Dental fossils and the fossil record

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Recent advances in developmental biology have provided a new matrix of questions which may be posited in investigating the operational processes involved in either the evolution or special creation of life on this planet. It is no longer enough to simply view a fossil as a static component of a phylogeny constructed largely on only morphological aspects. Developmental biology views the fossil as the end product of a long sequence of highly complex regulated processes which when subjected to mutational processes will exhibit perturbations in the system. The essential question when evaluating the fossil evidence will be: does the fossil record demonstrate evidence for the gradual establishment of the numerous developmental and regulatory developmental sequences, or does the fossil evidence support the sudden appearance of numerous complex forms which have already established developmental sequences? Furthermore, with respect to the creation hypothesis, does the fossil evidence support changes in animal dental morphology which can be explained by loss of information mutations in the developmental sequence cascade? This paper will examine the jaw and tooth (maxillary and occlusal) fossil evidence in light of emerging developments in developmental biology.

Due to their durability, fossil teeth and jaws may represent the only available evidence for the existence of an ancient animal. As a result, some phylogenies rely heavily on dental remnants in establishing the position of a particular animal. Many paleontologists have chosen to view jaw and dental morphology without regard for developmental biology, concentrating only on varying aspects of morphologies, either gross or microscopic, to establish to a supposed pattern of evolutionary development.

Recent research involving various aspects of the developmental cascade (the embryological origin) of the teeth and jaws has revealed an amazing complexity involving numerous subsystems which are very highly integrated, regulated, and constrained in every animal dentition studied. The fossil record of dental and jaw development must be re-examined in light of this new informational matrix.

It is no longer legitimate to investigate the evolution of the jaws and teeth without considering the operational processes which affect and control the developmental cascade. Complexity theory views the developmental cascade of the jaws and teeth as an interrelated system of subsystems which all require specific regulation and control. It is necessary to investigate the specific controls and feedback mechanisms present in this complex system and then search the fossil record for evidences of random mutations affecting this highly integrated system. The dental-jaw system provides an almost ideal system for such analysis, since perturbations in any of several selected subsystems are exemplified by such problems as cysts, tooth crowding, tooth and jaw malposition, tooth hypereruption (growing higher than normal) and/or enamel imperfections.

Genetic diseases known to affect the development of the teeth and jaws have provided further insight to malformations which might be encountered in the fossil record if random mutations were actually affecting or directing dental development. In fact, known jaw and dental genetic malformations only demonstrate loss of information mutations. Moreover, some of the genetic mechanisms directly impacting the specific components of the subsystems in the dental developmental cascade are able to be quantified using knockout animals—genetically altered animals with specific designed genes changed.

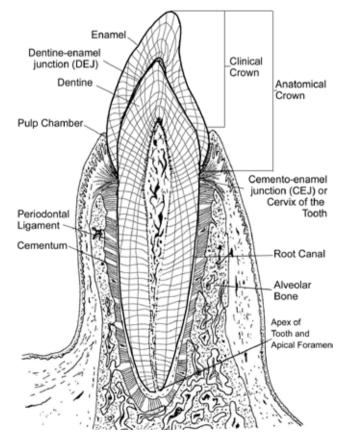


Figure 1. A diagram of longitudinal section of an incisor in situ. Note the highly complex structure of a tooth. Every portion of every stage must be regulated by a complex developmental sequence. Any developmental error or mutation always results in a less than perfect result in one of the subcomponents (from Avery). 44

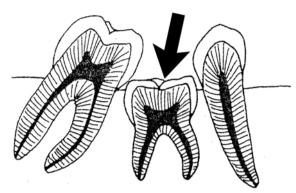


Figure 2. Diagram of submerged primary tooth. This represents less than perfect eruption timing. If evolution actually occurred the fossil record should have untold thousands of examples such as this. There are none (from Avery).44

The diversity of morphology of tooth shape, enamel microstructure, eruption sequencing (the timing of individual tooth emergence from the jaw), jaw shape and size present among the extant and fossil animals provides numerous opportunities for legitimate and necessary transitional forms to be identified, if they existed. In addition to this physical evidence, the supposed gradual evolution of the operational control mechanisms which determine the complex interactions of the numerous subsystems in the dental developmental cascade must be adequately explained by known genetic processes of random mutational effects on complex systems. The physical evidence must therefore be accounted for by available genetic models.

Review of dental and jaw science

Before undertaking an analysis of the evidence which I believe to be lacking in the fossil record, it is necessary to understand the precision and complexity of the dentomaxillary system. An animal depends on very few organs as much as it does its dentition. An inability to adequately obtain energy from one's environment results in death. Failure of any portion of the dentomaxillary system, a system composed of the teeth, the jaws, the jaw joints and the neurological system, could result in suboptimal performance or failure of the entire system. Teeth are formed as single separate units buried in the jaw in small cyst-like structures called developmental follicles. A crystalline structure called enamel is deposited around a developing core or matrix (dentine) so that the hard crown portion of the developing tooth is completely developed before the tooth root is developed, and before the tooth erupts into position (see Figure 1). The developed tooth is then guided into a specific position in the jaw, timed to arrive so that it may meet its counterpart in the opposing jaw (Figure 2). If an animal has a deciduous (milk) dentition, this process must occur twice. The deciduous tooth must not only hold a space for the arriving adult tooth but be able to be exfoliated as the permanent adult tooth erupts from below.



