AN ENIGMA FOR EVOLUTIONARY THEORY. THE ORIGIN OF BATS

IGOR POPOV

ABSTRACT. The rain forests of Southern Asia, those with the highest sparse arboreal tier, point to an environment in which the evolution of bat ancestors could have taken place. In these forests, gliding animals originated several times. The use of comparative methods have reached a dead end in the reconstruction of bat phylogenies, while biogeographic research turned out to be in this case promising. In the context of different evolutionary concepts, the "enigma" comes about with the problem of explaining the "tendencies" or "regularities" of the variations. This problem is stated clearly within the conceptual framework of directed evolution (orthogenesis).

KEY WORDS. Bats, rain forests, caves, biogeography, phylogeny, orthogenesis, Darwinism, punctualism, Lamarckism.

Small animals similar to modern insectivores or lower primates are considered as the starting point of the evolution of all mammals. The transition forms between such "non-specialized" animals and bats (Chiroptera) are not known, and it is difficult to imagine them. The suggested idea is that the bat's ancestors had underdeveloped wings. Those wings, however, since could not be used for flight, might lower the fitness of the animal carrying them. This means that to characterize the process of the origin of bats it is necessary either to explain how such unfit organisms could arise and evolve, or to substantiate the absence of the transition forms as a possibility, or to prove the adaptive value of the underdeveloped wings and other features of those hypothetical ancestors.

Numerous studies has been devoted to the evolution of bats, but their concern was mainly with the phylogenetic aspect of this problem, that is, the relations between various bat groups and their links to the closest relatives of bats—primates, insectivores and flying lemurs (Pettigrew 1986; 1999; Wible and Novacek 1988; Ammerman and Hillis 1992; Simmons 1994; Teeling et al. 2000, etc.). The evolutionary mechanisms that produced

Konrad Lorenz Institute for Evolution and Cognition Research, Austria.
IgorioshaPopov@mail.ru

the emergence of bats were passed over in silence; the answers to these questions could seem mere speculation. However, I think some indirect data could provide rather definite evidences in this respect. These data concern to the origin of other flying animals and the morphological features of some mammals, which could demonstrate the stages in the evolution of the nearest ancestors of bats.

What could be the transition forms between "normal" mammals and bats? They existed at all? What environment did they inhabit? How to explain their origin from the viewpoint of different evolutionary concepts? My study focuses on these questions; it demonstrates clearly the difficulties of evolutionary theory and could contribute to understand the motives of anti-Darwinism.

THE ORIGIN OF FLYING VERTEBRATES

The problem of the origin of any flying animal was always difficult for evolutionary theory. It was often related to creationist statements or to various heresies in evolutionary biology. "It is in vain to look for the intermediate forms, because they had never existed: the first bird hatched from a reptile's egg;" this famous statement of O. Schindewolf expresses the main idea of saltationistic concepts claiming the necessity of a radical change or the removal of Darwinism (Schindewolf 1936, p. 59). This statement can be called an exaggeration, since some intermediate forms between reptiles and birds are known. These forms are considered as "offshoots" of the main evolutionary trend of bird ancestors, and demonstrate some stages of their evolution. Anyhow, the origin of bats really looks like a sudden appearance of a new group without any intermediate forms. The most ancient extinct bat differs insignificantly from the modern ones, while it lived about sixty million years ago (Hill, Smith 1984).

Although saltationism is popular among modern evolutionists, it provokes objections in this case. Several hypotheses on the origin of flight are known, where the intermediate forms between flying and "normal" animals are considered. These hypotheses subdivide into two groups. The first one considers flight as the development of jumping upwards, the second, of jumping downward. The first group concerns first of all to birds. Some scientists believe that the closest bird ancestors could run rapidly and jump high up. In the process of evolution they acquired the capacity to jump higher and higher, acquired feathers and, finally, started to fly. It is presumed that at the early stages of this process feathers could be used as a butterfly net or as an arrangement to control the jumps (Padian 1985; Norberg 1990). This hypothesis is partly supported by the known fact that some cursorial dinosaurs, which were similar to birds in anatomy, had feathers and probably could run rapidly and jump high up (Wellnhofer 2002). The majority of modern birds are also capable of bipedal locomotion, and the indication of its cursorial ancestors could be seen in their anatomy. This hypothesis could seem convincing concerning birds, but it is not acceptable for bats. They are not only incapable to running, but can hardly move on any surface (except vampires). Their extremities and their whole structure do not indicate to their origin from cursorial animals.

According to the hypotheses of the second group, the ancestors of flying animals—birds, bats and pterosaurs—lived in the crowns of trees and were capable to parachute jumping. The wings appeared as the organs for gliding, and during the process of evolution they so improved that it was possible to use them for real flight. Some attempts to prove this hypothesis on the basis of aerodynamic calculations are known. The results of such studies are contradictory. Some specialists came to the conclusion that there is an insuperable gap between gliding and flight, because gliding means to fall downward, which cannot transform into an upward movement. However, the opposite viewpoint is also supported (see Norberg 1990). The hypothesis of the "arboreal" origin is not refuted at all, even in the case of birds, and it seems possible to develop it for bats. Maybe to analyze the modern gliding animals can clarify the mechanisms of the origin of bats.

