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A Literature Review on The Cardiovascular System of the Sauropod Dinosaurs, With an Emphasis on Their Thermal physiology

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1. Introduction

With their massive trunk, long neck, columnar limbs, and powerful tail, sauropod dinosaurs are the largest terrestrial animals known to have ever existed (Wilson, 2021). For this reason, they have fascinated humans for centuries. Sauropods' stratigraphic range extends from the late Triassic period until the late Cretaceous period of the Mesozoic era, and the locations of their remains indicate that they occupied all continents except for Antarctica (Wilson, 2021). In evolutionary terms, sauropod dinosaurs were presumably the most successful terrestrial herbivores to have lived on earth (Ruben, et al., 2012). 121 species of sauropods are recognized, which compromise nearly one fifth of all excavated dinosaurs to this date (Upchurch, et al., 2004).

In addition to researching sauropod dinosaurs to unravel their vast anatomy, physiology, and reason for existential success, dinosaurian studies have played a substantial role in the development of evolutionary theory in that each recovered taxon represent a different set of evolutionary experiments with disparate outcomes (Schweitzer, 2014). Furthermore, studying dinosaurs can aid in the comprehension of other scientific concepts, such as biogeography, plate tectonics, climate change, and the recovery of species and ecosystems following events of extinction (Novacek, 2012).

More has been learned about dinosaurs in the past 25 years than in the entire preceding century. The reason for this is that methodologies developed for other fields of science can be utilized in the study of dinosaurs as well (Reid, 2012). Advantageous information about dinosaurs has been garnered with osteo-histological techniques, computed tomography (CT) and surface- and allometric remodeling, to mention a few (Ganse, et al., 2011; Chapman, et al., 2012). By studying skeletal microstructures, soft tissue reconstructions can be accomplished (Chapman, et al., 2012). Moreover, extant phylogenetic bracketing and functional morphological approximation can be utilized in recreating the anatomy and physiology of the different organ systems of dinosaurs (Perry, et al., 2011).

To understand some aspects of how the biggest terrestrial tetrapods to ever exist functioned, literature concerning their cardiovascular- and respiratory systems will be reviewed in this thesis. The most plausible reconstruction of the sauropod dinosaurs' cardiovascular- and respiratory anatomy and physiology will be presented to investigate how their heart and lungs could support such a massive body and long neck. Next, the cardiovascular- and respiratory systems’ connection to thermoregulation and metabolic physiology with respect to gigantism will be covered. Lastly, certain additional facets holding a significant role in terms of sauropod thermo-physiology will be incorporated.

2. Classification of Dinosaurs: Taxonomy and Systematics

There are several ways to approach the subject of dinosaurian classification. On one hand, we can use the rank-based format of taxonomy to help us create a universal system of all extant and extinct life on earth. On the other hand, we can focus on the evolutionary aspect of life through systematics, finding the connections between living creatures, extinct beings, and their one common ancestor. In their studies of dinosaurian soft tissue anatomy, thermoregulation, and metabolic physiology (among others), researchers and paleontologists actively apply the dinosaurs' connections to extant organisms to demonstrate and explain their assertions (Perry, et al., 2011). Gaining knowledge of the different ways we can classify dinosaurs is important because it helps us understand how these scientists have drawn their conclusions. Therefore, the following chapter will present some of the most common forms of classification, before narrowing the focus onto the sauropod dinosaurs.

Taxonomy is defined as "the naming of names" (Holtz Jr. & Brett-Surman, 2012), and classifies, names, and identifies organisms by means of a hierarchical format. By providing internationally standardized names to organisms and their groups, taxonomy is a great tool in aiding communication among researchers. Starting on the top of the hierarchy, the taxonomic ranking is divided as such: domain, kingdom, phylum, class, order, family, genus, and species. This classification system was created by the Swedish natural historian and botanist, Carl Linné. Each group is called a taxon and is characterized by organisms possessing similar unique combinations of anatomical features. When climbing down the ladder of divisions, every taxon will get increasingly specific, i.e. the taxon of genus refers to a larger group of organisms than species do, and a genus consists of several species. When applying the taxonomic classification to the Sauropod dinosaurs, it looks like this: domain Eukaryota, kingdom Animalia, phylum Chordata, class Dinosauria, order Saurischia, clade Sauropoda. Hence, dinosaurs do not fit perfectly into the taxonomic method of classification. As observed, instead of utilizing the taxa family and genus, paleontologists switch their method to phylogenetic systematics.

Systematics is another, and arguably a more relevant, approach to dinosaurian classification. Systematics is defined as “The scientific study of the diversity of organisms within and among clades” (Holtz Jr. & Brett-Surman, 2012). It differs from taxonomy in that it aids in understanding the relationships among organisms rather than naming and sorting like organisms, yet it is similar in the way that it is a practice of identifying significant groups of organisms. There are two different methods of systematics utilized by paleontologists: evolutionary systematics (gradistics), and phylogenetic systematics (cladistics). Gradistics was the first method of systematics to be developed. It is based strongly on the Linnean hierarchy and has been criticized for being too subjective. Cladistics was developed as a response to this critique and is therefore meeting the need for a more objective approach, unattached from the taxonomic ranking (Holtz Jr. & Brett-Surman, 2012). Whereas gradistics focuses mainly on creating groups based on the level (grade) of evolution without considering total genetic relationships, cladistics focuses on creating a system closely connected to the evolutionary development of organisms. It does this by founding groups composed of one single ancestor, and all its descendants. These groups are called clades, the word used to categorize the sauropod taxon in the previous paragraph. Today, cladistics is the systematic method of classification preferred by vertebrate paleontologists.

When shifting our focus onto sauropod classification, the road has been lengthy and challenging. As a matter of fact, sauropod dinosaurs were not even classified as dinosaurs until 1869, and resolving their interrelationships was deemed extremely difficult for an additional one hundred years, the reason for this being a lack of complete skeletons (Romer, 1968). However, from around 1969 until the late 1990s, the number of excavations revealing fossil remains of sauropods steadily increased. Following the method of phylogenetic systematics, in 1998, Paul Sereno and Jeffrey A. Wilson published a monograph providing the first phylogenetic definitions of clades within Sauropodomorpha, basing their cladograms on the sauropods’ primitive broad-toothed feature (Wilson, 2021). Wilson later published a paper exploring the lower-level analysis of the sauropod clades. He sorted them by comparing various skeletal regions and finding the similarly derived characters between the taxa. Then, he looked at how these structures changed through time, before ultimately tallying the synapomorphies that characterized the various groups (Figure 1) (Wilson, 2021).

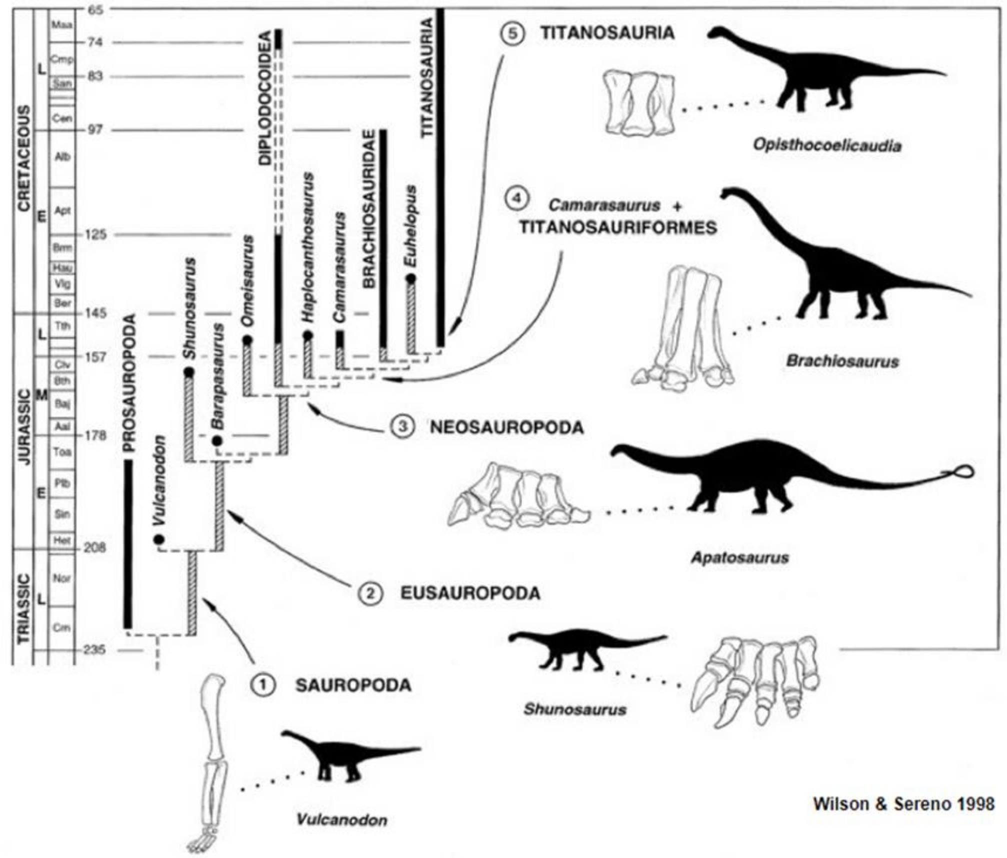

Figure 1: Evolution of anatomical- and postural changes in the sauropods' forelimbs and hindlimbs against a time scale of the Mesozoic era and its periods: Triassic, Jurassic, and Cretaceous. The highlighted nodes depict the development of a digitigrade posture, an elongated metacarpus, and the subsequent loss of manual phalanges. These are only a tiny fraction of anatomical characteristics that Paul Sereno and Jeffrey A. Wilson focused on when creating this calibrated phylogeny of sauropodomorphs based on their cladistic relationships (Sereno & Wilson, 1998).

