Serial homology: the crests and cusps of mammalian teeth

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I discuss the nature of serial homology. Mammalian teeth have a relatively dense fossil record, which permits an often close reconstruction of the evolution of patterns of serial homology. I identify the main crests of mammalian teeth, summarize their evolution, and provide new names where necessary. Serial homologies can change in evolution, originate, and disappear. They can be partial, unlike historical homologies. Teeth exemplify these phenomena, and their patterns can be viewed topologically as well as in other ways. Some, but not all, crests and cusps of upper teeth appear to be homologous to structures of lower teeth. The pure morphology of Goethe is a living science.

K e y   w o r d s: serial homology, teeth, crests, cusps.

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Introduction

The teeth of most mammals are complicated structures, and their form is not the same from one tooth to the next. Structures on one tooth are, though, usually recognizable on neighboring ones. Such serial homology has patterns, and it is the nature of these patterns which I discuss in this essay. To avoid clutter I give references of two kinds: general ones for nonspecialists, and particular ones where it seems necessary, but I do not try to document everything in detail. Tony Hoffman was a leader in theoretical paleontology, and I dedicate this paper to his memory.

Serial homology

Serial homology is real homology. Repetitive (within-individual) homology, of which serial homology is a special case, does seem to provide an alluring means of establishing historical (among-individual) homology. This is because the development of repetitively homologous structures is presumably, and in a few cases is partly known to be, controlled by copies of basically the same developmental program. A major criterion for the recognition of historical homology is also the possession of a similar developmental pattern. Therefore, if the developmental pattern was continuously similar during the evolutionary path between the forms being compared, repetition of this pattern in each of the forms compared is caused by repetition of basically the same developmental program as in the other form. The correspondence throughout is caused by continuity of information, which is the conceptual basis of homology (Van Valen 1982). (Information is not the same as DNA sequences; even the genes involved in the development of a structure can be lost and gained, as can the specific controls on their expression. It is rather, in this context, the network of developmental control ultimately specified by genes and by the vaguely glimpsed network which controls the genes. I simplify a little.)

Probably this alluring shortcut often gives correct results, but it cannot be relied on to do so, as also happened with the once-popular commonality criterion for the evolutionary polarity of characters (Van Valen 1978). This is because the developmental criterion for recognizing homology is not infallible. There are many cases known (e.g., de Beer 1971; Roth 1988) where homologous structures develop in different ways or in different locations on the individual. They are still homologous because the information controlling their development was continuous through the evolutionary path between them. Development, like anything else, can evolve, and I trust that no one would regard, e.g., the neural tube of vertebrates as representing nonhomologous structures in different groups despite its sometimes quite different modes of formation: folding of an epithelium or splitting of *a* cell mass. The converse, where nonhomologous structures have similar development, is harder to demonstrate because the evidence against homology must be more powerful than the positive evidence of the development itself. (It may also be that such cases are relatively rare ontically as well as epistemically, in reality as well as in our knowledge. I do not know how to investigate this possibility in a realistic way – relevant comparisons are biased from the start.)

But simple outgrowths often happen convergently and develop similarly, as with most of the elements of the auditory bulla of mammals or rhizoids of various organisms. The allantoic placenta of a number of vertebrates is a bit more complex but may rely on a pre-existing general response to the allantoic outgrowth (see Thomson 1988 for this kind of phenomenon.) The only complex case I can think of involves serial homo-

logy in mammalian dentitions. Thenius (1989)has given the best available depiction of the variety of mammalian dentitions and skulls.

Mammalian teeth

Premolars and molars often are quite different from each other in appearance, but they nevertheless seem to be constructed of homologous elements. The same is true for the more anterior teeth and the deciduous teeth, and separately for the roots, none of which classes I will discuss explicitly. Molars typically have more components than premolars do, but the components present on premolars can be identified, usually unambiguously, with corresponding elements of the molars.

