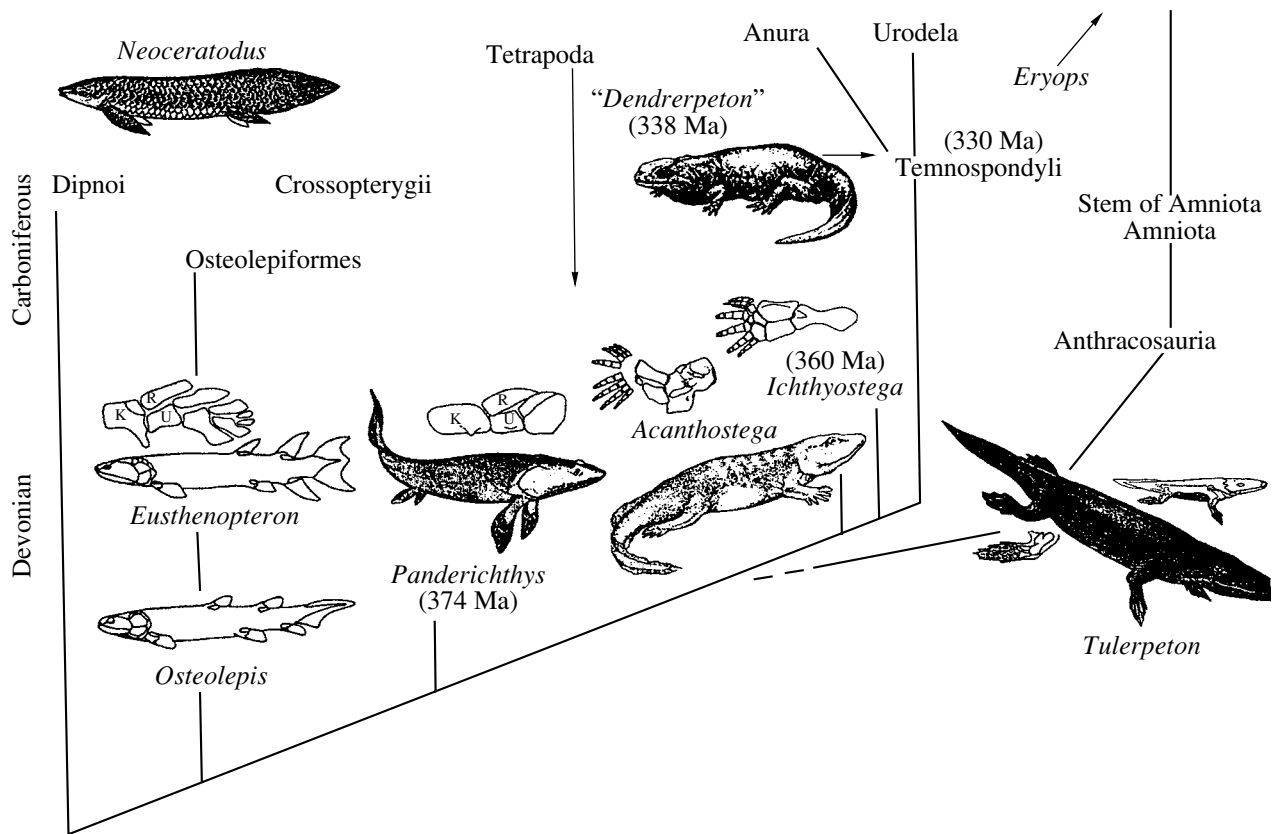


Fig. 1. Cladistic scheme of phylogenetic relationships of extinct and extant vertebrate groups (dipnoans, crossopterygians, early tetrapods); morphological variations in the skeleton of pectoral fins (*Eusthenopteron* and *Panderichthys*) and forelimbs of the earliest tetrapods (*Ichthyostega*, *Acanthostega*, and *Tulerpeton*) are shown.

whether special attention should be paid to the development of the molecular genetic foundation of morphology. W, whether or not morphology should be separated from physiology and genetics, and whether the preference in the study of morphological evolution should be given to extant or extinct forms. These discussions lead at the least to perplexity, since the levels of structural organization and the processes of their development and function are interlinked; thus, an important task is to comprehend their relationships and interaction. At the same time, true progress in science is determined by the knowledge accumulated, in which evolutionary morphology and paleontology have achieved valuable results, which should be widely used in further studies (Pavlinov, 2005) irrespective of future prospects of probable transition to the molecular mode of thinking (Shatalkin, 2005). It is hardly expedient to build artificial barriers between neighboring scientific fields, such as morphology and physiology; it is evident that the problem question of the 'whole organism' organism wholeness in ontogeny and phylogeny should be developed in through close cooperation of all scientific approaches (Schmalhausen, 1982; Vorobyeva, 2006). When dealing with morphological evolution, it is hardly possible to take a series of forms for a full-value morphological series if its beginning (represented by

extinct members, which throw light on subsequent changes) is artificially cut off (Fig. 1). In this connection, it is inconsequent methodologically meaningless to construct phylogenetic trees based exclusively on extant species (Platnick, 1980) and, subsequently, to extend these results to extinct taxa, as is proposed by contemporary transformed cladists. This approach is fraught with missing information on many patterns of morphological evolution, including estimation of the genesis of structural reorganizations reflected in phylogeny, and with the underestimation of the geochronological principle of phylogeny (see Novitskaya, 2002; Tatarinov, 2003; Vorobyeva, 2005; Kurochkin, 2006).

It is evident that morphological evolution is tightly connected with certain historical periods. This results in the wide use of such concepts as the time-forms dynamics, transitional forms, archetype, morphoclines and their polarity. In general, morphological evolution means changes in the shape and structures of organisms in the course of phylogeny, which implies clarification of their origin, features of establishment, character and rate of evolutionary changes. The central position in this consecutive process is occupied by the reconstruction of the archetype, i.e., the initial state, which is regarded as a variant in the evolutionary series of mor-

phenotypes combined in morphoclines (Hecht and Edwards, 1977). Their characteristics are tightly associated with ideas about general or typical plan of structure. This concept, taking somewhat different appearance, has gained a wide acceptance in morphology beginning from the time of Goethe, Owen, and Baer and provided the foundation of typological mode of thinking and the law of the type uniformity after Darwin (Vorobyeva, 1992). The term *Bauplan* (Riedl, 1975) became widely used, combining based on morphological affinity phyletically and hierarchically subordinated groups. From this point of view, morphological evolution is regarded as the exposure of the plan of structure, i.e., demonstration of its potentiality provided, in particular, by correlations and the dynamics of modular constructions (Dullemejer and Barel, 1977). In this connection, the concept of functional modules dynamics was determined as a linkage between functional and evolutionary morphology, demonstrating the “renaissance” of the 1970s (Wake, 1982).

The major aspects of the development of this renaissance were as follows: (1) biomechanical, intended to be a source of information for combining the evolutionary and functional approaches; (2) adaptational, focusing attention on the ecological aspect of morphological changes; (3) constructional, connected predominantly with the revelation of the structural organization of the shape; (4) theoretical, simulating parameters of changes in the shape (Raupp, 1966); (5) developmental biology, studying the mechanisms of formation (Delsol, 1977); and (6) phylogenetic, connected with the revelation of similarities based on relationships (homologies and autapomorphies).