In summary, we now understand that the best approach to classify the sauropod dinosaurs is to mix taxonomy and phylogenetic systematics. We can combine our gained knowledge of these methods to comprehend a diagram organizing the relative phylogenetic relationship between extinct sauropod dinosaurs and extant crocodilian species and birds (Figure 2). As mentioned in the beginning of this chapter, this is a fundamental part of reconstructing the sauropod soft tissue anatomy and physiology, as the combination of extant phylogenetic bracketing and functional morphological approximation build the foundation to evidence for theories laid down by experienced paleontologists.

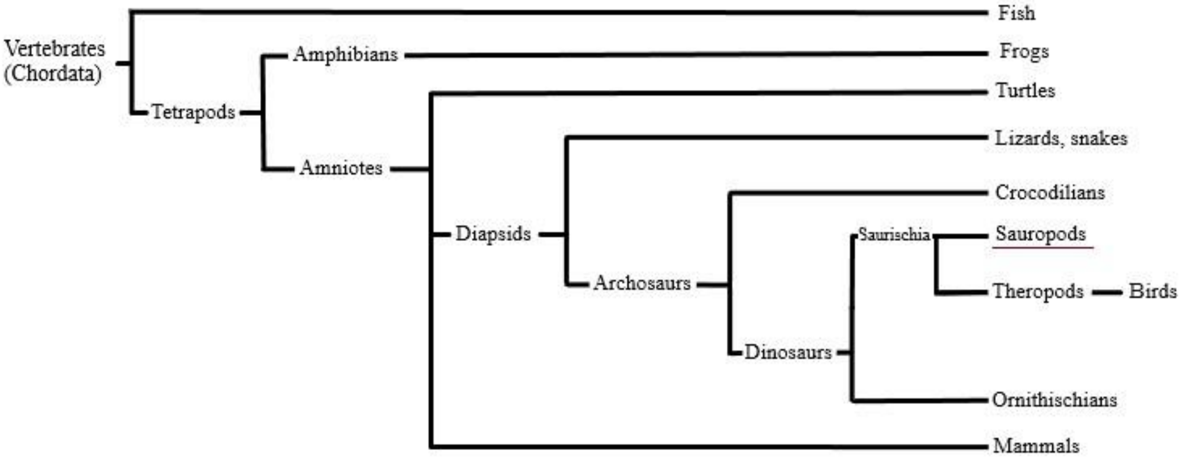

Figure 2: Cladogram (a diagram of cladistics) of major extant vertebrate groups, including an expansion of the line leading from Archosaurs to show the relative phylogenetic relationship between extant crocodiles and birds to extinct dinosaurs, including the sauropods (underlined). Figure created by the author of this thesis, with inspiration form (Rogers, 2002).

3. Anatomy & Physiology of the Cardiovascular- and Respiratory Systems

Before embarking on the topic of sauropod thermoregulation and metabolic physiology, it is essential to describe the structures of the cardiovascular- and respiratory systems, as well as their basic physiology. Without structural and functional comprehension, it will not be possible to explain the theories proposed by paleontologists regarding the processes that would have taken place in these dinosaurs. As stated in the introduction of this thesis, sauropods were the largest terrestrial beings ever discovered: they would reach 17 meters in height, 40 meters in length, and could weight up to 80 metric tons (Sander & Clauss, 2008). Their large body was supported by four columnar legs, and ended with a long tail caudally, while an extraordinarily long neck arose cranially, bearing a small skull on top. With such a level of gigantism at hand, the entire blueprint of the sauropod would have to change accordingly to support proper metabolic, locomotory, thermoregulatory, and cardiovascular function, among others (Ganse, et al., 2011).

3.1 The Cardiovascular System

3.1.1 Cardiac anatomy

Although the cardiovascular system of sauropod dinosaurs is polemically debated, there is a strong agreement among researchers in the palaeontologic field that they possessed a four-chambered heart (Paul, 2012). While fossil sauropod hearts have never been discovered, Fisher et al., (2000) have revealed structures suggestive of a four-chambered heart in an ornithischian dinosaur. This finding, along with the following arguments, make up the basis for this solid agreement.

The three-chambered heart seen in most living reptiles, except crocodiles, consists of two atria and one ventricle, meaning that the pulmonary circulation and the systemic circulation are connected (Reid, 1997). The result is relatively equal blood pressure levels in the lung- and systemic circulation, which benefits smaller reptiles in that they carry their bodies in a horizontal position and thus, the vertical hydrostatic forces formed by the vertical distance between the heart and the rest of the body are relatively low. However, this contrasts heavily to the sauropod dinosaurs, who have been demonstrated to carry their long necks in a vertically extended position (Taylor, et al., 2009), creating a distance between the heart and the brain of about 8 meters (Figure 3). These theories are based on anatomical evidence and comparative studies, where the dorsiflexed position of the neck is presently seen in extant amniotes walking on erect legs, like mammals and birds. In order to supply the cervical and cranial tissues with sufficient levels of oxygen, it has been estimated that the systemic arterial blood pressure of sauropods would need to reach 700 mmHg (Ganse, et al., 2011).

If a three-chambered heart was to produce blood pressure levels of the above-mentioned magnitude, it would immediately destroy the pulmonary vessels and hence, cause lung edema and inhibit gas exchange (Ganse, et al., 2011). Consequently, sauropods having a four-chambered heart – consisting of two atria and two ventricles – that separated the pulmonary- and systemic circulation is very likely, as it would allow low pressure levels and high pressure levels in the pulmonary and systemic circulation, respectively (Seymor, et al., 2004).

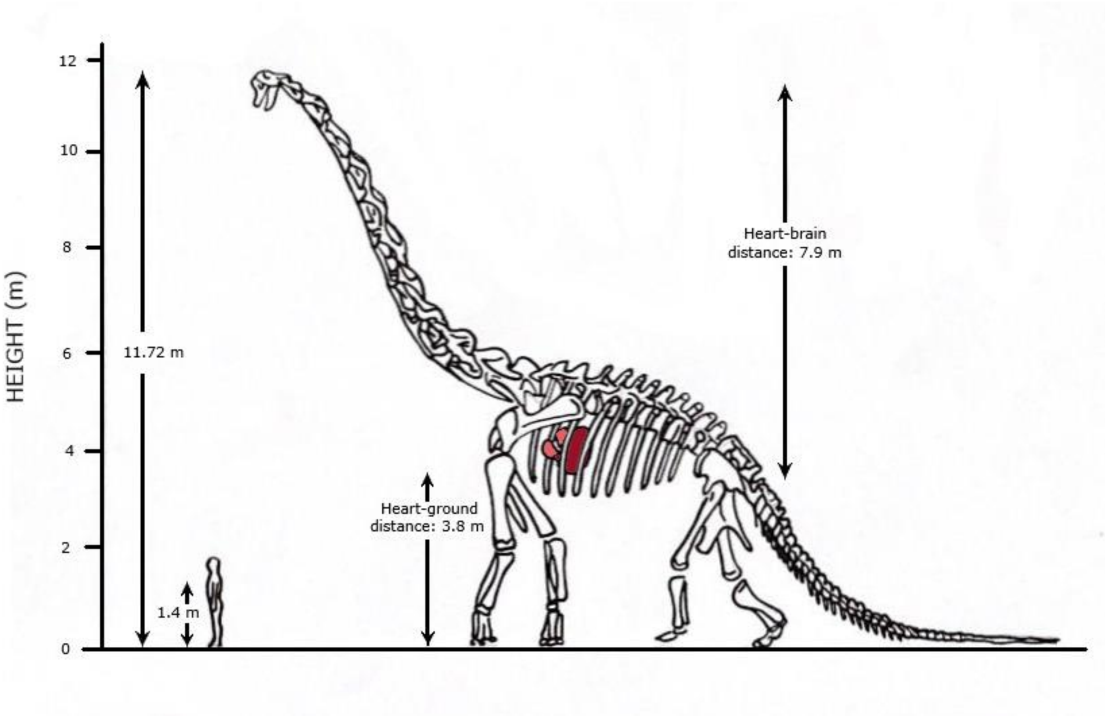

Figure 3: Comparison of the body- and heart size between a human and a sauropod (*Brachiosaurus brancai*). Additionally, the vertical distance between the ground and the heart, as well as the distance between the heart and the head, are displayed. Figure created by the author of this thesis.
Figure description source: (Ganse, et al., 2011).

It may be beneficial to note that the fossilized cardiac structures in the ornithischian dinosaur showed traces suggestive of a single aortic trunk. Furthermore, it was lacking the foramen of Panizza (Fisher, et al., 2000). Foramen of Panizza is an opening connecting the left and right aorta in crocodiles, aiding in the stabilization of blood oxygen levels when the animal is submerged (Ross & Wermuth, 2020). The presence of a single aortic trunk and the absence of foramen of Panizza further strengthen the hypothesis of a four-chambered, avian-mammalian heart in dinosaurs.

