DILAMBDODONT MOLARS : A FUNCTIONAL INTERPRETATION OF THEIR EVOLUTION

by

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ABSTRACT

In dilambdodont molars the primitive crest between paracone and metacone (*centrocrista*) is represented by a pair of crests that join the mesostyle (*postparacrista*, *premetacrista*). The cutting action of these crests against the crests of the hypoconid is described. Dilambdodonty is a derived adaptation for greater cutting efficiency. It has evolved several times and in more than one way.

RESUME

Chez les molaires dilambdodontes, la crête primitive entre paracône et métacône (*centrocrista*) est représentée par une paire de crêtes qui joignent le mésostyle (*postparacrista*, *premetacrista*). La fonction coupante de ces crêtes le long de celles de l'hypoconide est décrite. La dilambdodontie est une adaptation dérivée augmentant l'efficacité coupante. Elle a évolué plusieurs fois et de diférentes manières.

INTRODUCTION

It is with great pleasure that I am able to contribute to this volume in honour of Dr Don Russell. Starting with the classic memoir "Les mammifères paléocènes d'Europe" (1964), he has made a lasting contribution to knowledge of Early Tertiary mammals. Much of what is known about these, and especially the smaller ones that are loosely classified as "insectivores", depends upon studies of molar teeth, and it is about a particular type of molar, the dilambdodont type, that I have chosen to comment here.

Gill (1885) classified the Insectivora on the structure of the molars into Dilambdodonta and Zalambdodonta. In dilambdodonts the paracone and metacone are subequal, and in zalambdodonts the metacone is greatly reduced or absent. These terms were derived from the Greek letter lambda (λ); in dilambdodonts the molars, when seen in occlusal view, have two lambdas, in zalambdodonts they have one. There are corresponding differences in the lower molars: in dilambdodonts the talonid is subequal to the trigonid, in zalambdodonts it is reduced in length and height.

In 1941 I classified molars in a different way, according to the relative development of the protocone and stylar shelf. I used the term dilambdodont for those molars in which the paracone and metacone are placed midway across the crown, as in *Tupaia*, shrews and insectivorous bats. Teeth in which the stylar shelf is narrow and the paracone and metacone are buccal, as in erinaceids and *Ptilocercus*, I called tritubercular.

Gheerbrant (1992), in his study of adapisoriculids, has recently proposed a classification similar to that of Gill, laying emphasis on the degree of separation of the metacone from the paracone. Teeth in which the metacone is united with the paracone at the base (the primitive condition) he calls zalambdodont. Teeth in which the cusps are deeply separated are further distinguished into predilambdodont, where the paracone is