Plane of occlusion

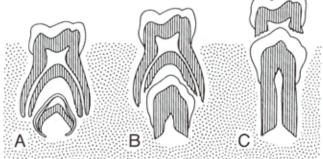


Figure 3. Progressive resorption and exfoliation of primary tooth as permanent tooth develops. Note the close coordination of root development and exfoliation of the primary and adult dentition. There is no fossil evidence for the gradual development of this system (from Avery).44

The rate of growth of the crowns in the developing juvenile must be precisely timed so that there is enough bone in the jaw to accommodate the newly arriving teeth. If the newly developing teeth cannot find adequate space in the jaw, they will be forced to remain unerupted, erupt in a malposition or become impacted (buried below the gum and bone)(Figure 3). While the jaws are developing, the cranium and face are developing as well. The different muzzle lengths of the various kinds of animals must be coordinated with facial and cranial growth as well. With the arrival of a new type of tooth shape, the jaw length must be changed to accommodate it. The jaw joint growth must be precisely controlled to allow for growth in facial height, cranial size, and tooth eruption. If the jaw joint does not coordinate its growth with tooth eruption, an open-bite may occur, preventing ability to incise or chew.

The crown size of the teeth must be precisely controlled in many species. The teeth of many animals are designed to chew against a similar shaped opposing tooth in the opposite jaw. If the teeth are misaligned by even a few millimeters, they may not touch or make contact in such a manner as to cause an open bite. Teeth points or cusps are supposed to contact valleys or depressions in the opposing teeth. If two opposing tooth points contact instead of a cusp and a groove contacting, the jaw will not close.

The teeth are held in the jaw by the periodontal ligaments which are highly developed and vary in structure among the different animals (Figure 4).

The hard outer coating of the teeth is composed of enamel (Figure 5). Enamel is composed of numerous microscopic crystalline structures which resemble soda straws lying parallel to each other. These enamel crystals project from the surface of the underlying dentine perpendicular to the chewing surface of the tooth. The microscopic structure of the enamel crystals varies significantly among the various kinds of animals.

The dento-maxillary complex is a very complex system with highly integrated subsystems which are precisely controlled. Against this backdrop of complexity is found

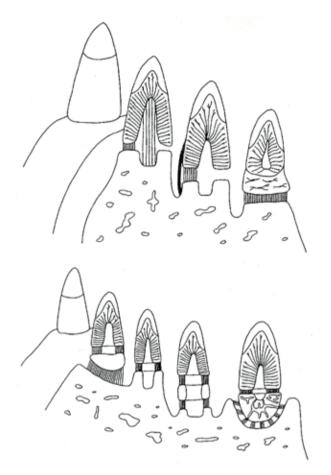


Figure 4. Periodontal attachment types. Note the diversity of attachment mechanisms. Each change would require a series of transitional types (Smith and Samson).¹¹

the highly disparate types of teeth and jaws found in extant and fossil animals. On a purely statistical basis, the fossils should provide ample specimens demonstrating gradual intermediate dento-maxillary morphology if it exists.

Dental apparatus of earliest animals

The presence of the dentomaxillary complex is seen from the earliest fossil specimens (Upper Cambrian 'dated' at 510 Ma) of either pre-vertebrates or vertebrates. These earliest evidences are seen in the tooth or tooth-like structures of conodonts (small, wormlike pre-vertebrate animals). These structures may or may not have been associated with jaws. This evidence challenges the classic theory proposing that skin denticles (structures like the scales on sharks) evolved into teeth as ectoderm* with denticle forming potential. A recent review¹ indicates that new phylogenies incorporating few fossil data challenge the theory that the first dentitions evolved in tandem with the transformation of a respiratory arch into the first biting jaws. Furthermore, Smith and Coates propose that 'in some of the most ancient agnathan vertebrates [jawless fish] a prepattern for gnathostome dentitions already existed in oropharyngeal

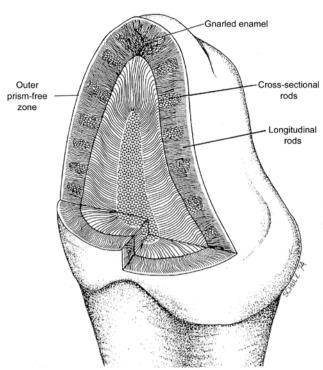


Figure 5. Diagram where the cross and longitudinal section of the human tooth are compared. Note the highly complex microscopic structure of the enamel. This enamel microstructure is different among different genera of animals (from Avery).⁴⁴

mineralized elements*. Moreover, at this stage, dermal and oral denticles were already under separate developmental controls'.² Controls for polarity, anteroposterior shape gradients*, bilateral symmetry, or opposing tooth sets and sequentially spaced unidirectional tooth generations (tooth families) already existed.³ Therefore, it appears as though the complex enamel-dentine developmental cascade was already functioning in the most primitive known postulated vertebrate.

