

古動物學中一些生物學基本觀念的討論

I. A. 叶菲莫夫

摘 要

要使生物科學當中的古動物學得到發展，必須深入理解化石生物體的構造和適應性。從上一世紀開始，古生物學利用功能比較解剖學的方法分析了各種絕滅動物的適應系統，從而得出了關於其生活方式的結論。

在本世紀裏，古動物學中有另一個相反的方向加速發展了，這個學科最後定名為古生態學。這個學科研究含有化石的沉積岩，從而瞭解絕滅動物身體構造上的適應系統有何功能。

由於受到化石動物骨骼的埋藏條件和石化條件的限制，古生態學不能掌握關於絕滅動物生活方式的可靠資料。所以，古生態學是與現生動物的生物學的發展現狀大不調和的。各種精確科學，首先是物理學和化學，已經取得了巨大的成就，給生物學家提供了新的研究方法，一切舊的研究方法根本不能與這些新方法相比擬。

所以，古生物學方向——功能比較解剖學、生理學、生物化學是古動物學上的最重要的研究方法和現實的基礎。相反地，對於研究適應系統和生存條件的關係，古生態學則並不十分相宜，因為古生態學採用的方法極為粗略，而適應系統與生存條件的關係又是那麼微妙、複雜，而且有時只發生間接的關係；古生態學的方法對此只能作出大略的說明。古生物學的研究方法如能從兩個方面辯證地分析適應性問題，則是大有成效的，文中列舉了這方面的例實。

(蓋培 譯)

SOME CONSIDERATIONS ON BIOLOGICAL BASES OF PALEOZOOLOGY

I. A. EFREMOV

(Institute of Paleontology, Academy of Sciences, USSR)

The initial development of palaeontology took place on the spur of the data of geological investigations. The study of fossil animals appeared to be the cheapest method of determining the stratigraphical succession.

Later the morphological investigations of extinct organisms turned paleontology into a biological science. This biological trend proved to be useful for geological practice as well. The remains of extinct animals became not only the documents of stratigraphical succession but also the indicators of physical environments of the past geological time, i.e. the palaeogeography and the paleoclimatology.

The extension of the possibilities of biological analysis of fossil remains became especially obvious on the background of the development of the branches of biology dealing with recent animals.

The reconstruction of the anatomy and mode of life of the animals of the past by means of incomplete fossil remains turned out to be very vague after finding out how complicated the anatomical structures and physiological processes in the recent animals are. Attempts of biological reconstructions seemed to be more satisfactorily made on the most complicated extinct organisms—vertebrates and arthropods. The peculiarities of their biology are better seen on the skeletal remains than in the low animal forms.

Therefore the doubt as to the scientific authenticity of biological analysis of palaeontological remains arose first in the invertebrate palaeozoology. Here specific methods of investigation were born, which were used to obtain biological characters of fossil forms so to speak in a roundabout way. This way leads to studying palaeontological remains as documents of geological processes having formed the chronicle of the Earth and Life.

Biostratonomy dealt with the study of the arrangement of organic remains in sedimentary rocks, deciphering the processes of embedding animal and plant remains. The other branch of palaeontology adequately named "actuopalaeontology" was devoted to analyses of the processes of destruction of the recent animals and of accumulation of their remains.

In the first two decades of our century there arose palaeobiology from the combination of the two above mentioned branches. That term was used from last century in various meanings. In the twenties of this century they begin to call it more definitely as palaeoecology. Very often in the Anglo-american literature the terms palaeoecology and palaeobiology are not distinguished, but combined with the trend of functional morphological analysis of skeletons of fossil organisms. That direction was of primary importance in the vertebrate palaeozoology beginning with the works of V. O. Kovalevsky, later on of L. Dollo, W. Matthew, O. Abel, P. Sushkin and others. However, palaeoecology deviated to auxiliary methods of investigation of fossils as indicators of certain geological processes forming the palaeontological documents. Investigators tried to acquire biological characteristic of the extinct creatures by a detailed analysis of the rocks containing their remains. The character of the facies of the rocks became so to speak a characteristic of life conditions and consequently of adaptation of the organisms found there.

The trend in question has been diligently developed by Soviet paleontologists with R. Hecker and L. Davitashvili at the head, who finally determined its profile and attached to it the term palaeoecology. This trend partly abandoned morphological examination of remains and shifted the general investigations to the lithological and stratonomical conditions prevailing. The trend of functional morphology in "palaeobiological" investigations having pure biological character remained prevailing in the Vertebrate paleontology.

The necessity of such biological way for the vertebrates appeared to be absolutely clear as soon as basic principles of taphonomy (the regularities of the formation of the geological

chronicle) were stated. Taphonomy proved the embedding of remains of land animals in continental sediments as well as the accumulation of the most fossiliferous strata to take place selectively with regular destruction of certain remains (and rocks) and regular preservation of others.