A widely accepted theory attempted to identify the original cusp (the 'reptilian cone') and some other elements of the molars on the basis of their serial homology with the premolars, which are usually simpler mesially, toward the front of the mouth. This was called the premolar-analogy theory, the name being a result of a long-standing confusion about serial homology. I reviewed the convoluted history of this theory, and its empirical disproof, in 1982. The morphogenetic process co-opts structures into new serial homology, whatever their previous serial homology, if they are appropriately situated.

When comparisons are made between premolars and molars, attention is usually focused on the cusps of the teeth. However, crests are of equal importance and may be critical even for finding the correspondence of cusps, as Patterson (1956) showed in his discovery of the real history of therian upper molars: arguably the finest paper ever written on vertebrate paleontology.

Vandebroek (1961, 1964, 1967) proposed a set of historical homologies of cusps and crests of therian cheek teeth, with a completely new set of terms for these structures. Perhaps because abandonment of existing terminology has seemed counterproductive, Vandebroeks proposal has been little discussed. [Also, as Hershkovitz (1971) noted, the homologies he gave are not always even mutually consistent. In addition, as can be seen by comparing Vandebroek's treatment with mine and with Butler (1978), most of the crests he named are either evolutionarily composite or convergently evolved neomorphs.] Hershkovitz (1971) modified Vandebroek's proposal, in a way which puts great weight on the exact position of cusps, and which does not, I think, mirror evolution in all respects.

Upper teeth

The basic pattern of the upper dentition is, or should now be, straightforward if a bit complex. Fig. 1 shows it in a relatively primitive placental. The *eocrista* (Vandebroek's term) is homologous to the original longitudinal crest on teeth of triconodonts and cynodonts. The later origination of the
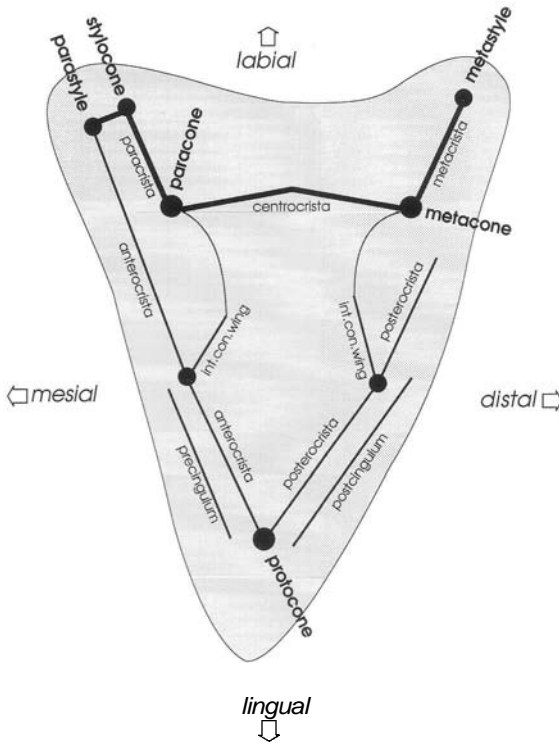
Fig. 1. Diagram of a stage in the evolution of upper molar teeth of placental mammals, a stage common at the end of the Cretaceous and the beginning of the Paleocene. A left tooth is shown. Heavy line: eocrista. Mesial is anterior for cheek teeth and labial is external.

protocone brought with it two new crests, one to the parastyle and one toward the metastyle but not reaching it because of the vertical shearing surface on the postvallum, distolabial to the metacone. These crests as such do not seem to have received names previously; I call the former the *anterocrista* and the latter the *posterocrista.* [Hershkovitz (1971) did call the former the protoloph or protocrista, but it is not primitively a loph and in 1966 I had used 'protocrista' for the crests between the protocone and the conules, which is now the established usage. I do not wish to change the latter usage, or other established usages, when a new term can avoid confusion.] The conules then originated, and their central wings sometimes continue to the apices of the paracone and metacone. The precingulum and postcingulum followed as the protocone lobe expanded.