Examples of Panderodontoid conodont elements (teeth), the oldest of which comes from Middle Ordovician rocks, demonstrate only minor variations in size and shape, which from a creationist standpoint would be variations within a kind. There seem to be no abnormally shaped or functionless conodont elements (teeth) which would indicate any mutational system operating or experimenting with tooth morphology. Polarity⁴ exists in all conodont teeth. No evidence of non-polarized elements exists which would indicate mutational experimentation with developmental cascade modification. In addition, each of the conodont elements is composed of enamel and dentine and they are arranged to oppose in pairs, exhibiting bilateral symmetry, and antero-posterior gradation (front to rear symmetry) of shape invariably with an anterior 'symphyseal*' symmetrical element.5

'These finds of early examples of dermal skeletons, together with the absence of any dermal armour or skin denticles in conodonts suggest that

... a divergence had occurred between the developmental controls for producing phosphatic skin denticles* and oropharyngeal denticle* in these three clades of earlies known vertebrates.'5

While scales, teeth, and oropharyngeal denticles each develop from similar odontogenic* units, they have either diverged or have always been distinct in the sense of not carrying the same pattern information. 6

The fine resolution of the fossil record with respect to conodonts indicates, although they are found in isolated elements, that in one family, Panderodontida, morphologic change can be followed in one phylogenetic lineage.⁷ It is unfortunate for the evolutionary model that this fine resolution does not provide any evidence for mutational mistakes or nonfunctional teeth. In fact, it merely demonstrates the genetic stability and tight developmental control of polarity and shape of the previously functioning and highly constrained dental complex. These conodont elements demonstrate minimal variation (possibly variation within a kind), preservation of polarity, and preservation of anteroposterior tooth shape with no significant pathological morphology for thousands of generations.

Dental apparatus of early cartilagenous fish

The earliest chondrichthyians (cartilagenous-like fish) have jaws bearing numerous whorl-like families of successional teeth (teeth which are replaced by other teeth)(Figure 6). In many chrondichthyan subgroups, such as the ratfish, these successional teeth are fused into whorls and/or crushing tooth plates. There are discrete boundaries of morphology which are not bridged by any fossil transitional forms. If the dentomaxillary developmental sequence were plastic enough to accommodate the sharp whorl-like teeth as well as the flat crushing type plates, there should be a fossil record of transitional forms as well. There are none. Smith and Coates note 'patterned differentiation along the biting margin as exemplified by *Heterodontus* [the Port Jackson shark] ... is apparent earliest in hybodontoid sharks whose overall anatomy is ... more advanced than that of cladodonts* and xenocanths*'.8 There is no evidence of a gradual transformation of tooth whorls or the traditional 'sharp shark teeth' to the smooth grinding surfaces of Heterodontus. Smith and Coates continue to add,

'Osteichthyans [fish which have a bony skeleton] ... probably evolved from primitive acanthodians. Teeth are entirely absent in the acanthodian genus known in greatest detail (Acanthodes) ..., but in more primitive taxa, teeth are present. These teeth may be ankylosed to the jaws or take the form of whorls of multicuspid teeth* ... attached to the jaw cartilages by connective tissue.'9

Even in the earliest chrondicthyan dentitions, a two-form gradient is already established for tooth size and shape, and each is dependent upon a 'complex system of reference points for positional information'. Nowhere in the fossil record is there evidence to substantiate the gradual evolution of this system. Therefore, the highly integrated and complex dentomaxillary complex is functioning in primitive chrondicthyans. Smith and Coates observe,

"... some of the most primitive chondrichthyans known in detail, ... Cobelodus and Stethacanthus ... show clear distinctions between teeth on the mandibular arch, in which the complex morphology appears to derive from morphodifferentiation at the cellular stage (cusps formed at the bell stage of tooth development), versus the oropharyngeal denticles which probably acquire morphological complexity at the tissue stage'11

The fact that complex subsystems are functioning in the primitive representatives of the chondrichthyans is beyond dispute. Mutational effects, if they occurred, would be characterized by eruption sequence failure, position alteration, abnormal and useless tooth morphologies and other evidences of experimentation with transitional dentitions. These are not seen. Only functioning useful forms are

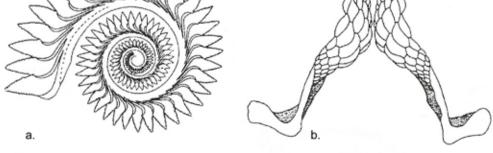


Figure 6. These disparate tooth forms represent but two of the thousands of different types of animal tooth morphology and eruption sequences. This is believed to give ample opportunity for the fossil record to demonstrate transitional developmental sequences. But it gives no such evidence (from Benton). 45

seen. The independence of the dental versus jaw developmental sequences allows for the possible explanation of agnathans. If the one or the other of these developmental modules is knocked out, the other is allowed to proceed in developing. Thus a primitive-appearing fish without a jaw could be the result of a mutation affecting a fish causing the jaw to not develop-possibly similar to a blind cave fish whose eye does not develop. What might be seen, therefore, are loss of information mutations which fits well within the predictions of the creation model. According to Huysseune and Sire, examples are given for a trend for loss of tooth producing 'odontode units in most taxa of vertebrates, except in the chondrichthyan lineage'. 12

Dentine

Dentine, the internal supporting structure of teeth, presents significant problems for a simplistic phylogenetic sequence. According to Smith and Sansom, 'the fossil record of dentine now extends back to the late Cambrian ... followed by rapid diversification of dentinous tissues into the succeeding Ordovician and Lower Silurian periods'. ¹³ The great variety of dentine-like tissues seen in this time period surpasses the diversity seen in the following 450 million years of vertebrate development. ¹³ According to Orwig, as reported by Smith and Samson,

'ascribing a hierarchical order to dentine diversity had been one of the early assumptions that dentine had evolved from bone and that some types in the fossil record represent a transformation series. Neither of these assumptions can now be supported.'14