3.1.2 Cardiovascular physiology

As for the physiological aspect of the cardiovascular system, several hypotheses have been put forward in attempts to solve certain difficulties connected to the sauropods' circulation and their expected high blood pressure. One hypothesis suggests an increased oxygen transport capacity of the blood (Ganse, et al., 2011). As a result, the heart's stroke volume could be reduced since each unit of blood would contain more oxygen. However, with increased oxygen transport capacity comes an elevated concentration of hemoglobin in the blood, and the viscosity of the blood would increase accordingly. This means that the pressure required to eject blood from the ventricles into the systemic circulation – the afterload – would need to be higher. For the chambers to accommodate the afterload, cardiac hypertrophy would occur. Therefore, this hypothesis is deemed unlikely (Ganse, et al., 2011).

Another hypothesis addresses the sauropod's cardiac size. This alone poses an essential question in terms of the space available in the thoracic cavity, but also concerning the forces required by the cardiac muscle to generate a proper blood pressure to reach across the enormous body of the sauropods. To support an arterial blood pressure of 700 mmHg, the heart of the sauropod dinosaur would have had to include a left ventricle of extensive size, "because cardiac muscle adaptively adjusts its dimensions to normalize the cross-sectional stress in response to pressure and volume loading." (Seymour & Lillywhite, 2000). This would lead to an extremely large and energy-demanding heart, which would pose subsequent problems concerning the diastolic filling of the heart wall vessels, as well as mechanical problems (Ganse, et al., 2011).

Other paleontologists have suggested the presence of several ancillary hearts positioned in the thorax and the neck:” In essence all the hearts, with the exception of the primary heart, would be “satellite” hearts located at intermediate points of the cerebral blood flow to provide a sequential forward pumping action.” (Choy & Altman, 1992). Ganse, et al. (2011) refute this theory. Additionally, adding to the concept of supplementary hearts, a cervical siphon mechanism hypothesis was brought forward by Hicks and Badeer in 1989, but this suggestion has been refuted, too (Ganse, et al., 2011).

It looks like scientists are closing in on the truth behind the function of the sauropods’ cardiovascular system. In 2015, American paleontologist Michael Habib presented an innovative hypothesis, when his excavation of a titanosaur in New Mexico revealed several huge, flexible cervical ribs (Balter, 2015). These ribs appear to be ossified tendons, running parallel to the cervical vertebrae. He proposed that their main function was to stabilize the sauropod’s neck during movement, but that they had a useful, auxiliary effect on the blood supply to its head. As the neck moved, the cervical ribs and -muscles would compress the corresponding arteries, pushing the blood cranially. Moreover, the longer neck, the more skeletal muscles would be present to aid the heart in pumping blood to the head. In turn, a 25% size reduction of the heart mass previously presumed required to get the blood to the brain would be possible (Black, 2015). This hypothesis has gained the support of many fellow paleontologists, including paleontologist Martin Sander of the University of Bonn in Germany.

Pertaining to the return of the venous blood to the heart from the sauropods’ extremities, scientists have looked to aspects of comparable physiology in horses and giraffes. In horses, a blood-collecting, digital cushion is positioned between the bones in each hoof. When compressed, the blood will move out of the cushion and towards the heart through veins (Ganse, et al., 2011). In giraffes, several mechanisms play a part in the prevention of fluid accumulation in the extremities: blood- and tissue fluid pressures, a tight skin layer, precapillary vasoconstriction, and a low permeability of capillaries to plasma proteins (Hargens, et al., 1987). If all, or the majority of, these mechanisms were present in sauropods, they would resolve the lasting pathological state of fore- and hindlimb edema that would otherwise occur (Ganse, et al., 2011).

3.2 The Respiratory System

In the body of all amniotes (a clade of tetrapod vertebrates including synapsids like mammals, and sauropsids, like reptiles and birds), the circulatory system and the respiratory system cooperate in supplying oxygen to the tissues, while also removing their cellular waste, such as carbon dioxide (Torday, et al., 2007). Amniote lungs can be separated into two morphologically distinct types: alveolar lungs and septate lungs (Ruben, et al., 2012). Alveolar lungs, seen in mammals, contain a vast amount of homogenously distributed, highly vascularized alveoli (Knudsen & Ochs, 2018). The alveoli make up the pulmonary parenchyma, where gas exchange occurs. With bidirectional ventilation, the alveoli will massively expand during inspiration – due to the formation of negative pressure and increased volume of the pleural cavity created by the expansion of the rib cage – and recoil during expiration (Ruben, et al., 2012). Septate lungs, however, works with a slightly different mechanism: large chambers serve as air storage, and gas exchange occurs in the chamber walls (Perry, et al., 2011). In other words, a septate lung “is functionally analogous to a single, oversized mammalian alveolus.” (Perry, 1983). The number of chambers, as well as the morphology of the lung parenchyma (homogenous to heterogenous), and whether the chambers are attached to the skeleton or not, vary greatly (Ruben, et al., 2012). The septate lungs are found in reptiles such as crocodiles, lizards, and turtles (Perry, et al., 2011). It is important to note that the respiratory system of birds possesses the most complete separation of air storage- and gas exchange units among extant amniotes (Torday, et al., 2007). Large bellow-like structures, called air sacs, are distributed throughout their bodies, and will expand and compress as they inhale and exhale, respectively. The gas exchange occurs in the neopulmo and the paleopulmo. These structures consist of numerous air ducts (parabronchi) surrounded by a blood capillary network and do not show any volume change during breathing (Perry, et al., 2011). A unidirectional ventilation is observed in the septate lungs of crocodiles and in the paleopulmo of birds (Brocklehurst, 2017). Figure 4 provides a visualization of the morphology of the different pulmonary types described above.

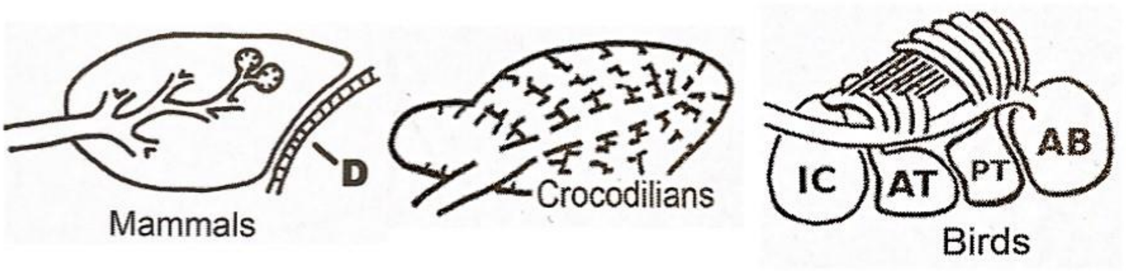

Figure 4: Lung diagrams with lateral views of the alveolar mammalian lung, the multichambered septate crocodilian lung, and the avian lung displaying complete separation of the gas exchange- and air storage unit. D – mammalian diaphragm; IC – interclavicular air sacs; AT – anterior thoracic air sacs; PT – posterior thoracic air sacs; AB – abdominal air sacs. Figure created by the author of this thesis, with inspiration from: (Perry, et al., 2011).

As fossilized sauropod lungs have never been discovered to this date, the reconstruction of their respiratory system relies heavily on indirect evidence (Perry, et al., 2011). It is also practical to utilize the combination of extant phylogenetic bracketing and functional morphological approximation to draw conclusions on the anatomy and physiology of the respiratory system of the sauropods (Perry, et al., 2011). Based on these techniques, the data strongly points towards an avian-like respiratory system consisting of separate regions for gas exchange and air storage in the thoracic cavity.

3.2.1 Indirect evidence

Examination of the sauropods' skeleton provides several indirect evidence of an avian respiratory system. A particularly substantial feature is the postcranial skeletal pneumaticity (PSP), which is well-documented in sauropod dinosaurs (Wedel, 2009). Although distinctive foramina and fossae of the vertebrae may vary within and between individuals (Taylor & Wedel, 2021), their presence indicate that the lungs must have been attached to the skeleton, while simultaneously ruling out the possibility of an alveolar, mammalian lung, as these glide on a fluid film in the thoracic cavity (Perry, et al., 2011). Furthermore, since the lungs could not have been the sole source of PSP of such an extensive degree as observed throughout the skeleton of sauropods, it indicates that air sacs with accompanying connections to the bones – pneumatic diverticula – must have been scattered throughout the body. These air sacs, from cranial to caudal, would be the cervical, clavicular, and abdominal air sacs (illustrated in Figure 5) (Wedel, 2009). Lastly, the presence of pleurocoels (hollow depressions positioned laterally on the vertebral body

(Holtz & Brett-Surman, 2012)) strongly suggest heterogenous lungs which – in all sauropsids – are always attached to the body wall (Perry, 1983).