Crests and cusps change their relations with each other in evolution as occlusal function changes. Such later evolution is beyond the scope of this paper but deserves detailed treatment for its own sake as well as as an adjunct to function. For instance, the hypocone (the distolingual cusp on a tooth with four main cusps rather than three) has convergently originated in a number of ways in many different groups, even from the original protocone. The term is, or should be, topographic rather than implying any historical homology. It is sometimes restricted to hypocones originating from the postcingulum, but these are as much convergent with each other as are hypocones originating from other parts of the tooth.
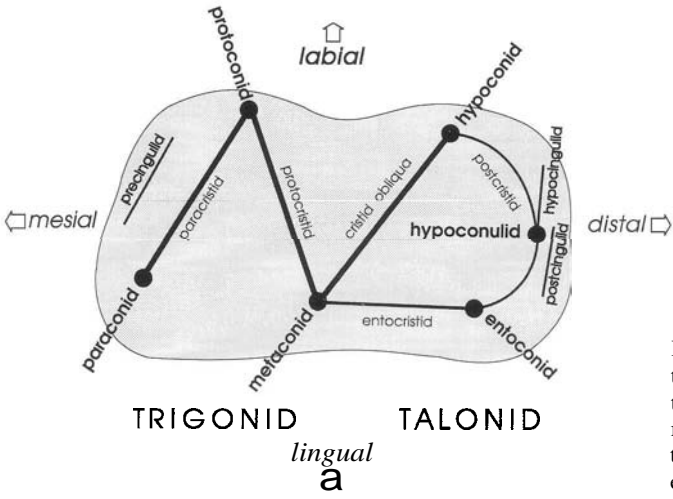
Fig. 2. Diagram of a stage in the evolution of lower molar teeth of placental mammals, as in Fig. 1. A right tooth is shown. Heavy line: eocristid.

Lower teeth

The evolution of the crown pattern of the lower dentition has been, in outline, obvious for the past century; it did not need a Patterson to decipher it, except for the Jurassic order Docodonta. However, some details have been obscure. Fig. 2 shows the basic pattern, although not quite the original one, for therians. The *eocristid* is, as with the eocrista, homologous to the longitudinal crest on triconodont teeth. The inclusion of the metaconid in the eocristid (Butler 1978) is based on the situation in almost all therians and nontherians before the late Cretaceous; the attachment of the cristid obliqua to the protocristid weakens and shifts labially with the enlargement of the talonid basin, and this derived but common situation has sometimes been taken as primitive. (Whether the therian-like teeth of the early Cretaceous monotreme *Steropodon* Archer *et al.* (1985) are homologous in derived ways with those of therians is questionable.) The hypoconid occurs even in triconodonts, and the hypoconulid is the next cusp to appear as the crest bounding the talonid extends beyond the hypoconid during the gradual evolution of the talonid basin. The *entocristid* was originally just a small mesial extension of the postcristid, as it is in the early Cretaceous genus *Aegialodon,* but its attachment to the trigonid is primitively on the distolingual side of the metaconid, where it often continues to the apex of the metaconid. A *hypocingulid* later is often separate from the *postcingulid*

Some complications

The very existence of serial homology in pattern is of interest. Homologous patterns of different teeth ordinarily evolve more or less together, and even the morphological individuality of specific teeth is not always preserved (Bateson 1892, 1894; Van Valen 1964). Therefore the developmental

information used in constructing the patterns for the various teeth is in part common to different teeth, as Butler (1939) noted in a different way. Nevertheless, in many mammals there are sharp morphological boundaries between some adjacent teeth, affecting and even obliterating the expression of most structures on one side of the boundary. The degree of individuality of specific teeth, and the sharpness of boundaries, are themselves subject to evolution in both directions. Such individuation and deindividuation occur widely, e.g., in the vertebral column or in the bristles of flies (Van Valen 1962).

In some mammals the incisors evolve additional cusps. Although the eocrista and eocristid are present on these teeth, the new cusps do not seem, in any case I know, to be homologous to any on the cheek teeth. This should not be surprising, because the intervening teeth are simple in structure. If there were homology, the pattern determinants would have to be suppressed on the intervening teeth. I have never encountered evidence of such an intervening suppression in any set of serially homologous structures in any organism. This apparent lack is one kind of evidence for the control of serial homology by gradients or similar phenomena in development.