PROBLEMS AND APPROACHES TO THEIR SOLUTION

To date, the list of questions of morphological evolution still includes such questions as relationships between the form and functions, the formation of adaptations, the relationship between ontogeny and phylogeny, the evolution of ontogeny and correlation systems, organismal holism with reference to differentiation and integration of internal and external factors and their interaction in ontogeny and phylogeny, the homology of parts of organisms and phylogeny, characteristics of morphophysiological and biological progress. These principal problems have changed with time, retaining their general directions, but defining more concretely their tasks in accordance with the demands of the times. Thus, in the problem of form–function relationships, the major stress is set placed on the origin and evolution of adaptive complexes and on the hierarchy of functions (Lauder, 1981; Iordansky, 1990). In the problem of relationships between ontogeny and phylogeny, the major attention is paid to the recognition of the role of developmental mechanisms in the establishment of morphological innovations and the formation of higher levels of organization and large taxa (Deviller, 1965;

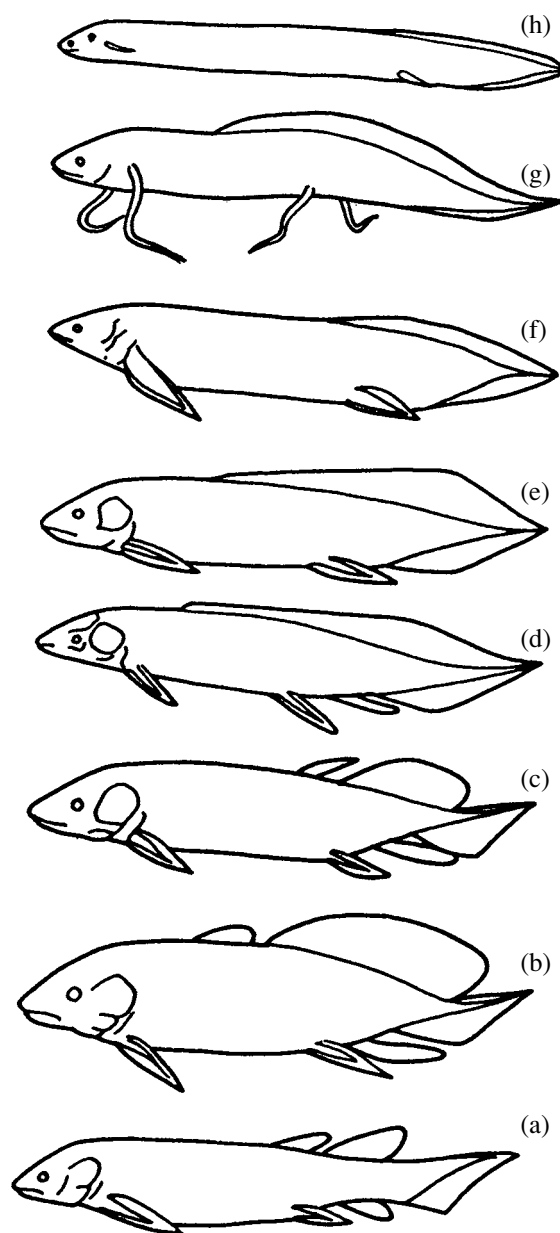


Fig. 2. Evolutionary series of morphofunctional changes in dipnoans, accompanied by pedomorphosis, including (a–e) extinct and (f–h) extant taxa: (a) *Dipterus valenciennesi*, basal Lower Devonian; (b) *Penilandia macropterus*, terminal Lower Devonian; (c) *Scaumenacia curta*, basal Upper Devonian; (d) *Phaneropleuron andersoni*, terminal Upper Devonian; (e) *Uronemus lobatus*, Lower Carboniferous; (f) *Neoceratodus forsteri*, Holocene–Recent; (g) *Protopterus annectens*, Holocene–Recent; and (h) *Lepidosiren paradoxa*, Holocene–Recent.

Hall, 1999; Korochkin, 2002; Kolchanov et al., 2003). A special place is occupied by the questions of evolutionary significance of heterochronies, in particular, pedomorphoses (Gould, 1977; Bemis, 1984; Carroll, 1986; Smirnov, 1991; Iordansky, 1994; Vorobyeva, 2003a; Rozhnov, 2005) (Fig. 2). In the problem of evolution of ontogeny, the regulatory mechanisms of

development, prohibitions and restrictions (including, genetic, morphogenic, morphophysiological, tissue, constructional, hormonal), and their role in the formation of the general plan of development, the *developmental bauplan* are brought into the foreground (Alberch, 1980, 1982a, 1982b; Carroll, 1985; Shubin and Alberch, 1986; Shubin, 1995; Vorobyeva and Hinchliffe, 1996; Hinchliffe, 2002; Smirnov, 2005). The concepts of a staged pattern of ontogenetic dynamics in evolution (Belousov, 1986) and relationships of molecular-genetic and epigenetic developmental programs were proposed (Delsol, 1977; Shishkin, 1984; Hall, 1999; Kolchanov et al., 2003; Shestakov, 2003). Special positions are occupied by the problems of the specificity of structural levels of organization and their hierarchy (Lieber and Lieber, 1983; Vorobyeva, 1992, 2005), the problem of organizational stasis (Gould and Eldredge, 1977; Alberch, 1980; Wake et al., 1983), connected with the problem of dynamic stability in morphology (Oster and Alberch, 1982; Vorobyeva, 1992), and the problem of directedness of evolutionary processes (Gilyarov, 1985; Tatarinov, 1987; Severtsov, 1990, 2005; Vorobyeva, 2003b).

The phylogenetic branch of morphology has also underwent essential changes. These changes primarily concern the approach to the study of homologies, which are inseparably linked with the search for relationships. In this case, in addition to the generally accepted criteria, which are based on the establishment of the origin, continuity, and topographical relationships between particular structures, the increasing significance is attached to the estimation of functional parameters of morphological changes, their rates, and the staged pattern of their transformations (Iordansky, 1990, 2004) as well as to the involvement in consideration of ontogenetic mechanisms, in particular, the influence of restrictions and the time of development on the results of macroevolution (Alberch, 1982a, 1982b; Gould, 1982). Finally, the transformed cladism changes the judgements concerning the nature of homologies, which are divided into general primitive (plesiomorphic) and advanced (synapomorphic) homologies, which reflect the morphological integrity of diverging taxa and are regarded as the characters of sister groups.

The interest in the question of organismal holism (*sensu* Schmalhausen, 1982) in individual and historical development has also increased (Alberch, 1982a, 1982b; Wake, 1982; Vorobyeva, 2006). As a result, attention is paid not only so much to the evolution of particular characters or structures, but also to their interactions in the course of evolution within the entire adaptive complexes, during the formation of the general plan of organization of a new macrotaxon (Iordansky, 1990, 2004). The dynamism of morphological evolution is regarded as a morphological process with a certain ontogenetic developmental trajectory of the formation. From the point of view of the integral-dynamic treatment of the organic form (Paaver, 1986), the following questions have become particularly topical: the

specificity and hierarchy of structural levels of organization as a means of providing its integrity; relationships between stability and dynamics of morphological components, which form a multiplex morphofunctional complex; the patterns of structural changes in biological systems at different stages of their evolution, in particular, the patterns of establishment and evolution of general plans of structure and their development, including their genetic and epigenetic foundation.