These authors note 'the terms mesodentine, semidentine, metadentine, and orthodentine are relics from such an approach'. ¹⁴ The apparently unrestricted range of entire types can be explained as a great phenotypic plasticity or a random pattern of histogenic diversity* based on relatively loose developmental controls. ¹⁴ Smith and Samson state,

'... it is not possible to determine the primacy of tissue types at this early time interval, because great phenotypic plasticity is apparent This great diversity of dentine in the fossil record poses a problem for meaningful discussion in cladistic analysis of early vertebrate relationships.' ¹⁵

Smith and Samson further elaborate

'... only then will it be possible to propose the order of tissue evolution and to discard the false concept of a transition series, the latter influencing the names such as, mesodentine, semidentine, and metadentine.' 16

The fact that dentine appears very early in the fossil record, has no legitimate transitional forms, and cannot be placed in any phylogeny lends more support to the creation model of plasticity within a biblical kind.

Tooth emergence sequence

Tooth emergence sequence, the specific order of appearance of the teeth in an animal's mouth, presents additional problems for phylogeny. Evolutionary models have contradictory traditions about the meaning of such eruption sequences. Smith states, 'one tradition is that sequence of tooth eruption is a good phylogenetic character, capable of showing genetic relatedness among species'.¹⁷

He continues, a 'striking finding is that ungulate tooth succession* is much like that of the primates/insectivores'. ¹⁸ A few comparisons cast doubt on the determinative effect of different or varied facial form and the size of the maxillary and mandibular arches or jaws. 'First, within primates there is little similarity among emergence sequences of *Saimiri*, *Cebus*, and *Homo* although all have short faces. *Lemur* and *Papio*, the more dog-faced species, are equally mismatched in sequence', according to Smith. ¹⁹ The same author relates primates and insectivores paired with best match in emergence sequence with ungulates. Smith states:

'... close resemblance pairs the Japanese shrew mole with the duiker, the tree shrew with the pronghorn, the night monkey with the impala, the true lemur with the caribou, the squirrel monkey with the peccary, the cebus monkey with the hyrax, and the chimpanzee with the hippopotamus. It is difficult to imagine a hypothesis about facial morphology that could explain pairings such as these.'20

The absence of a legitimate phylogeny based on eruption sequence is a serious detriment to evolutionary theory. Replacement sequences also do not allow an easy phylogenetic interpretation. The replacement pattern in reptiles occurs in waves, with every third tooth in a sequence being replaced until the last tooth is reached with the sequence beginning again to replace every next third tooth until the last tooth in the arch is again reached.²¹ The replacement method in mammals is complete. There is no intermediate part wave-part complete evident in any fossil. If the evolutionary model is true, there should be ample fossil evidence of two simultaneous events: the gradual transition from wave replacement of teeth to complete replacement of teeth, and the development of distinct species characteristic deciduous dentition. The fossil record does not record the gradual establishment of a characteristic deciduous dentition for any mammal. It seems obvious that intermediate forms of mixed wave and deciduous dentitions should occur in some phylogenies if evolution occurred. Failure of the deciduous dentition to function in space maintenance, as a result of mutations, would also result in abnormal positions of the erupting adult teeth. These failures are not seen in the fossils. The creation model or discontinuity model allows for such absence of transitional functionless intermediates in the fossil record.

Enamel microstructure

The enamel microstructure of the tooth is highly variable both within the teeth of each specific animal and among the animals themselves. The varying types of enamel microstructure do not fit well into any particular phylogeny. Sander states, 'the origin of prismatic enamel* is one of the central questions in the evolution of ectodermal hard tissues'. Numerous models have been proposed, 'however serious doubts emerged about the validity of these models'. Sander questions whether prismatic enamel evolved

'several times convergently in the synapsid clade above the level of the advanced cynodonts, or did it evolve only once in the Tritheledontidae* and then lost repeatedly during mammalian evolution in the Mesozoic?'23 He states, 'It is evident that the prism evolution process itself as well as the possible repeated loss or repeated convergent occurrence of prismatic enamel are in need of an explanation'. 23 There is no consistent pattern of supposed evolution of enamel microstructure which is abundantly obvious. Sander states that research on '43 taxa from all major reptile groups except the mammal-like reptiles indicates that the enamel of reptiles is characterized by great structural variety. A standard type of enamel as assumed by some earlier authors ... does not exist.'24 Sanders states 'the characters that define prismatic enamel such as continuity, perpendicular crystallite secretion and rounded sheath appeared all at once'. 25

Transition from primitive types of enamel to more advanced types and sequential intermediate steps are not found in the fossil record. One evolutionary hypothesis is the multiple convergent scenario in which one author states 'prisms must have evolved two, three, four, or more times, depending on the cladogram used to indicate phylogenetic relationships among synapsids. However, there is currently very little agreement on the interrelationship of the major mammalian taxa.'²⁶ A significant quandry arises from a theoretical standpoint in that the population of just so stories to account for the multiple loss of prismatic enamel have enormous facts to overcome. Sander states,

'there are a number of facts arguing against the multiple loss of prismatic enamel in Mesozoic mammals. The most important is that even taxa that have supposedly lost prismatic enamel show exactly the same kind of synapsid columnar enamel* (SCE) as all the other synapsids with prismless enamel.'²⁷

