e-ISSN 1734-9168
http://www.isez.pan.krakow.pl/en/folia-biologica.html

Folia Biologica (Kraków), vol. 69 (2021), No2
https://doi.org/10.3409/fb_69-2.09

Horse Tooth Enamel Ultrastructure: A Review of Evolutionary, Morphological, and Dentistry Approaches

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Accepted June 15, 2021 *Published online July 13, 2021* *Issue online July 13, 2021*

Review article

DEMESHKANT V., CWYNAR P., SLIVINSKA K. 2021. Horse tooth enamel ultrastructure: a review of evolutionary, morphological, and dentistry approaches. Folia Biologica (Kraków) **69**: 67-79.

This review searches for and analyzes existing knowledge on horse tooth anatomy in terms of evolutionary and morphological changes, feeding habits, breeding practices, and welfare. More than 150 articles from relevant databases were analyzed, taking into account the issues of our experimental research on the ultrastructure of Equidae tooth enamel. After our analysis, the knowledge on this subject accumulated up in the past, almost 50 years has been logically arranged into three basic directions: evolutionary-palaeontological, morpho-functional, and dentistic, which is also demonstrated by the latest trends in the study of enamel morphology and in the practice of equine dentistry. The obtained data show that in recent years we have observed a rapid increase in publications and a thematic expansion of the scope of research. It is caused by the need to deepen knowledge in theory and in the practice of feeding species in nature and in captivity as well as the possibility of using new technical resources to improve the excellence of such research. It is a summary of the knowledge of a certain stage of equine tooth enamel studies for this period of time, which serves as the basis for our experimental research (the materials are prepared for publication) and at the same time, defines research perspectives for the next stage of development.

Key words: Horses, teeth, enamel structure, morphology, pathology, treatment.

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Horses are a highly specialized, evolutionary mature group of mammals whose biology demonstrates a connection between morphology, function, and environment (EASLEY 1998; WINKLER & KAISER 2015). Teeth, as a part of the digestive system, are responsible for cutting and grinding the large amount of highly fibrous grasses that constitute the diet of horses (DIXON *et al.* 2013; BORKENT & DIXON 2017). The welfare of domestic horses is directly connected not only with health status or livestock conditions, but also with the appropriacy of their feed, which includes fibrous forage (MASLAUSKAS *et. al.* 2009; DE WINTER *et al.* 2016). Deficiencies in high fiber fodder always lead to digestive and oral disorders, primarily seen in a deterioration in the condition of the teeth (GRIFFIN 2013). Attempts to improve the welfare of horses should be based on the systems of their breeding and management, and should further take into account the specifics of the evolutionary development of horses (DU TOIT & RUCKER 2013).

In recent years, increasing attention has been paid to understanding the importance of animal welfare and in particular to horses concerning feeding, the process of foraging, and the condition of their dental system (RAMZAN & PALMER 2010; DIXON *et al.* 2013; SAHARA 2014; IACOPETTI *et al.* 2015). Such dependencies are largely due to the physical characteristics of the fodder, the morphological features of horses' teeth, and the masticatory system, as well as the conditions of existence. The problem is hardly novel and will be well known to both scientists and practitioners of veterinary medicine and animal feeding. To date, it has been partly covered in research papers (DU TOIT *et. al.* 2008a; COOK 2011; BORKENT & DIXON 2017).

As the understanding of the importance of an integrated approach to work in this area is increasing, there is also a need for more detailed anatomical studies of the structure and morphology of horse teeth, especially their chewing surface, as a functional structure (MUYLLE *et al.* 1999; HENNINGER 2003; CARMALT & ALLEN 2008; SHAW *et al.* 2008; SIMHOFER *et. al.* 2008; HOPKINS *et al.* 2016). Researchers have been working to show the relationship between tooth structure, feed, and the pathological manifestations that occur in functional processes (VERAA *et al.* 2009; WINDLEY *et al.* 2009; RAMZAN 2011).