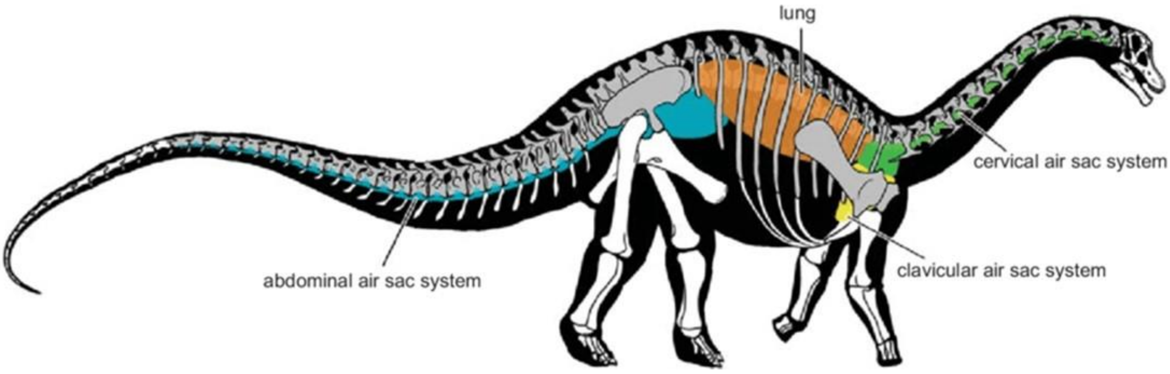

Figure 5: Reconstruction of the pulmonary anatomy in terms of PSP and air sacs in a *Saltasaurine* sauropod. The grey skeletal features are elements known to be pneumatized. The white bones are either apneumatic, or their condition is uncertain. The color coding of the pulmonary structures are as follows: green – cervical air sacs (pneumatize the cervical- and cranial thoracic vertebrae); yellow – clavicular air sacs (pneumatize the sternum, pectoral girdle, and possibly the humeri); orange – lungs (pneumatize the thoracic vertebrae and ribs adjacent to the lungs); blue – abdominal air sacs (pneumatize the caudal thoracic-, synsacral-, and caudal vertebrae, and possibly the femora and pelvic girdle as well). Source: (Ibiricu, et al., 2017; Wedel, 2007)

3.2.2 Extant phylogenetic bracketing

Another methodology utilized for the anatomical reconstruction of the sauropod dinosaurs' respiratory system is extant phylogenetic bracketing. With its foundation in cladistics, extant phylogenetic bracketing "is based on comparison of certain features of the nearest extant relatives in order to reconstruct these features in extinct animals" (Perry, et al., 2011). It was originally developed as a mean for inference of soft tissue anatomy yet can be applied to any palaeobiological aspect not normally preserved in the fossil record, such as function and behavior (Witmer, 1995). Sauropod dinosaurs are phylogenetically bracketed between birds and crocodiles (Figure 2) (Sereno, 1997). Hence, at least those structural traits shared by birds and crocodiles must have characterized the lungs of sauropods (Perry & Sander, 2004). Multichambered lungs with a cartilaginous cranial part, long and arching chambers emerging in spiraling rows, and an asymmetrical branching pattern, are some of the attributes common to both birds and crocodiles (Perry & Sander, 2004). Additionally, when studying the embryological development of avian- and crocodilian lungs, it is possible to reconstruct a gradual transformation from crocodile lungs to avian lungs: homologous to the crocodile lung’s anterior chamber is the bird’s clavicular air sac, and the crocodile’s terminal chamber foreshadows the bird’s abdominal air sacs (Perry, et al., 2011).

The internal subdivision of the thoracic- and abdominal body cavities is achieved by a postpulmonary- and a posthepatic septum in both birds and crocodiles. The first septum lies between the liver and the lungs, while the latter arises caudally to the liver (Perry, et al., 2011). Both membranes aid in the stabilization of the lungs. Nevertheless, a prominent difference between the birds’ and the crocodiles’ posthepatic septum is that in crocodiles, it gives rise to the *musculus diaphragmaticus*. This muscle inserts on Os Pubis of the pelvic girdle and holds both a respiratory and an aquatic function (Perry, et al., 2011). A prerequisite for the presence of this muscle is a mobile pubic bone. Sauropods lack a kinetic pubis and would therefore also lack the *m. diaphragmaticus* (Claessens, 2004). In addition to the high degree of PSP of the sacral and caudal vertebrae, this suggests a respiratory system inclined towards the avian kind (Wedel, 2009).

The bird-like ribcage of sauropods is a further remarkable feature. Some of the significant structures are the morphology of the ribcage and of the ribs, the articulation of the latter to the vertebrae, and the possible existence of gastralia. As in birds, the ribcage of sauropods is deeply corrugated, which is an accompanying indicator of an avian-like respiratory system (Paul, 2012). The ribs are long and spaced far apart, and each one has a two-headed construction: the tuberculum (dorsal head) articulates with the transverse process of the vertebra, and the capitulum (ventral head), articulates with the body of the vertebra (Perry, et al., 2011). This position of the articulation surfaces allows for the formation of robust hinge joints (Ruben, et al., 2012). In addition, there is a contentious debate concerning the presence or absence of gastralia in sauropods. Many paleontologists, including Tschopp & Mateus (2012), claim to have discovered bones correlating with gastralia in sauropod fossils. On the other hand, other paleontologists have repudiated all proposed theories (Claessens, 2004).

3.2.3 Functional morphological approximation

Based on the known analogs, functional morphological approximation can be applied for the physiological reconstruction of the sauropod respiratory system. There are several indices that sauropods possessed a costal breathing mechanism (Claessens, et al., 1998). Costal pulmonary ventilation is commonly seen in animals lacking structures with a diaphragmatic function (Paul, 2012). As mentioned above, sauropods presumably lacked a diaphragm. Instead, the hinge joint formation of the ribs' articulation surface to the vertebrae created a craniolateral abduction during inspiration, while simultaneously producing a dorso-ventral rotation of the sternum. This rotation would aid in the ventilation of the abdominal air sacs (Ruben, et al., 2012). If gastralia were present in sauropods, they would presumably aid in the stabilization of the pectoral gridle, support the breathing apparatus, and protect the abdominal organs (Tschopp & Mateus, 2012). However, if they were absent, abdominal collapse during inspiration would be prevented by the weight of the viscera, while also indicating a costal pulmonary ventilation (Claessens, 2004; Paul, 2012).

The postulation of highly efficient flow-through ventilation regarding the respiratory system of sauropods has been copiously researched. Unidirectional flow (caudal to cranial direction) is observed in alligators at rest (Farmer & Sanders, 2010), and also characterizes the ventilation of the paleopulmo in birds: during inspiration, the negative pressure generated by expansion of the cranial air sacs draws about 50% of the air into the paleopulmo. Concurrently, the other half of the inspired air flows through the parabronchi of the neopulmo and into the caudal air sacs. Subsequent compression of the air sacs guides air from the caudal air sacs to pass through the neopulmo again, and into the paleopulmo (Perry, et al., 2011). In birds, a prerequisite for the unidirectional flow in the paleopulmo is the presence of abdominal air sacs (Kuethe, 1988). Moreover, as demonstrated above, the ventilation of the neopulmo in birds is bidirectional (Perry, et al., 2011).

It is presumed that the gas exchange in sauropod lungs displayed a crosscurrent scheme (Perry, et al., 2011). The cross-current gas exchange is defined as a principle in which the blood flow in the vascular capillaries of the lungs is perpendicular to the direction of the airflow (Scheid, 1979). Additionally, the gas exchange is independent of the direction of the flow (Scheid, 1979). The crocodilian lung exhibits the anatomical prerequisites –

increased diffusing capacity – for cross-current gas exchange in its proximal chambers, and it is established that birds possess this mechanism of gas exchange as well (Perry & Sander, 2004). Thus, it is plausible that sauropods had cross-current gas exchange.

The combination of cross-current gas exchange and flow-through ventilation leads to a highly efficient respiratory system both during rest and exercise (Scheid, 1979), which allows for immense amounts of oxygen to be extracted from the air (Brown, et al., 1997; Perry, et al., 2011). Based on indirect evidence, extant phylogenetic bracketing, and functional morphological approximation, sauropod dinosaurs are likely to have possessed a highly heterogenous, bird-like respiratory system containing these mechanisms of gas exchange and ventilation. An avian respiratory system would make the development of the sauropods' long necks possible by overcoming the challenge of tracheal dead space, (Perry, et al., 2011; Wedel, 2007). Moreover, it would allow for the sauropods to reach their documented level of gigantism by supporting the extreme variations in metabolic needs throughout their lives, without a proportional increase in mass (Sander & Clauss, 2008; Perry, et al., 2011). Lastly, the hemodynamic concerns associated with large lungs would be solved with a capacious respiratory system and would also aid in thermoregulation by acting as an active cooling mechanism (Perry, et al., 2011).

4. Thermo-physiology of Sauropod Dinosaurs: Thermoregulation and Metabolic Physiology

When it comes to dinosaur biology, their thermoregulation and metabolic physiology are two of the most debated topics to exist. Alas, the engendered debates have led to the dismissal of accurate interpretations of objective evidence in relation to thermo-physiology (Ruben, et al., 2012). Adding to the complexity of the cause, paleontologists utilize the same arguments to support their claims both for and against the contrasting thermoregulatory strategies (Ruben, et al., 2012). Fortunately, the development of isotopic studies (Clauss, 2011), as well as an increased number of ecological and physiological studies of extant ectotherms (Quick & Hillenius, 2013) have given paleontologists the means for a more rigorous approach to the subject. Below, several terms utilized in the field of thermoregulation and metabolic physiology will be explained. Subsequently, the previously discussed topics of the anatomy and physiology of the cardiovascular- and respiratory systems, as well as some other relevant aspects, will be utilized to draw the most plausible conclusion regarding the thermo-physiology of sauropod dinosaurs.

4.1 Terms Utilized in Thermo-Physiology

Thermoregulation is defined as “the ability and the mechanics by which an organism regulates its body temperature in relation to ambient temperatures” (Ganse, et al., 2011). The speed of biochemical- and enzymatic processes in the body, as well as neural transmission of information in the tissues, is greatly influenced by body temperature (White & Seymore, 2003; Ganse, et al., 2011). To explain aspects in thermoregulation, pairs of contrasting terms are used.