Thus, in the approaches to morphological evolution, in addition to the principles of the historical point of view, Haeckel's Triad, and integrity, it is methodologically significant to apply the principle of system organization, focusing attention on the space-time consideration of the organic form; the principle of the initial morphofunctional archetypic diversity (Mamkaev, 2004; Rozhnov, 2005); the principle of dynamic stability (Vorobyeva, 1989, 1992); and the principle of preservation of processes (Vorobyeva and Meyen, 1988), which requires the classification of characters depending on the time of their origin. It is methodologically important to define the unit of morphoprocesses (the elementary object of morphological studies); it is expedient to regard the integral organism (i.e., phenotype) as this unit and oppose it to the unit of speciation, i.e., the population (Vorobyeva, 2006). This dualistic approach to the evolutionary process enables the avoidance of senseless discussions between typologists and population biologists and the attainment of dialectical integration of the statics and dynamics of the organic form, the unity of types and variation, macro- and microevolutionary levels of research. The development of this approach is mediated methodologically by the principle of dynamic stability, which implies that the evolution of morphological forms should be studied differentially, i.e., through the recognition of their stable constructions and plastic components providing this stability (Vorobyeva, 2006). These components may be represented not only by morphological structures, but also their position, developmental processes, functions, and mobility of biochemical, genetic, and behavioral bases. Thus, the morphological state does not always reflect the evolutionary process as it is perceived exclusively through the speciation. This characterizes the morphological evolution as a special phenomenon governed by special laws, which were characterized, in particular, by Severtsov (1939) through the analysis of anatomy and embryology of extant species of lower vertebrates.

PALEONTOLOGICAL ASPECTS OF MORPHOLOGICAL EVOLUTION

In paleontology, the morphological evolution means a number of special particular things. It usually considers the trends of morphological changes in the systems of organs and individual structures of particular extinct forms during certain historical periods. The informative significance of these changes depends directly on the

completeness of paleontological series, which provide the basis of phylogenetic reconstruction, while the general patterns of morphological evolution are taken out of context (see, e.g., Novitskaya, 2002; Vorobyeva, 2003a; Ponomarenko, 2005; Rozhnov, 2005; Saveliev, 2005; Kurochkin, 2006). In this context, a general task is the determination of the possible range of forms of organisms, including those not realized in evolution. This task is indirectly connected with the problem of biological diversity, which is reflected in morphological multiformity. It is associated with the solution of such questions as the modes and mechanisms of the formation of morphological types in the course of evolution; the status and morphological features of transitional and aberrant forms; model forms and species specificity of morphotypes; the rates and patterns of morphological evolution (gradualism, saltationism, directedness, relationships between divergent, parallel, and convergent development); morphogenic bases of evolution, in particular, the role of heterochronies in the formation of morphological innovations; morphological adaptations and their relationships with the formation processes. This list of these questions is not new; however, many of them have acquired a new meaning due to comparative analysis of new data on extinct and extant taxa.

MODES AND RATES OF MORPHOLOGICAL EVOLUTION

The evolution of morphotypes may follow two patterns, i.e., gradual and successive development (gradualism after Darwin), or long preservation of standard morphology, the *stasis* (Wake et al., 1983), which is replaced by abrupt structural changes accompanying spasmodic speciation, the *saltationism* (Gould and Eldredge, 1977) (Fig. 3). The first pattern is usually associated with the stable environment and gradually increasing fitness, as exemplified by the increase in the number of pygidial ribs in Ordovician trilobites (Sheldon, 1987). The second pattern may be caused by environmental fluctuations, for example, regressions and transgressions of the lake levels, which was shown in the evolution of some freshwater mollusks (Williamson, 1982), or connected with a large range occupied by populations and directed effect of natural selection, for example, in Devonian brachiopods (Boucot, 1975); or may be caused by various regulating mechanisms of development (Oster and Alberch, 1982), in particular, those functioning at the genetic level (Takhtajan, 1983; Kurochkin, 2002; Kolchanov et al., 2003; Shestakov, 2003). Morphological evolution does not necessarily result in divergence. The background of diverging lineages is overlain by the lineages developing in parallel (homoplasy) and convergently, which are responsible for the formation of new morphological characters and new combinations and for the emergence of new large taxa; this, on the one hand, provides the directed character of evolution (Tatarinov, 1987; Severtsov, 1990;

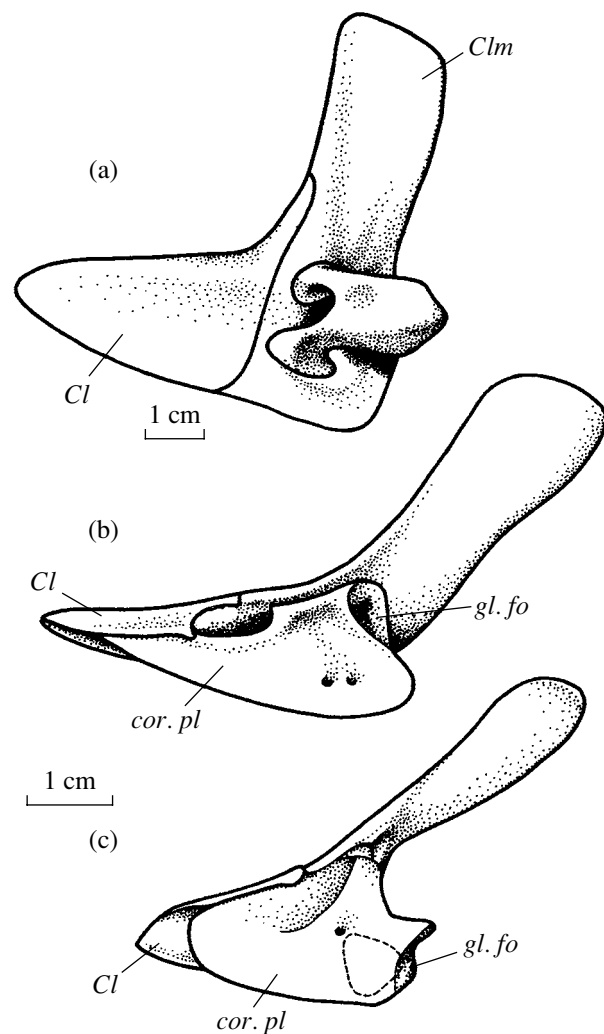


Fig. 3. Morphological saltation in the acquisition of the coracoid plate by (a, b) crossopterygians in parallel to (c) tetrapods: (a) typical condition, scapulocoracoid without a plate (*Eusthenopteron*); (b) *Panderichthys* with a well-developed coracoid plate; and (c) *Ichthyostega*. Designations: (*CIm*) cleithrum, (*Cl*) clavicle, (*cor. pl*) coracoid plate, (*gl. fo*) glenoid (modified after Vorobyeva, 1992).

Vorobyeva, 1992; Novitskaya, 2002; Kurochkin, 2006) and, on the other hand, makes it similar to a grassplot meadow rather than a branching phylogenetic tree (Ponomarenko, 2005). Parallelisms give the impression that morphological evolution follows a staged pattern, in the course of which different groups within the same lineage or successive lineages show certain levels of the formation of morphotypes, with primitive and more or less advanced conditions. The transition from one level to another does not always coincide with certain taxonomic ranks. Primitive features are often combined with rather advanced characters, resulting in the pattern of *mosaic evolution*. Earlier, this term was only applied to plants, some groups of invertebrates, and hemichordates (Asciadiacea), which are characterized by the autonomous morphogenesis. However, at present, the

mosaic pattern of evolution is known in a number of structural changes in many groups of invertebrates and vertebrates. This phenomenon is particularly widespread among the so-called transitional forms, which are positioned at the boundary of large taxa. They include *Archaeopteryx* (which provides a morphological link between reptiles and birds), ichthyostegids (semifishes–semiamphibians), and some theromorph reptiles with mammalian features. However, these animals are not true transitional forms, but show a mosaic of ancestral features and characters of descendant (derivative) taxa; therefore, they should better be termed *mosaic forms* (Schad, 1980).