THE GLIDING VERTEBRATES

Nocturnal cautious animals inhabiting tropical forests represent the main part of gliding vertebrates. Their existence seems exotic and rare, but they are rather numerous. Dozens of species of mammals, reptiles and amphibians demonstrate such capacity. The most numerous group among them is the mammal family of flying squirrels (Pteromyidae). It includes more then fifty species. They resemble common squirrels, but differ from them by having membranes of skin between their extremities. The flying forms are known in another family of rodents—scaly-tailed squirrels, Anomaluridae; these rodents resemble squirrels and flying squirrels. They have interesting structures—"scales" at the lower part of the tail, which enable these animals to keep themselves on strait trunks. There are flying and "normal" species among them. The flying forms are represented by two genera—scaly tailed squirrels, *Anomalurus*, and "flying mice", *Idiurus*, (they have quite normal tails). Beside flying squirrels and mice there are specific gliding forms among mammals differing greatly from "normal" ones. These animals—flying lemurs—are considered as a special order (Dermoptera). As it is takes very often, these placental species have analogies among Marsupials; three groups of possums are capable to gliding (fam. Petauridae).

On that account, gliding forms originated independently in several groups of mammals. Besides mammals, some snakes, frogs and lizards can also glide. There are some dozens of "flying" species among them—the "flying" snakes, *Chrysopelea*, the flying frogs *Rhacophorus* and flying lizards or "dragons," *Draco*.

The majority of these animals inhabit tropical forests. This fact does not seem strange, since tropical forests are especially suitable for this fauna. However, one feature of their distribution is remarkable: these animals are distributed over the world non-uniformly. Most gliding animals live in South-Eastern Asia and Northern Australia. The habitats of almost all genera of flying squirrels, flying lemurs, flying lizards, flying snakes and flying frogs overlap at the southeastern extreme of Eurasia. The rain forests of Africa are less rich in these gliding animals. Only two small groups of gliding mammals live there (scaly-tailed squirrels and flying mice). As to American rain forests, gliding animals are absent (some flying squirrels spread from Asia to Central America, but none of this animals originated in the rain forests of South America), while there are a lot of animals with tenacious tails instead.

Why does the capacity to glide appears in every possible group of animals in Asia, while it cannot appear in America? It seems that the conditions of rain forests in different continents are similar, so the animal forms inhabiting them should also be similar. Even so, significant differences exist among them. This case is cited sometimes to illustrate a "geographical style" incomprehensible in terms of adaptation. Such a "geographical style" could seem a mere chance in the evolution of vertebrates (Chaykovsky 1990). Anyhow, any "accidental" case in evolution often turns out regular, or even predetermined, if it is study profoundly.

Despite the fact that conditions in rain forests in different continents are quite similar, they are not identical. The differences in the character of arboreal tiers seem the most significant in this case (Richards 1952). Three such tiers are revealed in the tropical forests, and the difference in their density is strongly correlated with the absence or presence of gliding forms. In South America there are many trees in the highest tier, and the trees of the middle tier usually fill any gaps in it. Both tiers form a dense thick canopy (fig. 1a, Richards 1952). It is evident that the capacity to glide through a long distance cannot be realized in such conditions, in contrast to the capacity to clutch with the tail. The Asian tropical forests also have a dense canopy, but formed with the trees of the middle and lower tiers, while the highest tier is not dense (fig. 1b). Such a type of tier corresponds to the fact that the animals inhabiting the highest tier have the opportunity and the capacity to glide. In Africa the crown density is in the lowest tiers, so the distances between the highest trees is relatively big, and a considerable free space remains around the strait trunks of trees. The scale-tailed squirrels inhabit this space (fig. 1c).