This statement implies that 'in every case of loss, i.e. transition from prismatic enamel to prismless enamel, the reversal produced exactly the kind of structure that is seen throughout the non-mammalian synapsids ...'.²⁷ When consideration is given to the very complex developmental cascade controlling the microstructure of the enamel, especially at the molecular level, convergent evolution serves as a very weak explanation. In fact, Sander states 'it is obvious that the fossil record cannot currently and my never provide any documentation of this transition as the fossil material known today either exhibits primitive SCE or clearly prismatic enamel. Intermediate stages are missing.'²⁸

Further quandries arise in considering hypothetical ranking of complexity of enamel types. Recent research on the histological structure of hypermineralized tissues in various groups of actinopterygian (ray finned) and sarcopterygian (fleshy finned) fishes and some early tetrapods has revealed the presence of tissues apparently developmentally homologous with the enamel of the teeth of amniotes*. The enamels of some sarcopterygians have patterns of structural complexity described as resembling those found in the

prismless enamel of *Kuehneotherium*, an early member of the mammalia.²⁹ Clemens states.

'It must be stressed that we cannot regard the modifications of nonprismatic enamel into various kinds of complex prismless enamel and then prismatic enamel as an ordered progression. Although the available data suggest that these can be regarded as three grades of structural complexity, the precise evolutionary pathway remains unknown.'³⁰

Additional problems arise in establishing legitimate phylogenies when using enamel types (prismless and prism). There are numerous animals in which different types of enamel (primitive to advanced) are found on the same tooth and in the same dentition. Von Koenigswald states, 'various evolutionary levels can be found in a single dentition. In individual teeth, both primitive and derived enamel types are often combined'. Slavkin and Diekwisch state, 'These levels of control for tooth developmental processes are species specific'. They conclude 'The resultant of these features provide for species-specific enamel crystal patterns in enameloid sharks and bony fishes as well as the enamel of newts, crocodiles, rabbits, and mice.

Genetic mechanisms and the developmental cascade

Current research in genetics and developmental biology have added considerable difficulties to simplistic evolutionary proposals for mechanisms which could possibly account for the gradual development of a functioning dentomaxillary apparatus. The most recent advances in developmental biology provide an additional scaffolding by which the effects of random mutational events interfacing with a highly complex, coupled (several interdependent subsystems), and constrained system may be observed. A special informational characteristic of dental morphology (crown structure), that being lack of post developmental remodeling, allows discrete changes to be observed as a result of genetic interactions. Teeth seem to be a good and durable source of characters for phylogenetic analysis. Jernvall and Jung state 'Moreover these dental characters often appear discrete and heritable and they have different degrees of expression, i.e. different character states'.33 Dental characters reflect not only functional demands and dietary adaptations in the context of phylogeny but also developmental processes controlling morphogenesis.³³ There have been significant advancements in developmental biology, affected by new discoveries in the developmental genetics. This has led to the establishment of a new field of study, 'evo-devo'. A statement from Jernvall and Jung, reveals the importance of tailoring a reasonable genetic mechanism to fit a developmental model: 'Without a doubt, recent advances in developmental biology have enabled us to add new information on the early evolution of higher taxa previously beyond the resolution or reach of the fossil record'.34

The magnitude of the problem is further expressed by Jernvall as he poses the question:

'How can we connect expression data from an ever increasing number of known genes to morphologies that themselves are multivariate entities? This question is especially crucial in evolutionary studies where one needs to detect subtle changes during development because evolutionary patterns, as observed in the fossil record, unusually involve little initial modification of morphology.' 35

Great chasms of improbability loom for the evolutionary model. Tooth morphology is determined by numerous genes affecting a single trait (polygenic). How does a slow (1% or less) gradual change induced by occasional random mutations effecting a genome of thousands upon thousands of genes rise above the level of 'background noise' and beneficially effect any particular portion of the immensely complex dentomaxillary developmental cascade? Balancing selective processes presents an even greater detriment to establishing a small imperceptible change in single tooth or tooth group morphology. In 1982, Butler³⁶ realized significant problems. A characteristic of the dentomaxillary complex is the necessity for continued precision and function. Butler states:

'... this constancy of occlusal relations is presumably due to the functional continuity: transformation is possible only if all the intermediate steps are viable. A cusp that occludes in front of another cusp cannot come to occlude behind it, for at an intermediate stage the two cusps would meet tip to tip, resulting in malocclusion or the elimination of one of the cusps. The complexity of the occlusal system limits the number of ways in which it can change and increases the probability of parallel evolution.'³⁷

It seems that even minor differences in the teeth are subject to natural selection. In addition '... the ontogeny* and genetics of the dentition indicates that the relation between genes and morphological characteristics is very indirect'.³⁶ Furthermore, he states 'It is very difficult to imagine how a cusp, for example, which develops as a fold in a layer of epithelium, could arise as the specific consequence of a genetic mutation.'³⁶ More recently,