Another significant regularity of taphonomy is the absence in geological chronicle of any remains of land animals conserved in their life conditions. The more ancient the sediments are, the less exceptions this regularity has.

Localities of vertebrates and other land animals with the exception of some very late formations are accumulations of the remains transferred from regions of their habitation. Evidently the study of sediments with fossil remains of land animals can yield no direct information as to their life conditions. Only after having gathered many indirect facts one could in a complicated way restore the initial character of fauna which had undergone distortion in the "filters" of the burial process until the original biocoenosis turned into fossilized coenosis or oryctocoenosis.

Divergence of the ways of investigation in palaeozoology of vertebrates and invertebrates expressing itself in the primacy of functional morphology in the former and "palaeoecology" (bearing in mind Heeker's school) in the latter may in the future become sharper. The general character of palaeontological documents leads to wrong conceptions as to the correlation between animals and their life conditions. Extreme incompleteness the preservation of fauna along with good preservation of sedimentary rocks of different facies makes the palaeozoologist underestimate the variety of adaptations of living organisms and overestimate the number of biotopes and ecological niches as well as their changability (unsteadiness) in time.

In many of the present day palaeontological works we come across opinions concerning the insufficiency of the study of fossil remains only. Investigation must be accompanied by full analysis of the fossil-bearing rocks.

This conception would be absolutely correct if investigators saw in the fossil-bearing rock only the reflection of the embedding processes of the sedimentation and of the mineralisation of fossil remains. The analyses of these processes throw light on the conditions of peril and its reasons and consequently on the life conditions of fauna and its character. The reconstruction of the embedding processes may explain a selective character of the fauna and give an idea of its perished elements.

The "Palaeoecology" however deviates from this purely biological aim and introduces in the study a number of geological problems. In their latest works (1956—57) many palaeoecologists have an idea that benthic marine invertebrates are buried in their life conditions and consider the sediment which contains fossil remains to be the reflection of their habitat. Sedimentary facies in this case are interpreted as physiographic conditions of inhabiting.

But the authenticity and the universal importance of the foundation of this palaeoecological trend are being questioned. A great many localities of marine fossil faunas are

taphocoenosis. Regularities found in the processes of embedding of land animals in continental facies are quite adequate for marine sediments, containing sea animals. Therefore contained deposits cannot be indicative of the conditions of life.

The last citadel of the "palaeoecology" not yet gained is the bottom fauna of steady marine invertebrates. Sediments containing such fauna are undoubtedly precipitated at the place of the inhabitation of animals.

The investigation of modern marine biocoenoses showed that sedentary or immovable bottom animals were distributed unevenly along the whole area. They formed separate accumulations—"spots" with barren spaces in between. Such "spots" are situated in places where there are no sediments deposited and the intensive current is able to wash out the substratum.

If such biocoenosis or crowded areas of immobile forms go to perish as a result of natural death they do not get into embeddiments. Skeleton remains not being covered by sediments are readily dissolved in a very short period of time. Only in case of a sharp change of the sedimentation in the area of biocoenosis inhabitation is the accumulation of steady marine animals being covered by deposit, then it perishes and gets embedded. In most cases when we come across closed shells, they correspond to the bottom associations buried alive.

According to the taphonomic terminology the whole process of hydrodynamic transportation is left out in the course of embedding of marine steady forms. Thanatocoenosis passes into oryctocoenosis missing the taphocoenosis stage.

Obviously the sediments with such embedding do not reflect the conditions of life of the animal but show the conditions of their extinction. That is why the embedding of steady marine bottom animals does not coincide with the main demand of palaeoecology (to be correct, ecology) to explain the biological adaptation of animals by their life conditions. For this purpose palaeoecology may operate through applying chiefly indirect data in localities of land animals.

Reefs and bioherms taken by themselves naturally reflect the conditions of life of animals that have formed them. It must be pointed out however that the sedimentary rocks surrounding the reefs cannot characterize life conditions to the same extent as marine bottom fauna.

Reefs or some of their parts are covered with sediments only after they are dead.

Unfortunately palaeoecology with its study of fossil-bearing sediments as indicators of life habitat is not up to the level of modern biological science yet, though much has been done due to the development of physical sciences in general and methods of investigation of sedimental rocks in particular.

Li-hological investigations would be futile without a detailed functional morphology of extinct animals and recent animals analogous to them.

It goes without saying that the methods of modern physical sciences are and will be of great importance for indirect taphonomic investigation. Such are physico-chemical in-

vestigations of fossil remains, for instance, isotopical analysis of marine shells, which enables us to determine the temperature of the seas of geological past in relation to isotopes of oxygen O_{16} : O_{18} . It is a direct indication to the physical character of the habitat. This has nothing to do however either with the analysis of life environment judging from the organism structure ("palacobiological" or functional morphology method) or with the analysis of the organism concerning the nature of its habitat acquired by the study of the containing deposits ("palacoecology").