The upper premolars rarely present difficulties with respect to serial homology, although the then-unrecognized first disproof of the premolar–analogy theory was via P^3 of early horses (Gidley 1906). The central conule on the P^3 and P^4 of plesiadapid primates (Gingerich 1976) and their descendants exemplifies a situation where one structure is serially homologous to two different ones (the paraconule and metaconule) on more complex teeth. Such occurrences may be caused in a simple way (Van Valen 1970), but just how the serial variation in any pattern is really controlled remains unclear. The homeobox story (e.g., Thorogood & Hanken 1992; Morgan & Tabin 1993) for the most part provides an address, not a house; it gives a signal rather than a plan.

Serial homologies can thus be partial. This is not true for historical homologies, although it sometimes seems so. Whenever such cases are looked at carefully, though, they can be decomposed into aspects some of which are and some of which are not historically homologous. An evolutionary fusion or splitting involves a loss or duplication of a copy of a program, with some modification but not a merger of two variant copies. (If the change is a loss or insertion of a boundary like a suture between two bones, nothing else need be changed.)

In many Carnivora (and some other groups), from the Paleocene to the present, P_4 and often P3 have a cusp on the eocristid between the protoconid and the hypoconulid. This cusp is often relatively large, and it has been referred to in various ways, such as 'metastylid', 'hypoconid', and 'posterior accessory cusp'. The eocristid is nearly a straight line distal from the protoconid apex. The cusp is on the distal surface of the trigonid, above the level of the talonid but well below the protoconid apex. Its topographic position resembles that of the metaconid of molars of the primitive trico-

nodont *Eozostrodon* ('*Morganucodon*'; Kermack *et al.* 1973). However, in the Carnivora the cusp on the premolars cannot readily be homologized with either the metaconid or the hypoconid of the molars and perhaps its development combines information related to both, like the plesiadapid central conule.

There is an additional complication in this case, because one middle Paleocene species, the viverravid *Protictis vanvaleni* Mac Intyre 1966, almost as early as any known member of the order, has a distinct metaconid on P_4 lingual to the apex of the protoconid. No other carnivoran has this cusp, so far as I know. This metaconid is not on the eocristid, which extends in the usual carnivoran manner down the labial side of the tooth and which has the accessory cusp just discussed for Carnivora. The metaconid therefore appears to be a neomorph, related to a broadening of the tooth, although later Carnivora which broaden their P_4 lack such a cusp. (A few later genera with broad P_4s, such as the vivernd *Paradoxurus* and the mustelid *Enhydra*, convergently evolve a more distal cusp on P_4 which is more or less serially homologous to the molar metaconid.) The cusp on the P_4 of *P. vanvaleni* is therefore likely to be irrelevant to reconstructing the ancestral form of P_4 in the order, despite the temptation to consider it. The P_4 metaconid of *P. vanvaleni* is nevertheless serially homologous with the metaconid of the molars.

Similarly, the paraconid on the premolars of many mammals arises from the precingulid rather than from the mesiolingual side of the protoconid. Its apex is nevertheless usually connected to that of the protoconid by a distinct paracristid, the mesial part of the eocristid. (The eocristid occasionally extends down the mesial face of the paraconid, too; this is variable among Triassic and Jurassic mammals and I do not know if this extension is primitive for mammals.) The serial homology of this premolar cusp with the paraconid of the molars is not affected by its precise place of origination. This is because, again, serial homology is a developmental phenomenon and is consistent with different evolutionary paths.

The middle Paleocene genera *Gelastops* and *Acrneodon* are two related members of the Palaeoryctidae, a primitive family of proteutherian Insectivora, on which see Van Valen (1966). In these genera the P_4 has a metaconid, which is, as usual, connected to the protoconid by a crest. However, the eocristid maintains its straight direction on the labial side of the tooth, where it is continuous from the paraconid (which is variable intraspecifically in its differentiation from the precingulid) to the hypoconid. That the largest talonid cusp is the hypoconid is shown by related genera with simpler premolars (morphologically primitive in this case), which have a similar talonid. Therefore, as in *Protictis vanvaleni* the metaconid is a neomorph. Its crest continues distally and more or less merges with the entocristid on the talonid.