Despite the considerable number of publications on this matter, our knowledge about the anatomy of the dental system of horses and the results of its functioning are still limited. Mutual feedback is evident here, as tooth morphology is influenced by feed factors that can cause changes in their structure, with a corresponding reaction to the action of these factors (influences) (BOYDE 1997; MUYLLE *et al.* 1999; ŁUSZCZYŃSKI & PIESZKA 2011; ERICKSON 2014; MLAKAR *et al.* 2014). This is manifested through the fodder, the function of chewing, the physiological state of the horse, and its adaptive capacity, as well as the horse's conditions either in nature or in captivity. The existing data (KILIC *et al.* 1997a; SUSKE *et al.* 2016a; ENGLISCH *et al.* 2017) have provided us with new and important information about the morphology of the teeth and the ultrastructure of tooth enamel in equids (CURREY 1999; WANG *et al.* 2006a; HÖVENER *et al.* 2012; DE DIOS TERUEL *et al.* 2015), as well as the possible causes of the pathological condition of teeth and appropriate forms of treatment (EASLEY 1998; COOK 2011; CASEY *et al.* 2015; BORKENT & DIXON 2017). The evolutionary aspect of the problem provides the basis for understanding the dynamics of environmental conditions (BRIANT *et al.* 1996; BOARDMAN & SECORD 2013; JULIEN *et al.* 2013), diet history (SHARP & CERLING 1998; KITA *et al.* 2014), and vectorized changes in morphology (SEETAH *et al.* 2014).

Beyond the peculiarities and structure of their digestive system, the fact that horses tend to chew fodder throughout the day, significantly affects wear (MACFADDEN 2008; FERANEC & PAGNAC 2017) and dental disorders (MUYLLE *et al.* 1999). This functional connection of the morphological structures of the teeth, feeding system, and welfare status of horses was found in some of the reflections presented in the scientific publications explored in this research (UPJOHN *et al.* 2013; ERICKSON 2014).

In order to learn more about the problems described above, we carried out experimental studies on horse tooth enamel morphology. For this, genus *Equus* representatives were taken, which were conditionally divided into two groups. The first – small horses ("Tarpan" group), the second – large horses ("Caballus" group). The results of the experimental part made it possible to notice the difference in the enamel structure of the selected groups, resulting from their evolutionary state, and, accordingly, taxonomic differences, which was also reflected in the characteristics of phylogenetic relations. The basis of this publication consists of a short analytical overview of existing information on a given issue, starting from the second half of the 20th century. The review of the existing knowledge in a given article is a summary of the research stage on this issue, which, together with the new data, forms the basis for determining the perspectives of research in this direction. First of all, they are related to the comparative aspect of morphology and function studies in horse populations in wild nature and in captivity (stable keeping). Our research completes the existing knowledge on this subject to some extent. For the first time, a transition zone between enamel types I and II was noted by us, which is wave-like in small horses and simpler in the "Caballus" group. These characteristics have not been included in the publications we have analyzed so far. A detailed analysis of these results will be presented in subsequent publications. We also managed to more closely examine the ultrastructure of the enamel of selected forms of extinct horses (*E. sussenbornensis, E. latipes*, tarpans), characterize the specifics of their enamel structure and on this basis define (if possible) their phylogenetic relations. In summary, this allowed us to include additional morphological features (enamel structure) in the analysis for a deeper understanding of the history and evolution of equines.

The aim of this study was to search for and analytically review the existing information on the issues outlined above of horse tooth anatomy in terms of the evolutionary and morphological changes of horses, their feeding habits, husbandry practices, and horse welfare.

Materials and Methods

Forty years' worth of published papers that looked at the structure of tooth enamel, as well as at the dentin and cement of teeth in horses of the genus *Equus* were studied under the influence of animal welfare and health status using an evolutionary approach. The data presented were selected in 2020.

Information was sought via the scientific databases ISI Web of Science, Scopus, and Google Scholar.

The search resulted in more than 150 articles being found, these in turn being divided into three categories: I – "evolutionary-paleontological data" on the evolution of horses and their teeth (57%, 89 articles), II – "morphology and function" on the composition and structure of teeth (28%, 43 articles), III – "recent equine dentistry" – the medical aspect of the topic (15%, 23 articles) (see Fig. 1).

A core of 152 articles were published in the 1990s or more recently, this being a period associated with the

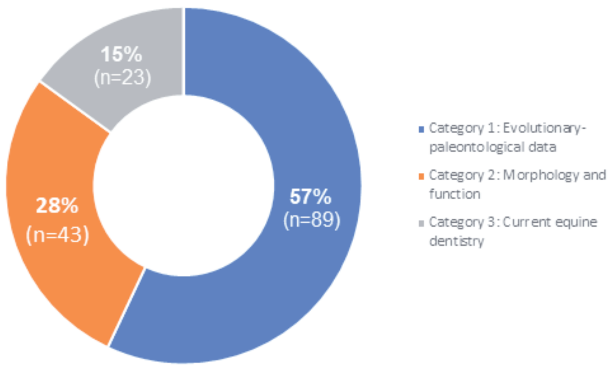

Fig. 1. The database (n = 155) of the articles we analyzed comprised of three different categories: 1 – evolutionary-paleontological data, 2 – morphology and function, 3 – current equine dentistry.

development of analytical methods. Only four of the articles found were published before 1990 (see Fig. 2). More publications based on the experiment were published after 1990.