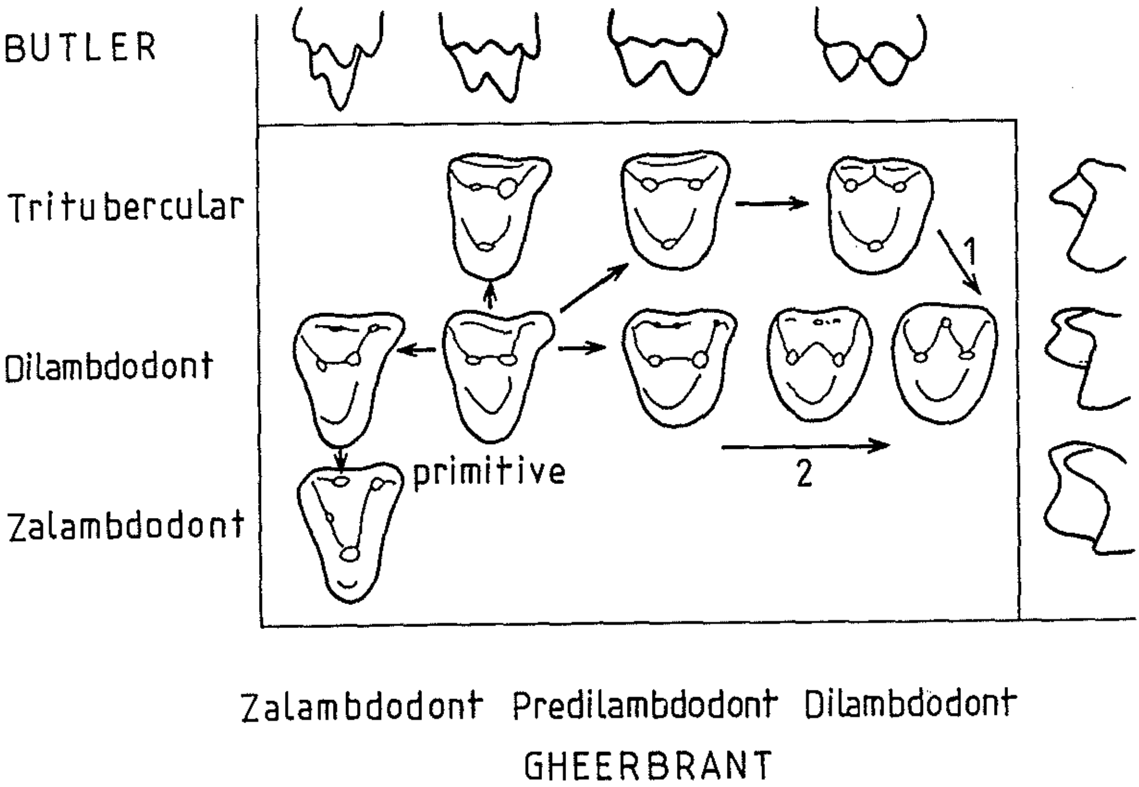

Figure 1.— Diagrammatic right upper molars, arranged to compare the nomenclatures of Butler, 1941 (based on the buccal-lingual position of the paracone), and Gheerbrant, 1992 (based on the degree of separation of the metacone from the paracone). The top row shows buccal views; the right-hand column shows anterior views. Arrows show evolutionary trends; those numbered 1 and 2 indicate two possible paths of derivation of advanced dilambdodont molars.

directly joined to the metacone by a longitudinal crest (*centrocrista*), and dilambdodont, where the *centrocrista* is diverted buccally, so that in many cases the paracone and metacone are connected to the mesostyle. Gheerbrant's classification can be combined with mine, because the metacone and protocone evolve independently (Fig. 1).

OCCLUSAL RELATIONS

The notch between the paracone and metacone is of considerable functional importance, as it is the path of the hypoconid in the transverse movement of chewing. Anterior and posterior wear facets on the hypoconid (facets 3 and 4 of Crompton 1971) occlude with the paracone and metacone respectively. The crests that form the leading edges of these facets operate as cutting edges.

