

The Unique Morphofunctional Structure of the Reptilian Heart

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Abstract—The paper analyzes the evolution of the thermoenergetic statuses of vertebrates and the associated evolutionary development of their heart. The analysis shows that, in most modern lepidosaurs and turtles, the heart is not completely, conditionally five-chambered: it has two atria and one ventricle, in which two incomplete septa divide it into three functional chambers. In some of them, these two septa were modified in evolution so that they turned into one with vertical and horizontal elements, as a result of which the heart became functionally four-chambered, with improved separation of arterial and venous blood flows. Crocodiles have a fully morphologically four-chambered heart. But the hearts of all reptiles, both recent and extinct, perform two opposite functions in parallel—the separation of arterial and venous blood flows and at the same time their regulated mixing. To do this, there are special morphological and physiological mechanisms in their hearts. Such a strange functional duality in the work of the reptilian heart aims to regulate the metabolism level by controlling the amount of carbon dioxide entering the blood flow: increasing the amount of CO₂ in the blood flow reduces the metabolic rate; reducing its amount increases the metabolism. Mixed blood in the blood flow of reptiles is not an immature, primitive state, but a physiological necessity. Moreover, this method of regulating the metabolic rate is most adequate to the initial, ancestral thermoenergetic state in reptiles, because basal terrestrial tetrapods and most ancient reptiles were meso- and even tachymetabolic, i.e., almost or completely warm-blooded, endothermic animals. It was just these endothermic animals that needed such type of metabolism regulation. As a result, all recent reptiles have a complex morphophysiological organization of the heart, which was functionally more suitable for their almost warm-blooded ancestors. Recent reptiles use part of their ancestral properties as an adaptation to new environmental conditions, new environmental requirements, and their new morphophysiological state. This unique organization of the heart is characteristic of all modern and extinct reptiles, and, importantly, it is characteristic exclusively of reptiles owing to their original endothermic state.

Keywords: vertebrates, anatomy and functions of the heart, evolution of thermoenergetic statuses, connection between the morphology and functions of the reptile heart

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INTRODUCTION

What are reptiles? First of all, when talking about reptiles, we need to decide what kind of animals we mean. The scope of the class of reptiles, which is more or less clearly defined in many scientific books and in most teaching aids, actually raises many questions. Many scientists quite reasonably express the opinion that the class of reptiles as a systematic category does not exist at all, since the class of reptiles (now living), according to modern ideas, includes groups of vertebrate animals that are too distantly phylogenetically related. Thus, modern squamates (beakheads, lizards, and snakes) and crocodiles are different branches of the development of diapsids (Diaspora): squamates are lepidosaurs (Lepidosauria), and crocodiles are archosaurs (Archosauria). The understanding of the origin of turtles is still far from clear, but it is already

obvious that turtles are also diapsids (Schoch and Sues, 2015), although not so long ago they were considered anapsids.

On the basis of the problems we solve, L.P. Tatarinov's position is the closest and most suitable to us, who, accepting the principle of horizontal classification for vertebrates (Tatarinov, 2009), considered reptiles not only the reptiles themselves, but also parareptiles, theromorphs and, with some doubt, seimuriomorphs. "Archosaurs and theromorphs are the most important subclasses of reptiles in phylogenetic terms," he wrote (Tatarinov, 2009, p. 324).

It is traditionally believed that reptiles are cold-blooded (poikilothermic, ectothermic, bradymetabolic) vertebrates. Most of them have a three-chambered heart: it has two atria and one ventricle, partially divided into two parts by an incomplete vertical or

horizontal septum. In addition, it is believed that warm-bloodedness is a higher, more developed, more evolutionarily advanced thermoenergetic¹ state, in comparison with cold-bloodedness, and also that one of the main directions of the evolution of vertebrate animals is expressed in the development from cold-bloodedness to warm-bloodedness.

However, research over the past 10–15 years using new technical means and techniques has introduced many new and unexpected things into our understanding of the biology of this group of vertebrates.

THERMOENERGETIC EVOLUTION OF VERTEBRATES

Traditionally, we divide vertebrates according to their thermobiological characteristics into two groups—cold- and warm-blooded, which are sometimes, in accordance with semantic nuances, called poikilothermic and homeothermic, ectothermic and endothermic, and bradymetabolic and tachymetabolic. Although, in essence, we mean division into the same groups.

Our research and analysis of published materials have shown that the evolutionary process in vertebrates is largely actuated, proceeds, and is directed as a result of the manifestation of a complex of key biochemical and physiological aromorphoses (Cherlin, 1988, 2017, 2021a, 2021b) associated with the development of their relationship to the factor of temperature (Cherlin, 2014, 2021a–2021d, 2022a, 2022b, 2023, 2024a). These aromorphoses are expressed in the fact that, during the evolution of initially bradymetabolic, ectothermic fish, in the first amphibian-like tetrapods formed on their basis—primary ectotherms (Cherlin, 2024a)—at a certain stage of their development approximately 350–330 million years ago, the intensity of oxidation in mitochondria sharply increased, basal metabolism increased, and then thermometabolism increased, and body temperature increased. Apparently, it was precisely thanks to these new qualities that, in these animals, the energy supply for activity increased significantly; they were able to go out onto land and begin to explore it. In other words, in the very first basal terrestrial tetrapods from their very evolutionary appearance, starting at least with stegocephalians with age of 331–326 Ma (Whitney et al., 2022) and seymuriomorphs with age of 290–270 Ma (Estefa et al., 2020), there were increased levels of basal metabolism; that is, the bradymetabolic ecto-