Being of great significance for biostratigraphy and consequently for geological practice, it must still be admitted that recent palaeoecological investigations are not up to the demands of the reconstruction of fossil animals as of living beings. The more detailed biological investigations of recent animals are, the better one realizes how complicated and subtle are the adaptations of the organisms to certain conditions of life. Former conceptions which had contemplated only a direct connection between an organism and environment now seem to be very primitive. Practically the ways of interrelation of an organism with the surrounding nature are invariably original and often unexpected.

Having at its disposal such mighty and subtle means of investigation that are engendered with the success of physics and chemistry, biology rises to a new much higher stage of perceiving nature.

Animal organism is a combination of special, physical and chemical structures getting energy by means of a very complicated metabolism, of structures regulating this metabolism as well as the growth, defence and wear of milliards of cell units.

Animal organism is a dynamical system which has been made up in the course of hundreds of millions of years of historical development. The subtler the methods of learning organism, the clearer the development of physical sciences which gives us an extreme complexity of work and regulation of these "biological machines" in high organisms especially.

Still more and more higher technical adaptations are revealed by physiological and biochemical investigations. They are for instance the ultrasonic location of bats and electromagnetic one of mormyrid fishes (Mormyridae), the use of polarized light for the so called "navigation" by birds and arthropods, an unusual gravitational orientation in height in such archaic marine forms as horseshoe crab (*Xiphidius*) and so on. We can only mention here peculiar biochemical distance-meters in the eyes of falcon birds as far as the using of infra-red light for distant vision in eagles and vultures or polarisers in the eyes of herbivorous tropical ungulates, living in Savannous, that always browse on the border of light and shadow (giraffes).

Sometimes the most complicated adaptations get very much ahead of the general physiological level of the class or order where they originate from for instance, embryonic cameras scorpions that are found at the roots of their middle extremities. The embryo is fixed in the camera on the organ like placenta. This mechanism anticipates higher placental mammals.

High organisation of the nervous system of Cephalopod mollusks seems to contradict a relatively low general physiological level of the class. Octopus for instance has rather big brain (fixed in hard cartilage-like skull) and binocular eyesight of large eyes. Binocular vision of land vertebrates first appears only among predatory dinosaurs and it is of a lower stage of development than in *Octopus*.

Some fishes (and tuna-fishes in particular) are characteristic of a high level of metabolism with intensive bloodcirculation that is due to the adaptation to extremely fast swimming. Such forms as sword-fish or sail-fish at the speed of a hundred kilometres per hour must have a very high physiological activity that is to be practically warm-blooded. Such warm-blooded animals with gills (but in a state of repose exothermic ones) are found among recent animals.

The attempts of palaeozoologists to elucidate the biology of extinct forms through the analysis of their habitat reflected in contained rocks seem to be exceedingly limited under complex conditions of modern adaptations. Palaeoecological data would be too general and vague concerning great complexity of the relationship between organisms and their habitat even if these rocks really reflected the conditions of life of animals.

In the course of the functional morphological study of fossil animals one may come across quite an insufficient preservation of fossil remains that hinders any detailed analysis needed for the comprehension of complex adaptations. There is still a great variety of different adaptation mechanisms in recent organisms enabling us to use methods of analogy. In modern fauna one can always find adaptations like those reflected on skeletal remains of extinct organisms.

The latest achievements in biology exceeded the limits of functional analysis that the past comparative anatomy had put up for palaeozoology before. The former made it possible to choose some analogous examples from the different classes fitting not for related forms but for analogous adaptations.

A radiolocation of recent Mormyridae living in mud may serve as a good example. According to Prof. D. V. Obruchev (oral information) the construction of weak electric battery of Mormyridae may be analogous to some Devonian Placoderm fishes also living in mud and with locatory orientation.

It is clear that the development of the brain of recent Mormyrids with their extremely great cerebellum as well as their organisation on the whole utterly differs from that of Placoderms, but the essence of adaptation remains as it is.

The reduction of the lateral osseous walls of nasal passages in some recent hoofed animals together with the shortening of nasal bones presents some kind of a device for cursorial animals. It is necessary during quick running when distended nostrils provide for the penetration of a sufficient volume of air at one breath.

Analogous organisation is characteristic not only of cursorial Ungulata (such as recent ruminants and Perissodactyls) but also of gigantic rhinoceroses *Baluchitherium*. The reduction of the nasal bones of the latter is connected not with a quick running but with the necessity of providing for the gigantic thorax to be filled with air. The head of these animals is relatively small (giraffa-like adaptation). The broadening of nasal passages in some other way would require the enlargement of the size of the head but it does not serve these adaptation. The essence of the adaptation remains the same as in cursorial animals but it becomes ever functioning.