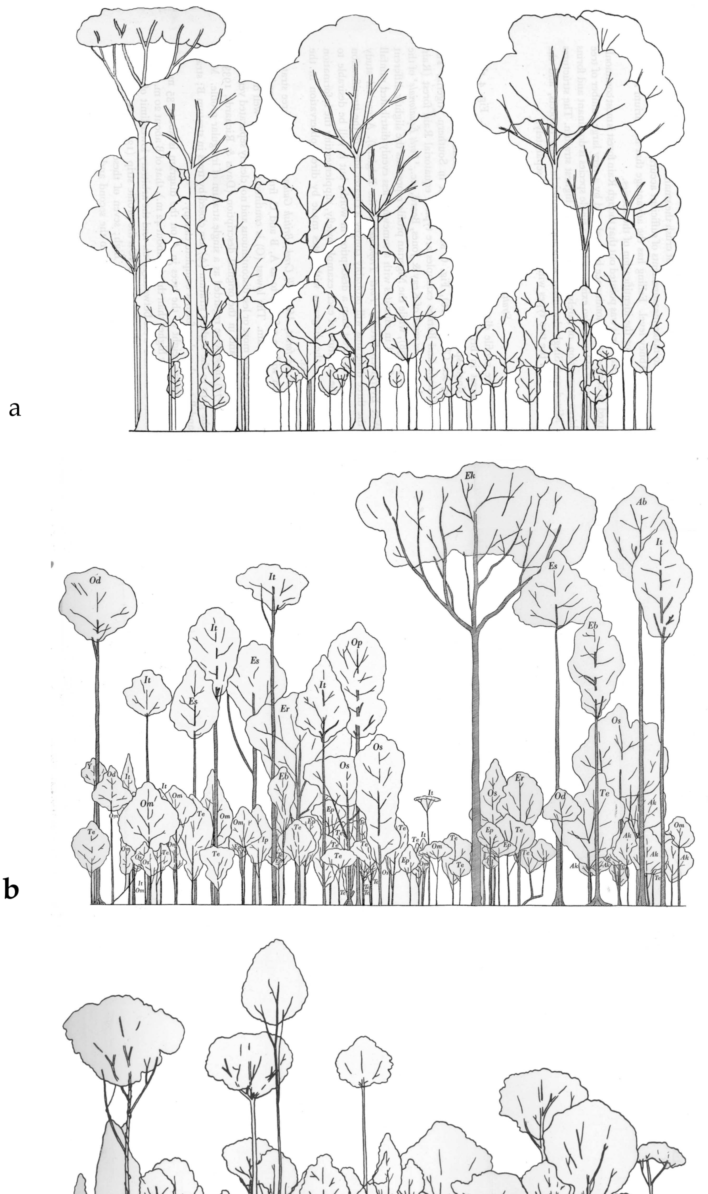

FIGURE 1.
The probable conditions of the environment in which bats could have originatedf.
Profile diagrams of primary rain forests in (a) South America, (b) Asia, Borneo, and (c) Africa (Richards, 1952).

For this reason, the analysis of the habitat of the gliding animals provides grounds for the conditions in which the capacity to fly was acquired. Those conditions are the rain forests with a sparse high arboreal tier. It seems promising to correlate these facts with the data on bats.

The order Chiroptera consists in two well-distinguishable groups: microbats (Microchiroptera) and megabats (Megachiroptera). They differ greatly from each other, and probably they had different non-flying ancestors. The megabats are close to primates, while the microbats to insectivores. Some features of the skeleton as well as the nervous and reproductive features indicate to these relationships; there are also well-notable differences. The microbats usually feed on insects and have a highly developed system of echolocation. The megabats are herbivorous, have a highly developed sight, and echolocation is uncommon; megabats present a claw at the wing, while microbats do not (Hill, Smith 1984). Some authors came to the conclusion of a diphyletic origin of Chiroptera just on the basis of morphological studies. If this scenario is right, it is necessary to find not one, but two non-flying ancestors of Chiroptera (Pettigrew, 1986) and two series of intermediate forms. Even so, at the same time, some morphological evidences—for example, the structure of the skull bones—indicate to the monophyletic origin of Chiroptera (Wible and Novacek, 1988).

Modern studies on the biochemical variation brought significant corrections in the phylogenetic studies of bats. In the context of such studies the morphological features seem to be something secondary, while data on molecular evolution are considered a description of the real phylogenetic history. The comparative studies on DNA, RNA and various proteins of Chiroptera are numerous (see Pettigrew 1999 for a review) and point rather to the monophyletic origin of bats. Anyhow, some doubts remain. The most recent studies in this field gave a more complex scenario: bats are a polyphyletic group. Still, "the problem is that *different families of microbats* are linked to the megabats in different studies." The disconcerting conclusion from these studies is that "The four or five different scenarios involving microbat polyphyly cannot *all* be right. Perhaps they are *all* wrong!" (Pettigrew 1999, p. 3).

The information on the closest relatives of bats is also contradictory. They were usually looked among primates, insectivores and flying lemurs. These animals were unified in the special super-order Archonta. Almost every possible hypothesis on the position of bats in this super-order was stated and supported by facts like this: all bats are close to insectivores (Kovtun 1987); at least some of bats are "flying primates" (Pettigrew 1986); bats do not have any special affinity to any other group (Wible and Novacek 1988). Moreover, some modern studies questioned the affinity of bats to primates and insectivorous, placing them closer to cetferungulates, a clade including Cetacea, Artiodactyla, Perissodactyla and Carnivora (Yu-Hsin Lin, Penny 2001).