thermy of their ancestors was replaced by mesometabolic endothermy. Thus, primary ectotherms turned into primary endotherms, one of the important characteristics of which was, among other things, the still insufficient development of systems for operational neurohumoral regulation of metabolic levels and thermometabolism (Cherlin, 2024a). And soon they experienced an increase in body temperature, and mesothermia and even a certain degree of warm-bloodedness appeared (Harrell et al., 2016; Legendre et al., 2016; Benton, 2020; Gregg et al., 2022). And these basal terrestrial tetrapods gradually evolved into the first amniotes, the reptiles (Cherlin, 2021a–2021d, 2022a, 2022b).

Subsequently, some of the sauropsids and synapsids independently gave rise to clades of meso- and tachymetabolic, endothermic, and almost or completely warm-blooded animals. This independent emergence of warm-bloodedness in two separate clades of vertebrates was possible because they all had common biochemical and physiological preadaptations to the manifestation of endogenous thermogenesis (Cherlin, 2023, 2024a). In addition, they had general patterns of evolutionary development that dictated the need to increase and stabilize high body temperature (Ryumin, 1940; Cherlin, 1990). At a certain stage of evolutionary development, most diapsids (most of the archosauromorphs and archosaurs), dinosaurs, and crocodylomorphs seemed to have become such meso- and tachymetabolic, that is, almost warm-blooded, animals (Cherlin, 2021a, 2021b).

But some of the diapsids evolved into tachymetabolic, completely warm-blooded animals—archosauromorphs and archosaurs—some dinosaurs and crocodylomorphs (Cherlin, 2021a, 2021b), sauropterygians (plesiosaurs), and ichthyopterygians (ichthyosaurs), as well as some lepidosaurs, for example, mosasaurs (Bernard et al., 2010; Harrell et al., 2016), became tachymetabolic, fully warm-blooded “secondary endothermic” animals.

Modern birds and mammals have become the same, only, apparently, even more advanced tachymetabolic, completely warm-blooded “secondary endothermic” animals, one of the important characteristics of which is the development of systems for operational neurohumoral regulation of metabolic and thermometabolism levels (Cherlin, 2024a).

But some of the sauropsids from different evolutionary branches, for various reasons, again switched to bradymetabolic ectothermy—crocodiles, lepidosaurs (beak-heads, lizards, and snakes), turtles (Cherlin, 2024a). All of these are secondary ectotherms (Cherlin, 2024a). But this secondary ectothermy differed significantly from the primary ectothermy of fish and basal amphibian-like tetrapods. The main differences are due to the fact that primary ectotherms, during their transformation into secondary ecto-

¹ Thermoenergetics is a term we introduced that characterizes a single functional and morphophysiological complex “temperature–metabolism.” The intensity of metabolism is inextricably linked with the animal’s body temperature, and, therefore, it is incorrect and simply impossible to study metabolic levels in isolation from temperature. The more logical term “thermometabolism” is already preoccupied and means that part of metabolism that is aimed at thermogenesis, and therefore, for our case, unfortunately, this term cannot be applied.

therms, went through the stage of mesometabolic primary endothermy (Cherlin, 2024a). Owing to this, the main differences between secondary and primary ectothermy should be noted: (1) the appearance of psilothermy in secondary ectotherms;² (2) secondary ectotherms, in contrast to primary, chamilotherms,³ were able to increase and withstand high body temperature and metabolism in order to use them to improve the most important evolutionarily significant characteristic—the quality of their activity⁴ (Cherlin, 2024a, 2024b).

WHY IS THE HEART OF REPTILES OF PARTICULAR INTEREST?

To describe the features of the thermoenergetic state of reptiles, we should again recall the scope of a nonsystematic group of animals in the strict sense of the word, which we denote by the term reptiles (Fig. 1; marked in the diagram with the letter “R”).

It is traditionally believed that, in the evolution of vertebrates, there was a gradual complication of the morphophysiological organization of the body, as a result of which reptiles, as an intermediate stage of this process, should have some transitional set of characteristics between the relatively simply organized cold-blooded, ectothermic amphibians and the much more complexly organized warm-blooded, endothermic birds and mammals. And it seemed that the data obtained earlier in the 19th and 20th centuries mainly in the study of the morphology and physiology of modern vertebrates and partly in the study of the anatomy of the bone fossils of their extinct ancestors confirm this point of view.

But research at the beginning of the 21st century using new methodological techniques and technical means produced many unexpected results that make us look at this process a little differently.

It turned out that, in fact, reptiles appeared on Earth and formed all their most important complexes of morphophysiological characteristics as mesometabolic, mesothermic, and psilothermic endotherms a little later than 300 million years ago. Moreover, according to modern data, the overwhelming majority

² Psilothermy is a thermoregulatory reaction aimed at periodically or constantly increasing body temperature (Cherlin, 2021e).

³ Chamilothermia is a thermoenergetic state, the status of animals characterized by the absence of a psilothermic reaction; that is, these animals do not have a focus on an obligatory increase in body temperature (Cherlin, 2021e).