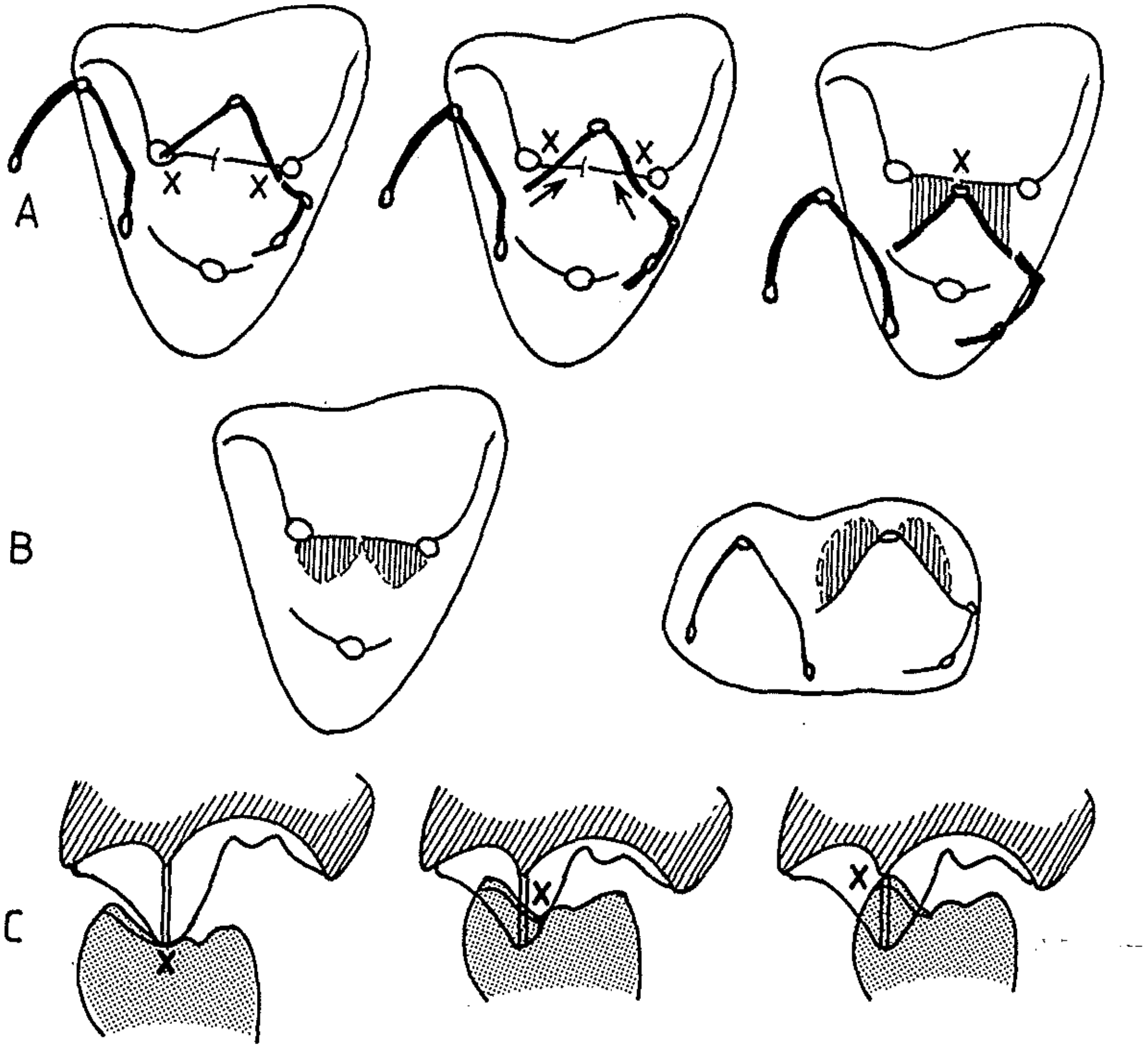

Figure 2.— To illustrate relations between the hypocone and the *centrocrista* in predilambdodont molars. A, Stages in the transverse passage of a lower molar across an upper molar. Anterior is to the left. x indicates crossing-points of crests. B, The facets (shaded) so produced. C, Relations of hypoconid to metacone. Upper molar represented as sectioned along the path of the hypoconid, to show anterior surface of metacone; posterior side of talonid of lower molar seen as transparent. As the lower molar moves lingually (from left to right in the figure), the crossing-point (x) moves from tip to base on the metacone, and from base to tip on the hypoconid.

Cutting is performed by crests which cross like the blades of scissors. The force is concentrated at a crossing point which travels along the blades as the scissors close. Food tends to be pushed towards the end of the blades; this is avoided in teeth by the crests being concave or notched, so that there are two crossing points which approach each other, imprisoning the food between them. Cutting crests on teeth usually lie between two cusps (Crompton 1971, Every 1972, 1974, Rensberger 1973).