In the analytical processing of the data, attention was paid mainly to the thematic focus of each work, the vast majority of which were complex and based on factual material. The use of techniques, their effectiveness, and the depth of data analysis in the discussion were the criteria for the articles chosen for the review. Of particular noteworthiness were the comparative works, which immediately allowed the evaluation of the research data. The data obtained were linked and remain linked to a certain period in recent history and characterize the stage and the degree of advancement in the accumulation of knowledge about the problems of horse tooth morphology and anatomy. When an evolutionary approach to the evaluation of scientific data was used for determining the study object, that being the tooth enamel ultrastructure in horses including their keeping; this would consequently offer an outline of prospects for future research. This comparative and analytical approach allows for the observation and evaluation of the

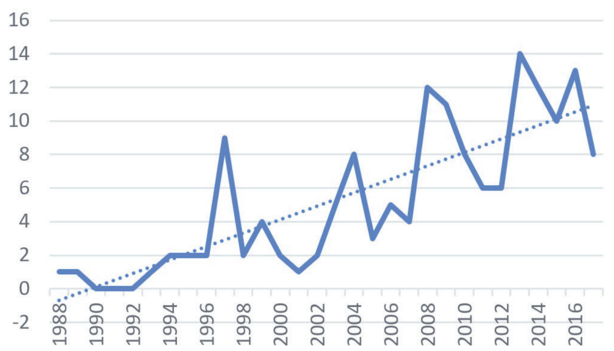

Fig. 2. Distribution of the number of articles published in various years (1988-2017).

"missing link" and determines the topic of current and prospective research. Each work was evaluated not only by the new information it provided, but also by the prospect of the problem solved in the paper. Finally, the subject of tooth enamel ultrastructure studies in relation to nutrition and tooth functionality was recognized through the use of the evolutionary approach, as a basic component of the studies presented.

Results

The results were interpreted in the areas of evolutionary, morphological, and recent dentistry research, thus allowing a better understanding of the existing knowledge about horse tooth enamel for the prevention of diseases, treatment, and the improvement of animal welfare in husbandry practice.

Evolutionary and paleontological data

According to their morphological characteristics, teeth possess a specific combination of constituent elements (MLAKAR *et al.* 2014; DE DIOS TERUEL *et al.* 2015). They have a strong structure, (MACFADDEN *et al.* 1994; BOWMAN *et al.* 2017); they resist the effects of external factors well (CHOUBISA 2013; ECKER *et al.* 2013); they survive longer in the fossil state (KOVÁCS *et al.* 2012; JOHNSON & GEARY 2016). The process of tooth fossilization occurs slowly in comparison with the bones of the skeleton, converting them into solid fossils in the orictocoenosis of different geological epochs, making them available for study (NUNEZ *et al.* 2010; DOMINGO *et al.* 2016). Therefore, it is no coincidence that the tooth as an object and subject of study (morphology) is traditionally used to study the evolution of both extinct and modern forms (NUNEZ *et al.* 2010), in paleoecological (biocenoses) and climatic reconstructions (HOPPE & KOCH 2007), as well as to build knowledge of the relationships in the system "man and nature" in historical times (PELLEGRINI *et al.* 2008; BENDREY 2011; YRAVEDRA *et al.* 2016). This complex of evolutionary and morphological issues in the scientific publications researched here occupies one of the leading places and accounts for almost 57% (89 articles) of the articles available for analysis (see Fig. 1).

This relative abundance of studies may be due to the fact that publications in different thematic areas tend to favor studies that consider the history of the area of study or the history of the taxon studied. With due consideration to the goals of the research the articles from the group "evolutionary and paleontological data" were divided into three separate categories: 1 – clarification of diet, including extinct forms, 2 – reconstruction of conditions with respect to climate and paleobiocenoses, and 3 – studies of the evolution and systematics of horses. Various methods of morphological and paleoecological analyses were tested and used for such purposes (Kempson *et al.* 2003; Zhang *et al.* 2012; Rekovets *et al.* 2014; Domingo *et al.* 2015, 2016; Hopkins *et al.* 2016) including the isotope characteristics of forage and tooth structure (Bryant *et al.* 1994; Bryant *et al.* 1996; Ciner *et al.* 2015).

For the reconstruction of paleo-diets of ungulates, various methods have been proposed and employed, including tooth abrasion analysis (Fortelius & Solounias 2000), biogeochemical markers (MacFadden 2008; Pérez-Cuzmina *et al.* 2016), and paleoecological comparative analyses (Kuzmina 1997). Several works rely on complex research and combine data from traditional "morphological" and "high-tech isotope" methods (Bryant *et al.* 1996; Feranec 2007; Nunez *et al.* 2010).