⁴ The quality of activity is a term we introduced that denotes a complex of characteristics manifested in an increase in speed, coordination, and accuracy of movements, the intensity of internal processes, optimization of life activity owing to the development of the nervous system, increased energy supply of activity and life activity, increased endurance, adaptability, etc., which give animals selective advantages in competition with other groups of animals and create the preconditions for their evolutionary success.

of reptiles that have ever lived on Earth were meso- or tachymetabolic, primarily endothermic, that is, warm-blooded animals to varying degrees, and not at all cold-blooded, bradymetabolic ectotherms, as is written in all our textbooks! Only a few of the most ancient reptiles (primary ectotherms) were such, that is, bradymetabolic ectotherms, and now all modern reptiles (secondary ectotherms) are. It was the cold-blooded state of modern reptiles that misled researchers of the 19th and 20th centuries about the thermoenergetic status of this group of animals.

Various variants of endothermic and ectothermic reptiles and the paths of their evolution are illustrated in Fig. 1. It shows that all modern, bradymetabolic, psilothermic, secondary ectothermic reptiles are descendants of meso- or even tachymetabolic, warm-blooded ancestors to varying degrees (Cherlin, 2021a–2021d). It is also quite obvious that the key link, the original core of the evolution of vertebrates, is the group of basal terrestrial tetrapods. Now there is already quite definite information that, from the very beginning of their appearance and development, they were mesometabolic endotherms (Estefa et al., 2020; Whitney et al., 2022).

If we simplify and slightly modify the diagram shown in Fig. 1 (Fig. 2), then we can see another important pattern, which is also not reflected in our textbooks: the evolution of vertebrates is not at all clearly aimed at developing from ectothermy to endothermy. The functional focus on the development of endothermy appears in parallel in the clades of synapsids (mammals) and sauropsids (birds). But at the same time, the evolutionary development of ectothermy (secondary) is observed among sauropsids. It is very important to understand that ectothermy is not a more evolutionarily primitive state preceding endothermy, but an independent evolutionary direction from primary to secondary ectothermy, parallel to the development of endothermy.

Thus, in the evolution of vertebrates, reptiles are the first, later very developed and evolutionarily promising group of endothermic, meso- or even tachymetabolic psilothermic animals. As we have already said, bradymetabolic ectotherms were among the groups of primary ectotherms, and they were mainly the most recent, modern secondary ectotherms. Consequently, the evolutionary development of reptiles occurred for the most part in the environment of meso- and tachymetabolic psilothermic endotherms, that is, warm-blooded animals to varying degrees.

In accordance with this circumstance, in the evolution of vertebrates, the development of the morphophysiological organization of their heart occurred, which is most directly related to changes in the thermoenergetic status of animals. It is important to note here that, since the earliest, basal terrestrial tetrapods, transformed into reptiles, turned out to be mesometabolic,

