What is 'Pseudo' in Pseudotribosphenic Teeth?

ALISTAIR R. EVANS[1,2]

[1] School of Biological Sciences, Monash University, VIC 3800, Australia (alistair.evans@monash.edu)
[2] Geosciences, Museum Victoria, Melbourne, VIC 3001, Australia

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The discovery of a 'pseudotribosphenic' lower tooth row in 1982, with a basin anterior to the trigonid rather than posterior, caused a large stir in mammalian palaeontology. This indicated that a tooth shape of equivalent complexity to the tribosphenic tooth form could evolve more than once. The upper tooth predicted to occlude with the pseudotribosphenic molar was reconstructed with a 'pseudoprotocone' to occlude with the pseudotalonid basin. Here I discuss the relative merits of naming the major upper lingual cusp of pseudotribosphenic molars as 'protocone' due to its likely similar developmental and functional relations as the protocone of tribosphenic molars. The use of a different name implies greater morphological distance between tribosphenic and pseudotribosphenic upper molars than is perhaps warranted, and likely exaggerates the perception of the difficulty in evolving both tribosphenic and pseudotribosphenic. The choice between the evolution of the alternative forms of tribosphenic may in fact be related to the degree of anterior-posterior bias in lower molar development – tribosphenic with a posterior bias, while pseudotribosphenic with an anterior one.

Keywords   tribosphenic, pseudotribosphenic, *Shuotherium*, protocone, pseudoprotocone.

Introduction

'Tribosphenic' was the term Simpson (1936) coined for the basal tooth type of all extant therian mammals, from its dual functions of grinding ('tribo') and shearing (wedge or 'sphen'). The key structures of this tooth form are the occluding blades leading from the main cusps (forming a W-shaped ectoloph on the upper molar, and a disconnected W on the lower molar), and the mortar-and-pestle crushing of the protocone on the lingual side of the upper molar into the talonid basin that sits at the posterior of the lower molar behind the elevated trigonid (fig. 1a). For decades, the complexity and intimate relationships between these teeth led workers to the conclusion that it would be 'almost inconceivable' that such a tooth shape could have evolved more than once in the history of mammals (Simpson, 1936:797). After Simpson's work, Patterson (1956) outlined the stages of evolution of the tribosphenic molar. Based on a functional analysis of occluding crests, Crompton (1971) detailed a scenario for the evolution of the tribosphenic dentition from pre-tribosphenic forms. The importance of the tribosphenic form in the evolutionary history of mammals was emphasised by Tom Rich's graduate advisor, Malcolm McKenna (1975), using it to diagnose a clade of crown therians (Tribosphenida).

The single origin of the tribosphenic form began to look more doubtful with the discovery of *Shuotherium dongi* by Chow and Rich (1982), in which a small basin was positioned at the anterior of the elevated, triangular trigonid of the lower molars (fig. 1b). Chow and Rich (1982) termed this basin the pseudotalonid, in analogy to the shape and function of the true talonid. For this to be analogous to the talonid, it must be a crushing basin that receives a protocone-like structure. Chow and Rich (1982) predicted that the upper molars of *Shuotherium* would have such a cusp, which they termed the 'pseudoprotocone'. This prediction was borne out by the discovery by Wang et al. (1998) of an upper molar of *Shuotherium* with a lingual cusp in general agreement with the predicted position and shape.

The purpose of this short note is to discuss the usefulness of the conventions currently used for naming cusps in the pseudotribosphenic dentition, and the potential for names to colour our interpretation of evolutionary scenarios. Here I will consider what does 'pseudo' mean, and which parts of teeth may consistently be called 'pseudo'?