Gelastops and *Acrneodon* go a step further. Incipiently in *Gelastops*, and more fully developed in *Acrneodon,* there is a cusp on the eocristid as it descends the distal surface of the protoconid, rather like the accessory

cusp of carnivorans. In the present case it is clearly not historically homologous to the hypoconid, although there may be some developmental influence in that direction because the hypoconid of P4 is about in the position of the hypoconulid of the molars and may therefore have become serially homologous to it. The new eocristid cusp is morphologically in the position of a metaconid, being on the eocristid on the trigonid just past the protoconid apex, but it is clearly a new cusp and a different cusp is serially homologous to the metaconid of the molars.

In the most primitive rodents and lagomorphs the metaconid of the molars and of P4 (and occasionally P3) is larger and taller than the protoconid, which on P4 is sometimes only a weak cusp. Therefore the possibility arises that here the protoconid of P4, not the metaconid, is the neomorph, as Wood (1962) proposed for the primitive rodent *Franimys*. If this is the case, the new protoconid arose labial to the eocristid, and a new protocristid and paracristid evolved concomitantly with the cusps as serial homologs of the corresponding structures on the molars. Unlike rodents, the primitive lagomorph *Eurymylus* has a paraconid at least on P3 and P4 (the molars being too worn in specimens I know to establish presence or absence of the cusp there). This premolar cusp would also have to be a neomorph on the interpretation provisionally suggested here, thus weakening the hypothesis a bit.

The last upper premolar, although not the last lower premolar, of the primitive middle Cretaceous placental Prokennalestes Kielan-Jaworowska and Dashzeveg (1989) is semimolariform. Whether this condition is primitive for placentals is still unclear, as is the primitive state for the last lower premolar. (Prokennalestes has five lower premolars and probably five upper premolars, which may possibly be the primitive number.)

Sometimes molars become simplified, premolariform or even simpler. In the Paleogene family Mesonychidae, itself ancestral to whales, the talonid basin is gradually lost, leaving only a large hypoconid on a strong eocristid. The eocristid extends through the protoconid to the paraconid; the metaconid is gradually lost and does so without regaining contact with the eocristid.

The distal premolars of many placentals become more or less molarized in evolution, this occurring convergently and often differently in a number of clades in various orders. (Whether this is in part an evolutionary remolarization, after an earlier demolarization, does not affect the processes involved.) The usual morphological appearance for lower teeth is that the metaconid is a neomorph, occurring lingual to the eocristid by a forward extension of the metaconid-inducing mechanism of the molars (cf. Van Valen 1970). In some cases, though, as in the basal primate *Purgatorius* (see Clemens 1974) and the basal ungulate Oxyprimus [Archibald (1982) gives the best published figure], the eocristid of P4 is diverted lingually to a mesially extended entocristid, and a metaconid may form at this junction. The metaconid is still perhaps a neomorph, but in such a case it convergently attains the primitive topological relationship.

Topology

For crests and cusps can be viewed topologically, as well as in the more familiar approaches such as morphology, development, and function. Topology, which should not be confused with topography, comprises those relations of the elements of a space which are preserved under continuous deformations, such as change of size or shape. The criterion of morphological contiguity (the 'principle of connections' proposed by E. Geoffroy Saint-Hilaire in 1818), which is used, with good if imperfect results, in inferring homology, is topological. Geoffroy's 'principle of similarity', on the other hand, is not topological. Homology itself can in a sense be regarded as a topological relation, with information rather than morphology as the continuous variable, and such a perspective may be useful in cases like paralogy, repetitive genetic elements, or historical plus repetitive homology.