Recent cheetahs—"grey-hound" cats developing speed over one hundred kilometers per hour are also characterised by extremely broad nasal passages and by the ability to broaden them.

It seems to me that the main trend of the development of the biological base of palaeozoology follows the way of a detailed functional physiological and biochemical study of adaptations which will offer in the end the possibility to estimate and compare organisms as energetical systems.

The elucidation of the energetical essence of adaptations leads us to the comprehension of the environment as an energy basis. It makes our conception of the geological past more exact even if the geological chronicle is not full enough.

The examination of the whole series of adaptations of modern fauna presents a gigantic problem unsolved yet by relatively little developed contemporary biological sciences.

The urgent task of the coordination of zoological and palaeozoological investigations is to choose the most suitable archaic forms for the comparison with the extinct ones. Most of such archaic forms of vertebrates are presented by the animals now living in very old conditions of life in such biotopes as large swampy lowlands, deltas of rivers, swamps situated in tropical or subtropical zones, hylas and so on. Relic archaic forms, preserved in almost unreachable areas, i.e. high mountains and thick forests in the gorges of mountains of tropical and subtropical zones, are exclusively rare.

Many such forms are for a long time known to the man, but their adaptations are not in the least studied yet. Such are, for instance, two kinds of longsnout crocodiles, *Gavialis* and *Tomistoma*, that greatly differ from each other in the construction of the jaw and teeth. They are undoubtedly of different adaptations.

Quick as lightning movements of archaic marten-like asiatic beasts of prey, or viverras from Africa as well as genettes, are reflected in a peculiar structure of the brain. Physiology of these animals however has not yet undergone examination.

Monotremes and marsupials, armadillos and sloths as well as archaic ungulates are also little examined. The gaps in the investigation of archaic fishes, insects and higher molluscs are not less.

It is just among rare animals that we come across striking adaptations that change old conceptions not only of separate forms but also of the stage of development of the

whole group or class. This is quite natural because relics have survived to this day on account of that they have special adaptations to very narrow ecological niches.

As an example of surprises in connection with the examination of archaic and rare animals we may take giraffas with their exceptionally sharp seeing eyes that polarize light, with a very mighty heart, thick vessels and blood pressure reaching three hundred (according to the indices accepted in medicine). Antelope gerenook is notable for the development of the organs of equilibrium in the inner ear characteristic for only biped animals. This is natural since gerenook gets its food from the branches of acacias balancing on its hind legs. Very long feathers on the back of the birds of paradise that were thought to be useless decoration practically serve as a signal of alarm. Settling down on a bough for the night the bird arranges its feathers along the branch. The slightest vibration is immediately sensed by the feathers, their roots having sensitive nerve endings in the skin. Thanks to the length of the feathers the bird has time to fly up, being inaccessible to the persecutor (1954).

The last example cited shows how most unostentatious things sometimes signify important adaptative peculiarities. There are no things of little importance in nature. Almost each peculiarity of the structure of recent animal explicable in the course of functional morphological and physiological investigations offers for palaeozoologists an opportunity to penetrate into the past by means of precise methods of modern biology.

There is one more reason for studying the rare archaic animals of the present without delay. The areas of their habitat become limited and their extinction is going on very fast. At the growing rate of mastering virgin areas it is quite evident that most of the rare relict animals will cease to live in some decades. If we care for the future of science we must make every provision for the proper study of archaic animals before they disappear from the planet.

Simultaneously with the disappearance of ancient animals there disappears archaic mode of life of men but the disappearance of the latter goes on more rapidly.

Together with the vanishing of the hunting tribes of various lands we lose the precious experience-long standing observations of the mode of life of rare animals and those inhabiting almost impassable regions.

That experience of peoples passing through generations possesses detailed information which is difficult to overestimate.

The bushmen of South Africa were known to guess individual characters of large beasts by judging from the outer habitus of the organism. The hottentott tribes of shepherds of South Africa distinguish 350 shades of colour of cattle and there is a separate name for each shade.

In the experience of nomadic tribes there have been accumulated a great many purely ecological data. These data together with recent functional-morphological investigations will help us to find out adaptative peculiarities without making gigantic efforts to renew observations which are partially impossible now.

The accumulation and generalization of the experiences of the hunting tribes is a matter of more importance than the examination of extinct forms as the greater part of them will vanish before the end of the seventies of this century. If so, we might have missed most important observations of man on nature of animals.

The examination of the structure of various organisms of the present in its full complexity that is revealed by exact sciences with modern methods, gives every opportunity of finding out analogous adaptations in the organisms of the past.