Cusp Development

In an embryo, the future tooth surface begins as the interface between epithelium and mesenchyme cell layers in the tooth germ. Soon after the initiation of the tooth germ, the primary enamel knot forms. The enamel knot is the main signalling centre of the tooth, expressing dozens of genes. Certain gene products of the enamel knot prevent proliferation of the epithelium adjacent to the knot, and the proliferation of surrounding epithelium continues. This differential proliferation bends the epithelium-mesenchyme interface, creating a local topological maximum that is the site of a

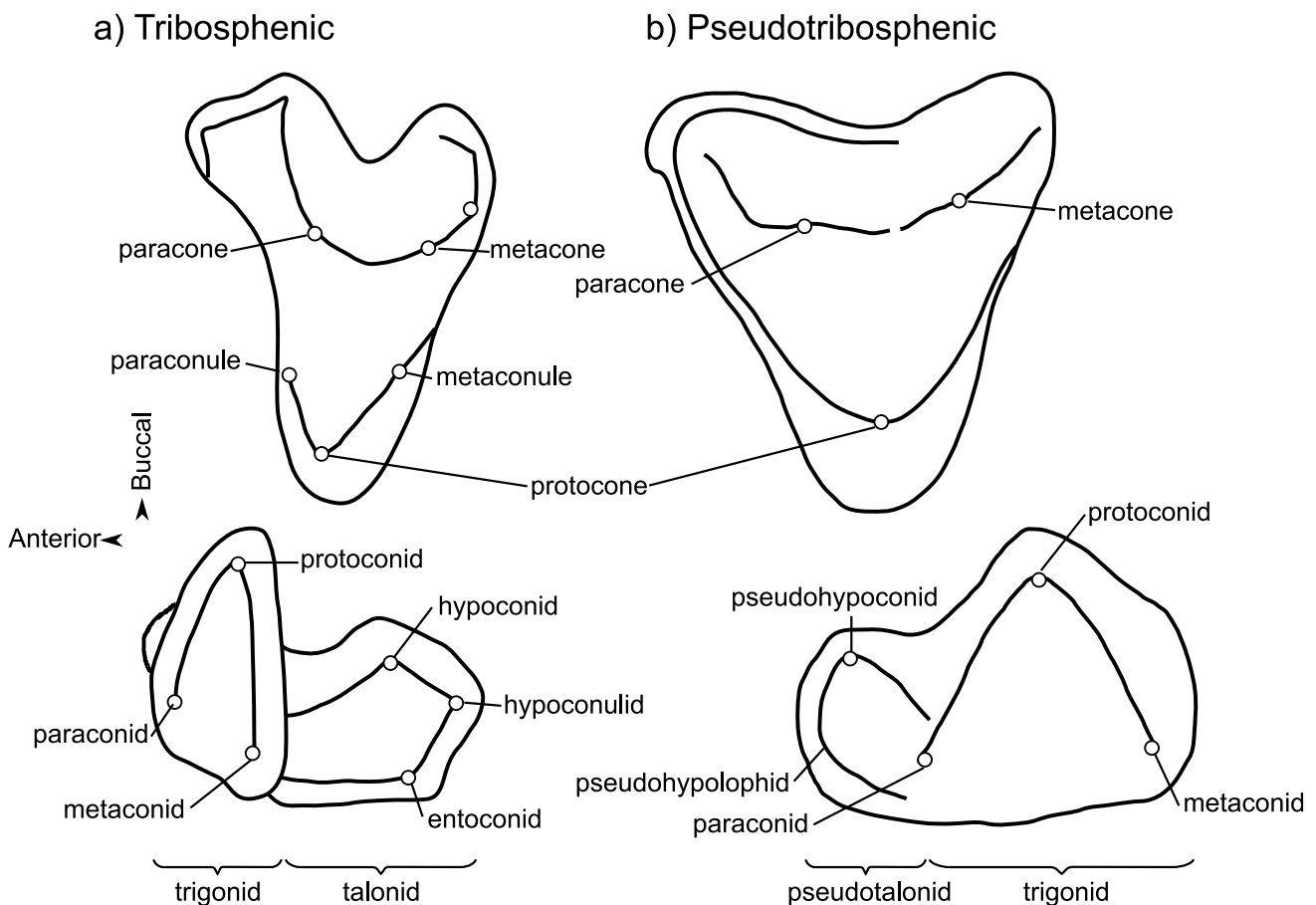## a) Tribosphenic

b) Pseudotribosphenic

Fig. 1. Comparison of tribosphenic (a) and pseudo-tribosphenic (b) morphology for upper (top) and lower (bottom) molars, with basins and cusps labelled according to the nomenclature proposed here. The main upper cusps of both forms are labelled protocone, paracone and metacone, while the structures associated with the pseudotalonid basin on the lower are suffixed with 'pseudo'. (a) upper is *Peramus* and lower is unidentified lower from Crompton (1971), redrawn from Wang et al. (1998); (b) upper and lower are based on *Pseudotribos*, redrawn from Luo et al. (2007).

future cusp. At some distance from the primary enamel knot, additional knots can form, called secondary enamel knots, that also produce local maxima in the folded interface. The result is the general topography of the tooth represented by the epithelial-mesenchyme interface. After folding at each cusp is completed, mineralisation commences, starting at the cusp tip, with dentine deposited from the interface towards the interior of the tooth, and enamel on the outer surface.