The first pair of contrasting terms used in the mode of thermoregulation, is homeothermy and poikilothermy. These terms describe the internal temperature stability of an organism (Holtz Jr., 2021). A homeothermic organism has the ability to maintain a stable internal body temperature (Sapkota, 2021). Homeotherms are, to a certain extent, independent of the environment, and deviations can be tolerated to a small degree (Ganse, et al., 2011). Poikilothermic organisms possess a varying internal temperature, often influenced by – and subsequently matching – the environmental temperature (Sapkota, 2021).

The second pair of contrasting terms is endotherm and ectotherm. These refer to an organism's source of energy (Holtz Jr., 2021). An endothermic organism regulates its body temperature by means of internally produced heat such as shivering, metabolic activity, and intestinal heat production (Ganse, et al., 2011). To prevent heat loss, an endothermic organism often relies on insulating elements like feathers, fur, and subcutaneous fat (Sapkota, 2021). Additionally, they might resort to hibernation or migration in case of very low external temperatures, or in the absence of adequate food sources (Sapkota, 2021). Conversely, an ectothermic organism acquires heat from external sources (Ganse, et al., 2011). Its level of activity will be influenced by ambient temperatures, resulting in a torpid state during nocturnal hours and at low temperatures (Holtz Jr., 2021).

Metabolic rate is another aspect of thermo-physiology that is closely linked to thermoregulation. Standard metabolic rate is defined as the amount of post-absorptive energy expended at rest at neutral temperature (Ganse, et al., 2011). As with thermoregulation, there is a pair of juxtaposing terms used to describe the types of metabolic rate: tachy-metabolic and brady-metabolic. A tachy-metabolic organism has a high resting metabolic rate, often resulting in homeothermy and endothermy (Holtz Jr., 2021). The obsolete term warm-blooded implies homeothermy, endothermy, and tachy-metabolism (Ganse, et al., 2011). On the other hand, a brady-metabolic organism holds a low resting metabolic rate, but will have an active metabolic rate similar to that of a tachy-metabolic organism (Holtz Jr., 2021). Cold-blooded generally refers to poikilothermy, ectothermy, and brady-metabolism (Ganse, et al., 2011).

There are three terms in thermo-physiology that do not contain a contrasting counterpart. Heterothermy is seen in endothermic organisms whose core temperature exhibit a greater variation than that which defines homeothermy (Landes, et al., 2020). This variation of core temperature may be nychthemeral or seasonal. For instance, heterothermy is seen in small endotherms who are poikilothermic and brady-metabolic during sleep, yet homeothermic and tachy-metabolic during activity (Ganse, et al., 2011). The second term to be presented is terramegathermy. As the name reveals, this term deals exclusively with larger terrestrial animals, and asserts that tachy-metabolism is a prerequisite for evolving body masses exceeding one ton in 1 G (Paul & Leahy, 1994). Thus, no brady-aerobic ectotherm can become gigantic (Paul, 2012). The last term also encompasses gigantism and has three names that define the same hypothesis: Gigantothermy, inertial homeothermy, or mass homeothermy (Gillooly, et al., 2006). Gigantothermy suggests that an ectotherm organism can become homeothermic during ontogeny due to the fact that heat dissipation in a large organism will be smaller in relation to its surface area (Holtz Jr., 2021; Ganse, et al., 2011). Additionally, they will be able to display high levels of activity diurnally, as well as a low metabolic rate nocturnally (Ganse, et al., 2011).

It is believed that previous views on dinosaur thermo-physiology have been too narrow, firmly constricted to the combinations that is cold-blooded and warm-blooded (Ganse, et al., 2011): initially, it was believed that dinosaurs were similar to reptiles, exhibiting poikilothermic, ectothermic, and brady-metabolic features (Ruben, et al., 2012). Later, a notion of mammal- or bird-like homeothermic, endothermic, and tachy-metabolic dinosaurs were presented (Ruben, et al., 2012). In reality, it is feasible that the thermo-physiology among different taxa of dinosaurs differed greatly (Reid, 1997). Nevertheless, when it comes to sauropod dinosaurs, current research proposes a homeothermic, endothermic, and tachy-metabolic thermo-physiology.

4.2 Thermo-physiology and Extant Phylogenetic Bracketing

Over the years, most researchers have assumed that endothermy developed after the divergence of the bird lineage and the crocodilian lineage (Holtz Jr., 2021). The reason for this is that crocodiles are ectothermic poikilotherms, whereas most birds are homeothermic endotherms (Craig, 2018; Holtz Jr., 2021). However, crocodile anatomy reveals certain features more consistent with endothermy than with ectothermy: a unidirectional ventilatory flow and a four-chambered heart (Holtz Jr., 2021). Moreover, a parasagittal stance that allows for an increased aerobic exercise capacity (tachy-aerobiosis) is seen in extinct outgroups of extant crocodiles (Paul, 2012; Holtz Jr., 2021). These observations have led to the conjecture that crocodiles reverted to an ectothermic physiology after the divergence of their lineage (Holtz Jr., 2021).

The insinuation that crocodiles' thermoregulation developed from an endothermic physiology is in accordance with new evidence demonstrating that ancestral archosaurs possessed some level of endothermic tachy-aerobiosis as well (Paul, 2012). The combination of this new evidence and the above-mentioned endothermic anatomical features in crocodiles indicate that dinosaurs – including sauropods – did not develop tachy-energy independently (Seymor, et al., 2004). Instead, they inherited and further developed this thermo-physiological characteristic (Paul, 2012).

4.3 Thermo-physiology and the Cardiovascular System

4.3.1 The circulatory anatomy

Endothermy is seen together with high oxygen consumption levels. To support the elevated levels of oxygen utilization, structural and functional modifications that facilitate oxygen uptake, transport, and delivery are observed. Increased lung ventilation rates, expanded cardiovascular function, and the full separation of the pulmonary and systemic circulation, are some of the supporting modifications seen in endothermic organisms (Ruben, 1995).

As mentioned in subchapter 3.1.1 of this thesis, sauropod dinosaurs most likely possessed a four-chambered heart and a full separation of the pulmonary and systemic circulation. These features would be able to support the high-pressure circulatory system required for the proper functioning of a sauropod's extensive body mass and tall posture (Paul, 2012). Operating this type of circulatory system would require high levels of work, which would subsequently increase the resting metabolic rate (Seymor, et al., 2004). Contrastingly, the reptilian ectothermic, brady-metabolic respiratory- and cardiovascular systems would not be able to generate enough aerobic power to support the sauropod body's oxygen demands (Paul, 2012), nor would it be able to support the high-pressure circulation needed to overcome the elevated hydrostatic pressure associated with a vertically raised, long neck (Figure 3) (Ganse, et al., 2011). With the four-chambered heart and the separated pulmonary- and systemic circulation, the circulatory demands of sauropod dinosaurs would be supported, while also being indicative of endothermic tachy-metabolism (Fisher, et al., 2000).

4.3.2 Blood volume, oxygen saturation, and erythrocyte dimensions

Ruben (1995) explains that increased blood volume, a higher concentration of hemoglobin in the blood, and high tissue aerobic enzymatic activities are further indications of endothermy. Although making direct measurements of the blood volume in sauropod dinosaurs have not been possible, the cross-sectional examination of the nutrient foramina in long bones has exposed an interrelationship between the foramen size, the blood flow requirements of the internal bone cells (Seymour, et al., 2012), and the general blood flow rate (Holtz Jr., 2021). Furthermore, the scaling of foramen size positively correlates with exercise metabolic rate (Seymour, et al., 2012). With respect to body size and femur length, the long bones' nutrient foramina are larger in dinosaurs compared to both reptiles and mammals (Figure 6). This finding suggests fast growth and an active lifestyle with tachy-aerobic metabolic rates for dinosaurs (Seymour, et al., 2012).

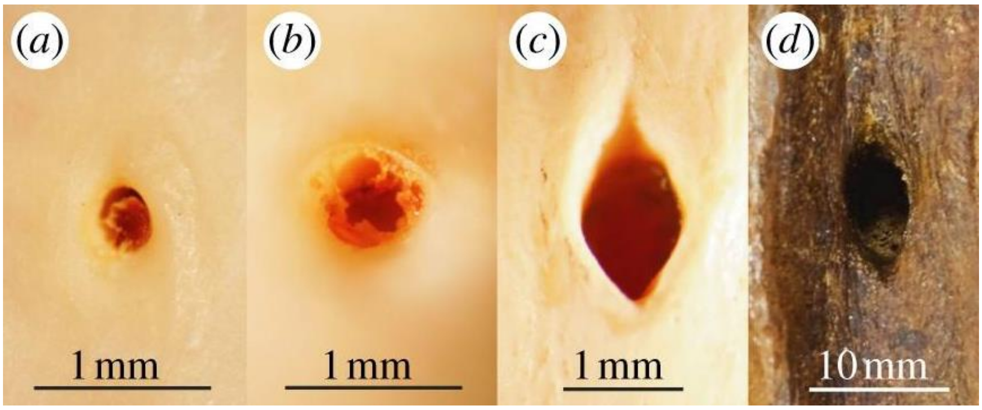

Figure 6: Nutrient foramen of the femur of a non-varanid reptile *(a)*, a varanid reptile *(b)*, a mammal *(c)*, and a dinosaur *(d)*. Figure source: (Seymour, et al., 2012).