Some data, observations, and conclusions are based on dental morphology, such as crown height and root development, enamel loops on the chewing surface, and cement development. These criteria provide the foundation for knowledge of the evolution of horses and the reconstruction of their phylogenetic relationships (Forsten 1993; Eisenmann & Baryshnikov 1995; Cucchi *et al.* 2017).

The leading role in the evolution of the natural populations of horse species belongs to the specific conditions of life, and the diet of the horse (Woodburne 2007; Koufos 2016). These were dynamic and determining factors in the process of adaptation, and morphologically changed the most functionally important organs required for motion and grazing (Kaiser & Fortelius 2003; Ecker *et al.* 2013). In onto- and phylogeny, adaptations were of benefit in the struggle for existence in the permanent aridization of the climate in Eurasia (Forsten 1993; Eisenmann & Baryshnikov 1995; Kuzmina 1997). The evolution of the dental system was determined by the herbal fodder being much tougher in mechanical composition, by the function of chewing, and by the strengthening of the chewing system (mainly the muscles involved) as a whole (Kuzmina 1997; Kaiser & Fortelius 2003). This is related to the odontological problems in the ancestors of horses and the problems of dentistry in their modern forms (Griffin *et al.* 2016).

Tooth morphology and the degree of wear in performing the function are essential criteria in the adaptation to the prevailing conditions and the survival of the Equid family over time. Herbivorous mammals, and ungulates in particular, combat the effect of tooth enamel wear by combining the following changes: functionality due to the features of the occlusion of the chewing surface; hypsodonty through gradual root reduction; and enamel line length through folding (Seetah *et al.* 2014; Suske *et al.* 2016b; Cucchi *et al.* 2017). Changes in these features are most noticeable over time in extinct forms (Li *et al.* 2016), as they had adapted to live in the wild (cool, dry habitat) and fed exclusively on grasses or the shoots and leaves of trees and shrubs. Early Pliocene ancestors (*Astrohippus, Dinohippus*) mainly consumed fibrous grasses and the leaves of trees and shrubs, but their diet changed constantly according to the dynamics of the climate as it headed toward aridization (Famoso *et al.* 2013).

These findings serve as one of the most convincing pieces of evidence in the process of the reconstruction of the ecology of paleobiocenoses, mainly phytocenoses, as a food site for extinct herbivorous mammals. The environmental data obtained are often supported by the results of studies of carbon isotopes of teeth and enamel (MacFadden & Shockey 1997; Wang *et al.* 2008; Feranec *et al.* 2009; van Dam & Reichart 2009).

Studies have shown that the multi-proxy approach characterizes the ratio and action of carbon and oxygen isotopes in enamel, as well as the meso- and microwear of horse teeth, which thus characterizes the diet of extinct forms of equids (Zhang *et al.* 2009; Ecker *et al.* 2013; Tütken *et al.* 2013; Gocke *et al.* 2014). Stable isotopes in the bioadaptation of extinct horse forms and the dependence of their ratio (oxygen and carbon) on seasonality and temperature provide good, strong indicators for paleoecological reconstruction (Palmqvist *et al.* 2003; Koch 2004; Hoppe 2006; Desantis *et al.* 2009; García García *et al.* 2009; Tütken & Vennemann 2009; Kohn & McKay 2010; Matson & Fox 2010; Fabre *et al.* 2011; Yann *et al.* 2013; Zanazzi *et al.* 2015), that is, the reproduction of species habitat in paleobiocenoses (Hoppe *et al.* 2004a; Hoppe *et al.* 2004b; Koch 2004; Hoppe *et al.* 2005; Deng 2006; Rink *et al.* 2008; Biasatti *et al.* 2012; de Winter *et al.* 2016). The analysis of stable isotopes in tooth enamel is one of the most reliable methods of determining the diet and use of fodder resources by extinct mammals through the conservation of the original carbon isotopic position under certain environmental conditions (Iacumin *et al.* 1997; Deng *et al.* 1999; Fox & Fisher 2004; Higgins & MacFadden 2004; Feranec& MacFadden 2006; Joannes-Boyau & Grün 2011; Tian *et al.* 2013; Domingo *et al.* 2016). Microwear also testifies to the effect of seasonal changes in the natural diet of horses and opens the possibility of testing hypotheses about the size of natural populations or the qualitative composition of horse taxa at different stages in their evolution (Kaiser & Fortelius 2003; Grün *et al.* 2010; Rivals *et al.* 2015).