In this fashion, concerning the genealogical history of bats not one common viewpoint exits, and even to choose among any version does not say anything about the nature of bat ancestors. The comparative method reaches a deadlock in this evolutionary study. This fact provides grounds for doubts concerning the effectiveness of its theoretical basis. Two approaches were used in the studies mentioned. The first one consists in revealing the similar "valuable" features among groups. For example, the special kind of connection of the retina and the brain was found only in megabats and primates. The conclusion was that these groups are closely related to each other (Pettigrew 1986). Even so, an objection was made in such cases: every morphological feature could arise as a convergence, and the data on them can hardly be used for the reconstruction of phylogenies. The second approach consists in the arrangement of groups on the basis of comparing numerous features (it is desirable that these features should be biochemical or genetic): the more similar features are present between groups, the closer they are in the phylogenetic tree. This procedure is based on the postulate of the permanency of the evolution rate of the features studied. This postulate is questionable. Moreover, as the first approach, this one does not take into account the convergences, or at least tend to hide them (see Moore and Willmer 1997 for a detailed analysis of hiding convergences in modern comparative studies).

Despite their theoretical weakness, such approaches are used because it is difficult to propose alternatives. Maybe using J. C. Willis's (1868-1958) hypothesis of "age and area" or "space and time" could be promising in this situation. His main idea is the following: the first representatives of the groups of the higher taxonomic level arise rapidly, and then they spread very slowly. In process of distribution they subdivide in several subgroups. Such spreading takes place very slowly in natural conditions, since new forms have to find some place in the territory, which is already occupied by other organisms. It follows that the groups with vast habitats are the most ancient ones; on the contrary, if the group has a restricted habitat it means that it originated relatively recently (Willis, 1922, 1940. The detailed analysis of the phylogenetic reconstruction according to Willis's hypothesis was conducted in the paper "Quintessence of evolution", Popov, Sendek 2003).

This hypothesis corresponds well to the ideas on the conditions favorable for the flight origin cited above. The distribution of one group of bats—megabats—demonstrates the same regularity as the gliding animals. Despite the absence of geographical barriers to the spread of flying animals, the megabats are absent in America, abundant in Southern Asia and Australia, and less abundant in Africa. Is this coincidence accidental?

It can be considered so at the present stage of our knowledge, but the existence of a "regularity" can be assumed. Maybe a long time ago the tier structure of the forests differed in the continents as it does now. The ancestors of megabats inhabited the same highest low-density tiers as the modern gliding animals and were also capable to glide. They originated relatively late, since they still live around the centers of origin.

The analysis of the geographic distribution of microbats does not indicate any conditions on their origin. They are widely distributed over the world. Other fact could give some information in this respect: the capacity to echolocate. All microbats have very complicated echolocation systems pointing to the long duration of its evolution. Moreover, there are some indications on the existence of the echolocation in the most ancient bats (Novacek 1985). This feature seems to be an adaptation to nocturnal life, albeit is well known that a lot of nocturnal animals do easily without it. Further, some authors claim that the adaptive significance of echolocation is dubious: the appropriate organs of the system increase the weight of the animal and restrict its size, thus why the megabats lost this system (see Speakman and Racey 1991; Rayner 1991; Teeling et al. 2000). Echolocation develops as the main system of orientation if the animal spends a lot of time in total darkness (where even the moon light is absent) and moves freely in a three-dimensional space, i.e., flies or swims. The capacity of echolocation has been noted in some other animals, but only as an additional and not highly developed type of orientation system. As a highly developed system it is found among aquatic animals (whales) and in animals living in caves—bats and some birds (Konstantinov 1980). The development of echolocation was one of the main features of the evolution of bats. This means that some early stages in the evolution of bats were related with caves. Perhaps the analysis of the cave fauna could provide some data on the origin of microbats.

Some caves are populated by strange fishes, insects and crustaceans. The cave animals manifest several specific features: reduction of sight organs, discoloration, and highly developed tactile organs. In their study sometimes they are called "anomalies" in evolutionary biology. As any anomaly they are considered either a curiosity of little value for serious research or, on the contrary, as the window to the superfine mechanisms of evolution. Darwin considered cave animals as relicts of ancient fauna, which were conserved in conditions of lower concurrence. Such hypothesis was not proved: the recent origin of a lot of populated caves was established. The results of the first studies on cave fauna were cited as a confirmation of Lamarckism. The appearance of the specific "cave features" was explained by "the exercises and non-exercises" of organs. Later, the Lamarckian explanation was gradually rejected, while the orthogenetic one prevailed. It means that the specific conditions reveal the latent possibilities of evolution, which could not be realized in "normal" conditions (see Vandel 1964; Bocking 1988). For example, the tendency to the lengthening of fins and the reduction of sight in fishes was one of such latent possibilities. This tendency led to the emergence of features that are anomalous with respect to the relatives. Perhaps the structure of bats was a result of the same anomaly, i.e., the tendency to the hypertrophy of the length of upper extremities, the formation of skin membranes and so forth.