The hypothesis of an increased hemoglobin concentration in the blood of sauropods has been refuted due to the resulting cardiac hypertrophy connected to the increased viscosity of the blood (see subchapter 3.1 of this thesis). Alternatively, it has been argued that higher oxygen levels in the atmosphere during the Jurassic and Cretaceous periods would allow each unit of inspired air to contain more oxygen, which in turn would aid a higher metabolism and faster growth (Holtz Jr., 2021). However, recent research suggests that an increased concentration of oxygen in the atmosphere during the above-mentioned periods may not have been reality after all, and theories basing their conclusions on this postulation – among them certain aspects of sauropod gigantism and metabolism – must be reassessed (Perry, et al., 2009; Clauss, 2011; Tappert, et al., 2013).

The size of erythrocytes may be indicative of different thermoregulatory types (Holtz Jr., 2021). In fact, red blood cell size is shown to negatively correlate with metabolic rate, meaning that smaller erythrocytes imply higher metabolism (Bertazzo, et al., 2015). The reason for this is that small entities have a larger surface area/volume ratio. Thus, smaller erythrocytes may dispose of carbon dioxide and bind to oxygen at a higher rate than larger erythrocytes manage (Holtz Jr., 2021). In dinosaur bones, researchers have identified structures reminiscent of erythrocytes (Bertazzo, et al., 2015). These concave structures have a size comparable the small erythrocytes of emus, and although some possible shrinkage during fossilization cannot be disregarded, their size indicates tachy-metabolic endothermy (Bertazzo, et al., 2015).

4.3.3 Vascular heat dissipation and its link to metabolism

Several paleontologists have claimed that gigantism poses a fundamental constraint on heat dissipation, resulting in an increased risk of overheating (Ganse, et al., 2011). Nevertheless, in the study of elephant body temperature, metabolic rate, and geographical distribution, no problems concerning potential overheating has been observed (Ganse, et al., 2011). Upon these discoveries, researchers suggest that the immediate vascular transport of heat to subcutaneous tissues has not been appropriately considered in terms of sauropod heat dissipation (Clauss, 2011). It is argued that sauropod dinosaurs had the ability to adjust their body temperature by actively controlling their metabolic rate and their vascular flow of heat from the core to the surface of the body via vasodilation and vasoconstriction (O'Connor & Dodson, 1999; Ganse, et al., 2011; Henderson, 2013). This type of temperature control indicates homeothermy (Henderson, 2013).

It appears that enhanced blood flow to certain areas of the sauropod body emphasizes that thermal exchange occurred at predilect sites, suggesting a more focused thermal strategy (Porter & Witmer, 2019). These areas show increased neuro-vascularization, and for large sauropod dinosaurs, their heads – specifically the oral- and narial regions – act as predilection sites (Figure 7) (Porter & Witmer, 2019). Here, a vast palatal vascular plexus in the oral cavity, as well as palatine vessels supplying the nasal region, would aid greatly in heat dissipation (Porter & Witmer, 2019). Later in this chapter, other regions of the sauropod body and their role in thermoregulation will be discussed.

4.4 Thermo-physiology and the Respiratory System

4.4.1. Thermoregulation in the upper airways

In terms of the sauropod respiration, the suggested avian-style respiratory system would provide credible mechanisms of thermoregulation (Perry, et al., 2009). The main function of the upper respiratory tract – the nasal cavity and the trachea – is to moisten the air and cool down the venous blood (Perry, et al., 2009). Assuming that the inspired air would be cooler than the body surface temperature and less than fully saturated with water vapor, the air would be humidified and cooled off in the upper respiratory tract. Subsequently, the highly vascularized plexus in the oral cavity (Figure 7) (discussed in section 4.3.3. in this thesis) would be cooled by transforming water from the liquid phase to the vapor face on surfaces moistened by secretory serous glands, followed by thermal conduction within loose connective tissue (Perry, et al., 2009).

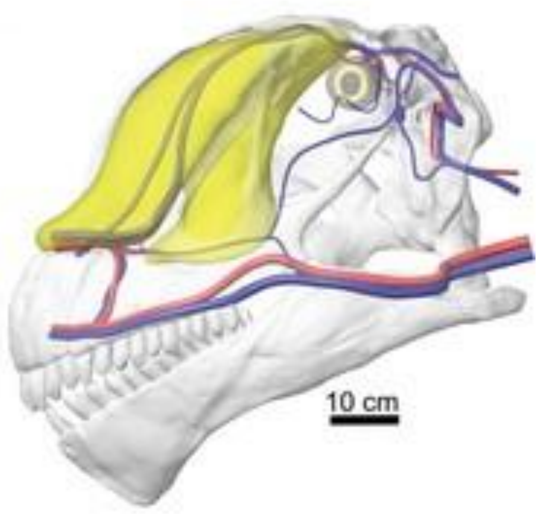

Figure 7: left lateral view of a *Camarasaurus* sauropod. The yellow area represents the airway, and the blue and red structures illustrate the rough vascular anatomy of the head. The *Camarasaurus* shows a focused thermoregulatory strategy, meaning that one or two of the main sites for heat exchange (main sites being the orbital, nasal, and oral region) are emphasized through increased vascularization. This specimen displays emphasized vascularization of the nasal and oral region, indicating that these sites acted as principal sites of heat exchange. Figure source: (Porter & Witmer, 2019).

During expiration, the warmed air would pass through the trachea and into the nasal cavity. From here, most of the expired air would be exhaled into the atmosphere, yet a certain amount would be retained to aid in the recovery of moisture to avoid desiccation of the lungs (Perry, et al., 2009). In mammals and birds, the method of retention is accomplished through respiratory turbinates protruding into the airways (Ruben, et al., 2012). Respiratory turbinates represent a direct indicator of endothermy in that they create an intermittent countercurrent exchange of respiratory heat and water between the respired air and the turbinates' epithelial lining (Ruben, et al., 2012). There has been found no evidence of the presence of respiratory turbinates in sauropod dinosaurs (Perry, et al., 2009; Clauss, 2011). However, it is plausible that a well-developed air sac system may have replaced their function (Perry, et al., 2009).

4.4.2 Thermoregulation in the lower airways

With the suggested avian-like respiratory system, the sauropod dinosaurs' lower respiratory tract would consist of lungs and air sacs (discussed in section 3.2 of this thesis). These structures are indicative of a tachy-metabolic endothermic physiology (Perry, et al., 2009). In the abdominal air sacs, metabolic heat produced by organs such as the liver, intestine, and cecum, would be conducted through the walls of the sacs, warming up the humid and cool inspired air (Perry, et al., 2011). Hence, the air sacs would aid in temperature regulation by acting as sites of heat transfer (Perry, et al., 2009; Ganse, et al., 2011). During expiration, the warm and humid air would pass through the parabronchi. At this place, additional body heat could be transferred from the blood to the air (Perry, et al., 2009).

In the avian respiration model, the combination of the low work of breathing and its high efficiency implies that the heat-producing activity of the respiratory muscles is low, due to the estimated low breathing frequency and power output per breath (Perry, et al., 2009). In fact, it has been calculated for sauropods that they most likely possessed a breathing frequency of 3.5 breaths per minute (Gunga, et al., 2008). Additionally, the low air convection requirement characterizing the avian respiratory system means that sauropods with this kind of respiratory system would only need to obtain about half as much air for the same amount of oxygen as an equivalent mammal. Furthermore, they would only need to use the inspiratory muscles ¼ as much as the mammal (Perry, et al., 2009). These reconstructions provide a plausible theory suggesting that sauropod dinosaurs possessed efficient temperature control, indicating homeothermic endothermy and a high metabolic rate (Perry, et al., 2009).

4.5 Other Aspects of Sauropod Thermo-physiology

While the cardiovascular- and respiratory systems are major contributors to the mechanisms of thermoregulation and metabolic physiology of an organism, there are several other structural and functional aspects that aid in defining and describing the presumed thermo-physiological type of sauropod dinosaurs. Hence, not presenting some of these aspects would give a skewed perception as to what type of thermo-physiology sauropods possessed.

4.5.1 The growth of juvenile sauropods

Ganse et al. (2011) believe that one of the strongest arguments for an endothermic physiology in sauropod dinosaurs is found in their rapid growth rate. To reach a body mass of more than 50 metric tons during a reasonable lifetime, sauropods must have possessed a high resting metabolic rate for at least parts of it (Ganse, et al., 2011). This is consistent with evidence showing that maximum body size of brady-metabolic terrestrial vertebrates is limited to approximately one metric ton, even in the highest ambient temperatures (Head, et al., 2009).

By utilizing skeletochronology, the maximum growth rate for dinosaurs can be calculated (Holtz Jr., 2021). It has been estimated that juvenile sauropods increased their masses more than ten thousand times over merely a few decades. Such an achievement would be incompatible with ectothermic poikilothermy (Sander & Clauss, 2008). For swift growth, a relatively stable body temperature would be necessary to optimize the internal conditions (Paul, 2012). In effect, the most critical factor may have been the ability to deliver sufficient amounts of nutrients to be converted into body tissues. This would require a vast amount of food to be consumed per unit time, which in turn would demand high-capacity digestive-, circulatory-, and respiratory systems (Paul, 2012). Following the rapid growth period of juvenile sauropods, it has been suggested that their metabolic rate would then decline as they reached maturity (Sander & Clauss, 2008).

4.5.2 Bone histology and growth rate

Through the examination of bone histology, researchers have managed to differentiate between ectothermic heterotherms and endothermic homeotherms (Paul, 2012). Hence, utilization of the relationship between growth rate and bone histology for the determination of dinosaur metabolism is thought to be an optimistic approach (Ganse, et al., 2011).