This is the case of the *centrocrista*. Although it looks straight in crown view, it is really V-shaped, as may be seen in lateral view. Consider predilambdodont molars as in

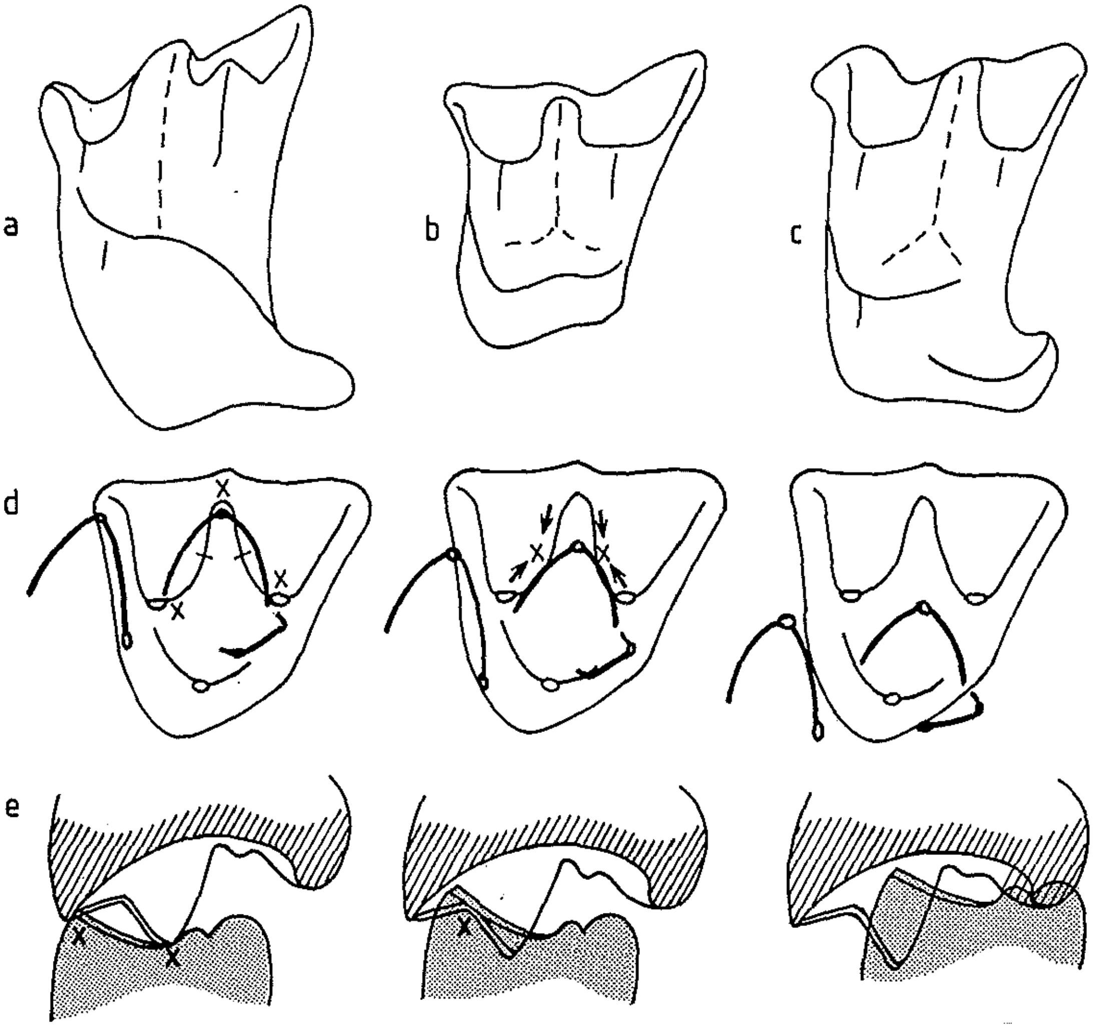

Figure 3.— **a-c**, Left upper molars seen in partially lingual view. **a**, *Suncus* (soricid); **b**, *Tupaia* (treeshrew); **c**, *Vespertiliavus* (chiropteran). **d**, Stages in passage of a lower molar across an upper molar; compare with fig. 2A. Note the additional contact of hypoconid with mesostyle, and convergence of the crossing-points (x) on the *postparacrista* and *premetacrista*. **e**, Relations between the hypoconid and metacone; compare with figure 2C. There are two crossing-points (x) on the posthypocristid and *premetacrista*.