The morphology of mosaic forms demonstrates a combination of interlacing features of the previous and new organizations. Thus, *Ichthyostega* (Fig. 1), the earliest primarily aquatic tetrapod, combines the limbs of the lever type with the rudimentary gill cover, closed sensory canals, scales, and the caudal fin with lepidotrichia, while the limbs were rather used for swimming, having six digits, probably, with a swimming membrane between them. An even more aquatic appearance is characteristic of *Acanthostega*, which retained inner gills and limbs with eight long digits (Coates and Clack, 1990).

Tetrapod characters were acquired at the fish level following both gradualistic and saltation patterns; this is supported in particular by the finds of panderichthyids, which are regarded as a sister group of ichthyostegids (Vorobyeva and Schultze, 1991). These crossopterygians resemble *Ichthyostega* even in appearance (Fig. 1), showing similarity in the skull design, with a rostrum; the nares located ventrally, near the mouth edge; the topographically similar choanae; and the closely positioned orbits located dorsally and bordered medially by superciliary ridges; the composition of the skull roof bones, in particular, the presence of frontalia; the presence of a deep spiracular fissure (corresponding to the ear notch of tetrapods); the structure of the lower jaw and teeth; the morphology of the pectoral girdle (Fig. 3); and the composition of the proximal elements of the forelimb (Vorobyeva, 1992, 2003a). However, the endoskeleton of the distal region of the fin of *Panderichthys* is distinguished among other rhipidistians by its unusual specialization. Instead of something like a pentodactyl limb, the pectoral (Vorobyeva, 1992) and abdominal (Boisvert, 2005) fins of this fish have an ulnar plate that is not subdivided distally (Fig. 1). Such a limb could have appeared as a result of fusion of the prochondral elements and arrest of development due to pedomorphosis.

The pedomorphosis, i.e., the preservation of embryonic or juvenile characters of the ancestor in the definitive state of its descendants (Gould, 1977), apparently played an important role in morphological evolution and divergence of taxa. It could have been manifested in individual characters or sets of characters, providing a way out of an evolutionary dead end by returning the

previously lost morphological characters through the reactivation of latent developmental potentialities (Oesche, 1965). Consecutive pedomorphic changes were probably realized by dipnoans, which resulted in significant changes in their appearance in both Late Paleozoic and extant taxa (Bemis, 1984) (Fig. 2). The modular skull structure of crossopterygians is probably a pedomorphic feature, with the anterior and posterior modules corresponding to the trabecular and parachordal regions of the embryonic vertebrate skull, respectively. Pedomorphoses could have been responsible for the loss of the cosmoid cover on the bones and scales of bony fishes, reduction of some membrane bones of vertebrates, the development of nonplicate or poorly plicate teeth in early amphibians, the preservation of shagreen plates on the jaws of coelacanth, the formation of different vertebral types in fishes and tetrapods (Carroll, 1986). Pedomorphoses could have given rise to new species and large taxa. Thus, grasses are compared to the juvenile phase of trees (Kolchanov et al., 2003). The extant amphibian groups developed against the background of pedomorphoses, which were primarily manifested in the underdevelopment of cranial elements; this was even regarded by some researchers as evidence of morphological degeneration. At present, pedomorphic development is commonly recognized as one of the major phenomena of amphibian evolution (Shishkin, 1973; Smirnov, 1991; Jordan-sky, 1994; Hall, 1999; Vorobyeva, 2003b), which provided their morphofunctional diversity and the ability of to mastering of narrow ecological niches (Duellman and Trueb, 1986).

Pedomorphoses may be obligatory or facultative characters of amphibians, which are manifested in somatic or sexual neoteny and often accompanied by a decrease in the size of animals (miniaturization). Similar features also occur in fishes, for example, dwarf males of salmonids.

A wayn opposite route to pedomorphic evolution is phylogenetic outstripping in the development of structural conditions in members of the same lineage, which look like a saltation developing beyond the typical states characteristic of this lineage and often resembling more advanced groups. Examples are provided by the development of the lower jaw flanges (Fig. 4), the complex microstructure of teeth, the intense branching of nerve trunks in Devonian crossopterygians, etc. (Vorobyeva, 1992). Since these events are widespread in many groups, we regarded them as a special evolutionary mode, which reflects the directedness of morphological evolution (Vorobyeva and Nazarov, 1988) and is comparable to the principle of characters overlapping (see Mamkaev, 2004). From this point of view, phylogenetic outstripping may be regarded as a searching strategy (preadaptation) on the route of morphophysiological progress. The results of this search could have been stabilized by further natural selection (usu-