Thus the eocrista and eocristid, despite the zigs and zags which they evolve, remain topologically single crests until they are interrupted, as the eocristid usually is in therian molars by the postvallid (the distal surface of the trigonid). The relations of cusps on these crests are also invariant, although it is possible for a cusp like the stylocone or the paraconid to become detached from its corresponding crest in evolution. Such detachment is a topological threshold, as is the interruption\ of a crest or the merger or joining of two previously separate structures such as the eocristid and entocristid of *Purgatorius* just described. Cusps also sometimes merge with each other or, more commonly, a single cusp becomes subdivided. The distinction between serial and historical homology, even though a slightly fuzzy distinction in several ways (Van Valen 1982), applies to topological relations just as it does to any morphological structures. Similarly, topological relations, like others, evolve (and are maintained) by the interaction of development and function.

Evolution of serial homology

Serial homology itself evolves. I don't mean the concept, of course, but the ways in which it manifests itself in repeated series. This evolution is of at least two kinds, corresponding to the repeated units themselves (such as teeth, digits, or arthropod segments) and the patterns within these units. Primitively, as with vertebrate teeth, tetrapod digits, or trilobite segments, the number of units is at least often not fixed. Such variation in number occurs concomitant with relatively little differentiation among the units, as one might expect soon after their evolutionary reduplication from a single ancestral pattern. The later progressive evolution of serial differentiation ('Williston's Law') is too well known to belabor; I actually can think of no case of a reversal. The developmental determination of the addresses of serial units obviously evolves, and the existence of two kinds of such

evolution is now known within the Vertebrata (Holland 1992; Hunt & Krumlauf 1992), but just how it relates to the increase in precision of counting is not clear. Moreover, the number of serial units often changes in evolution, and as we have seen a specific morphology is not always associated with a particular unit when the number of units varies.

The other kind of evolution of serial homology is in the patterns expressed in the serial modules, or rather in the relationship of these patterns along the sequence of modules. Structures and topological invariants are mostly expressed along only part of the sequence, and the interval in which they are expressed often varies among the features examined. Moreover, the position of maximum expression, and the relation of the expression in other modules to this, is even more variable (cf. Van Valen 1970). The interval of expression of a feature can be regarded as an aspect of the pattern of expression of this feature, with a threshold. The evolution of these patterns of expression, which are of course not independent of each other at least functionally, would be valuable to study. The next level would be comparative evolution of such patterns, both among clades for the same repetitive structures and among different kinds of repetitive sequences.

Homology between upper and lower teeth

An individual vertebrate has four jaws, not one: two upper and two lower. The homology of corresponding structures between right and left sides is trivial, although patterns of variation between sides can be interesting (Van Valen 1962). The other correspondence, between upper and lower jaws, is less well understood and even its existence is often denied for mammals. Belief in the correspondence dates at least to the Cope-Osborn theory of homologies of molar cusps (see Osborn and Gregory 1907; Gregory 1934). Patterson's (1956) disproof of that theory did not affect the existence of homology itself between the jaws, as he noted.

In triconodonts and most symmetrodonts, upper and lower teeth are generally similar to each other in structure. The following description applies to the large majority of known genera, and nearly so to the rest, which are derived in their small deviations (see, e.g., Lillegraven et *al.* 1979). A central crest extends longitudinally along the tooth. This is the eocrista in an upper tooth and the eocristid in a lower tooth, and it is already somewhat bent in most symmetrodonts (not in the Amphilestidae, which Mills and I transferred to the Symmetrodonta in separate papers in 1971). The tallest and most massive cusp of the tooth is about central on the crest. This cusp is the paracone on upper teeth and the protoconid on lower teeth. Mesial to it, also on the crest, is the stylocone on upper teeth and the paraconid on lower teeth. Distal to the main cusp, and on the crest, is the metacone on upper teeth and the metaconid on lower teeth. The crest continues distally to a small metastyle on upper teeth and the

Tab. 1. Proposed homologies of elements of upper and lower teeth of therian mammals.

Lower teeth			Upper teeth
Eocristid	←	→	Eocrista
Paracristid	←	→	Paracrista
Protocristid	←	→	Centrocrista
Cristid obliqua	←	→	Metacrista
Protoconid	←	→	Paracone
Paraconid	←	→	Stylocone
Metaconid	←	→	Metacone
Hypoconid	←	→	Metastyle
Precingulid cuspule	← ?	→	Parastyle

hypoconid on lower teeth. Often the crest continues mesially from the stylocone to a very small parastyle on the upper teeth, and from the paraconid to a very small precingulid cusp on the lower teeth. Whether these most mesial cusps, and the crest extensions to them, are primitive for mammals is not clear; their presence sometimes varies even within individuals.

