New frontiers in proboscidean research

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SUMMARY: The early proboscideans like anthracobunid and moeritheres were lophodont and cuspidate, whereas the modern elephant are hypsodont. The proboscidean dental enamel ultrastructure also shows a great deal of variation since the time of their evolution in Eocene. The change in mammalian dental morphology and enamel microstructure is related to dietary habit and function. The enamel types are responsible to accommodate and dissipate particular kind of tensile stresses produced during various masticatory functions of the molars. Despite so much available data no work has been undertaken to study the driving forces that brought about the change in dental morphology and enamel microstructure among the proboscideans and their interrelationship.
In order to solve these issues it would be important to develop some Finite Element Analysis (FEA) models of proboscidean molars. The FEA has enormous flexibility of applying load from various angles and observing stresses in a structure in three dimensions. The stresses, mainly tensile stresses, may be accommodated by changing either composition or the structure of the material. The composition of enamel has remained same throughout the evolutionary history of the enamel but enamel structure has been found to vary considerably. This change in structure is to provide better reinforcement to the dental enamel against different loading conditions.

1. Origin of the Concept

Proboscidean evolution and dental morphology have been studied in great detail by many workers. The latest works on these topics have been compiled by Shoshani & Tassy (1996) in a comprehensive volume on Proboscidea. In contrast, the work on the proboscidean molar enamel has not attained much significance and attention of many scientists. Though the biomechanical study provides important clues to study the functional evolution of molar morphology in relation to the enamel microstructure among Mammalia, it has not been studied systematically among the proboscideans. Proboscidea is one of the important groups of mammals, which have greatly changed their molar morphology and enamel microstructure since the time of their origin during middle Eocene time.

In the evolutionary history of the proboscideans, the teeth of early anthracobunids and moeritheres were lophodont and cuspidate, whereas the modern elephant developed large hypsodonty (Kozawa 1978). This change in dental morphology from lophodonty to hypsodonty has frequently been noticed among various groups of mammals. Pfretzschner (1992a) noticed this evolutionary pattern in larger mammals and suggested a biomechanical model for hypsodonty in large mammals.

Despite these studies it still remains the topic of the debate as to how enamel microstructure is related to dental morphology, especially among proboscideans. Further, it is also so far unknown what the driving factors were that brought about the change in dental morphology and enamel microstructure among the proboscideans.

The proboscidean molar possesses a complex enamel microstructure (Kozawa *et al.* 1991). This complexity in structure has evolved through time with the functional evolution of dental morphology (Kozawa *et al.* 1986; Pfretzschner, 1992a).

The structural complexity in proboscidean enamel occurs at the prism level. The prisms as defined by Koenigswald & Sander (1997) are the bundles of apatite crystallites which extend from the enamel-dentine junction (EDJ) to the outer enamel surface (OES) without interruption. The prisms do not split or merge and are equal in size with a distinct prism sheath. The prisms have the ability to decussate in layers (Hunter Schreger Bands) in groups and individually (Koenigswald & Sander 1997).

Eocene forms such as anthracobunids and moeritheres possess simple enamel type in lophodont molars, in which the Hunter Schreger Bands (HSBs) are slightly curved and arranged in an orderly manner. The enamel prisms are arched with a prism diameter of about 5-6 microns. The recent hypsodont elephantids such as *Elephas* and *Mammthus* possess a special gingko-leaf like prism pattern, which is 7 microns wide.

Kozawa (1993) and Kozawa *et al.* (1989) suggested that the changes in proboscidean molar morphology and enamel microstructure were the result of change in dietary habit. This indicates the functional significance of the different molar types and enamel microstructure in proboscideans.

In order to comprehensively tackle these issues it is essential to examine the molar morphology and enamel microstructure in extinct and extant proboscidean genera. There is a general consensus that development of a particular type of enamel microstructure depends on the type of stresses produced during various masticatory functions of the molars like chewing, crushing, grinding and slicing. Pfretzschner (1992a, b) studied the development of three types of dental enamel in herbivorous mammals. He offered a biomechanical analysis to study the relationships between the load and enamel prisms orientation in hypsodont molars. In addition, Srivastava (1998) and Srivastava *et al.* (1999) also studied the relationships between the load and enamel types among rodent incisors and also among the unicuspid teeth of mammals and reptiles. Such analysis has so far not been done for the proboscideans, which possess a 3-D enamel microstructure with a large variety of lophodonty and hypsodonty (Pfretzschner 1992a).

3. Definition of the Concept

Major categories of enamel are “prismless”, which is present in almost all the extinct and extant reptiles (except *Uromastyx*), and “prismatic” (present in almost all mammals). The prismatic enamel in mammals with hypsodont teeth possesses three different enamel patterns, namely vertical HSBs in Rhinocerotoidea and Astrapotheria, modified radial enamel (MRE) in Artiodactyla, Perissodactyla, Marsupialia etc., and 3-D enamel in Proboscidea. Pfretzschner demonstrated (1991) that these three types of enamel in herbivore mammals are due to the changed mechanical situation in hypsodont teeth. For his studies Pfretzschner (1992a) used a computer program based on the Finite Element Method and calculated different types of stress patterns in the enamel of hypsodont molars.