The difference in evolutionary development, time and place of inhabitation must not discourage the palaeozoologist. A great deal of convergence testifies to relative scantiness of combinations of physico-geographic conditions of inhabitation occurring in different geological epochs of the earth surface.

Convergence is characteristic not only for the common character of outer environment, but also of similar adaptive reaction of organisms to certain conditions of life. This "similarity" of adaptations is conditioned by identically constructed organs acting similarly in certain physicochemical parameters. This inevitable physiological convergence becomes the more "universalized", the more important systems of organs, with which it is connected. For instance there is not any difference in the mechanism of light conception in the eye of recent mammal and archaic crustaceans. Even for the adjustment to a definite part of the spectrum: yellow-greenish rays are identical.

Here lies the cause of the appearance of many similar adaptations of different animals as to their origin and level of advance. Physiological convergence will be a mighty weapon for modern biological palaeontology. Its power will depend on the number of adaptations that will be fully studied nowadays.

The use of dialectical method will make the application of biological data in palaeozoology more fruitful. I wish to dwell on it because this method which will in future substitute the "monolineal" formal logics is being hardly developed. The essence of dialectical analysis of biological and palaeontological and any other phenomena lies first of all in the revelation of dual discrepancy of any phenomenon and any development. The analysis of the development of contradictions and unity of opposites must give good results when combined with inevitable historical approach to palaeontology.

It is interesting to recall that at the dawn of the Middle Ages in secret books available only to the initiates (in Hermes Trismegist's for instance) dialectics was called "a Great Secret of the Double" and considered to be the most refined mighty knowledge. This "Secret of the Double" is to play an important role as it is the reflection of genuine process of contradictory historical development of organisms and organic world on the whole.

The disclosure of the other "negative" feature of each adaptation leads to interesting considerations.

If we take the most general stages of the historical evolution of animals, the first thing observed is the steady increase of the individual energy of the organism chara-

cteristic of all forms from low up to high ones. Among low forms we come across great energy of reproduction to the detriment of individual energy. As early as in 1930 V. Vernadsky pointed out the gigantic energy of reproduction of bacteria, fungi and algae. In high organisms the expenditure of energy for reproduction sharply decreases and is substituted by the expenditure for a long standing postembryonic period of individual evolution of a complex and long-living organism.

The increase of energy is due to the acceleration of metabolism and of the strength and speed of movement, the extension of receptorian ability of the sense organs and accordingly the complication of the whole nervous system. The other aspect of this evolution is concerned with the steady increase of the necessity in the nourishment of high quality. This necessity gets greater in the high forms as compared to the low ones. This process is consequently accompanied by a keen struggle for food and enlargement of area of life, and by weakening the resistance to starvation. This general regularity is applicable to molluscas as well as to birds. Development of rapid movement enables the animal to make use of large areas to nutrition. In fact all the quickly moving forms are in need of much food; that being their weakest point and under unfavourable conditions it results in mass death.

Some peculiar deviation from former ecological niches due to the competition with high forms may be witnessed among certain poikilothermic land vertebrates of a low organization. The biggest recent amphibians, the former inhabitants of warm climate adjust themselves to different conditions of life in the cold water of mountainous rivers (*Megalobatrachus*, *Ranodon*). The general lowering of the body temperature sharply lessens mobility, metabolism and consequently want of food. The animal can live only on catching occasional prey.

It is of note that the latest Stegocephalian (*Capitosaurus*, *Mastodonsaurids* and others) being obliged to compete with physiologically more active reptiles, have come to a passive-predatory life.

However the lack of possibility to diminish metabolism in warm climate by low temperature made it necessary for the beasts to develop huge trap-Mouths, the only means of providing food enough for the passive, catching hunter of the prey.

The smallest warm-blooded animals—little shrews cannot preserve the minimum of constant temperature of the body necessary for hibernation. During winter they manifest such great want of food, that can be satisfied only by permanent motion. Practically endless eating and movement keep the small animal alive in severe frosts. These two examples are good illustration of the diametral use of the contradiction: food-motion.

Once again it can be pointed out that the higher the organization of the animal is, the more it is independent of physico-geographical conditions and accidents. The long living animal acquired the greater individual experience. Still such animals are easily wounded after sharp violations of their routine existence. They can stand only short period of hunger, still shorter period of thirst. The break-off of any normal breathing

results in immediate death. Therefore the highly organized animals are much more easily subjected to quick and mass loss. It is especially true for the highly specialized forms.

The optimal conditions of work of biological mechanism, i.e. of living being (an animal with high organization in particular), comprise "four step",-in other words four degrees, from death. That is the difference between the optimal temperature of 37° and the lethal one of 42°. So, the greater the energy of the vital activity is, the closer the organism is to the lethal bound.