Alphadon. When the lower molar first meets the upper molar at the beginning of the chewing stroke the protoconid touches the parastyle, the paracone is near the anterior end of the prehypocristid ("cristid obliqua"), and the metacone is near the hypoconulid, at the posterior end of the posthypocristid. The tip of the hypoconid is then buccal to the paracone and metacone. As the lower molar moves lingually and upward in relation to the upper molar, the protoconid travels along the precingulum and penetrates into the interdental embrasure. Relatively to the lower molar, the upper molar moves buccally and downward: the paracone travels down the groove between trigonid and talonid (hypoflexid), and the metacone moves along the posterior cingulum. At the same time the tip of the hypoconid passes through the notch in the *centrocrista*.

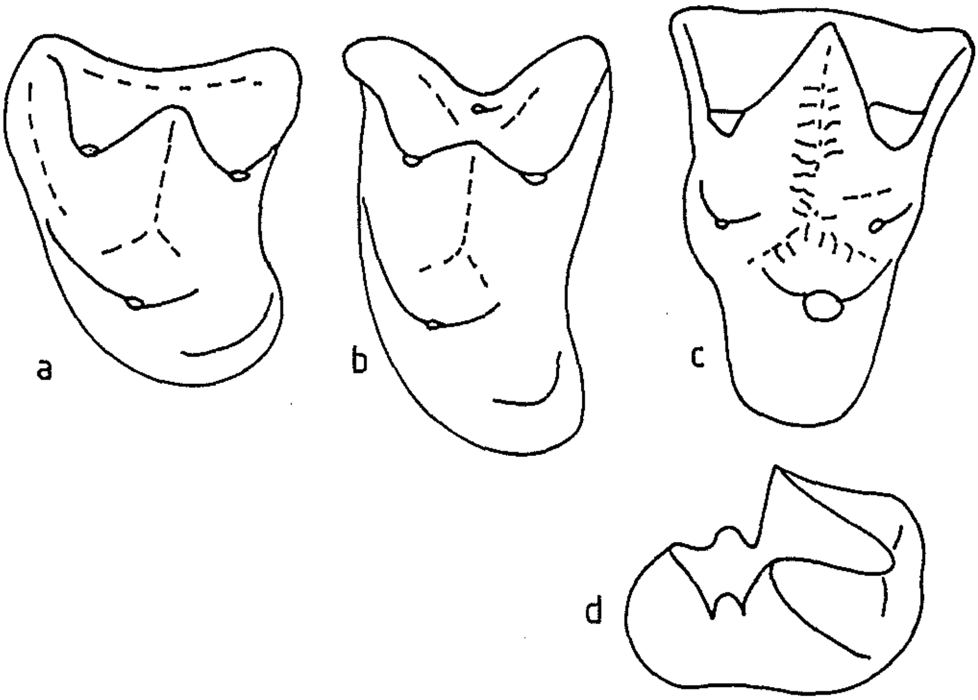

Figure 4.— Left upper molars in which crests of the paracone and metacone are straight, and the mesostyle is not involved. **a-c** in partially lingual view. **a**, *Ageina* (primitive chiropteran); **b**, *Scotophilus* (chiropteran with secondarily reduced hypoconid); **c**, *Cynopterus volans* (dermopteran). **d**, *Cynocephalus variegatus* (dermopteran), posterior view.