Weiss, Stock, and Zhao,³⁸ indicated that examining development in the context of micro-and macroevolution can be used to estimate the extent of phylogenetic drift and defined how much genotype can evolve without a corresponding change in phenotype. Jernvall and Jung state, 'phenogenetic drift is a crucial issue because if phenogenetic drift is common simple genetic reductionism is unwarranted and some higher level developmental principles must be discovered in order to understand the developmental basis of

morphological evolution'.34

It is readily apparent than that given a polygenic trait determined structure (tooth and jaw) operating in a precise and highly constrained system (masticatory) with only limited change tolerated (constrained) and with unknown genotypic and phenotypic drift, current random mutations operating in a balancing selection genetic scenario could not account for the evolution of dentomaxillary apparatus using a reasonable evolutionary driven mechanism. To further complicate the evolutionary model, the enamel types found in the various vertebrates are unable to be accounted for by any known mechanism. Specifically ' ... in this regard we know of no genes who evolutionary arrival corresponds to the origin of a new dental trait, '39 Zhao, Weiss, and Stock summarize by stating 'a number of spontaneous and induced mutations in animals and humans affect dental patterns but none has been demonstrated to play a direct role in specification of tooth type. '40

Recent research seems to be indicating that the dentomaxillary system is actually quire resistant to the effects of random mutations on the developmental cascade.⁴¹ This is necessary to preserve the precise nature in which the occlusal (chewing) system functions. If polygenic effects were not enough to derail any hopes of developing a dentomaxillary complex gradually, the pleiotropic* conundrum adds additional complicating factors. It is well known that there are certain genes which cause far reaching effects, beyond an immediate limited small change in a single organ or structure (pleiotropy). In humans there are about one hundred reported tooth number anomalies⁴² or syndromic conditions that appear to be familiar. These are heterogenous, usually involve some of the teeth of a given type and are typically syndromic, associated with other numerous non-dental anomalies.40 Currently, all known human and animal mutations of the dentomaxillary system seem to indicate a loss of information when they occur. The *Tabby*, *Crinkled*, and *Crooked-tail* laboratory knockout mice share similar phenotypes of smaller teeth (incisors and molars), reduced or fused or missing cusps, and missing third molars.40

Missing incisors in both upper and lower jaws frequently occur in *Tabby* (knockout mice) homozygotes (Tb/Tb) and hemizygotes (Tb/-).⁴⁰ This 'coupled' abnormality of

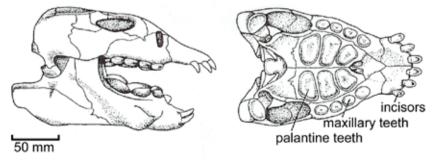


Figure 7. Dentition of a 'Placodont' marine reptile of the triassic. Note the highly diverse palatal dentition (from Benton). 45

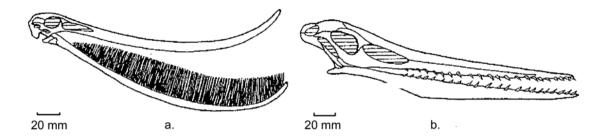


Figure 8. Diversity of pterosaurs. Note the diversity of the dentition especially (a) Pterodaustro with very fine comb -like teeth and (b) Ornithocheirus. There are no transitional forms between these types (from Benton).⁴⁵

multiple dental changes indicates that there is currently no known genetic mechanism which can selectively modify single tooth morphology, which the evolutionary theory requires. Considering the incredible number of different types of teeth (shapes) of vertebrates, logic would mandate that a specific mechanism must be proposed in any theory which attempts to explain the appearance of such diversity. Zhao, Weiss, and Stock state 'whatever the mechanisms are that cause the development of crown morphology, no existing theory adequately explains how the number and arrangement of cusps is produced in the first place.'43

The explanation of a mechanism which can account for the diversity in the numerous types of enamel microstructure is also lacking in evolutionary theory. Amelogenesis imperfecta, a defect in the enamel crystal structure, is the only currently known genetic disorder which singularly affects enamel microstructure and not other components of the dentomaxillary system. However, it affects the enamel of all the teeth present in the dentition. Evolutionary theory must account for the ability to change only specific portions of enamel on only certain classes of teeth. For example, to change the enamel microstructure of the bicuspids and not the incisors, or to change the enamel microstructure of the molars and not the premolars, etc.

It is well known that numerous animals have different types of enamel crystal structure present on a single tooth. The evolutionary genetic mechanism must therefore provide a means to change enamel microstructure in various portions of a single tooth. Experimental evidence demonstrates that this is not currently possible. Furthermore, the only mutations known to affect enamel and dentin are deleterious, and would not improve the strength of an animal's teeth. Control of the development of the jaws and teeth are believed by some researchers to be under the control of separate homeoboxes—homeoboxes are specific microscopic embryonic areas which control animal developmental sequences.⁴⁰

If this is found to be true, incredible improbabilities arise for the evolutionary paradigm. The precision and complexity of the dentomaxillary system has already been established. Separate homeobox control of the different components of the dentomaxillary system would mean that

simultaneous mutations affecting sub-systems such as eruption speed, root length, crown length, periodontal support, tooth arch position, and jaw size would need to occur to maintain the precision of the dental apparatus.