Concerning the conditions favorable for the origin of flight, some other hypothesis can be stated: elevated oxygen levels in the mid to late Mesozoic would have facilitated aerodynamic force production and enhanced muscle power output in ancestral birds, as well as for the precursors to bats and pterosaurs (Dudley 2000); the warming caused the burst of insects, and to eat them some corporal forms may have taken place (Seamons 2005). Maybe these factors contributed to the origin of bats. Still, they are not sufficient, because they do not explain the geographic patterns of distribution among flying animals.

In this way the environment favorable for the origin of bats can be characterized. Most likely, it was the tropical rain forest with a specific tier structure and, probably, caves. However, to describe the process of their origin it is necessary to characterize the intermediate forms. To imagine a bat with underdeveloped wings, i.e., the extremities with underdeveloped skin membranes, seem not to be viable. Even so, modern animals demonstrate all possible stages in the development of membranes between legs and fingers. A lot of mammals have skin membranes between fingers; usually related to the aquatic mode of life, but not necessarily. Some aquatic mammals do not have them (otter-shrews, fam. Potamogalidae), and some non-aquatic mammals do (siamang, *Symphalagus syndactylus*, fam. Hylobatidae). The monkey lemurs (genus *Propithecus*) have an underdeveloped skin membrane between the legs; it is not quite clear how these lemurs use it. Maybe, it is used as something like a brake parachute when lemurs jump from tree crowns. The following stages of the development of the skin membranes could be seen among various species of flying squirrels, scale-tailed squirrels and flying possums. Some of them have the membranes only between the legs, some between the legs and tail, even between the legs, tail and neck together. The flying lemurs demonstrate the highest possible development of such membranes. Their skin membranes embraces all possible prominent parts of the body, i.e., legs, fingers, tail, and neck. To "transform" into Chiroptera only one feature fails: the disproportion of the extremities so that the upper ones would be bigger than the lower. This feature could be seen in other mammals, for example, apes or aquatic mammals.

All the possible features of the bat ancestors, taken separately, can be seen among modern mammals. It means that they could have appear in the ancient ones, and it is possible to assume that intermediate forms between bats and "normal" mammals existed. In the whole of arboreal mammals every possible stage of the development of membranes of skins could be seen among viable organisms. Usually these membranes find a use for jumps or gliding. Concerning other possible functions of membranes in ancient mammals some ideas were expressed—nets to catch insects, flippers, heat exchangers (Crompton 1968; Paniutin 1980; Kovtun 1990). Small mammal, with sun batteries in their hands, or a mammal with nets instead of hands, or the small insectivore mammal similar to gobies seems absurd. Even so, it is difficult to formulate a conclusive scientific disproof of these hypothesis. It is possible just to state that a gliding animal seems to be more "natural" because it reminds modern animals.

It is possible to precise these speculations on the transition forms if we pay attention to some phenomena described in palaeontology. The transition forms always provoke problems even within the groups that are well known in the palaeontological sense. In every possible genealogical tree the transition forms are situated somewhere beside the main stem. It is difficult to find such a transition form that can be put just at the point of divergence in phylogenetic branches. It would be more correct to draw the phylogenetic schemes not in the form of a tree, but in the form of separate strokes. All known transition forms are "lateral branches" with the features of specialization, which demonstrate that the stages in the evolutionary process are not the direct ancestors of the following taxon.

For example, the group of fishes Sarcopterygii existed a little before the emergence of quadrupeds. These fishes had a lot of features common with the most ancient amphibians. It is possible to establish among them subgroups that are especially close to amphibians (Crossopterigii among Sarcopterigii, Rhipidistia among Crossopterigii, Osteolepiformes among Rhipidistians), but it is impossible to find a group that is a direct ancestor of quadrupeds; neither the most ancient amphibians—ichtiostegs—are considered as the ancestors of all quadrupeds. They are transition forms between fishes and amphibians that are not the direct ancestors of the following group. It is the same in all other groups, up to man, situated in the palaeontological record (Carroll, 1988).

Accordingly, the transition forms between the groups at a high taxonomic level exist, but the gaps in the fossil record and the rapid evolutionary changes also exist. It is difficult to overcome this contradiction and that is why the discussions on saltationism continue to this day. For example, E. Mayr writes about the ancestors of man the following: "*Australopithecus* is a disharmonious type having primitive and progressive features, it could not be the direct ancestor of man, but it demonstrates the stage which was passed by the ancestors of man, but this ancestors are not yet found" (Mayr 1971). His opponents claimed that such ancestors would never be found, because the new species arise in discrete steps. The problem of the origin of bats falls into the same situation, even more clearly. In this case some transitive "lateral branches" could not hide the gap, which is always revealed in the fossil record in the process of detailed research. If such forms were to be found, they will remind either flying lemurs, or primates, or other specialized group.