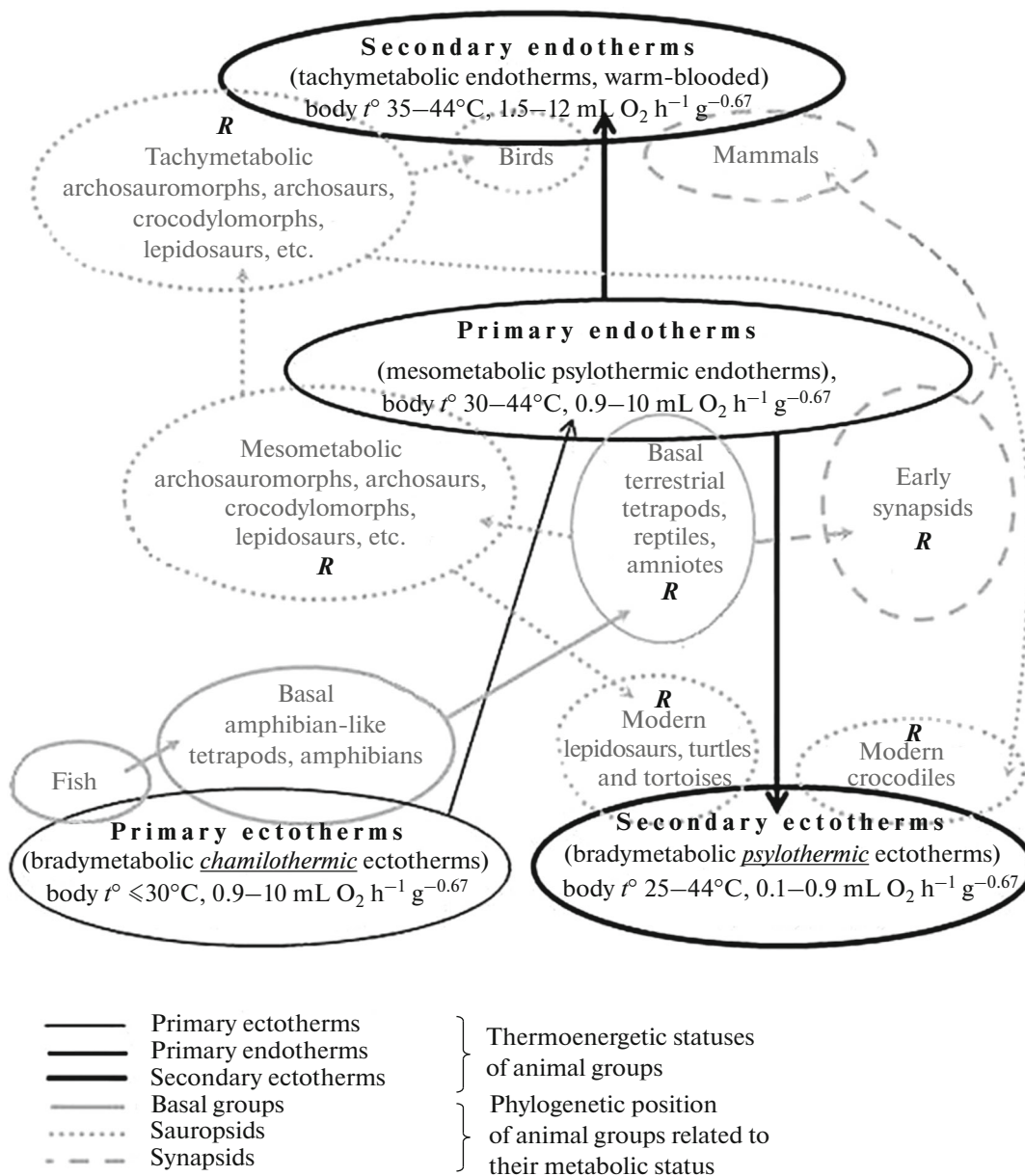


Fig. 1. Simplified diagram of the evolution of thermoenergetic statuses in vertebrates, their main indicators, and specific groups of animals that followed different paths of this evolutionary development. Letters “R” on the diagram show groups of vertebrate animals which, in accordance with the position of L.P. Tatarinov assuming a horizontal type of taxonomy of vertebrates (Tatarinov, 2009), can be considered reptiles. The partial overlap of gray ellipses denoting phylogenetic groups of vertebrates with black ellipses denoting a thermoenergetic state indicates that these phylogenetic groups have a given thermoenergetic status.

bolic primary endotherms, this circumstance confronted them all with the most important common problem—the need to regulate their initially elevated metabolic level. Without this regulation, an uncontrolled increase in metabolism and therefore thermometabolism and body temperature would lead to fatal consequences. And these primarily endothermic animals clearly had not yet developed operational neurohumoral regulation of metabolism, which could not have appeared in them simultaneously with an

abrupt, anormorphic increase in the levels of mitochondrial and general metabolism. For this, it was necessary to use some other regulatory mechanism, which was already present in these animals, but was used for other purposes.

The following physiological pattern is present in the body of vertebrates: an increase in the amount of carbon dioxide in the bloodstream reduces the metabolic rate, and a decrease in its amount in the blood increases metabolism. It is this already existing pattern

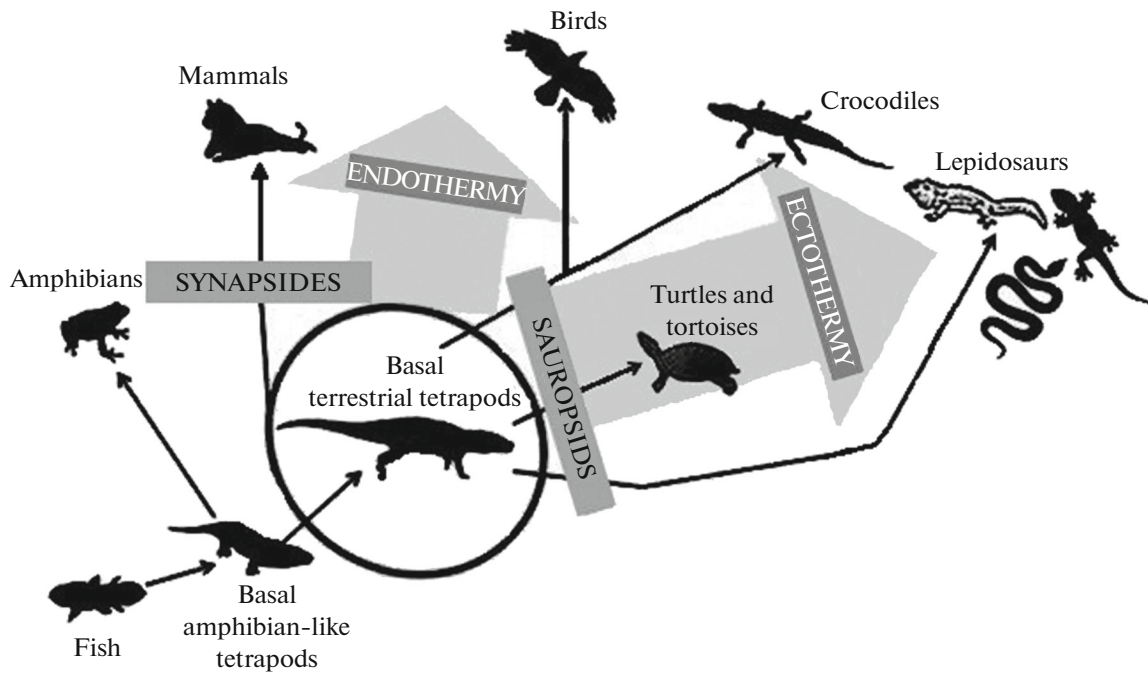


Fig. 2. Modern ideas about the evolution of vertebrates and their thermoenergetic statuses.