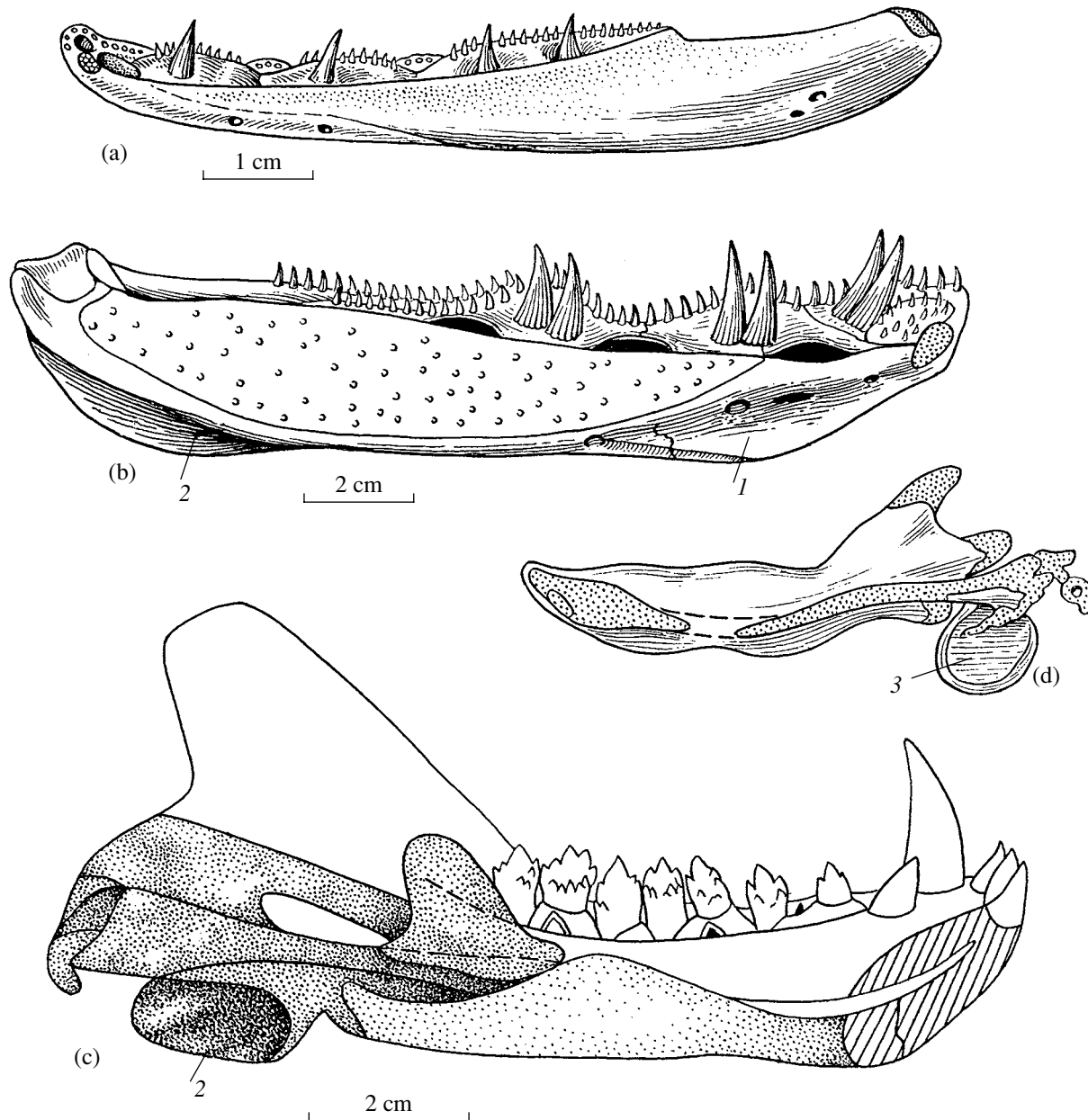


Fig. 4. Phylogenetic outstripping, using the example of morphofunctional transformations of the lower jaw in the evolution of vertebrates: (a) crossopterygian *Eusthenopteron säve-söderberghi*, basal Late Devonian, infradental flanges are absent; (b) crossopterygian *Platycephalichthys bischoffi*, terminal Late Devonian, (1) anterior and (2) posterior infradental flanges are well-developed; (c) mammal-like reptile (theriodont) *Cynognathus*, Lower and Middle Triassic, the angulare has a plate (2), corresponding to the posterior infradental flange of crossopterygians and, topographically, to the cavity of the middle ear; and (d) mammal, region of the tympanic (3), corresponding to the angular flange of theriodonts (after Vorobyeva, 1992).

ally in a modified form), become a typical condition of large higher taxa or only a result of random search, which is observed in isolated representatives of these taxa. Thus, crossopterygians stabilized the skull roof through the preservation of serrated sutures characteristic of the juvenile stage (*Eusthenopteron* and *Panderichthys*) or the acquisition of posterolateral projections on the anterior shield (*Elpistostege*). The second variant was rejected by further evolution, while the first was fixed at the level of stegocephals.

Thus, morphological diversity was formed by both retarded and accelerated development of structures (principle of an acceleration-retardation of Cope-Hayatt). In paleontology, the results of such nonuniform rates were fixed as more or less advanced or, on the contrary, primitive conditions, which were sometimes retained for millions of years. These phenomena give rise to the concepts of archetypic appearance of representatives of various groups, of the pronounced plesiomorphic characters. Note that almost all groups

include conservative and advanced lineages, which are often closely related. Some high-rank groups or their parts show primitive features that were lost in their potential predecessors; for example, in a number of characters (proportions and particular elements of the skull), parareptiles are more similar to crossopterygians than brachiopods (the earliest amphibians), which were formed under a significant influence of fetalization, i.e., pedomorphic development. In this and similar cases, one criterion of homology (continuity of structural series in phylogeny) is violated; therefore, the recognition of homologies is based on the other two criteria (structural similarity and topography). However, these two can also show substantial deviations. It is possible to put them under control only in the case that rather complete paleontological series are available, which allow the direction and character of structural changes or their general trends to be reconstructed.

The restoration of lost characters and the acquisition of new characters through outstripping development or pedomorphosis may give the impression of morphological saltations, which are based on responses of the threshold type and latent potentialities. This is illustrated using the example of intensive branching of the occipital veins on the skull roof of the crossopterygian *Eusthenopteron* and the echidna (among mammals), the presence of an unusually well-developed dermintermedial process in the nasal cavity of the Late Devonian crossopterygian *Platycephalichthys* and the extant anuran amphibian *Hypopachus* (Vorobyeva, 1992).

MOSAIC FORMS

Mosaic forms provide prominent examples of the patterns of morphological development of higher taxonomic levels, which show many ancestral features at the early stages of their formation. This is demonstrated by the example of *Archaeopteryx* (Schad, 1980), in which reptilian features clearly prevail, avian features are developed to a lesser extent, while transitional characters are almost absent. The assignment of this taxon to reptiles or birds is conditional and depends on the assumption concerning relative significance of its characters, i.e., which features (wings with feathers and pneumatic bones or dentition and a number of reptilian characteristics of the postcranial skeleton) are taken for the key characters. To date, it has been clearly shown that *Archaeopteryx* has many advanced tetrapod characters, which are in common with coelurosaurs. Therefore, it is often regarded as an offshoot of theropod evolution rather than a sister group or ancestor of birds (Kurochkin, 2006).

Comparisons of neighboring mosaic forms belonging to the higher and lower lineages are of particular interest. This concerns, for example, Devonian *Ichthyostega* and *Panderichthys*, which represent sister groups at the boundary between fishes and tetrapods. In this and similar situations, it is possible to recognize the sequence of the loss of ancestral features and the acqui-

sition of new characters. In particular, scales, lepidotrichia, closed sensory canals, subdivision of the skull into modules, remains of the gill cover and gill cavity, and the presence of the humerus are evidence of the "processual preservation" of the inherited morphophysiological organization in early tetrapods (Vorobyeva and Meyen, 1988). In contrast, the absence of dorsal and anal fins, the widely spaced pectoral and abdominal fins, the acquisition of the coracoid plate (Fig. 3), and the monolithic shields of the skull roof of *Panderichthys* suggest that a number of typical tetrapod features could have been acquired at the fish level of organization (Vorobyeva, 1992). Due to the mosaic pattern of changes, a distinct boundary between neighboring morphophysiological levels disappears, so that it can be recognized only by the analysis of typical representatives of either lineage, mostly at rather late phylogenetic stages. It is important to distinguish taxonomic transitions (mosaic forms) from morphophysiological transitions, which provide successive series of changes from primitive to advanced conditions.

TRANSFORMATION RULES AND VARIATION PATTERNS OF MORPHOLOGICAL FORMS

The discovery of transitions in morphological (paleontological, comparative anatomical, and ontogenetic) series provided the foundation not only for gradualistic concepts but also gave rise to the principle of hypothetically common ancestor, the concept of unity of structural types in paleozoology, and the telome theory in botany (Vorobyeva and Meyen, 1988). In actual evolution, however, series of transitional states are observed mostly in dead-end lineages (*Archaeopteryx*) or in morphological series corresponding to a small time period, as is exemplified by the formation of the rostrum in belemnites, the change of the suture in ammonoids, and the transitions from phyllosperms to cladospores in higher plants.

However, in the case where many species of the same lineage are compared, particularly, when they have lived for a long time, the typological approach (which predominated in comparative anatomy and paleontology in the past centuries and was based on the recognition of model or reference forms) seems inadequate in practice, since the diversity of morphological forms usually does not fit in the framework of these models. As a result, each model form appears to be something averaged, approaching to a greater or lesser extent the type condition (depending on luck of more or less random choice). This does not mean, however, that the typological approach should be rejected. A more correct conclusion is to develop this approach, although using an essentially new foundation. First of all, when constructing interconnected morphological series, morphologists usually try to reduce the diversity of each organ to only one initial state. This approach seems to follow from the principle of monophyly used in phylogeny and taxonomy, although this relationship is

optional. The initial organ may vary within species and genera (Lebedkina, 1986) or even within particular populations; in the course of evolution, this variability produced dominant modalities that were manifested in descending taxa. The rank of these characters could have increased. In particular, in the first gymnosperms, the symmetry of the copula was a character of low value; however, subsequently, it became a key character, even at the level of classes (Meyen, 1984). At the same time, the pattern of polymorphism could have changed considerably in the course of evolution. According to the principle of the initial morphofunctional diversity (Mamkaev, 2004), this diversity provided the basis for the formation of type features; subsequently, polymorphism within particular lineages of the type was established in connection with their adaptive radiation. The change of this kind in the pattern of morphological diversity occurred, in particular, in Paleozoic bryozoans, i.e., colonies of Fenestrata showed nine structural types in the Carboniferous and only four in the Ordovician, when they were formed by the combination of the initial characters during gemmation and changes in the spatial orientation of zooids. The formation of these types was accompanied by profound parallelisms at the level of families (Morozova, 1987).