In Finite Element Analysis (FEA) a body or structure may be divided into smaller elements of finite dimensions. The original body or structure is then considered as an assemblage of these elements connected at a finite number of points called nodes. Then stresses and strains in the structure are evaluated using the material properties of the body or structure like Young’s Modulus and Poisson’s Ratio values, and shape and dimensions of the body. The formulations are evaluated and solved in a software program based on FEA. Proboscideans offer some of the best material for such analysis because they have greatly changed their molar morphology from lophodonty to hypsodonty, and the enamel microstructure from the arched pattern of *Moeritherium* and other Eocene proboscideans to the key-hole pattern of *Steogodon* and *Mastodon* (Miocene to Pleistocene), and finally to gingko-leaf pattern of *Mammut* and *Elephas* (Pleistocene to Recent). This classification of proboscidean molar enamel is based on the characteristics of enamel prism cross-section, distribution and orientation of prism-sheath, and Hunter-Schreger bands (Kozawa 1978, 1993; Pfretzchner 1992b).

As stated earlier, the main functions of proboscidean molars are chewing crushing and grinding (Pfretzschner 1992b). To see the effect of these functions and developmental patterns in the molar enamel, some mathematical models may be proposed using FEA. With the help of FEA deformation and stresses in a structure can be calculated at the given load conditions and accordingly changes can be made in the structure to withstand the load. These changes can be made either in the material properties by changing the composition of material and/or in the structure. In molars, the constituent material "hydroxyapatite" is the same throughout the evolutionary history of enamel but internal structure has been found to vary considerably. This structural variation obviously provides better reinforcement to the dental enamel against different load conditions. Apart from these, in proboscidean molars, the molar morphology has also been found to vary greatly throughout their evolutionary history. The change in the proboscidean enamel microstructure needs to be studied in detail in relation to the change in molar morphology, and thus offers special consideration and attention.

4. Review of research and development in the Subject

The biomechanics of hard tissues in general and dental enamel in particular have not been studied by many workers. Priviously, Koenigswald *et al.* (1987) and Pfretzschner (1992a, b) have made attempts to study the development of HSBs and hypsodonty in mammals, using the Finite Element Method. Lately Srivastava (1998) and Srivastava *et. al.* (1999) studied the biomechanical evolution of rodent incisor enamel and conical teeth. While studying biomechanics of conical teeth and rodent incisors, Srivastava (1998) and Srivastava et. al, used mechanical data (Young's Modulus and Poisson's Ratio) for enamel and dentine as suggested by Waters (1980). Pfretzschner (1992a) used mechanical data as suggested by Grenoble *et al.* (1972) for the hard tissues apatite.

In addition to these studies, Rensberger & Koenigswald (1980), Rensberger & Pfretzschner (1992) and Rensberger (1995) studied the functional significance of the enamel structures in rhinoceroses and astropotheres and the stress pattern in some Cenozoic mammals.

The proboscidean enamel study remains an area which has never been dealt with systematically except in the work of Kozawa (1977) and Kozawa *et al.* (1986). Kozawa studied the variation of enamel structure in elephant molar teeth (Kozawa 1977a, b; Kozawa & Tateishi 1983; Kozawa 1993) and tusks (Kozawa 1982, 1985; Kozawa *et al.* 1989). A comparative histology of four lineages of Proboscidea was studied by Kozawa in 1987. In 1991 Kozawa *et al.* related the pattern of HSBs to the molar form and masticatory function. They found that HSBs developed from a simple form to a complex one. They classified the developmental pattern of HSBs as (1) irregular, (2) horizontal, (3) vertical, (4) reduced, or absent and (5) special type.

The enamel is an anisotropic material but for biomechanical study, its not possible to consider anisotropy, which inturn would affect the mechanical properties of the material. For comparative study the enamel may be considered as an isotropic material and then the mechanical properties of isotropic hydroxyapatite may be computed for comparative results. The mechanical properties of hard tissues apatite were calculated by Grenoble *et al.* (1972) and Waters (1980). Besides these, the mechanical properties of animal horn, hoof and hair were calculated by Rama Rao and Ahmad (1993). Apart from these studies no biomechanical data have been generated so far.

5. Significance of the Concept

Biomechanical studies have not attained the importance they deserve and there is no data on biomechanics of various calcified tissues apart from some isolated work. Biomechanics has tremendous application in calculating the tensile and compressive strength of calcified tissues.

The biomechanics of dental enamel provides evidence for determining various evolutionary grades in the dental enamel and studying their stability at various load conditions. In the future, human dental enamel can also be studied in a similar way to determine its strength in different individuals and may suggest artificial ways to better its performance.

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