In extant vertebrates, two histological types of bones have been recognized: lamellar-zonal bone and fibrolamellar bone (Paul, 2012). The degree of vascularization, as well as their fibril organization, are used to distinguish the two types (Paul, 2012). The lamellar-zonal bone exhibits a lower degree of vascularization and is the primary bone of ectothermic amphibians and most reptiles. On the other hand, highly vascularized fibrolamellar bone characterizes the skeleton of mammals, birds, and dinosaurs (Paul, 2012). This type usually correlates with high growth rates requiring rapid calcium deposition. Allegedly, such swift growth is only possible in organisms with elevated metabolic rates associated with endothermy (Paul, 2012; Holtz Jr., 2021).

It is important to note that several opposing arguments to the usage of bone histology in the determination of metabolic type exist. For instance, fibrolamellar bone is seen in extant ectotherms showing rapid growth, such as turtles, crocodiles, and lizards (Reid, 1997). This suggests that a high basal metabolism is not a prerequisite for fibrolamellar bone deposition (Paul, 2012). Additionally, long bones in numerous genera of dinosaurs reveal regions of both fibrolamellar and lamellar-zonal histology (Reid, 1997). Therefore, bone histology cannot be the only distinguishing factor in the determination of an organism’s metabolic physiology and thermoregulatory type (Paul, 2012).

4.5.3 Body mass

When it comes to endothermic organisms’ basal metabolic rate, this parameter displays a negative allometric trend when plotted against body mass (Ganse, et al., 2011). This means that the mass-specific basal metabolic rate decreases as the animal gets larger. Thus, sauropod dinosaurs most likely possessed a relatively low basal energy expenditure per kilogram per day (Ganse, et al., 2011). Additionally, it is noteworthy that the basal metabolic rate-exponent probably varied slightly in the different sauropod species, as well as exhibiting certain interindividual fluctuations (Ganse, et al., 2011).

Due to the low mass-specific metabolic rate of giants, it takes several hours for the body temperature to increase a few degrees if all internal heat was retained, even if the tachy-aerobic metabolic rate is scaled to the ¾s power (Paul, 2012). Therefore, having the low surface area/volume ratio, like gigantic sauropods would have had, is advantageous in that they can prevent most of the heat gain from the environment (Paul, 2012). During the day, large tachy-aerobic terrestrials may allow their internal temperature to rise above 46^{o} Celsius. Consequently, the excess heat will be unloaded during the nights (Paul, 2012). The effectiveness of this system increases along with the size of the animal (Figure 8). Hence, the argument concerning the possibility of hyperthermia in sauropod dinosaurs has been refuted once more (Paul, 2012).

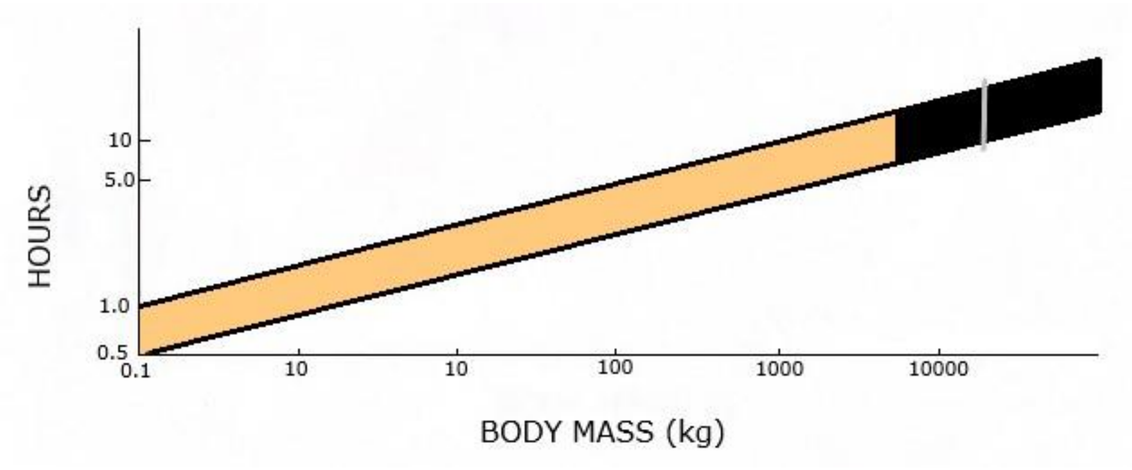

Figure 8: Estimation of the time it takes for tachy-aerobic terrestrial animals to overheat if they store all internal body heat and exclude external heat, with body temperatures rising to 46^{o}C. The yellow zone covers extant examples, solid black covers extinct giants. The line on the right indicates the size of the largest mammals. Picture made by the author of this thesis. Figure description: (Paul & Leahy, 1994; Paul, 2012).

Terramegathermy argues that to become gigantic, an animal must have a high-power aerobic system (Paul, 2012). Moreover, a massive and/or tall animal is, or always displays anatomical evidence of being, a tachy-aerobic endotherm (Paul, 2012). This is consistent with the suggested anatomy and physiology for sauropod dinosaurs (see chapter 3 of this thesis). Including the fact that there is no gigantic extant organism present on earth exhibiting a brady-aerobic physiology, any hypothesis proposing such a physiology for giant terrestrials is therefore illogical (Paul, 2012). As a matter of fact, the slow growth inherent to brady-metabolism would prevent any terrestrial organism to grow at a rate that would allow them to become gigantic (Paul, 2012). Hence, while these data are fully compatible with and aid in the verification of terramegathermy, they also refute gigantothermy (Paul, 2012).

4.5.4 Heat dissipation from body surfaces

As the oral and narial regions of the head of sauropods have already been defined as predilection sites for heat dissipation (subchapter 4.3.3. of this thesis), it is natural to consider the potential thermoregulatory role of other parts of the body as well. Research has been conducted on the possible heat regulation connected to the neck, body, and tail of sauropods. The study is based on the assumption that metabolism is directly proportional to body mass raised to the ¾ power (Henderson, 2013). It is important to note that PSP and the air sac system was taken into consideration in this study. With respect to metabolic rate, the total body surface area and the tail area showed negative allometry, whereas the neck area showed positive allometry (Henderson, 2013). The positive allometric trend for neck surface area to increase with increasing metabolic rate is a significant indicator that the neck contributed to heat dissipation and thermoregulation in sauropod dinosaurs (Henderson, 2013).

4.5.5 Skin type

Although the presence of feathers and bristle-like structures have been discovered in the fossils of some dinosaurs, there are no implications that sauropod dinosaurs possessed such insulating integument (Ganse, et al., 2011). The first finding of fossilized sauropod skin suggests that they had reptile-like, scaly skin, even at an embryonic stage (Figure 9) (Chiappe, et al., 1998). Accordingly, the sauropod dinosaurs' means of heat dissipation was presumably through radiation, convection, and conduction and not through sweating, assuming the lack of sudoriferous glands (Ganse, et al., 2011). However, the absence of evaporative heat dissipation does not seem to have posed a problem. The reason for this would be the air sac system providing increased conductive heat loss via the lungs (Ganse, et al., 2011), as well as the previously discussed subcutaneous heat loss, and the head and neck acting as predilect sites for thermal release in sauropods. Additionally, data suggests that sauropod cruising speeds are compatible with those of tachy-aerobic elephants, peaking at approximately 3.5 km/hour (Paul, 2012). Hence, though they moved at a pace well-above the anticipated speed of reptilian giants, sauropods still did not move very fast, and would thus avoid excessive heat production generated form physical exercise (Ganse, et al., 2011; Paul, 2012).

5. Conclusion

The study of dinosaurs provides valuable insight into evolutionary theory. Through a diverse array of scientific methodologies, it can expand the understanding of how and why extant organisms have evolved in the way they have. Interestingly, the opposite is also true: extant organisms may increase our knowledge of dinosaur biology. By utilizing the phylogenetic relationship between dinosaurs and both their ancestors and living relatives, dinosaurian soft tissue anatomy and physiology can be reconstructed. Additionally, in sauropod dinosaurs, looking to similarly constructed extant organisms may assist in deciphering certain physiological challenges associated with their size.

Due to their level of gigantism, sauropod dinosaurs' circulatory- and respiratory anatomy and physiology, as well as their thermo-physiology, have been of great interest to paleontologists. Because of the differing pressure demands of the systemic and pulmonary circulation, as well as the excavation of a fossilized ornithischian heart, a four-chambered heart has been suggested for sauropods. Subsequently, sauropods are assumed to have had an avian-like respiratory system, with a full separation of the gas exchange- and air storage units. This postulation is based on the presence of extensive PSP throughout the axial skeleton, robust hinge ribs, and the fact that the efficiency of an avian respiratory system would be able to meet the operative demands of the gigantic sauropod body. Concerning thermoregulation and metabolic physiology, new research has found evidence that diverge from the formerly proposed reptilian thermo-physiology for sauropods. Based on the reconstructed anatomy and physiology of the circulatory- and respiratory systems, as well as on growth rates, body mass, and on the concept of terramegathermy, it is currently believed that sauropods were homeothermic, tachy-metabolic, and endothermic dinosaurs.

In summary, researchers believe that sauropod dinosaurs had characteristics more compatible with birds, but also with mammals, than with reptiles. Following the prodigious development in technology that can be utilized in the study of dinosaurs, advancement in the understanding of dinosaurian biology may only increase as well. Hopefully, this will result in less disputes and uncertainties regarding dinosaur reconstruction, leading to increasing agreement among paleontologists.