While it is conceivable that the developmental-genetic process may exist such that tooth cusps are in some way encoded in a gene or genes, there are no unique gene signatures in any single cusp that has been investigated. In fact, because of the pleiotropy of genes (the effect of a gene on many phenotypic features) and the network nature of gene expression and signalling pathways, most tooth features including cusps are interlinked in development by shared genes and signalling pathways. In this sense, the cusps are not independent at the level of developmental processes (Kangas et al., 2004). The spacing and timing of each enamel knot controls the relative position and height of the resulting cusps. This mechanism

appears to be conserved among therian mammals (placentals: Jernvall and Thesleff, 2000; marsupials: Moustakas et al., 2011). Therefore, we cannot identify a cusp based on any particular gene or specific combination of genes, i.e., there is no 'protocone gene'. However, there may be a gene or genes that control aspects such as lingual bias in growth of the upper tooth. The increase in such a signal may produce sufficient space for a cusp, which would then be called a 'protocone'.

Some genes are known to affect cusp formation. *Ectodysplasin* (*Eda*) is a tumor necrosis factor (TNF) gene that is expressed in the developing tooth (Kangas et al., 2004; Harjunmaa et al., 2014). When the EDA protein is absent, as is the case in the spontaneous null mutant in the mouse called Tabby, the molars are simpler and smaller, but when EDA is overexpressed in the epithelium, they are more complex compared to the wild type (Kangas et al., 2004; Harjunmaa et al., 2012). Fine-tuning of the amount of ectodysplasin generates intermediate tooth shapes, and replicates the order in which these cusps appeared in evolution (Harjunmaa et al., 2014).

Cusp Homology

The lack of specific genes for each cusp and the lability of the developing tooth to changes in gene products such as EDA appear to be somewhat at odds with the palaeontological perspective, which tends to view the positioning and relative size of major cusps as highly conserved and very stable. Evolutionary change appears very gradual compared to the havoc that can be wreaked by the modification in a single gene like *Eda*. This implicit view has led to the use of presence/absence or shape of tooth features as cladistics characters for phylogenetic reconstruction. If the developmental process were so labile, then there would be no phylogenetic signature in tooth cusp patterns at all. The phylogenetic signature in teeth at high taxonomic level is relatively low, presumably due to high degrees of homoplasy (such as the repeated evolution of the hypocone; Jernvall et al., 1996), but still can be informative at lower levels.

The use of tooth characteristics in phylogenetic reconstruction assumes homology among cusps. Homologies of cusps among tooth forms, and even between upper and lower teeth, have been proposed for over a century (Osborn, 1888). While it is now clear that it is very unlikely that there is a simple relationship of 'homology' among cusps, naming conventions have at least in part been based on criteria of homology. Wang et al. (1998) proposed these to be morphology, topographic position and occlusal relationships. Based on differences in topographic position, the lower basins of tribosphenic and pseudotribosphenic teeth are justified in their divergent names.

Protocone and the Meaning of 'Pseudo'

The major lingual cusp on upper molars of pseudotribosphenic dentitions has been analogised to the protocone, given its similarity in position, shape and inferred function to the protocone in tribosphenic dentitions. However, because it occludes with the basin on the anterior of the lower, the prefix 'pseudo' has been used to indicate that it is in some way different from the standard protocone.