The complex functions of the nervous system of the animal are in accordance with its organisation. Embryonic development is not at all sufficient for the manifold actions and perceptions of the nervous system. The animal in its postembryonic life is forced to undergo a long period of training which is possible only if care is taken to the offspring. It makes its first steps in life when having learned elementary sense-conceptions, walking, flying, crawling and having been already used to the surroundings. This sharply decreases mortality. From the point of view of the preservation of energy, the duration of life of the species becomes much more economical. But on the other hand this significant achievement has a certain disadvantage that tells as a rule on the parents (especially of rapidly developing forms)-it is a burden to force the individual to fight for more food and shortening the longevity of the latter. This reflectively results in the lessening of individual experience and training, all that being unfavourable in the struggle for existence of the species.

If we reject the principle of classification of the adaptive radiation to movement formulated by H. Osborn, many phenomena of adaptive radiation in palaeozoology become clearer. Food is undoubtedly the main factor in adaptive radiation and nearly all kinds of motion are designed to get it.

The way of moving is in full accordance with the ability to subsist on the limits of a certain fodder zone.

The mastering of the steppe and half-desert areas by the large animals could take place only after the appearance of the animals moving with little loss of energy. Then meagre food scattered on large areas could offer fodder for a large and physiologically active animal as, for instance, recent ruminant. The large steppe areas could not have been fit for reptiles, for instance, even on the condition that there was vegetation there adequate to the modern one.

Dialectical analysis compels us to give up the idea of inequality between the adaptive and the inadaptive development of the ungulates suggested by Kovalevsky. The ability of the extremities to pass through ancient biotopes-swampy areas with moist soil is what is really called the "inadaptive". The extremities adjusted to new biotopes-dry plains with hard soil were taken by Kovalevsky for the "adaptive" ones, which he considered to be a higher type of organisation. But from the point of view of expediency and universality of adaptation both types are absolutely equal.

The examples were cited from the field of "external" contradictions in the evolution of animals. Here are some examples of other contradictions in the structure of the separate organs and the entire organism as well.

The structure of the eye of the vertebrates is a most striking example of conflicting contradictions in the physiology.

Two main elements of the structure of retina, i.e. rods and cones serve different purposes. Rods provide for the sensitivity of the eye, cones-acuity of eyesight. The two functions are vitally important. For millions of years a process has been going on for the conjugation of sufficient sensitivity to light and acuity of eyesight as to the adaptations of the eyes of the vertebrates. Prevalence of acuity over sensitivity is specific for birds and for Sauropsida in general. The latter sees in the daytime better than Mammalia but the acuity of their eyesight is abruptly reduced at twilight and in dark forests. It is well known that birds go to bed early. Everbody knows how hens get under shelter in the evening but the essence of this biological peculiarity is not explained in any of the text-books. It goes without saying that I do not mean any night forms, their eye adaptation being specific.

The Mammalia have inherited the structure of the retina from the inhabitants of thick forests, tree-climbing twilight animals. That is a reason for their higher sensitivity but less acuity of eyesight as compared to Sauropsida. This shortcoming of the highly organized representatives of the class is to a great extent compensated by the development of the cerebrum with "the psychological" eyesight intensified, i.e. the intensification of cerebral perception of the image and of visual memory. At the early stages of the evolution of mammals the shortage of eyesight in comparison with that of Sauropsida was counterpoised by the sense of smell that has survived as the dominant sense of the whole class.

Binocular vision is necessary for the beast to estimate the distance to catch the prey. The same is true for some of the herbivorous animals that need to judge the distance for jumping in trees (these are monkeys and lemuroids).

Among the animals with the prolonged front part of the skull (especially birds with their beaks) the necessity of crossing the axes of the central vision sometimes contradicts the development of the beak which hinders the binocular vision. This contradiction is usually settled by the development of the second supplementary fovea of the maximum acuity on the retina. Supplementary fovea of falcons are placed on the back temporal surface of the retina. It serves the bird when looking in front. The crossing of the axes of the central vision of the birds with a very long beak (some predatory herons and littersns) cannot be achieved by the additional temporal fovea. Such birds have the fovea on the upper part of the retina. Under the necessity of binocular vision the bird raises its beak vertically and looks at the prey from under it. The setting with the beak raised up to the sky is specific for littersns for example, but it was incomprehensible until special examinations were conducted.

Here is an example from palaeozoology.

Only such fishes as crossopterygians have been assimilated to the littoral zones, gotten into delta and later on passed to the land in spite of the fact that at that very time there existed sharks and Dipnoi of high organization.

The deltaic zone is rich in food which is enough for the only slightly mobile forms of fishes and invertebrates. These forms are supplied as a rule with hard armours which protect them from the teeth of a predatory animal. Millstone-like teeth which can overcome the fast clenched shells are not universally good. The mobile armoured animals must not only be "opened", but also killed. Labyrinthodont teeth appear in accordance with the peculiarities of inhabitation in deltaic zones and it is not of an accidental nature that they are passed to all large Stegocephalians and even to Batrachosaurs, their very names denoting the nature of their food.