Discussion and summary

The fact that the dentomaxillary apparatus is highly complex has been established. The importance of the numerous subsystems involved is demonstrated by investigations with knockout animals which display the mutational effects of the interruption of a portion of the developmental cascade. These interruptions should be seen in the fossil record if evolution were occurring. Teeth and jaws are very durable and account for a large proportion of the fossil remains of many animals. Close examination of the fossil jaws and teeth should represent a 'snapshot in time' of many of the intermediate steps in the evolution of the dental developmental cascade if they occurred. Mutational 'improvements' as well as mutational failures should be evident. Failures in one of the subsystems would appear as some type of pathology. This could be dental crowding, unerupted teeth, teeth erupting in the wrong positions, hypereruption or hypoeruption, discoordinate jaw size, mismatching of jaw and tooth size, etc. Given the tremendous disparity in the types of teeth and jaws present in fossils, there should be innumerable examples of intermediate (see Figures 7 and 8) successes and failures of almost every subsystem component of the dental developmental cascade. What is observed, however, is a complete lack of pathology indicating the gradual development of the dentomaxillary apparatus. Considering the enormous amounts of fossil dental and jaw material available, it is statistically unrealistic to assume that no fossil evidence exists of any intermediate dental types. Just because it is possible to arrange different appearing dentitions in a phylogeny, this does not indicate support for the position that they evolved. The engine of evolution, that being genetic mutations, has great difficulty in accounting for the gradual modification of a highly complex integrated and coupled system in small increments. Genetic theory has an even greater difficulty in accounting for such changes in small isolated populations. Tooth and jaw development is

directed by a polygenic mechanism.

This process is even more resistant to modification by random mutational effects. Incrementally small changes in dental morphology caused by mutations would most likely not rise above that of background genetic 'noise', and have absolutely no effect on survival value. To get a glimpse of the immensity of the problem an example should suffice. If a mutation increased the length (mesio-distal or front to back) of a lower premolar, the opposing premolar on the upper jaw would need to have a simultaneous change in its size as well to take advantage of increased chewing efficiency the new mutation might cause. Furthermore, the teeth of the same class (premolars) on the opposite side of the jaw would need to increase in size as well so the bite would not be asymmetrical.

The deciduous tooth occupying the site for the incoming premolar would need to increase its size simultaneously in all four quadrants (upper and lower jaw) in order to save space for the newly mutated premolar. If the deciduous tooth did not simultaneously increase its size, the new premolar could not erupt as there would not be enough space for it to do so. Jaw length would need to be increased simultaneously. Eruption speed, eruption height, root development, etc. must also be coordinated in both the upper and lower jaws and on both the right and left sides. If the new premolars erupted to a greater or lesser height than the previous premolars, there could be additional crowding. Additional problems arise with respect to the mechanism of dental development. Teeth are formed and their crowns are completed before eruption begins. Tooth anatomical form is complete before the structure in which they reside (the jaw) is complete or has reached its adult size.

Therefore any mutational effects on tooth crown morphology would not have any selective advantage unless additional simultaneous mutations occur with respect to jaw size, eruption sequence, or deciduous tooth exfoliation, which would allow the new tooth a timely and precise positioning in the dental arch. Genetic mutations are known to affect the cranio-maxillary dental apparatus and they are all characterized by numerous simultaneously occurring abnormalities (pleiotropy). There is no simple relationship between a small mutation and a small change on a particular tooth. Single mutations have a widespread effect. Therefore it is very legitimate to examine the fossil record for examples of pleiotropic changes. These are simply not seen. It is well known that numerous animals have different enamel microstructure on different portions of specific teeth. Therefore evolutionary theory requires a mechanism to modify the enamel crystal type as it covers different specific portions of different classes of teeth. Once again, there is no mechanism for this in the genetic inventory. In summary, the fossil record demonstrates numerous highly complex coupled dento-maxillary developmental systems which can not be accounted for by any known evolutionary mechanism.

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Glossary

- Amniotes = animals which develop an amnion, an early embryonic structure, including reptiles, birds, and mammals.
- Anteroposterior shape gradients = shape which differs as one proceeds from front to rear. The opposite would be teeth which are essentially the same shape in the front as the rear.
- Cladodonts = most Devonian and Carboniferous shark teeth have a pattern with a single major cusp and smaller lateral cusps above a broad base.
- Ectoderm = outer embryonic germ layer that forms skin, salivary glands, hair, sweat glands, sebaceous glands, nerves, and especially teeth.
- Histogenic diversity = differences based upon the formation or development of tissues from the undifferentiated cells of the germ layers of the embryo.
- *Multicuspid teeth* = teeth which have more than one point or cusp.
- Odontogenic = having to do with the development of teeth
- Ontogeny = the sequence of anatomic development of an embryo to its adult form.
- *Oropharyngeal denticle* = toothlike structures found in the pharynx, or throat area, of early primitive animals.
- *Oropharyngeal* = having to do with the mouth and throat area.
- Oropharyngeal mineralized elements = toothshaped mineralized elements which occur in the pharyngeal, or throat, area.
- *Phosphatic skin denticles* = skin denticles containing phosphates instead of enamelin.
- Pleiotropic = producing many effects in the phenotype, the quality of a gene to manifest itself in more than one way.
- Prismatic enamel = the structural units of the tooth enamel, consisting of parallel rods or prisms composed mainly of hydroxyapatite crystals and organic substance and held together with a cement substance, each prism being enveloped in a sheath, also called enamel rods.
- Symphyseal = having to do with the frontmost portion of the lower jaw where the right and left halves join.
- Synapsid columnar enamel = a subtype of columnar enamel. The columnar units are small, 5–10 microns in diameter.
- Tritheledontidae = a member of the cynodont group—an animal which appears to be very close to being a mammal. The two halves of the lower jaw remained separate (not fused by bone) in the symphysis.
- *Ungulate tooth succession* = the sequence of tooth eruption

and development in the horse like animals.

Xenocanths = a chondrichthyian—an 'early' shark Order Xenacanthidae.