Paleoecological studies in recent years and the resulting evolutionary-morphological data on horse nutrition indicate that most Late Pleistocene Equidae had mixed feeding patterns in nature and had optimal habitat conditions (Brasser 2012; Pushkina *et al.* 2014). Such conditions could be related to a variety of environmental factors such as ecotope differentiation, temperature dynamics, taxon migration, etc. (MacFadden *et al.* 1994; MacFadden & Higgins 2004; Wang *et al.* 2006b; Zhang *et al.* 2012; Pérez-Crespo *et al.* 2016; Pérez-Crespo *et al.* 2017; MacFadden 2008). Equid ancestors evolved from biocenoses with large, occasionally rare, nutrient-rich herbs, to drier biocenoses (Vollmerhaus *et al.* 2002; Famoso & Davis 2014).

The complexity of the occlusal surface of teeth and enamel in horses was fixed at the time of the Middle Miocene to the Holocene, the evidence for this being drawn from current knowledge of long-term climate changes, the steady direction of climate aridization, and periods of climate cooling. These changes to dental structure were accompanied by a process of increased rate of tooth abrasion and the establishment of the evolution of hypsodont and rootless teeth (Famoso & Davis 2014). In this process, phytoliths played a significant role in the overall evolution of both grasses and horses (Strömberg *et al.* 2007; Erickson 2014; de Winter *et al.* 2016).

Other paleoclimatic reconstructions should also take into account other factors such as the position of the teeth and the jaw rows, the mechanics of functionality, and seasonal variations in feed mineralization, among others (Bryant *et al.* 1996; Weeks *et al.* 2003).

The history of the evolution of the genus *Equus* in the Pleistocene of Eurasia includes representatives of different geological ages in the following sequence: *Equus stenonis – E. sussenbornensis – E. mosbachensis – E. taubachensia – E. abeli – E. latipes – E. caballus*. They may form one cladogenetic group. The other group includes *Equus gmelini* and *E. przewalskii*. Scientific discussions regarding the ranking of the taxonomic representatives together with their status continue (MacFadden *et al.* 1994; Cucchi *et al.* 2017).

Morphology and function data

This is one of the most theoretically and experimentally important chapters in studies of horse teeth. Different fields of study of teeth have considered the morphological changes to onto- and phylogenesis (Wolf & bernor 2013; Lazaridis & Tsoukala 2014), the structure of their constituent elements, the features of the process of picking and chewing food, and the characteristics of the various factors influencing these processes (Odor *et al.* 1999; Pasteris & Ding 2009; Hövener *et al.* 2012; Dixon *et al.* 2013).

The problem of the functionality of the teeth of equids and their wear are both analyzed (Boyde 1997; Dixon & Dacre 2005; Bendrey *et al.* 2009; Bendrey 2011; D'Ambrosia *et al.* 2014). Herbivores among terrestrial animals are a good example of adaptative and correlated evolution, which is particularly evident in the phylogeny of horses (Currey 1999). Horse teeth wear with relative intensity and often due to the effect of phytoliths, this providing an example of the interdependent evolution of ruminants and plants (Erickson 2014).

Enamel and dentin ridges are of paramount importance when grinding feed material. Since these ridges are contained within the outer cement, it is logical to assume that if the structure decreases in size over time, so too do the anatomical details contained within it (Carmalt & Allen 2008).

The process of natural compensation for the relatively high rate of tooth tissue loss in herbivorous mammals includes 1) a relatively large area of chewing surface (Famoso & Davis 2016); 2) the replacement of deciduous teeth with permanent teeth (the horizontal replacement sequence is unique to elephants and manatees) (Upjohn *et al.* 2013); 3) continuous growth due to root loss as observed in, for example, rodents and lagomorphs (du Toit & Rucker 2013; Griffin 2013); and 4) hypsodonty, which is also associated with root loss, and is evident in the evolution of horses (Rivals *et al.* 2015; Barrón-Ortiz *et al.* 2017).

Effective chewing function is achieved through the somewhat rough and complex chewing surfaces of teeth due to the enameling of the enamel loops and the perfection of the ultrastructure (Wang *et al.* 2006a). This improves the process of enzymatic digestion in the gut of horses. The presence of the rough friction surface of the teeth increases the risk of the rapid wear of the teeth opposite. There is here a certain functional and, accordingly, mechanical contradiction – the preservation of the rough and, at the same time, the solid chewing surface (Boyde 1997).