Labyrinthic teeth made of complex folds of dentine bone (and partly of enamel), are very much like Damask steel that is a kind of hard, unbreakable material "invented" four hundred million years before it was invented by man.

Such "Damask" teeth enabled slow crossopterygians to assimilate in coastal deltaic zones with its supply of fodder. Massive structure of this fish is not accidental either. To struggle with the somewhat strong currents in deltaic channels and further in rivers, crossopterygians (as well as dipnoans) have developed four strong fins that rest against the bottom and keep the fish in the current without using too much of energy. Dipnoan fishes with their specific teeth fitting for the thin-shell mollusks could not get deep into the continent and survived in land conditions. Crossopterygians had practically crawled deep into the continent on their fins and later on became the ancestors of all Tetrapoda. Though mobile sharks with comparatively high organization could swim fast and wanted more food, their unspecified teeth did not meet this necessity. That was the cause of their failing to compete with crossopterygians. Later on under the need of a more universal dental apparatus, labyrinthic teeth in accordance with their complexity in growth and changes came in contradiction with the structure of land tetrapods and gave way to the codont ones. They appeared again however looking different among herbivorous mammals when only hard fodder was available on dry areas of the land. If it had not been for them there would not have been recent hoofed animals.

The creeping kind of motion of the extinct reptiles was considered an archaic "survival" as if inherited from their fish-like ancestors. In fact the adaptation to swampy land was so common in ancient continents, that the former being the main biotops of the most ancient quadropedal caused the development of this type of walk. A very low position of the body is of primary importance for the animals' motion in half-watery ground as its weight was to be allotted not so much to the extremities but to the belly as well. Slow-moving kind of locomotion contradicted the usual way of opening the mouth. Instead of depression of the lower jaw it was necessary to raise the upper one in a way as recent crocodiles do it. Special "tongs" structure of the jaws has been developed with the shifting of the depressory mechanism of the lower jaw further back to the

tabular processes of the occiput and retroarticular processes of the mandibula. Now we are sure in determining a slow-moving type of locomotion in any forms having such a structure of the jaws even if the skeletons of these forms are unknown. The mode of opening of the upper jaw of such fish as *Dinichthys Arthrodira* is a prompt indication of their former creeping along the bottom.

The opening of the upper jaw instead of the lower one results in the drawback—the weakest point of all slow-moving predatory animals, recent crocodiles included. When the animal's jaw is open, the beast ceases to see anything in front as its eyes are hidden behind the raised skull. That is the explanation why predatory animals with reptile-like motion could hunt mainly by watching their prey (catching-hunting).

A significant disagreement between the mode of feeding and moving arose among reptiles with the appearance of herbivorous forms. The flat body of the predatory creeping reptiles could contain small portions of meat enough for the animal. Herbivorous and insectivorous reptiles that demanded larger size of the belly certainly could not agree with creeping motion. To provide for the necessary volume of the body i.e. digestive apparatus and lungs (because in herbivorous animals metabolism requires greater expense of air for oxidizing processes) it became necessary to lift the body from the ground. The first herbivorous four-legged cotylosaurs and deinocephalians passed to a different mode of walking with the body raised. Cotylosaurs walked with the whole body raised while Deinocephalians had only the front part raised, thanks to strong development of the front legs and shoulder girdle. Recent large herbivorous Iguanas of Galapagos Isles (*Amblyrhynchus*, *Conolophus*) resemble Deinocephalia with the front part of the body lifted.

The new kind of motion appeared to be not fit for the half-watery swampy soil that had been the habitat of the most ancient four-footed animals. It made the herbivorous inhabitation drier than the temporal regions of lowlands. There they came across coarser vegetation, that was badly digested with weak teeth of the most ancient herbivorous reptiles. In the end cotylosaurs and deinocephalians disappeared. Anomodontia with extreme strength of jaw apparatus succeeded the former in borderland biotopes of marshes and later on of some high areas of eating. The mentioned adaptive faculties were the foretokens and imperfect analogues of the very second palate of higher theriodonts, that undoubtedly became warm-blooded animals.

An example of non-dialectical approach to the deciphering of the adaptations can be seen from Prof. A. P. Bystrov's researches with regard to the analysis of microstructure of dermal bones of the Stegocephalian skull. Bystrov pointed out two types of adaptation of Permian and Triassic Stegocephalians:

- a) strong vascularisation of dermal bones testifying to the intensive gaseous exchange through the skin- "hydrophilous" type and
- b) weak vascularisation with feeble gaseous exchange through the skin- "xerophilous" type. On the basis of the prevalence of the "xerophilous" forms in Permian and "hydro-

philous" in Triassic, Bystrov made a formal conclusion that in Permian there was a dry climate and in Triassic a damp climate.