References

- Smith, M. and Coates, M., Evolutionary origins of the vertebrate dentition: phylogenetic pattern and developmental evolution, *European J. Oral Science* 106(Suppl 1):482–500, 1998.
- 2. Smith and Coates, Ref. 1, p. 483.
- 3. Smith, and Coates, Ref. 1, p. 482-483.
- 4. Characteristic whereby asymmetrical shapes have cusp arrangement directed in a uniform antero-posterior position.
- 5 Smith and Coates, Ref. 1, p. 484.
- 6. Smith and Coates, Ref. 1, p. 486.
- 7. Smith and Coates, Ref. 1, p. 488.
- Smith and Coates, Ref. 1, p. 491.
- 9. Smith and Coates, Ref. 1, pp. 492-493.
- 10. Smith and Coates, Ref. 1, p. 494.
- 11. Smith and Coates, Ref. 1, p. 497.
- Huysseune, A. and Sires, J-Y., Evolution of patterns and processes in teeth and tooth-related tissues in non-mammalian vertebrates, *European J. Oral Science* 106(Suppl 1):442, 1998.
- Smith, M. and Sansom, I., Evolutionary origins of dentine in the fossil record of early vertebrates: diversity, development and function; in: Teaford, M., Smith, M. and Ferguson, M. (Eds), *Development, Function* and Evolution of Teeth, University Press, Cambridge, p. 70, 2000.
- 14. Smith and Sansom, Ref. 13, p. 66.
- 15. Smith and Sansom, Ref. 13, p. 77.
- 16. Smith and Sansom, Ref. 13, p. 78.
- Smith, B.H., 'Schultz's Rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates; in: Teaford, M., Smith, M. and Ferguson, M. (Eds), *Development, Function and Evolution of Teeth*, University Press, Cambridge, p. 212, 2000.
- 18. Smith, Ref. 17, p. 218.
- 19. Smith, Ref. 17, pp. 221-222.
- 20. Smith, Ref. 17, p. 222.
- Berkowitz, B.K., Tooth replacement patterns in non-mammalian vertebrates; in: Teaford, M., Smith, M. and Ferguson, M. (Eds), *Development, Function and Evolution of Teeth*, University Press, Cambridge, p. 186, 2000.
- Sander, P.M., Non-mammalian synapsid enamel and the origin of mammalian enamel sprisms: the bottom-up perspective; in: Von Koenigswald, W. and Sander, P.M. (Eds), *Tooth Enamel Microstructure*, Balkema Publishers, Rotterdam, p. 42, 1997.
- 23. Sander, Ref. 22, p. 43.
- 24. Sander, Ref. 22, p. 44.
- 25. Sander, Ref. 22, p. 54.
- 26. Sander, Ref. 22, pp. 55-56.
- 27. Sander, Ref. 22, p. 56.
- 28. Sander, Ref. 22, p. 57.
- Clemens, W.A., Characterization of enamel microstructure terminology and application of the origins of prismatic structures in systematic analyses; in: Von Koenigswald, W. and Sander, P.M. (Eds), *Tooth Enamel Microstructure*, Balkema, Rotterdam, p. 92, 1997.

- 30. Clemens, Ref. 29, p. 105.
- Koenigswald, W., Evolutionary trends in the differentiation of mammalian enamel ultrastructure; in: Von Koenigswald, W. and Sander, P.M. (Eds), *Tooth Enamel Microstructure*, Balkema, Rotterdam, p. 206, 1997.
- Slavkin, H. and Diekwisch, T., Evolution in tooth developmental biology: of morphology and molecules, *The Anatomical Record* 245(2):143, 1996.
- Jernvall, J. and Jung, H-S., Genotype, phenotype, and developmental biology of molar tooth characters, *Yearbook of Physical Anthropology* 43:172–188, 2000; p. 172.
- 34. Jernvall and Jung, Ref. 32, p. 174.
- Jernvall, J., Keranen, S. and Thesleff, I., Evolutionary modification of development in mammalian teeth: quantifying gene expression patterns and topography, *Proc. Nat. Acad. Sci. USA* 97(26):14444–14448, 2000; p. 14444.
- Butler, P.M., Directions of evolution in the mammalian dentition, Systematics Association Special Volume No. 21, p. 241, 1982.
- 37. Butler, Ref. 36, p. 240.
- Weiss, K., Stock, D. and Zhao, Z., Critical Review of Oral Biology and Medicine 9:369–398, 1998.
- Weiss, K., Stock, D. and Zhao, Z., Development and evolution of dentition patterns and their genetic basis; in: Teaford, M., Smith, M. and Ferguson, M. (Eds), *Development, Function and Evolution of Teeth*, University Press, Cambridge, p. 165, 2000.
- 40. Weiss et al., Ref. 39, p. 164.
- 41. Sequence of ordering the various processes of the dental development pathway.
- Shum, L., Takahashi, K., Takahashi, I., Nagata, M., Tan, D., Semba, I., Tanaka, O., Bringas, P., Nuckolls, G. and Slavkin, H., Embryogenesis and the classification of craniofacial dysmorphogenesis in: Fonseca, R. (Ed.), *Oral and Maxillofacial Surgery, 6*, W.B. Saunders Co., Philadelphia, p. 167, 2000.
- 43. Weiss et al., Ref. 39, p. 157.
- Avery, J.K., Oral Development and Histology, 2nd Edition, Thieme Medical Publishers, New York, 1994.
- 45. Benton M., Vertebrate Paleontology, Blackwell Science, 2000.

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