With the possible exception of the most mesial cuspules, I propose that all the correspondences noted (see Tab. 1) are homologies, i.e. that a continuity of causal information occurred between the development of the corresponding structures. This continuity may still have been present within individuals in some or even all of these mammals, but some of it may alternatively have weakened or disappeared at some earlier time. Cynodonts, the ancestors of mammals, have teeth with an eocrista (-id) and some homologous cusps. (The structure of these teeth has been surprisingly neglected in most work and deserves careful comparative treatment.) At some point the development of the simple pattern of upper and lower teeth was caused in the same way, by the same set of developmental instructions acting in different places just as it does between the right and left jaws. Even if this continuity of developmental information between upper and lower jaws decreased, by evolution of greater individuation of the jaws, historical homology can still be recognized in lines of descent. Therefore, even in remote descendants, the corresponding structures in upper and lower jaws are still repetitively homologous, with historical continuity of information through each lineage and repetitively between the jaws at an early stage.

What of later-evolving correspondences? If there is real repetitive homology, their initial appearance was caused by the same change in developmental information acting on tooth primordia in different jaws. For

instance, the evolution of bunodonty in omnivores, the conversion of cusps to low, crushing mounds as in our own cheek teeth, is presumably caused in the same way in each jaw and is therefore repetitively homologous. Perhaps this is also true for some more specific structures.

This does not mean, though, that structures which evolve together need be homologous. The protocone evolved concomitantly with the talonid basin, into which it occludes, and these structures enlarged together. To regard them as homologous as well as functionally related is without warrant. Olson & Miller (1958) and later workers have nevertheless given some evidence that teeth (and their parts) which occlude with each other tend to vary together among individuals. Even nonoccluding teeth at corresponding positions can vary together (Gingerich & Winkler 1979). This must have a developmental basis, because teeth are formed before they erupt, but how it happens is mysterious. Perhaps homeobox addresses are relevant.

Cauda

This essay has been on pure morphology, a now much underappreciated subject. It is not functional morphology, it is not evolutionary morphology, it is not phylogenetic morphology, it is not developmental morphology, it is not mathematical morphology, it is not population morphology, it is not structuralism, although it touches all of these. Pure morphology is the study of form for its own sake, what Goethe meant about 1795 when he coined the term 'Morphologie' for 'die Lehre von der Gestalt, der Bildung und Umbildung der organische Korper' (quoted from Goethe 1963: p. 92): the study of the configuration, formation, and modification of organic forms.

It is not much less appropriate to read Goethe for modern morphology than it is to read Darwin for modern evolution. Each was a century or more ahead of his followers. One should be careful not to read modern views into the eighteenth century, but conversely one should be careful not to impose later adverse stereotypes. Goethe, especially, has suffered from the latter, although perhaps not as much as Aristotle. (I do wish, though, that commentators would use the modern term 'premaxilla' instead of the eighteenth-century 'intermaxillary' when discussing Goethe's prediction and confirmation of it in humans.) Arber (1946) and Brady (1987) have given good and complementary accounts of Goethe's morphology.

Pure morphology is inherently comparative, but the comparisons are adjunct to the study of the nature of the form itself. Form exists and form is potential; forms change and forms are controlled. Goethean archetypes are not those of Owen or Darwin; they are for repetitive homology rather than for historical homology. They are the developmental potential of different kinds of organisms. And therefore they evolve.

Acknowledgments

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Streszczenie

Korespondencja poszczegolnych elementow pomiędzy roznymi zębami tego samego osobnika jest wyrazem homologii seryjnej, w odróżnieniu od homologii historycznej odnoszącej się do stosunków pomiędzy roznymi osobnikami. W obydwu wypadkach przyczyną zaistnienia homologii jest ciągłość informacji.