In fact, a reverse correlation takes place. The skin of Amphibians lacks the moisture isolating scaleous horned cover, a characteristic for the reptiles. Therefore Amphibians can be the active (nonself-buried) land forms only in the conditions of very damp climate, in biotope overshadowed by vegetation. It is especially essential for large amphibians like Stegocephalians unable to survive in microclimatic ecological niches. So the existence of amphibians of land appearance, i. e. "xerophilous" type is an indication of damp climate, but not of dry one.

On the other hand the motion of the raised body along the soft ground at horizontal position of the roots of extremities— a structure inherited from the creeping way of walking—required great muscle power. Therefore herbivorous Cotylosauria and Deinocephalia develop monstrous massive bones with extremely thick muscles. The waste of the muscle energy was contradictory to the fodder base which is also fatal to the animals' existence.

There are many localities of herbivorous cotylosaurs that are strictly selective. Taphocenosis in such a locality is presented by one or two forms as a result of the mass death of the animals in marshy silts where their contemporaries moved freely.

With the development of intensive movement, organisms of ancient Theromorphous Reptiles were getting more and more complex that resulted in an inevitable change to a higher kind of energy of the animals, the latter becoming warm-blooded. Accordingly, the want in nutrition of higher quality and bigger quantity as compared to that of lower reptiles grew greater and greater. So metabolism to its intensification in turn required the increase of frequency of respiration. Complex palatal processes, interchoanal ridges and transverse flanges of pterygoid bones— all these formations in the skull of Thermorph reptiles remained obscure up to the recent time. They are assigned to push the food from the palate in the moment of chewing and to let the stream of air move above the food that is to provide for breathing during the process.

The hydrophility that is a strictly limited adaptation to the aquatic life is a result of dry climate in which the large Amphibians cannot survive outside the water.

The main point of the bilateral dialectical analysis of biological adaptations lies first of all in the discovery of the opposite "negative" side of each adaptation that is in its disadvantage, incompleteness and weakness in certain conditions of life. By the analogous analysis of the destructive aspect of the geological processes it was possible to state in taphonomy important regularities of the geological chronicle formation.

The "bilateral" estimation of every adaptation would to a great extent restore the peculiarities of different trends of evolution, the causes of the vanishing of various groups and the appearance of new ones in exceedingly complex processes of the evolution of living organisms.

Applying the dialectical method that excludes one-sided conception of duplex processes in nature and drawing comparative information from an enormous variety of recent animals, adaptations, modern palaeozoology overcomes the difficulties it faces.

Only then it would be able to determine the historical formation of the structures of organisms and the correlations in the animal world only then it would gain the right to stand in line with other biological sciences that have now acquired primary importance in the knowledge of the origin and comprehension of the world.

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НЕКОТОРЫЕ СООБРАЖЕНИЯ О БИОЛОГИЧЕСКИХ ОСНОВАХ ПАЛЕОЗООЛОГИИ

И. А. Ефремов

(Резюме)

Развитие палеозоологии в ряду биологических наук потребовало углубленного понимания строения и адаптаций ископаемых организмов. Еще с прошлого века, палеобиология, методами функциональной сравнительной анатомии, анализировала приспособительные устройства вымерших животных и отсюда выводила заключения об образе жизни.

Наш век характеризуется усиленным развитием другого, противоположного направления в палеозоологии, которое окончательно определилось под названием палеоэкологии. Это направление, путем изучения осадочных горных пород, вмещающих ископаемые остатки, пытается восстановить условия жизни животных и отсюда выяснить назначение приспособительных устройств, наблюдаемых в строении вымерших организмов.

По ряду причин, определяемых условиями захоронения и фоссилизации остатков ископаемых животных, палеоэкологическое направление не может

располагать достоверными данными об образе жизни организмов. Это обстоятельство приходит в особенное противоречие с современным развитием биологии ныне живущих животных. Гигантские успехи точных наук и прежде всего физики и химии, дает в руки биологам новые методы, исследования несравнимые со всеми прежними.

В результате, палеобиологическое направление—функциональная сравнительная анатомия, физиология, биохимия животных становится важнейшим путем исследования, реальной биологической базой палеозоологии. Наоборот, палеоэкология, с ее весьма приближенными методами, оказывается мало пригодной для изучения тончайших, сложных и нередко косвенных связей адаптационных структур с условиями обитания, которые могут характеризоваться методами палеоэкологии лишь в весьма общих чертах. Палеобиологический путь исследования особенно плодотворен при двустороннем, диалектическом анализе адаптаций, примеры которого даны в статье.