Consider the crossing points between the *centrocrista* and the hypoconid crests. At the beginning of the stroke these lie near the tips of the paracone and metacone, and as the lower molar moves lingually they converge at the notch. On the hypoconid they travel up to the tip of the cusp. Food is thus forced towards the notch where it is carried by the tip of the hypoconid lingually into the trigon basin, to be crushed between hypoconid and protocone. The relationship is illustrated diagrammatically in figure 2. This relationship is found also in primitive placentals such as *Kennalestes*, but there the paracone-metacone notch is smaller, and the hypoconid is correspondingly small, so that its cutting function is less than in *Alphadon*.

In dilambdodont molars such as *Tupaia* and soricids, the *centrocrista* is represented by two crests, *postparacrista* and *premetacrista*, which connect with the mesostyle at the buccal edge of the tooth. Owing to the elevation of the mesostyle these crests are concave. The valley between them, starting at the mesostyle, is the path of the hypoconid. Superimposing drawings of upper and lower molars in occlusal view, it is seen that the tip of the hypoconid meets the mesostyle early in the chewing stroke. This contact introduces second crossing points, which travel lingually along the *postparacrista* and *premetacrista*, and on the lower molar they travel from the tip of the hypoconid down its anterior and posterior crests. They converge towards the primitive crossing points that start at the tips of the paracone and metacone. Thus both

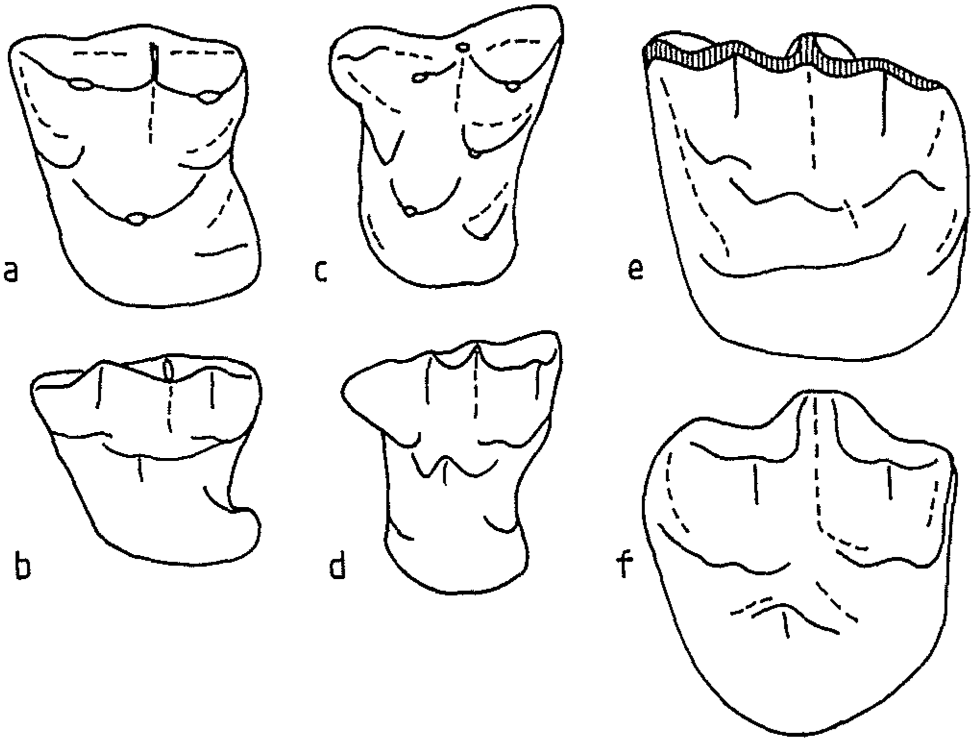

Figure 5.— Left upper molars with mesostyle and buccal paracone and metacone, i.e. narrow stylar shelf. **a,b,** *Mixodectes*, crown and partially lingual view. **c,d,** *Pontifactor*, the same. e, *Lambdotherium* (perissodactyl) and **f,** *Dacrytherium* (artiodactyl), partially lingual view.

postparacrista and *premetacrista* function like the *centrocrista* of *Alphadon*, and the cutting power of the tooth is approximately doubled (Fig. 3).