With all this going on, the transition forms not always demonstrate adaptive features. There are some organs of plants and animals which make sense only after being developed to their maximum possible stage, since the first stages of their development hold no adaptive value. Such organs are called "aristogenes" (Osborn, 1934) or "morphological mysteries" (Willis, 1940). H. Osborn analyzed this phenomenon in detail for the first time using the examples from the evolution of several groups of mammals; for instance, the evolution of the group of horned mammals Titanotheria was described. It is accepted that the highly developed horns provide a great benefit for the animal. However, the ancestors of horned Titanotherians, which lived for a long time, had only small primordial tubercles instead of horns. The existence of these tubercles in the first stage of their evolution seems senseless for the early Titanotherians, while favorable for the latest.

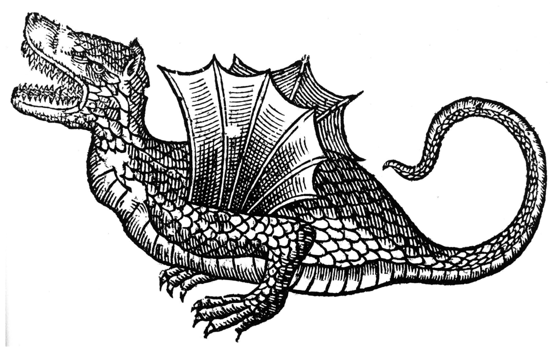

FIGURE 2.
Dragon. Konrad Gesner. *Historia Animalum*. Book I-IV. 1551-1563. (From Gesner K., *Curious Woodcuts of Fanciful and Real Beasts*. A selection of 190 sixteenth-century woodcuts from Gesner's and Topsell's natural histories. New York, Dover Publications, 1971, p. 84.)

Maybe the skin membranes, which could not be used to fly, were also "aristogenes", that is, organs without adaptive value. If this is the case, the existence of animals manifesting every possible stage in the development of wings is possible, even if they have the wings reminding those of a dragon from K. Gesner's book (figure 2). What caused the appearance of the aristogenes? The author of the aristogenesis theory, H. Osborn, thought it is as mystery, such as the appearance of the horn rudiments on the skull of Titanotherians.

How do the adherents of different evolutionary concept explain all these facts? Modern punctualists or saltationists would propose the simplest explanation: a "normal" animal gave birth by accident to a "monster", which turned out to be in evolutionary perspective fit and so established a new group of organisms. The Lamarckians also would not find difficulties in explaining the origin of bats. Jean-Baptist Lamarck himself analyzed this case without considering it enigmatic. On the contrary, he cited it as "the very convincing evidence" of the action of exercises to shape animal's forms. According to him, the squirrels acquired the habit to stretch their legs during a jump; because of frequent exercises the skin stretched and formed the membrane. The flying lemurs acquired this habit earlier, that is why they have a more developed membrane. Such habit within bat ancestors was much more ancient, and they brought it to perfection (Lamarck, 1873). The modern Lamarckians could precise the description of the environment, which caused the appearance of such peculiar habits; it was the tropical rain forest with sparse high arboreal tiers. Moreover, it would be necessary to stress the duration of this process. Lamarck was not so naive as very often considered: if the animal trains the fingers, it does not mean that he would give birth to a flying offspring at once. This process took place very slowly through very fine steps.

According to Darwinism the selection of small deviations in several features explain the evolution of bats. At first, for example, small skin webs appeared, then fingers became elongated a little, or in the reverse order. The combination of features necessary to fly appeared in such a winding way: one feature varied in one direction, then other feature in another, and so forth. Every step had some adaptive value, and this fact can be confirmed by the examples from modern fauna. Some Darwinists may add that the bat ancestors had a "tendency" to vary in some direction or discuss "functional objectives" imposed by the environment: the arboreal mode of life demanded the elongation of fingers, the jumps demanded the development of skin membranes, and the like.

According to the concept of directed evolution, orthogenesis, this case could be considered as follows. It is possible to imagine several trends in the evolution of mammal extremities: elongation of upper extremities, elongation of lower extremities, elongation of both extremities, elongation of fingers. Every trend is realized in the evolution of mammals and in every case the appearance of skin membranes is possible. In such a way a "definite direction", i.e., the combination of various trends could arise: the elongation of fingers, the elongation of upper extremities, and the development of skin membranes. According to the law of inertia, if the evolutionary trend has formed, it develops up to the maximum, like the growth of crystals, even if it leads to a non-adaptive direction. Almost everywhere this direction was doomed to extinction, but in some specific conditions (the rain forests with a specific tier structure or caves) it kept safe. The developing features could be non-adaptive in some stages, but at least not too harmful.