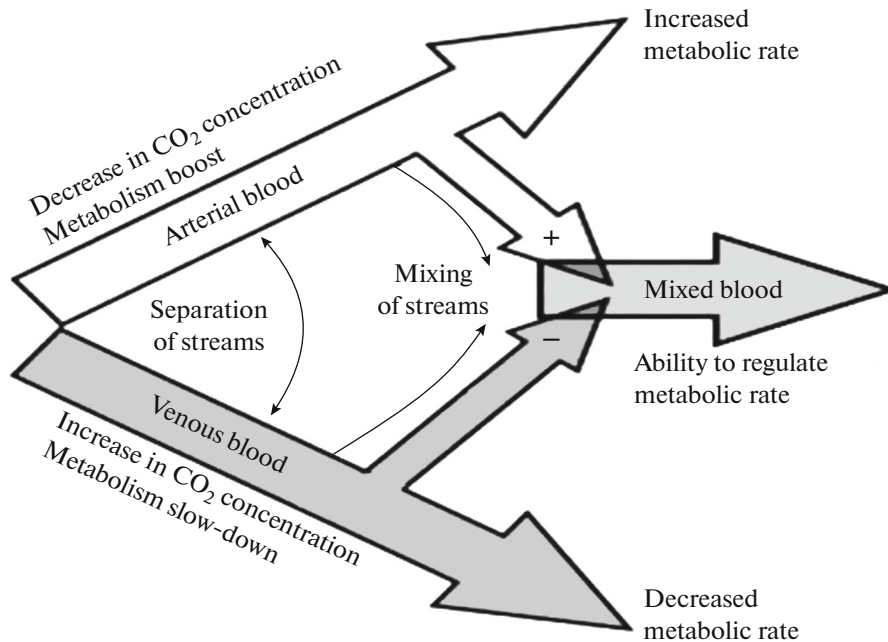


Fig. 3. Two directions of manifestation of cardiac functions in reptiles in relation to arterial and venous blood flows: a decrease in CO_2 concentration in the blood increases the level of metabolism; increasing the level of CO_2 reduces metabolism.

that reptiles use to regulate metabolism. This requires mechanisms to control the amount of CO_2 in the blood or, in other words, control over the proportion of venous blood entering the bloodstream.

Thus, it is in reptiles that there are two parallel, simultaneously acting and at the same time functionally oppositely directed mechanisms in the cardiovas-

cular system: (1) separation of arterial and venous blood flows and (2) controlled mixing of these flows. The meaning of this mechanism is the regulation of metabolic levels (Fig. 3).

It should be noted that, for fish and amphibians with their low metabolic rates and the unambiguous, complete or almost complete mixing of oxygenated

and deoxygenated blood flows in the undivided ventricle of a two- and three-chambered heart, control over the degree of this mixing is simply irrelevant. In warm-blooded, tachymetabolic birds and mammals, with their four-chambered heart and, therefore, complete separation of these two flows, it is simply pointless to control mixing, since this mixing does not exist at all.

Thus, it is for reptiles that the problem of mixing arterial and venous blood and control over the degree of this mixing turns out to be not only relevant, but vital. This circumstance sets reptiles apart and makes their cardiovascular system unique among all other vertebrates.

MORPHOFUNCTIONAL STRUCTURE OF THE HEART IN LEPIDOSAURS AND TURTLES

The morphofunctional structure of the heart can be directly studied only in modern animals. Therefore, let us look at how the hearts are structured and work in various groups of living vertebrates.

In classical bradymetabolic animals, that is, in primary ectotherms—fish and amphibians, the heart is two-chambered or three-chambered, in which the blood is mixed, in some cases with the first signs of partial, slight separation of arterial and venous blood flows. These are lungfishes with an atrium almost divided in two and one ventricle with an incomplete septum in it (Jollie, 1962; Ishimatsu, 2012) and amphibians with two divided atria and one ventricle with many incomplete septa that prevent the free, complete mixing of arterial and venous blood (Dzerzhinsky et al., 2013; Shakhporonov, 2017).

In modern lepidosaurs and turtles, the heart has a unique structure. Most of them have two barriers in the ventricle, partially (functionally, but not completely morphologically) dividing it into three functional chambers—arterial, venous, and pulmonary (Fig. 4a). Thus, in general, their heart becomes incompletely, conventionally five-chambered. In some cases, modification of the septa—their partial connection or fusion—leads to the fact that, instead of two, one septum with vertical and horizontal components appears, which turns their incompletely five-chambered heart into a conditionally, functionally four-chambered one (Figs. 4b, 4c), in which the separation of arterial and venous blood flows is not yet final, but, nevertheless, more complete.

Here it is important to pay attention to the functional component of the hearts described above. The fact is that the absolute need to regulate the level of metabolism is primarily relevant for animals whose metabolic level is elevated. This only partially applies to modern reptiles: they only periodically, most often during periods of activity, increase their body temperature owing to heat coming from outside, as a result of which their metabolic rate also increases. But it is

unlikely that such a situation can cause large-scale morphophysiological changes in the heart and other organ systems, because even some amphibians (for example, toads with dry skin) periodically increase their body temperature to 34–39°C owing to the influx of external heat (Pearson and Brandford, 1976; Meek and Jolley, 2006), but their heart structure is the same as that of other amphibians, with consistently low levels of body temperature and metabolism. It is likely, therefore, that many reptiles could probably get by with slightly modified three-chambered hearts, somewhat similar to those of modern amphibians.