EVOLUTION

Dilambdodonty has evolved many times. It occurs not only in lipotyphlan insectivores (shrews, moles, *Nesophontes*), tupaiids, bats and dermopterans, but also in a number of herbivores such as *Pantolambda*, chalicotheres and brontotheres. Its adaptive significance seems to be the improved cutting power required for chewing fibrous food.

Crochet (1980) distinguished a type of dilambdodonty, which occurs in Tertiary didelphines, where the *centrocrista* forms an inverted V in crown view, but it does not reach the buccal margin of the tooth and does not incorporate a mesostyle. He called this condition "dilambdodontie didelphidienne", to distinguish it from "dilambdodontie talpidienne" in which the mesostyle is involved. In these marsupials, style C is present in the position of a mesostyle but, by looking at the tooth along the paracone-metacone groove, it is seen not to be high enough to touch the hypoconid (except in some cases after wear, e.g. *Amphiperatherium ambiguum*). The crests that make up the *centrocrista* function against the hypoconid crests in the same way as in predilambdodont teeth, except that, as the notch is situated more buccally, the tip of the hypoconid reaches it earlier in the transverse chewing stroke; this means that the contact points travel along the crests more rapidly. Didelphidian dilambdodonty occurs in some placentals, notably in L. Eocene bats such as *Ageina* (Russell *et al.* 1973), where there is no mesostyle on the buccal cingulum. In later bats the *centrocrista* crests reach the buccal margin and a mesostyle is incorporated. In the living dermopteran *Cynocephalus* the crests reach the buccal margin but they are not notched (Fig. 4).

Many mammals possess a mesostyle in combination with a narrow stylar shelf. It is situated opposite the notch in the *centrocrista*, and its function may be to protect the gum from food escaping through the notch. When the notch is deep enough the hypoconid touches the mesostyle just before it passes through the notch, so that a transverse wear facet appears on the mesostyle, branching off the *centrocrista* at the notch. Examples may be seen in species of *Microsyops*, *Plesiadapis* and *Notharctus*. Dilambdodonty could evolve from this condition by retreat of the paracone and metacone lingually, giving the *centrocrista* an inverted V shape. An early stage, where the cusps have not retreated very far, can be seen in *Mixodectes* and *Pontifactor* (Fig. 5). The central position of the paracone and metacone in dilambdodonts would in that case not be a primitive survival but a derived character, which evolved subsequently to the mesostyle connection. (Compare the arrows 1 and 2 in Fig. 1). Possibly shrews and moles have evolved in this way from a nyctithere source, passing through a *Pontifactor*-like stage. If *Ptilocercus*, with a narrow stylar shelf, represents the plesiomorphic state in the Tupaiidae, the centrally placed paracone and metacone of *Tupaia* may also be derived (Butler 1980).

CONCLUSION

Dilambdodonty is an adaptation that has evolved many times independently, and not always in the same manner. In some cases it appears that the primitive *centrocrista* was diverted buccally in molars with a wide stylar shelf; in other cases the paracone and metacone were displaced lingually in molars where the stylar shelf was originally narrow. Involvement of the mesostyle, resulting in concavity of the cutting crests, may take place at different stages in the process. Dilambdodonty illustrates the propensity of teeth to parallelism and convergence, that causes so much trouble to taxonomic palaeontologists who have to rely to such a large extent on dental characters. Thus Crochet and Sigé (1983) misinterpreted the adapisoriculid *Bustylus* as a didelphid (Gheerbrant 1991), and Van Valen (1965) regarded *Adapisoriculus* as a tupaiid.

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