Which explanation is the best one? Saltationism-punctualism seems to reject any. The appearance of a "monster" is considered a fortuitous event. To confirm such a possibility, the emergence of viable forms having hereditary abnormal features is often cited. For example, cats without tails, sheep with short legs, mammals without hair, etc. However, such anomalies do not demonstrate the occurrence of new families and classes of animals, and they have nothing in common with the "hopeful monsters" postulated by R. Goldschmidt. Such abnormalities account only for separate features, and to consider them as an explanation by analogy to the bat's origin, they prove that animals either with skin membrane, or elongated fingers or abnormal lower extremities, or whatever, could appear, but not with all these features simultaneously. It is interesting that the history of saltationism (at least the recent one) is not related to the studies of anomalies, while all researchers of this phenomena, beginning from E. Geoffroy Saint-Hilaire or even Aristotle, stressed the regularities in the appearance of monsters and claimed that anomalies could not be a matter of semblances (see Popov 2000, for the review). In this way the saltationistic model should be supported with the analysis of the regularities of variation or with some orientation within evolution. Such an analysis is more characteristic in other evolutionary models.

Lamarckism seems extremely archaic in this case. Lamarckian speculations appear sometimes in modern biology, but they take place mainly in the context of microbiology, immunology, and virology (see Golubovsky 2000, for the review). "Adaptive mutations" and some other atypical kinds of hereditary variation could hardly be applied to the processes discussed above. Moreover, the high rate of the bat's evolution does not correspond to Lamarckism (as well as to classical Darwinism); they appeared instantly in the scale of the fossil record.

Darwinism and orthogenesis provide some general explanation; still some aspects remains unclear, namely the "tendencies" or "definite directions." The problem with the investigation of this phenomenon is put more clearly with the concept of directed evolution, orthogenesis. The facts count in favor of this concept. The formation of promising research programs was often considered as the main achievement of this evolutionary concept; Darwinism in its time was often supported for this very reason. Guided by orthogenesis, evolutionary studies would focus on the regularities of variation, evolutionary constraints, the problem of norm-anomaly, morphogenetic correlations, etc., that is, the very problems which seem rather unsolved in terms of modern Darwinism. It turned out that in this case some traditional research programs reached a deadlock, meaning they do not correspond to the objectives of the evolutionary studies. Despite the numerous, thorough and detailed comparative phylogenetic studies, they do not provide any information neither on the genealogical history nor on the ancestors of bats. It is appropriate to mention here that during the development of evolutionary morphology at the end of nineteenth century, a lot of biologists came rapidly to the conclusion on the faultiness concerning the inclination "to build hastily the countless genealogical trees, rotten trunks which fall to the ground, covering the soil of forest and preventing the young growths" (L. Rutimeyer, from Deperet 1921, p. 91). Such a critical evaluation has a certain attitude toward modern cladistic studies.

CONCLUSION

It is possible to definitely characterize the environment in which the evolution of bats could have taken place. The extant rain forests of Southern Asia, that is, forests with a sparse high arboreal tier, point to such an environment. Various "flying" or gliding animals originated there, and it seems possible that real flight appeared in such conditions. The evolution of microbats (one of the two bat groups, which probably had different non-flying ancestors) was closely related with caves. The highly developed system of echolocation indicates to this fact.

All the features of the possible intermediate forms between "normal" mammals and bats could be seen separately among modern species in various groups. The skin membranes, elongated fingers, hypertrophy of the upper extremities, occur in modern mammals. This fact could be considered indirect evidence of the vital capacity of the transition forms between "non-specialized" mammals and bats.

The details of the evolutionary development of the whole complex of the bat features remain unclear. In the context of various evolutionary concepts the "enigma" come about from the characteristics of the tendencies or regularities of the variations. The problem with this investigation is to precise the orthogenesis concepts more clearly. Moreover, the analysis of the regularities of variation using J. Willis's hypothesis of "age and area" and biogeographic analysis seems to be promising in this case. It turned out, at least, that this approach can eliminate some unclearness regarding the emergence of gliding animals. At the same time, the comparative studies on the evolution of bats have reached a deadlock.

BIBLIOGRAPHY

Ammerman L. K.; Hillis D. M. (1992), "A molecular test of bat relationships: monophyly or diphyly?" *Systematic Biology* 41: 222-232.

Bocking S. (1988), "Alpheus Spring Packard and cave fauna in the evolution debate," *Journal of the History of Biology* 21 (3): 425-456.

Carroll R. L. (1988), *Vertebrate Paleontology and Evolution*. New York: Freeman and Company.

Chaykovsky Yu. V. (1990), *Elementy evolutsionnoy diatropiki*. Moscow: Nauka. (In Russian, *The elements of evolutionary diatropics*).

Crompton A.W. (1968), "The enigma of the evolution of mammals," *Optima* 18 (2): 137-151.

Deperet Ch. (1921), *Le transformation du monde vivant*. (Russian edition, Petrograd: Sabashnikov).

Dudley R. (2000), "The evolutionary physiology of animal flight: paleobiological and present perspectives," *Annual Review of Physiology* 62: 135-155.

Golubovsky M. D. (2000), *Vek genetiki: evolutsia idey i poniaty*. Saint-Petersburg: Borey art (*The century of genetics: evolution of ideas and concepts*).