To understand the real reason for the appearance of an incompletely five-chambered heart in many reptiles, it is probably worth turning to their evolutionary history. As we have already mentioned, the first basal terrestrial tetrapods that came onto land, which later turned into reptiles, were already at least mesometabolic, primarily endothermic animals. Moreover, the huge variety of archosauromorphs, archosaurs, lepidosaurs, crocodylomorphs, turtles, and other groups that developed on their basis apparently began precisely with animals that had an increased level of metabolism. And it was for them that the incompletely five-chambered heart acquired paramount importance, which developed on the basis of a three-chambered one with a large number of incomplete muscular and connective tissue septa and which became capable of partially separating the flows of oxygenated and deoxygenated blood and simultaneously mixing them, thus contributing to the regulation of the amount of CO₂ in blood.

Thus, a not completely five-chambered heart is most relevant, first of all, for mesometabolic, primarily endothermic reptiles. And it was from them that this type of heart passed on to their descendants—to modern secondary ectothermic bradymetabolic reptiles, in which their body temperature and metabolic rate periodically but significantly rise, as a result of which they temporarily turn into mesometabolic high-temperature ectothermic animals. And it was in this periodically mesometabolic and high-temperature state that the five-chambered heart turned out to be very useful for modern reptiles.

It is even possible that such a five-chambered heart acquired in the process of adaptation to high levels of temperature and metabolism became a trigger for primarily endothermic reptiles for further successful exploration of land, allowing them to significantly improve the quality of activity by improving its energy supply and other benefits obtained owing to high body temperature and metabolic rate.

MORPHOFUNCTIONAL STRUCTURE OF THE HEART IN CROCODILES

Modern crocodiles have a completely four-chambered heart. One would expect that this four-chamber