6. Summary

Sauropod dinosaurs are the largest terrestrial tetrapods to have ever existed, and they roamed the earth in the Mesozoic Era. 121 species of sauropods are currently recognized, which makes up nearly one fifth of all excavated dinosaurs to this date. Due to prodigious advancements in scientific technology, more has been learned about dinosaur biology in the last few decades than in the entirety of the past two centuries. Research has been conducted on the sauropod dinosaurs' circulatory and respiratory anatomy and physiology to see how these systems supported their gigantic bodies. Additionally, studies on their thermoregulatory type and metabolic physiology have been carried out to understand the principles of temperature stability, generation, and dissipation in sauropods. For their cardiovascular system, a four-chambered heart and a separated pulmonary- and systemic circulation are suggested. These findings are also indicative of endothermy. Paleontologists postulate an avian-like respiratory system for sauropods. This type of system will provide efficient temperature control, also indicating homeothermic endothermy and tachy-metabolism. Then, further aspects connected to sauropods' thermo-physiology are discussed, such as growth rates, bone histology, body mass, heat dissipation from different regions of the body, and skin type. With varying degrees, these features point toward endothermy and tachy-metabolism as well. Overall, current knowledge suggests that sauropod dinosaurs possessed characteristics more compatible with birds and mammals, than with reptiles.

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2. **Figure 2:** Roger S. W., 2002: Allosaurus, Crocodiles, and Birds: Evolutionary Clues From Spiral Computed Tomography of an Endocast. *The Anatomical Record,* 257. 5. p. 162-173 p.
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8. **Figure 8:** Paul G. S., 2012: Evidence for Avian-Mammalian Aerobic Capacity and Thermoregulation in Mesozoic Dinosaurs. In. Brett-Surman M. K., Holtz Jr. T. R., Farlow J. O. (eds): *The Complete Dinosaur.* Bloomington, Indiana University Press, p. 819-871.
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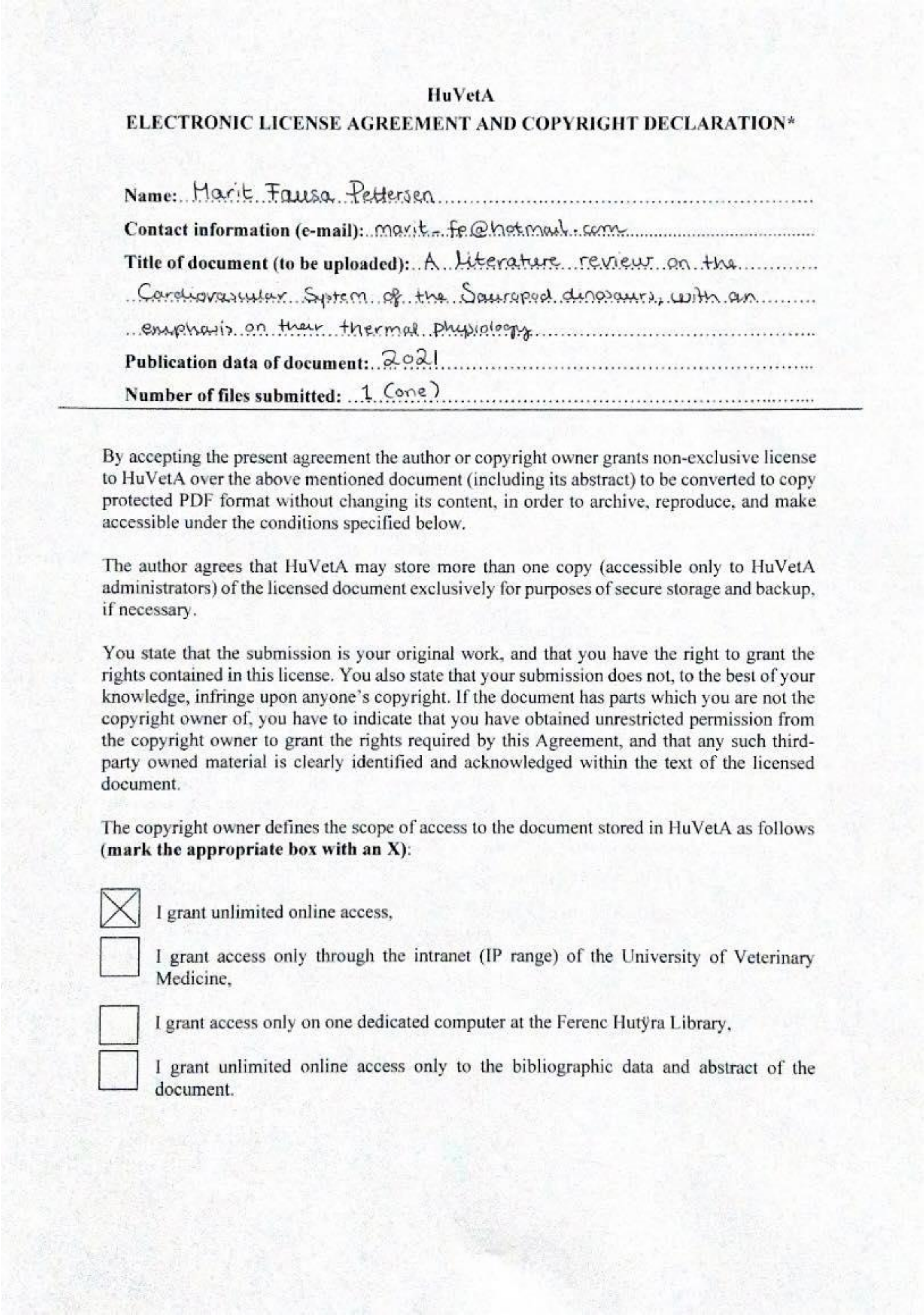

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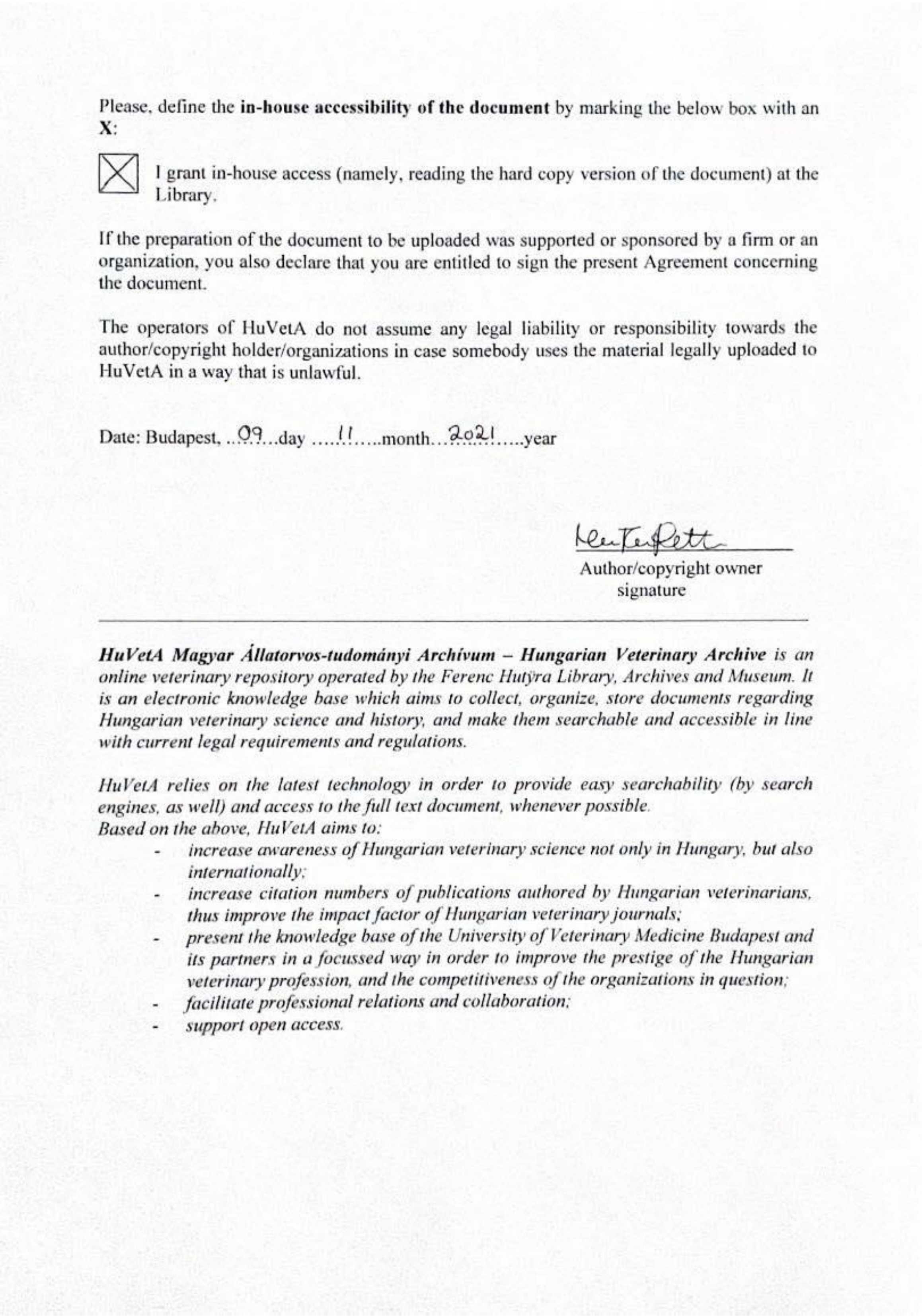

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