Hill J. E.; Smith J. D. (1984), *Bats. A Natural History*. Austin: Univ. of Texas Press.

Konstantinov A. I. (1980), "Prichiny vozniknoveniya ekholokatsii u rukokrylykh", in *Voprosy teriologii. Rukokrylye (Chiroptera)*. Moscow: Nauka, pp. 271-276. (In Russian, "The causes of the appearance of echolocation").

Kovtun M. F. (1988) "Morphologicheskiy aspect evolutsii organov locomotsii rukikrylikh (Chiroptera)", in *Sovremennyye problemy evolutsionnoy morphologii*. Moscow: Nauka, pp. 104-117. (In Russian, "Morphological aspect of the evolution of the locomotion organs of bats").

Kovtun M. F. (1989), "On the origin and evolution of bats," in Hanák V., Horácek I. and Gaisler J. (eds), *European Bat Research*. Praha: Charles Univ. Press, pp. 5-13.

Kovtun M. F. (1990), "Problemy evolutsii rukokrylykh", *Vestnik zoologii* 3: 3-13. (In Russian, "The problems of the evolution of Chiropterans").

Lamarck, J.-B. (1873), *Philosophie zoologique ou exposition des considerations relatives a l'histoire naturelle des animaux*. Paris: Libraire C. F. Savy.

Mayr E. (1971), *Populations, Species, and Evolution*. Cambridge (Mass.): Harvard University.

Moore J. and Willmer P. (1997), "Convergent evolution in invertebrates," *Biological Reviews of the Cambridge Philosophical Society* 72 (1): 1-61.

Norberg U. M. (1990), *Vertebrate Flight*. Berlin: Springer Verlag.

Novacek M. J. (1985) "Evidence for echolocation in the oldest known bats," *Nature* 315: 140-141.

Osborn H. F. (1934), "Aristogenesis, the creative principle in the origin of species," *American Naturalist* 68: 193-235.

Padian K. (1984), "The origins and aerodynamics of flight in extinct vertebrates," *Palaeontology* 28 (3): 413-433.

Paniutin K. K. (1980), "Proiskhozhdeniye poliota rukokrulukh," in *Voprosy teriologii. Rukokrylye (Chiroptera)*. Moscow: Nauka, pp. 276-286. (in Russian, "The origin of the Chiropteran flight").

Pettigrew J. D. (1986), "Flying primates? Megabats have the advanced pathway from eye to midbrain," *Science* 231: 1304-1306.

Pettigrew J. (1999), "Summary of studies on primate phylogeny and 'flying primate' hypothesis," in P.A. Racey and S.M. Swift. (eds.), *Symposium of Zoological Society of London* 67: 3-26.
Popov I. Yu. (2000), "El problema de los monstruos en la evolución", *Ludus Vitalis* VII (13): 35-50.
Popov I. Yu. Sendek D. S. (2003), "Quintessentsia evolutsii", in *Evolutsionnaya biologia: istoria y teoria*. Saint-Petersburg: RAN (In Russian with English abstract, "Quintessence of evolution").
Rayner J. M. V. (1991), "The cost of being a bat," *Nature* 350: 383-384.
Richards P. W. (1952), *The Tropical Rainforest. An Ecological Study*. Cambridge: Cambridge University.
Schindewolf O. H. (1936), *Paläontologie, Entwicklungslehre und Genetik. Kritik und Synthese*. Berlin: Bornträger.
Simmons N. B. (1994), "The case for chiropteran monophyly," *American Museum Novitates* 3103: 1-54.
Simmons N. B. (2005), "An Eocene big bang for bats," *Science* 307: 527-528.
Speakman J. R. and Racey P. A. (1991), "No cost of echolocation for bats in flight," *Nature* 350: 421-423.
Teeling E. C.; Scally M.; Kao D. J.; Romagnoli M. L.; Springer M. S.; Stanhope M. J. (2000), "Molecular evidence regarding the origin of echolocation and flight in bats," *Nature* 403, 6766: 188-92.
Vandel A. (1964), *Biospéléologie. La biologie des animaux cavernicoles*. Paris: Goutier-Villars.
Wellnhofer P. (2002), "Die befiederten Dinosaurier Chinas", *Naturwissenschaftliche Rundschau* 651: 465-477.
Wible J. R. and Novacek M. J. (1988), "Cranial evidence for the monophyletic origin of bats," *American Museum Novitates* 2911: 1-19.
Willis J.C. (1922), *Age and Area*. Cambridge: Cambridge Univ. Press
Willis J. C. (1940), *The Course of Evolution by Differentiation or Divergent Mutation Rather than by Selection*. Cambridge: Cambridge Univ. Press.
Yu-Hsin Lin, Penny D. (2001), "Implications for bat evolution from two new complete mitochondrial genomes," *Molecular Biology and Evolution* 18: 684-688.