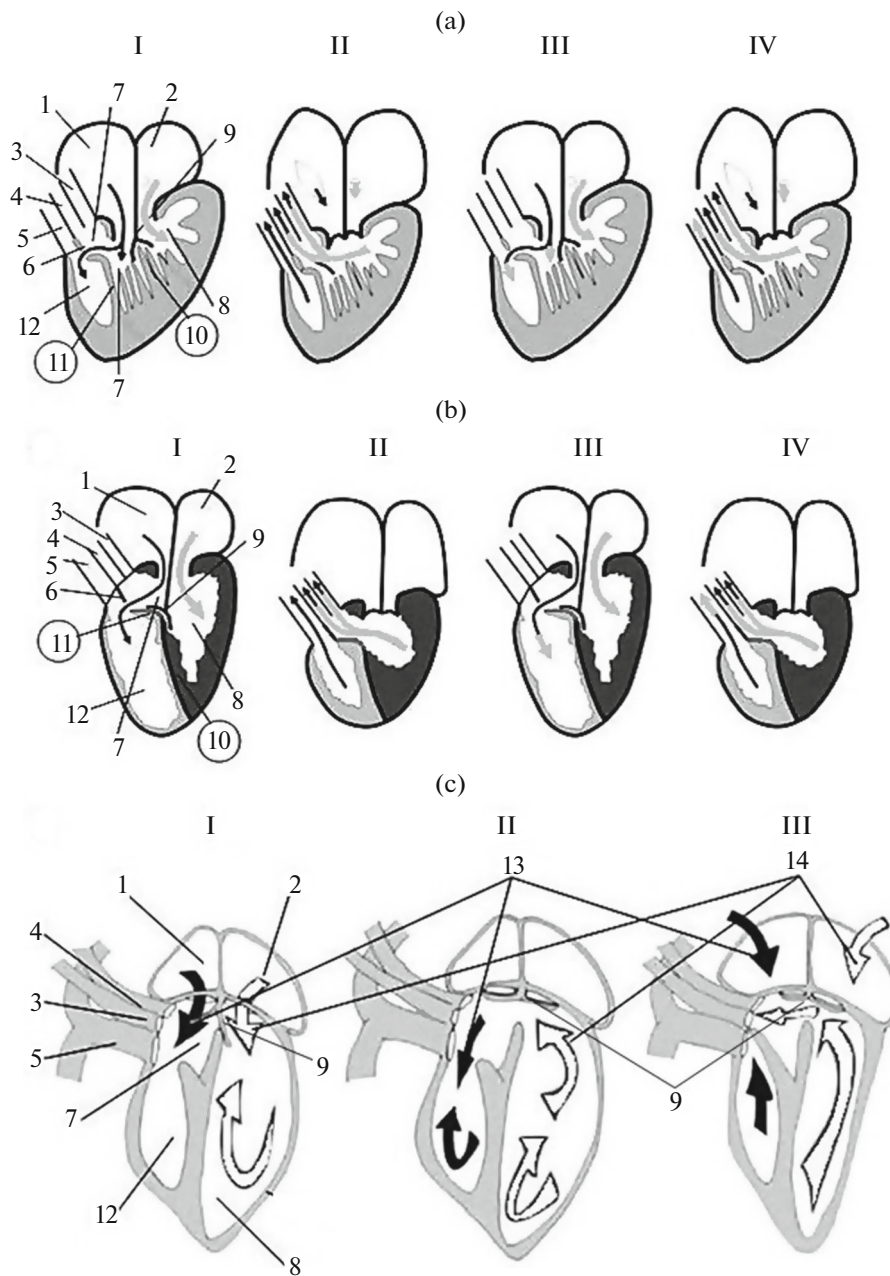


Fig. 4. Simplified diagram of the structure of the heart of some reptile species and the blood flow in it. (a) Most squamates, tuataras, and turtles; (b) pythons (according to Jensen et al., 2014). In fact, most squamates and turtles have trabeculae in the arterial (8) and pulmonary (12) chambers of the ventricle, but in the figure they are erased so as not to interfere with the understanding of the division of the ventricle into chambers. Black thin arrows—deoxygenated (venous) blood; gray wide arrows and parts of arrows (in the figures numbered II and IV)—oxygenated (arterial) blood. (I) First diastole, (II) first systole, (III) second diastole, (IV) second systole. (1) Right atrium, (2) left atrium, (3) right aortic arch, (4) left aortic arch, (5) pulmonary artery, (6) bulbous septum, (7) venous chamber, (8) arterial chamber, (9) atrioventricular valve, (10) vertical septum, (11) muscular crest, (12) pulmonary chamber, (13) deoxygenated, venous blood, (14) oxygenated, arterial blood. (c) Diagram of the structure and operation of the functional four-chamber heart of the royal python *Python regius* (by Starck, 2009; Bogan, 2017). (I) Early diastole. Deoxygenated blood flows from the right atrium into the venous chamber. Oxygenated blood flows from the left atrium into the arterial chamber. The leaflets of the atrioventricular valves close the intraventricular canal, preventing the mixing of oxygenated and deoxygenated blood. (II) Late diastole. The atrioventricular valves close, and oxygenated blood flows from the venous chamber to the pulmonary chamber. (III) Ventricular systole. Deoxygenated blood flows from the pulmonary chamber to the outside through the pulmonary artery. Oxygenated blood flows from the arterial chamber through the venous chamber and exits through both the left and right aortas. With this structure, the conventionally five-chambered heart of pythons turns out to be not morphologically, but functionally four-chambered.

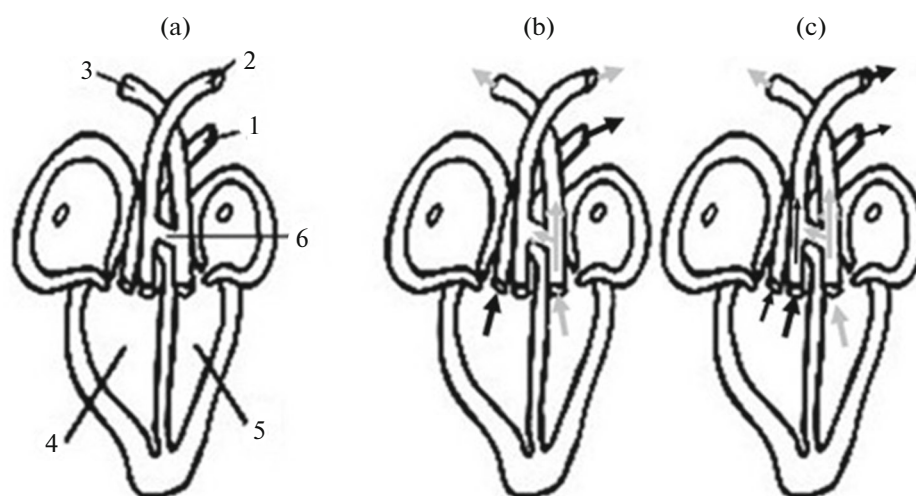


Fig. 5. Diagram of the structure and operation of a fully morphologically four-chambered crocodile heart (according to Benton, 2020). Black arrows—venous blood; gray arrows—arterial. (a) Anatomy of the heart, (b) blood circulation on land, (c) blood circulation during diving. (1) Pulmonary artery, (2) left aortic arch, (3) right aortic arch, (4) right ventricle, (5) left ventricle, (6) foramen of Panizza.

structure is aimed primarily at separating the flows of arterial and venous blood as completely as possible. But in fact, the situation with the functions of their heart is much more complicated.

It is now quite obvious that the ancestors of modern crocodiles were terrestrial, predatory, active, meso- and tachymetabolic, practically warm-blooded animals (Legendre et al., 2016; Cubo et al., 2020; Faure-Brac and Cubo, 2020). And in this warm-blooded state, a four-chambered heart was absolutely mandatory for them.

Subsequently, the evolution of crocodiles followed the path of mastering a specific ecological niche: a near-aquatic lifestyle and long periods of hiding in shallow water to hide from dangers, to conduct ambush hunting, to drown prey, etc. In other words, they developed adaptations to long periods of apnea, which required a periodic sharp weakening of metabolism at least for the duration of these apneas; that is, regulation of metabolic levels became vital. And this, naturally, affected the structure of the heart. More on this in the next section.

Thus, the entire volume of information about the evolution of thermoenergetic statuses in the history of the development of crocodiles, about the morphophysiological and functional characteristics of their heart, indicates that modern crocodiles are the descendants of practically warm-blooded ancestors, and it was from them that they received their four-chambered heart as an organ with atavistic properties (Fig. 5).