The idea of morphological diversity of the archetype, which is based on the recognition of plasticity of primitive forms and their polymorphism, was opposed to the idea of the prototype. The typological approach implies in this case the search for stable (type) characters, to which the morphological diversity is reduced. This reduction implies the recognition of modes of morphological transformation and their role in different groups of organisms at different stages of their historical development in different ecosystem conditions. This point of view gave rise to the meronomic approach in morphology, as a part of constructive-morphological studies, which was developed by Meyen (Vorobyeva and Meyen, 1988). According to this approach, the organism is divided into different types of characters, *meronomes* (at the level of organs, their systems, tissues, and cells), which are subsequently classified based on the three major criteria of homology: the position, special quality, and discontinuity (of the series of transitional forms). In the study of morphological evolution, it is most important to recognize the order of forms within a morphological series. Morphological series in which the transformation rules and variation patterns of forms are recognized were named *refrains* (Meyen, 1984). Refrains can be established in the subdivision of leaves of extant and extinct plants, in the transformation of the shell shape of foraminifers and cephalopods, in the location of endoskeletal elements and the shape of the caudal fin and the tooth crown of Paleozoic elasmobranchs, in the changes in different systems of organs of Turbellaria, in the increased branching of ducts of dermal glands in living mammals, in the complication of dental plication in Paleozoic crossopterygians, etc. (Vorobyeva and Meyen, 1988).

When recognizing the major type parameters, which comprise the diversity observed in available forms, it is possible to reconstruct the potentiality of the archetypic state (in other words, to determine the morphogenetic potential). Thus, the diversity of gastropod shells is reduced to two parameters, which, with the use of computer analysis, allow the reconstruction of all actually realized shell shapes. The experience of paleontology suggests that the shell shape and size are usually species-specific or subspecies-specific characteristics and play a minor role in the recognition of higher taxonomic categories. In particular, the size and shape of bivalve shells varied very widely during evolution, ranging from strongly extended to spherical or cup-shaped. In ammonoids, the pattern of the suture is recognized as a key character in the diagnoses of genera and species, while the shell shape varies widely. At the same time, the ontogenetic developmental pattern of the suture is regarded as one of the best diagnostic characters of families and also used for the determination of superfamilies, suborders, and orders. Due to a wide range of the suture variation, it is highly improbable to record the same suture pattern in phylogenetically remote taxa (Ruzhentsev and Bogoslovskaya, 1971). The complication of the suture, which results in the consolidation of the shell, reduces the mollusk mass and simultaneously increases the speed of its movement and maneuverability, which is associated with biological progress. These situations may be described as a manifestation of high plasticity (variability) of a character, which provides increasing specialization and crucial significance of this character in evolution. As the specialization, i.e., the complexity of the suture increases, the participation of genes in its development probably increases; this reduces the mobility of other structures and restrains thereby the morphophysiological progress, which was probably accompanied by a decrease in the size of ammonites in the Carboniferous (Berdnikov, 1990).

At the same time, the evolution of many lineages led to an increase in size up to the appearance of giant animals; this phenomenon is named known as Cope's law (Fig. 5). It is commonly associated with a high level of energy consumption and regarded as an indicator of morphophysiological progress, usually accompanied by the complication of working structures connected with somatic functions. The number of such structures is determined by the complexity of adaptive zones and the action of mobilizing selection, which provides the working structure with a large number of special genes and is accompanied by an increase in its plasticity. From this point of view, *degeneration* (reduction) of organs is correlated with the swapping of superfluous genes and complication of gene programs of the development of appropriate structures and amplification of their functions. According to Cope, the law of nonspecialized ancestor may be explained by the fact that primitive forms, which have underdeveloped structures, provided the best ground for mobilizing selec-

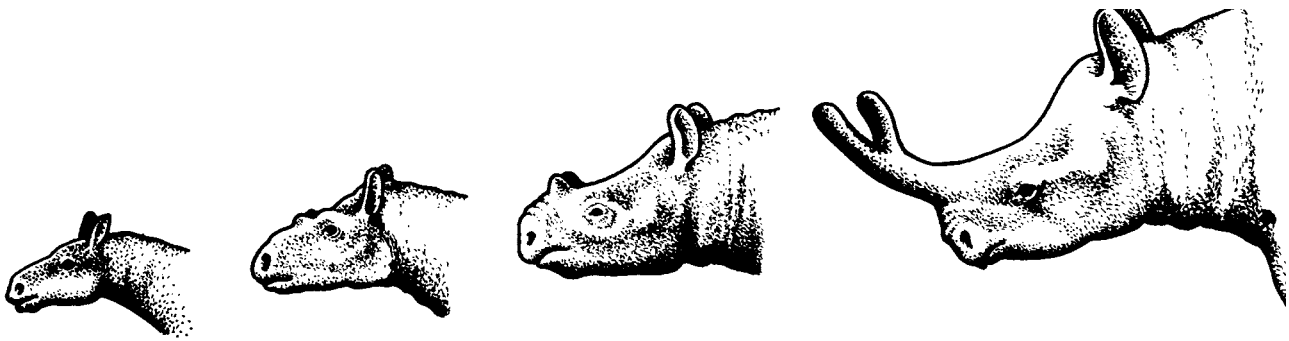


Fig. 5. Progressive increase in body size and positive allometry of horns in a series of extinct titanotheres.

tion, since they were distinguished by a high level of competitiveness and low mobility of appearance of a new physical principle (Berdnikov, 1990). However, this should not be confused with the plasticity of the initial states, implying their morphofunctional variability (see above).

SPECIALIZATIONS AND THE WAYS OF THEIR REALIZATION

An important point in the estimation of morphological evolution is its character, i.e., divergence or independent similarities (parallel and convergent development). The widespread of the latter, on the one hand, complicates the search for homologies and, on the other hand, can be used as a corroboration of phylogenetic affinity of particular forms, particularly, in the case where they are manifested in complex structural reorganizations, in particular, correlated reorganizations. The parallelisms are responsible for independent achievement of similar levels of morphological organization in different lineages. This concerns, for example, morphological parallelisms between theriodonts and mammals, between tetrapods and different crossopterygian lineages, and convergences between vertebrates and insects connected with the transition to land. The greatest number of independent similarities is usually observed in similar environmental conditions and, hence, many morphological similarities suggest similar adaptations. In particular, early tetrapods show the greatest number of parallelisms with stegocephal-like crossopterygians, which were probably adapted to a semiamphibiotic mode of life. These taxa are designated as strictly specialized (Vorobyeva, 1992), confined to an adaptive zone that is in general atypical for the lineage (implying that the superorder Rhipidistia inhabited nearshore shoals). The organizational prerequisites acquired by this group for transition to land are often regarded as potentially polyfunctional preadaptations. Because of the polyfunctional nature, these structures can follow the way of intensification, replacement, or differentiation of functions in further evolution. In particular, the choanal passage, which connects

the nasal and oral cavities of crossopterygians, was initially used for water flow providing branchial breathing or smelling, while, later, in connection with the transition to land, it was involved in lung breathing.

It is reasonable that the pronounced polyfunctional potentiality of structures provides their evolutionary plasticity and the possibility of adaptive radiation. At the same time, specialization imposes restrictions on the evolutionary plasticity, predetermining further course of specialization in certain directions, which agrees with Deperet's law. From this point of view, it is possible to comprehend Cope's law about nonspecialized forms, especially as it is supplemented by the idea of the initial morphofunctional diversity. This law is in conflict with the principle of heterobathmy (sensu A.L. Takhtajan), which asserts that transitional mosaic forms combine primitive and advanced characters. At the same time, the presence of conservative groups, which retain primitive appearance for a long time, as well as the secondary return to the primitive state through pedomorphoses strongly restricts the range of application of Cope's law. This law is a particular regularity rather than a general law, it indicates a usual increase in structural specialization in the course of phylogenetic development. Deperet's law also has restrictions, which are imposed by dedifferentiation and underdevelopment of pedomorphic forms, as, for example, in brachiopoid amphibians (Shishkin, 1973).