Comparisons between the position and shape of the protocone and pseudoprotocone reveal a reasonable concordance between them (fig. 1; see also Wang et al., 1998, fig. 6). They both fulfil the same function of supporting crests that occlude with the lingual crests of the talonid basin. Wang et al. (1998) suggest that *Shuotherium* was not able to closely approximate the buccal surface of the pseudoprotocone with the lingual surface of the pseudotalonid basin, and so may not be able to 'crush' or 'grind' as many, but not all, tribosphenic molars can do (Crompton and Sita-Lumsden, 1970). Regardless, their overall functional relationships remain the same, although they are mirrored in the anterior-posterior axis. In what ways are these lingual cusps different? Since we currently understand that there is not a unique gene signature that could distinguish these two, and they are in the same position of the tooth with approximately the same shape, we could conclude that there is no major difference in their development or function. Therefore, I propose that there is no need to use the qualifier of 'pseudo' for the large lingual cusp

on the upper molars of pseudotribosphenic teeth, and that it be called 'protocone'.

In the hypothetical upper pseudotribosphenic molar, Chow and Rich (1982) named the posterobuccal cusp metacone, using the same topological convention as tribosphenic molars (as did Luo et al., 2007 for the new pseudotribosphenic mammal *Pseudotribos robustus*). Wang et al. (1998) label this cusp the 'pseudometacone', which occludes between the pseudohypoconid of the opposing lower tooth and the protoconid of the tooth posterior to it. The 'pseudometacone' of the pseudotribosphenic teeth has an equivalent position and shape to the metacone of tribosphenic teeth. The justification for the 'pseudo' designation is likely because of its different occlusal relationships with the lower compared to the tribosphenic metacone, which occludes in the space between the hypoconid and protoconid of the same lower tooth. An equivalent difference in occlusal relationships exists for the paracone, and so following the same convention it would be the 'pseudoparacone'. This shows an inconsistent use of the 'pseudo' prefix in exactly what is different or 'pseudo' about the feature. I propose here that the 'pseudo' be used only for the new topographical structure, the anterior basin of the lower molar, and its associated cusps and crests, such as the pseudohypoconid and pseudohypolophid (fig. 1b).

Importance of Names

Why is it important to reconsider the naming of this cusp, in what looks like a purely nomenclatural discussion? The term pseudoprotocone implies some substantive difference from the protocone, and suggests major developmental and/or functional distinctions between these cusps.

In order to evolve a tribosphenic-like tooth from a basal reversed-triangle tooth, three features must be added: a basin on the lower tooth, a lingual cusp on the occluding upper, and an additional buccal cusp (either paracone or metacone) also on the upper. The biggest difference between evolving a tribosphenic tooth and a pseudotribosphenic tooth is whether the basin is anterior or posterior. This will affect the shape of the protocone, paracone and metacone, but the protocone and two buccal cusps must still be present. From a developmental perspective, then, the protocone is essentially the same for the two tooth forms.

Anterior-posterior Bias

Using 'pseudo' gives the impression of substantial difference in shape and function from tribosphenic, while in fact the differences are relatively minor. It is likely only the anterior-posterior bias in the lower molar that makes the difference. Recent developmental experiments show an inherent bias in the morphogenesis of mouse molars, such that a posterior extension is more likely than an anterior one (Harjunmaa et al., 2014; Luo, 2014). It is likely that such a bias existed in the ancestor to all modern toothed mammals. This begs the question of whether pseudotribosphenic mammals had an anterior bias rather than a posterior one. How labile may this anterior-posterior bias be? Could a switch in the bias have

changed several times in the history of mammals? Depending on the postulated evolutionary relationships among tribosphenic and pseudotribosphenic mammals, this switch may have occurred once or several times (Luo et al., 2007; Rich and Vickers-Rich, 2010).

The origin and evolution of anterior-posterior developmental bias in lower molar development relative to the upper appears to be a bigger question than the convergence of the tribosphenic-like form itself. If a lower molar has a posterior bias in producing a basin, then it can occlude with a nascent lingual cusp that can later evolve to become a protocone. A basin produced by an anterior developmental bias can also occlude with a nascent protocone.

Currently there are no obvious molecular signals that may produce this anterior-posterior differential bias in tooth development, but this is a significant line of enquiry for future research.

Conclusion

While the tribosphenic tooth is an intricate, precisely-occluding device (Evans and Sanson, 2003; Evans and Sanson, 2006), equivalent structures have evolved a number of times, at least in tribosphenic and pseudotribosphenic mammals. But the difficulty of evolving such a shape may have been overestimated, and is perhaps exaggerated by the 'pseudoprotocone' terminology.

Acknowledgements

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