REGULATION OF METABOLIC LEVEL

Figure 6 shows a diagram of some intra- and extracardiac mechanisms that ensure mixing of arterial and

venous blood flows and regulation of the degree of its mixing in modern crocodiles. They have an intracardiac shunt—this is the foramen of Panizza between the right and left aortic arches. Some groups of reptiles also have a canal located inside the myocardium and connecting the arterial and venous chambers of the heart (Kargdong, 2012). Whether all groups have such a channel, and if not all, then which ones, remains to be seen.

In crocodiles, a serrated valve is located at the entrance to the pulmonary artery. With its help, crocodiles change the amount of venous blood that enters the pulmonary artery. In addition, by passing arterial blood from the right aortic arch through the foramen of Panizza into the left arch, the crocodile regulates the amount of venous blood entering with mixed blood through the left arch into the bloodstream. In other reptiles, this regulation is carried out by changing the lumen of the pulmonary artery itself with the help of its smooth muscles (Iordansky, 2015).

CONCLUSIONS

One of the most important, unique functional features of the hearts of all groups of reptiles, which distinguishes them from other vertebrates, is that in them there is simultaneously a partial separation of the flows of arterial and venous blood and, in parallel, their partial, regulated mixing. It is this dual function that is the main mechanism for regulating metabolic levels, since an increase in the concentration of carbon dioxide in the blood (an increase in the proportion of venous blood in the bloodstream) reduces the metabolic rate, and a decrease in the concentration of carbon dioxide in the blood (a decrease in the proportion

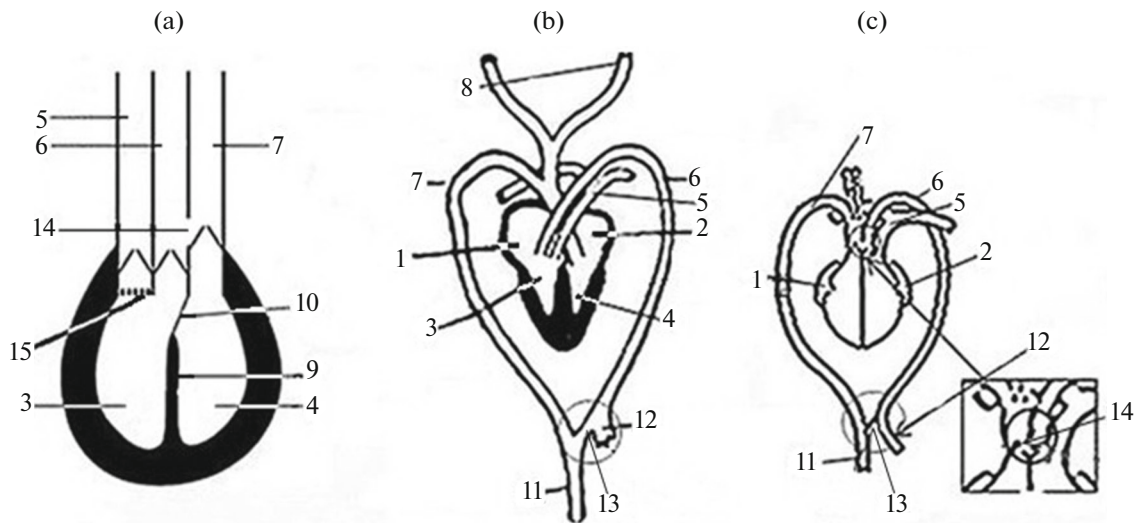


Fig. 6. Diagram of shunts and valves that ensure mixing of two blood streams and regulation of the degree of mixing in crocodiles. (a) According to Seymour et al., 2004; (b) according to Boas, 1884; Polezhaev and Shimkevich, 1891; Shmalhausen, 1947; (c) according to Grigg et al., 2022. (1) Right atrium, (2) left atrium, (3) right ventricle, (4) left ventricle, (5) pulmonary artery, (6) left aortic arch, (7) right aortic arch, (8) carotid arteries, (9) interventricular septum, (10) membranous septum, (11) dorsal aorta, (12) celiac artery, (13) extracardiac shunt, (14) foramen of Panizza (intracardiac shunt), (15) cog-tooth valve.

of venous blood in the bloodstream) accelerates metabolism.

Thus, mixed blood in the reptilian bloodstream is not an underdeveloped, primitive condition. The presence in the heart of reptiles of special morphological structures and special physiological reactions that create mechanisms for regulating the proportion of venous blood entering the bloodstream, that is, regulating the level of metabolism by controlling the amount of carbon dioxide in the blood, suggests that we are dealing with physiological necessity and evolutionary focus on the development of secondary ectothermy. And the pinnacle of this evolutionary direction are modern reptiles.

Such regulation of the level of metabolism was most relevant primarily for the ancestors of modern reptiles, which for the most part were meso- or tachymetabolic, and not at all bradymetabolic animals. Thus, the morphophysiological organization of the heart of all modern groups of reptiles is to a large extent connected with their evolutionary, phylogenetic history. They received certain types of hearts that were characteristic and most relevant to the physiology and ecology of their mesometabolic, endothermic ancestors. In modern reptiles, the ancestral types of hearts have largely changed their functions. These animals used part of their ancestral properties as adaptations to new environmental conditions, to new environmental requirements, and to their new morphophysiological state. The materials of this article were presented on November 27, 2022, at the Department of Vertebrate Zoology at St. Petersburg State University; on November 21, 2023, at a scientific conference at the Paleontological Institute, Russian Academy of

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving humans and animal subjects.

CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

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