The widespread belief that narrow specialization (telomorphosis after A.N. Severtsov) leads to evolutionary dead ends is not always supported by factual material. Thus, in the case of narrow specialization under conditions of a transitional adaptive zone, there may be prerequisites for the enlargement of this zone by taxa that have a wide evolutionary plasticity, in particular, mosaic forms. In this situation, it is possible to say that narrow specialization leads to aromorphosis, which is determined as the complication of morphophysiological organization in connection with the acquisition of large-scale adaptations (Schmalhausen, 1982). The transition of vertebrates from aquatic to terrestrial mode of life (Vorobyeva, 1992) and transition of

aquatic insects to land habitats (Gilyarov, 1985) represent such aromorphoses. Since these aromorphoses give rise to large taxa, they can be designated as key aromorphoses (Iordansky, 1990).

Profound changes in organization are usually regarded as morphophysiological criteria of aromorphoses. For example, the tetrapod limb, at least its endoskeletal proximal part, developed structurally at the level of crossopterygians (Vorobyeva and Hinchliffe, 1996) (Fig. 1). As concerns functional characteristics, the biological significance of these structures most likely corresponded to that of fishes, although some taxa, such as panderichthyids, apparently used its limbs for short-term travelling on a solid substrate. The forms of this kind initiated new trends of morphological evolution through testing particular variants under conditions of fluctuating environment, although they remained connected with the initial habitats. It is noteworthy that the first tetrapods apparently remained primarily aquatic for a long time. In this respect, adaptation of tetrapods to terrestrial habitats can be regarded as a gradual process of expansion of their adaptive zone, which later resulted in complete shift in adaptive zone, i.e., transition to land.

It was indicated that narrow specialization, which correlated with the narrowing of ecological niche, could have led to morphological stasis (Wake et al, 1983). This was shown, for example, in Jurassic *Phoenicopsis*, which were indistinguishable from Cretaceous taxa even at the ultrastructural level. At the same time, during biosphere crises, with presumable intense competition, conditions were similar to those of the transitional zone. Pioneer species, the strategy of which is designed for unstable environment, appeared on the scene and paved the way for more competitive species adapted strategically for similar environment (Krassilov, 1986). In these conditions, morphophysiological specializations that provide adaptive advantage acquire special importance. In particular, the appearance of mammals is believed to be connected with the acquisition of homoiothermy, high activity, well-developed brain, and, what is more important, early maturity, which was undoubtedly atypical for reptiles.

A special specialization category comprises hypermorphoses, which are characterized by excessive development of organisms (giantism) or particular organs (Fig. 5), and katamorphism, which lead to degeneration because of transition to parasitic or sedentary mode of life. These specializations are connected with rearrangement and disturbance of interactions between parts of the organism, i.e., in its coordination systems. Three major types of coordinations are recognized: biological, topographical, and morphophysiological (dynamic); they differ in evolutionary stability and tightness of inner relationships.

COORDINATION SYSTEMS AND THEIR ROLE IN EVOLUTION

Biological coordinations are most mobile (easily replaced), showing connections with environment; they have been widely known from the times of Cuvier. They are manifested in different aspects of vital activity of organisms: changes in the shape of body and organs, in connection with clearly adaptive character, modes of locomotion and food treatment. The reorganization of these coordinations is often connected with hypermorphoses, in particular, giantism, which, in addition to endocrine disturbance, is caused by predator-prey coevolution, abundance of food resources, etc., and often manifests itself in the development of secondary sexual differences (e.g., giant antlers of *Megaloceros*, tusks of mammoth, canines of saber-toothed tiger, etc.). Hypomorphoses, which are based on pedomorphic processes, are opposed to hypermorphoses. They are manifested, for example, in miniaturization of amphibians.

The two specializations may be combined, as, for example, in *Diplodocus*, which combines a huge size (up to 15 m in length) and body mass with an extremely small brain. These taxa, assigned to the persistent type, were extremely stenotopic, so that the change in ecological situation (balance of feeding, shallowing or a decrease in salinity of water bodies, climatic cataclysms, etc.) resulted in their extinction due primarily to a sudden disturbance of historically typical coordination systems.

Just before extinction, some groups demonstrated certain morphological changes, increased variability, extreme specialization, and manifestation of abnormalities. In particular, many extinction events in the history of trilobites were accompanied by the disappearance of relief elements on their shields or, on the contrary, development of excessive ornamentation, which is explained in part by racial aging. A period of distinct degradation of the shell shape occurred in ammonites just before extinction at the end of the Cretaceous, which is usually correlated with marine regressions and transgressions (Ruzhentsev and Bogoslovskaya, 1971). Pachyostotic expansions on skull and limb bones occurred in the evolution of a number aquatic vertebrate groups from the Paleozoic to the Cenozoic, which coincided with the exhaustion of their evolutionary potential, giantism, and extinction, in accordance with O. Abel. The variability of osteological characters in the cave bear just before disappearance is regarded as an indication of ecological optimum (Severtsov, 1990). However, the skeletal pachyostoses of fishes, which presently inhabit red water of the Amazon, are apparently accounted for by disturbance of the calcium exchange under conditions of changed water-chemical mode, which could have taken place in the history of other vertebrates.

It is possible to obtain a reliable estimation of fluctuations of variability by population-morphological studies. Thus, using samples of subfossil and recent

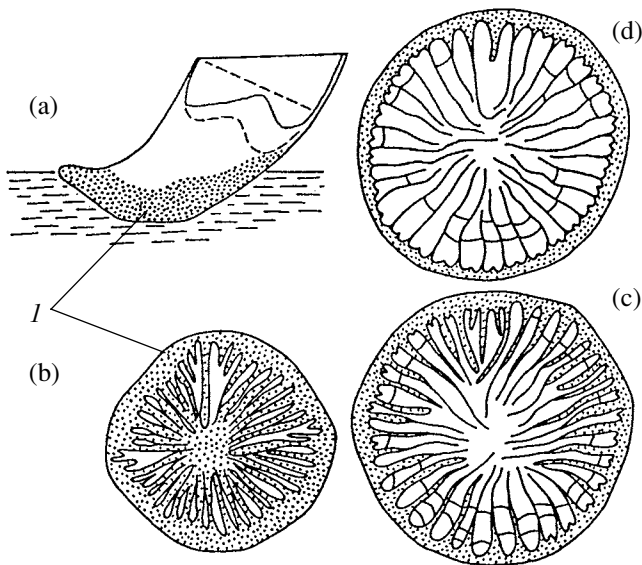


Fig. 6. Position of single streptelasmatid corals (a) on the substrate and (b–d) skeletal elements lightening in the course of evolution by the reduction of sclerenchyma (I) (cross sections): (a) curved trochoid corallite (scheme); (b) *Kenophyllum*, Middle–Late Ordovician; (c) *Dinophyllum*, Llandovery; and (d) *Porfirieviella*, Late Llandovery (after Latypov, 1982).

mammals from the Baltic Region, K.L. Paaver has shown that a decrease in variation ranges of some characters, in particular, certain proportions of teeth and cranial features connected with them, depends on stabilizing selection in favor of the norm, resulting in the disappearance of extreme values of characters from the population.