The protein organic matrix in enamel is largely mineralized and replaced by hydroxyapatite and this mineralization is a relatively long process (Shaw *et al.* 2008; Bendrey *et al.* 2009; Bendrey 2011; Bendrey *et al.* 2015). However, after the long period of mineralization, the enamel becomes relatively solid. For example, in the third permanent molar of a human there is a temporary delay between the process of "maturation" of the enamel on the conid tips and its appearance over the dental bone (eruption), and this may take as many as 10 years to complete. Horses do not have such a long time in their life spans to allow the mineralization process to slow to such an extent, and their enamel never reaches the desired hardness found in mammals where the development process can afford to be slower, such as in the Proboscideans (Boyde 1997).

During the evolutionary process there was an attachment of cement to the tooth enamel in the majority of herbivores, this being achieved due to the natural roughness of the enamel as a result of the sudden termination of the secretion process. In horses, however, the completed, mature enamel surface is released by the maturation stage ameloblasts (Vollmerhaus *et al.* 2002; Ferguson *et al.* 2004).

Problems of tooth hardness and features of tooth abrasion as the most functionally active structures are always relevant (FORTELIUS & SOLOUNIAS 2000; FAMOSO *et al.* 2013; TÜTKEN *et al.* 2013; FAMOSO & DAVIS 2014; VIRANTA & MANNERMAA 2017). This issue relates specifically to the incisors (SCHROCK *et al.* 2013) and to the molars (RAMZAN & PALMER 2010; SAHARA 2014). The problem is found in the microstructure of enamel and cement, and has been studied in a number of papers in recent years (FALGUÈRES *et al.* 1997; MUYLLE *et al.* 2000, 2001; DU TOIT*et al.* 2008a; RAMZAN & PALMER 2010). In this microstructure, the bundles of hydroxyapatite crystals (prisms) have an orientation that is more or less perpendicular or at a slight angle to the surfaces of wear or abrasion (VON KOENIGSWALD & SANDER 1997).

It is established that the constituent parts of enamel are 96-97% a mineral substance, up to 4% organic substance, and about 1% water (CURREY 1999; DIXON *et al.* 2013). Data on the layered structure of mammalian teeth, including enamel (VON KOENIGSWALD 1980; FERGUSON *et al.* 2004), dentin, and periodontium (DU TOIT *et al.* 2008a,b; DIXON *et al.* 2013; STOCK *et al.* 2014) were confirmed. The peculiarities of the alveolar structure of teeth and jawbones are characterized (HENNINGER2003; IACOPETTI *et al.* 2015). KILIC *et al.* (1997a, 1997b, 1997c) isolated different types of structures in the radial enamel of horses, their findings being presented in a series of publications in 1997 and later confirmed and detailed by other researchers (ODOR *et al.* 1999; DU TOIT *et al.* 2008b; DIXON *et al.* 2013). At the turn of the century, studies were conducted to investigate the ultrastructural morphology of mammalian enamel and dentine (BOYDE 1997; WANG *et al.* 2006a) followed by a more in-depth study of the chemistry and functionality of these structures (PASTERIS & DING 2009; DE DIOS TERUEL *et al.* 2015; DE WINTER *et al.* 2016; HOPKINS *et al.* 2016).

The use of new techniques characterizes the current stage and level of research in equine dentistry (HÖVENER *et al.* 2012; BARATT 2016; VERAA *et al.* 2009; ENGLISCH *et al.* 2017). This is especially true in areas such as tooth fluoridation (MACICEK & KROOK 2008; PASTERIS & DING 2009; CHOUBISA 2010, 2013) and in-depth studies of dental morphology and enamel based on computed tomography (VERAA *et al.* 2009; WINDLEY *et al.* 2009; ENGLISCH *et al.* 2017). Advances in this field have made it possible to learn more about the phenomenon of dental fluorosis and to protect teeth from the effects of acids, as well as the processes of the negative impact of water enriched with fluoride (F^-) on enamel (MACICEK & KROOK 2008; CHOUBISA 2013). The results of the computed tomography of the jaw are widely used in the diagnosis and treatment of animal tooth disease, including in horses (FITZGIBBON *et al.* 2010; BARATT 2016).

Isotope analysis of the solid structures of the skeleton and teeth has found widespread application in practical horse dentistry (DELGADO HUERTAS *et al.* 1995; BRYANT *et al.* 1996; WEST *et al.* 2004; BENDREY *et al.* 2009). The scope of this method is widely known and relates to the improvement of the technique in application with horses (ZAZZO *et al.* 2012), determining the diet of the animal (WEST *et al.* 2004), especially extinct forms with subsequent reconstruction of their habitat (DE WINTER *et al.* 2016), and the influence of isotopes on the structure of enamel by considering damage to the enamel (PASSEY *et al.* 2002; BENDREY 2011).