The compensatory character of biological coordinations, which demonstrates their mobility, is usually observed in connection with changes in natural conditions, for example, with the transition of invertebrates or vertebrates from aquatic habitats to land (Gilyarov, 1985; Vorobyeva, 1992), transition of tetrapods to crawling, flight, climbing, digging, secondary return in aquatic habitats, when new coordination relationships are formed on the basis of available and modified structures, which is particularly distinct in the case of changes in the biological role of organs. Numerous examples of such changes were provided by Gregory even 50 years ago.

The topographical coordinations, which reflect relationships between organs during phylogeny and are determined by the general structural plan and the type of development of organisms, are more stable than biological coordinations. Examples of such coordinations are relationships between the pattern of the suture and the shape of the septum in ammonites, the correlation between the shape and weighting (position of the sclerenchyma) in single diaphragmatic corals (Fig. 6); the correlation between the flattened skull shape of

fishes and stegocephals with the dorsal position of orbits, the passage of the trigeminal nerve in the trigeminal notch of the palatoquadrate, and the position of the frontals between the orbits; relationships of the nucleus of gymnosperms and the megasporangium of cryptogams with the megaspore. Coordinations of this kind provide the basis for the application of the criterion of position, as structural elements of organisms are homologized. In addition, they are used for the reconstruction of missing elements of the skeleton (for example, the shell) and soft tissues related to them. However, they are often of limited significance, particularly, in the case of dispersed parts, and in connection with the wide occurrence of convergences. For example, until recently, the assignment of rhyncholites to cephalopods, the function of aptychi in ammonoids, the position of the dental spiral in *Helicoprion*, and the nature of conodonts remained open questions.

Finally, morphophysiological (dynamic) coordinations are interrelations of parts of the organism that determine conjoint transformations in phylogeny. They are based on functional interactions that provide a greater or lesser autonomy from the other systems. An example of this coordination is a multiplex morphofunctional complex of the jaw apparatus, which consists of the following major components: the mouth cavity, jaws, muscles moving the jaws, innervation and blood supply, teeth, and tongue. This apparatus, or, more precisely, its coordination system includes ectosomatic (directly connected with the environment) and entosomatic structures. They interact according to the principle of direct and feedback connections, performing in general hierarchically subordinated functions, which are integrated in the entire system of the jaw apparatus as a multiplex adaptive complex (Iordansky, 1990, 2004). Changes in ectosomatic structures are clearly adaptive, while entosomatic structures are connected with them by a complex system of correlations and coordinations.

DYNAMIC STABILITY OF MORPHOLOGICAL STRUCTURES AND PROCESSES

As was shown based on the principle of dynamic stability (Vorobyeva, 1989), the complex jaw apparatus, which performs in vertebrates uniform tasks, including capturing, primary treatment, and swallowing of food objects, is most dynamic in its peripheral (i.e., ectosomatic) part. In this connection, it is possible to indicate the stability of the general skeletal–muscular pattern of the jaw apparatus and stability of the scheme of its movements as a whole, which are combined with the plasticity of a number of peripheral coordinations. These coordinations include different development of muscular portions, their innervation and blood supply; the structure of tendons; the structure, attachment, and replacement patterns of dentition; the

shape and mobility of the tongue. Due to the plasticity of these components, both morphological diversity (polymorphism) and protection (and, consequently, stability) of the basic construction in the course of evolution were formed. The components of the complex system of morphophysiological coordinations were replaced basically through this mobile reserve, using the compensatory ability of particular elements; for example, the change of the tooth shape and attachment in lizards (Vorobyeva and Chugunova, 1995).

Thus, the same adaptive task could be accomplished by different morphofunctional variants of the same systems. For example, a decrease in the cranial kinesis of different crossopterygians, extinct and extant amphibians, and reptiles developed differently, although followed three basic directions: consolidation of bones of the skull roof, fusion between the regions of the braincase, and strengthening of its connection with the palatoquadrate complex.

The basis of coordination changes is formed of complex correlation systems, or interactions developing during ontogeny (Lebedkina, 1986). The appearance of morphological innovations, or developmental variants is recently often correlated with epigenetic potentialities of organisms, in particular, with the morphogenesis. From this point of view, morphological evolution is regarded as a result of differential natural selection of new structural formations, which arise not only on the basis of random genetic mutations and indeterminate variation, providing material for natural selection, but also as a process controlled by regulatory genes and historically typical inner epigenetic factors of development. In particular, these regulations promote the appearance of phylogenetic parallelisms and convergences.

The dynamism of stability of ontogeny implies the combination of the stability of general organizational morphogenic foundation with certain plasticity of processes and mechanisms. Thus, the stability of early stages, which is manifested, in particular, in von Baer's law of embryonic resemblance, is accompanied by well-pronounced variability, which obscures the picture of recapitulation. This diversity provides the basis for qualitative reorganization of ontogeny, i.e., archalaxes, which, however, are rather infrequent because of the stability of the morphogenic bases and occur mostly in plants. In this connection, the morphogenesis is not only a result of natural selection, but also a restrictor of its action (Alberch, 1982b; Shishkin, 1984), which determines the potential range of structural changes. The wide occurrence of phylogenetic parallelisms and convergences is explained by the stability of general organizational foundations in close and remote lineages, which is manifested in similar developmental situations and, then, is fixed by natural selection. The phenomena such as outstripping, which are provided by the revivification of latent potentialities, are evidence

that the uniformity of morphogenic foundations of large lineages and the ability to realize this uniformity were established much earlier than they appeared in the evolutionary history. At the same time, the presence of outstripping, along with pedomorphosis and prolonged ontogeny, is evidence of the plasticity of morphogenic foundations, which is provided by the hierarchy of structural levels and processes, their mutual compensatory ability, different degree of autonomy of systems, and integration in the organism. Since the phenomena of outstripping, consequences of pedomorphoses and prolonged development are fixed in phylogeny in the form of definitive morphological conditions, they should be assigned to a special category designated phylogenetic heterochronies and regarded as a consequence of the evolution of morphogenic foundations, or historical morphogeneses. These heterochronies can be regarded as a mechanism of morphological macroevolution. They are based on the stability of historically typical designs and processes, which recapitulate in a series of generations. Such reproduction is only possible due to the combination of stability and certain plasticity of ontogenies, which is clearly seen in the variability of developmental processes, regulatory ability, heterobathmies, and others.

Consequently, the dynamism of the stability of ontogeny is an indispensable prerequisite of morphological evolution. From the point of view of the principle of dynamic stability (Vorobyeva, 1989, 1992, 2005), the morphotype is regarded not only as a result of natural selection, but also as the connection of the stable organizational foundation and a certain reserve of plasticity, particularly, in the leading systems of organs, directly responsible for the survival of organisms in the given period. All other systems changed in coordination with the leading systems. As the conditions of development and functioning changed, individuals and species with the most plastic (dynamic) systems persisted. The plasticity of systems, which is displayed in population polymorphism, allowed them to survive, particularly, under conditions of a fluctuating environment. This was the prerequisite for the formation of species with a high potential plasticity, which was manifested in structural mosaic (heterobathmies) and in a wide range of pedomorphic changes.

The complex interaction of correlation and coordination systems, which are controlled at the genetic and epigenetic levels (Kolchanov et al., 2003; Shestakov, 2003) and integrated in the entire organism through direct and feedback connections with the environment (Vorobyeva, 2006), provided, on the one hand, the historical preservation of inherited foundations and, on the other hand, the ability of accumulation of minor deviations or saltation shifts in a series of generations. This, in turn, supported polymorphism and, hence, the plasticity of populations as an indispensable condition of evolution of species.

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