Recent equine dentistry

The analytical data presented in this study on the achievements in the field of tooth structure and enamel at the level of ultrastructure and their chemical composition have almost always been aimed at the prevention of diseases, treatment, and the improvement of animal welfare in husbandry practice. A large amount of experimental work was devoted in this field of research to practical recommendations for the correction of common health issues (UPJOHN *et al.* 2013). The latest techniques in the study of pathological changes in teeth and enamel are also offered (COOK 2011; BARATT 2016; BORKENT & DIXON 2017; ENGLISCH *et al.* 2017). In 2011, the most recent analytical work on the scientific and practical achievements in horse dentistry was published (RAMZAN 2011).

Diseases, pathologies, and injuries to the teeth in horses, their heterogeneity, types, and causes of the consequences of these processes were analyzed (EDMUNDS *et al*. 1988; CARMALT & ALLEN 2008; MASLAUSKAS *et al.* 2008; SHAW *et al.* 2008; COOK 2011; CHINKANGSADARN *et al.* 2015; BORKENT & DIXON 2017). The set of studies in this area relates to the interrelation of the action of microorganisms in periodontal diseases (DIXON *et al.* 2013), the condition and structure of the enamel (SIMHOFER *et al.* 2008; HOPKINS *et al.* 2016), and the tissues of the digestive tract (DU TOIT & RUCKER 2013). On this basis, preventive recommendations for annual dental care, especially for young equines, as well as for individuals with pre-existing dental problems, were developed and proposed (UPJOHN *et al.* 2013; SUSKE *et al.* 2016b). Several articles deal with dental disorders and their impact on horse well-being (MASLAUSKAS *et al.* 2008; SIMHOFER *et al.* 2008; BORKENT & DIXON 2017). Considering the clinical importance of dental disorders and their role in maintaining the health and welfare of horses, disease prevention is considered a priority area of research (MASLAUSKAS *et al.* 2008, 2009; DU TOIT & RUCKER 2013; BARATT 2016).

The pathogenesis of equine dental pulpitis using computed tomographic and histological findings in extracted teeth has been analyzed, and equine dentinopulpar mineralization described (CASEY *et al.* 2015). The main causes of caries formation due to dysbiosis, bacterial action, and the presence of an acidic environment, which are both necessary for the processes of digestion of food, are named (EDMUNDS *et al.* 1988; HOPKINS *et al.* 2016; BORKENT & DIXON 2017). The morphology and anatomy of tooth enamel, including caries and their manifestations, causes, and methods of treatment have been analyzed (BORKENT & DIXON 2017).

The use of 2D and 3D CT as a new clinical diagnostic tool for dental disease and to assist in the selection of the most appropriate treatment protocol was described by the sequential sectioning of individual horses' teeth and subsequent histological examination (WINDLEY *et al.* 2009). Evidence of changes in tooth morphology was provided, especially in the early stages of pathological condition. Digital radiography confirms the evidence of extensive alteration to peripheral tooth enamel when the enamel infundibula distort the radiological endodontic anatomy of the teeth. The clinical results obtained and further laboratory studies confirm the effectiveness of the endodontic treatment of equine teeth (SUSKE *et al.* 2016). The general application of this seemingly simple and accessible method in practice is not yet generally accepted, and experts continue to engage in research in this direction.

Many studies have shown that in ontogeny the tooth begins to develop at the moment of the mutual interplay of two tissues – the ectomesenchyme and its covering plate of ectodermal origin. The mutual induction of the cells of these tissues is the main mechanism in the initiation of tooth morphogenesis. Next comes the process of forming a layer on the tooth, with this determining its shape, and the last phase is histogenesis or the formation of mineral structures (dentin, cementum, and enamel) and organic structures (miasms and periodontium) (DIXON *et al.* 2013). The ectomesenchyme becomes thick and forms a tooth particle from which the cement and periodontium enamel arise. Ameloblasts produce very tall cells that secrete a substance from which an interprismatic matrix is formed (a structure similar to a honeycomb). In these cells, a substance is formed from which prismatic crystals of hydroxyapatite arise. The primary enamel separates the ameloblasts and odontoblasts. Ameloblast cells produce proteins, and an enamel-dentine structure is formed. At that moment, the mineralization of the enamel begins. The finalization of enamel maturation often takes a long time (FERGUSON *et al.* 2004; HOPPE *et al.* 2004b; BENDREY *et al.* 2015).

The embryonic stage of development of separate tooth structures is a relatively well-researched topic in previous research. It was noted, that hydroxyapatite crystals come into contact with the primary enamel. Amelogenins are the main proteins in the organic matrix of enamel, actively participating in the next stages of mineralization. Amelogenins can form sphere-shaped densities, named nanospheres. These bind to the surfaces of the initial crystals, concentrate around them, and stabilize the organic matrix of the enamel. Consequently, the crystals have no fusion, rise in height, and are coarser. In the final stages of crystallization, the nanospheres disappear, and the crystals remain surrounded by amelogenin, preventing their fusion and stabilizing the crystals (PASSEY *et al.* 2005; RAMZAN *et al.* 2010).

A brief review of the above data presents the embryogenesis of teeth as an evolutionary process resulting from changes in the primary oral epithelium and mesenchyme with subsequent differentiation of enamel structures into ontogeny and phylogeny. Their further evolution took the direction of more effective adaptation to environmental conditions, mainly taking and processing food in animals of different directions of ecological radiation, mainly herbivorous and predatory. Food intake and chewing, as well as the structure of the tooth and especially the enamel, developed in horses in the direction of the more efficient grinding of cellulose and the more efficient processing of this cellulose by bacteria in the digestive system (EDMUNDS *et al.* 1988; MLAKAR *et al.* 2014). The chemical composition of the enamel also changes during this process (HOPKINS *et al.* 2016) along with its microstructure (MLAKAR *et al.* 2014) and microhardness at the first and second ontogenetic levels (MUYLLE *et al.* 2001; FITZGIBBON *et al*. 2010; DU TOIT & RUCKER 2013).

Important data are obtained in the analysis of isotopes of oxygen, phosphorus, carbon, and calcium in the teeth of different taxa (HUERTAS *et al.* 1995; BRYANT *et al.*1996), in determining the growth rate of enamel in ontogeny (three growth zones are highlighted: mature enamel, maturing enamel and enamel matrix formation) (BENDREY *et al.* 2015) as well as determining the individual age of teeth (ŁUSZCZYŃSKI & PIESZKA 2011).

Our experimental studies supplemented the data on enamel ontogenesis, namely a more tight connection (fusion) of ameloblasts in dentin with enamel structures at the EDJ boundaries was noted. In contrast to the OES border, the EDJ border has a very rough surface, which greatly strengthens the tooth structure, minimizing the possibility of its cracking during functional loading (pressure).

Conclusions

This review of articles that consider horse tooth enamel allowed for the definition of the basic directions of research on the analyzed topics in theoretical and practical aspects. It has been confirmed that in the last 50 years there has been a rapid increase in the quality of publications, caused by an increased interest in the problem of horse tooth morphology, function, and health in connection with the requirements of veterinary medicine. There has also been an expansion of the publications' thematic orientation based on the formulation of bold hypotheses and the devising of experiments. The expansion in this field of study coincided with the introduction of new, modern techniques and a more technically advanced laboratory-experimental base. Progress has been made in functional morphology, ontogenetic, and evolutionary processes with the use of x-ray, digital radiography, 2D and 3D computed tomography, analysis of stable isotopes, tooth fluoridation, and histological findings.

Particular attention should be paid to the achievements in the study of enamel ultrastructure and the related structures of dentin and cement, made possible by the use of the scanning electron microscope. In-depth histological studies of the processes of enamelogenesis, cementogenesis, dentinogenesis, microhardness, and tooth abrasion are likewise of great importance.

Studies of the chemical composition of teeth and enamel using isotope analysis methods (including phytoliths) have shown increased activity, the results of which are now effectively employed in paleoecological reconstruction, determining the quality of plant food, determining the individual age and rate of tooth growth, and preventing and treating the diseases of the dental system in equids. A considerable number of publications in the field of veterinary medicine are devoted to these last topics along with the development of recommendations in dental practice. The layered structure and crystalline-prismatic structure of enamel, represented in the form of three (I, II, III) types with decussations, has allowed the causes and processes of the manifestation of dental disease to be better understood and accordingly, for treatment to be more effective.

An important outcome of this study of the data of the last ~50 years is the recognition that mathematical methods for the confirmation of results in experiments on the dental system and the chewing apparatus as a whole have become much more common in the theory and practice of odontology. Almost 40% of the published papers contained statistical analysis data in the form of tables, graphs of dependencies, diagrams, and schemes. The findings thus obtained are perceived as scientifically sound, substantiated, and convincing, especially with respect to the biology of horses, their evolution, as well as animal husbandry and veterinary practice.

Funding

This review was supported by the International Visegrad Fund (52010462).

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https://doi.org/10.1016/j.epsl.2012.04.013

Author Contributions

Research concept and design: P.C.; Collection and/or assembly of data: V.D.; Data analysis and interpretation: V.D.; Writing the article: V.D.; Critical revision of the article: K.S.; Final approval of article: V.D.

Conflict of Interest

The authors declare no conflict of interest.

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