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Counting premolars in early eutherian mammals

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The primitive number of premolars for most eutherian groups is four. A growing number of Cretaceous taxa, however, had five. Regardless of the hypothesis used to explain the discrepancy, or what the primitive condition was, it is generally agreed that the middle (third) tooth of five-premolared taxa is the one not represented in mammals that have only four premolars. Hence the current practice of labeling the teeth as the first through fifth and the first through fourth, depending on how many teeth are observed in the jaw, results in incorrect implied homologies for the last two premolars of the series. Given the long-standing tradition of referring to the premolars as the first through fourth, for most eutherian groups, together with the uncertainties involved in interpreting the difference, the most practical solution is to refer to the disputed tooth by a neutral term, 'Px', as advocated several decades ago.

For more than a century, many eutherian mammal groups have been recognized to have primitively had four premolars. Hence, it has become standard practice for students of fossil and recent mammals to refer to these teeth as the first through fourth premolars (P/p1-4 hereafter[1]). Where one or more of these teeth is missing from the series, the remainder are conventionally referred to by their homologies (established or inferred) with the original four (e.g., Romer 1966). It came as a surprise when specimens of *Gypsonictops*, from the Late Cretaceous of North America, showed evidence for the presence of five premolars (Lillegraven 1969; Clemens 1973). The third tooth is smallest and is lost ontogenetically in *G. hypoconus*, but apparently retained through life in the geologically older *G. lewisi* (see Fox 1977). Five upper premolars were found to be present in *Kennalestes*, a primitive eutherian from the Late Cretaceous of Mongolia (Kielan-Jaworowska 1981). Here, too, the third in the series is small and is lost in mature individuals (Fig. 1C). The homologies of P1-2 and P3-4, in *Gypsonictops* and *Kennalestes*, with those of other eutherians is well established and has not been questioned: it is the third in the series that is supernumerary, and for this reason it was termed Pc (e.g., Lillegraven 1969; Clemens 1973) or Px (Kielan-Jaworowska 1981).

McKenna (1975) reinterpreted the dental formula in non-tribosphenic *Peramus* as including P/p1-5, M/m1-3 (traditionally thought to be P/p1-4, M/m1-4, see Clemens & Mills 1971) and proposed an hypothesis that was to become enormously influential: that the pres-

[1] Eutherians generally replace all antemolar teeth except the first premolar, which technically is thus dP/dp1 (see review by Luckett 1993). Herein I follow convention in referring to it simply as P/p1.

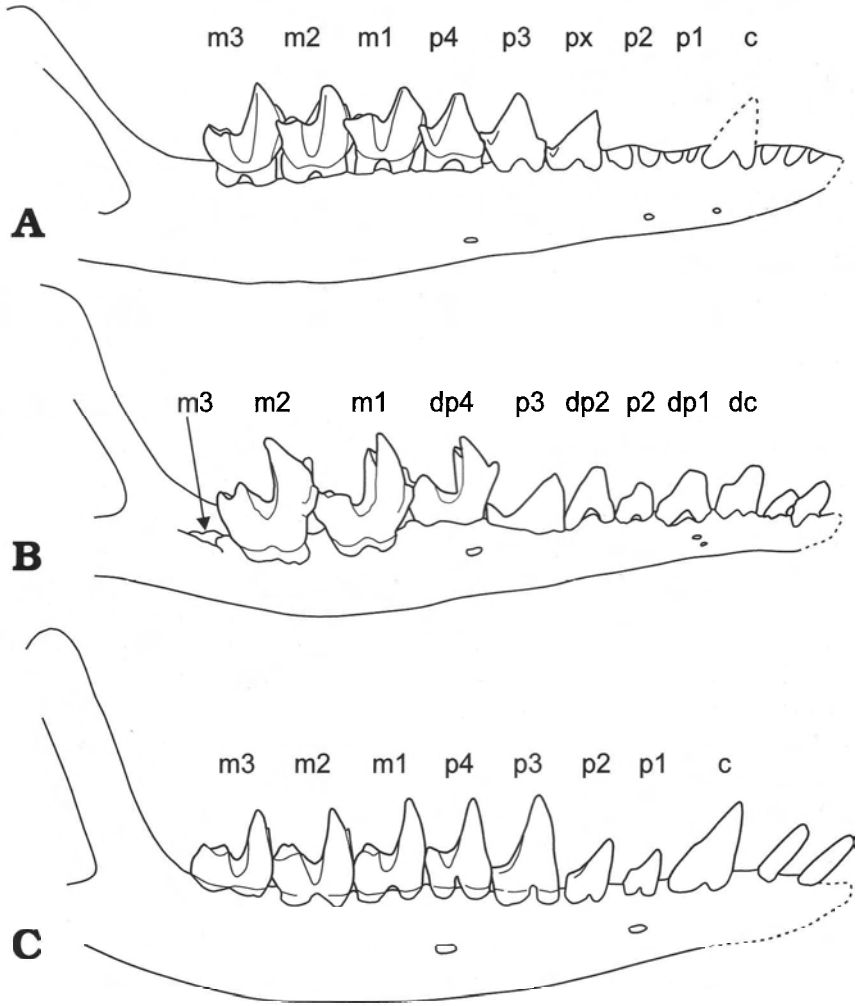

Fig. 1. Dentaries of Cretaceous eutherians in lateral view, showing variation in the premolar series (not to scale; reversed as necessary). **A**. *Prokennalestes* (composite, based on specimens described by Kielan-Jaworowska & Dashzeveg 1989; Sigogneau-Russell *et al.* 1992), showing five premolars, the third labeled px following system advocated in the text. **B**. *Daulestes* juvenile, showing the retention of dp2 after the eruption of the successor p2 (modified after McKenna *et al.* 2000). **C**. *Kennalestes* adult, showing the 'typical' primitive eutherian complement of p1-4, although juveniles retain dp2 after eruption of p2, as in *Daulestes* (modified after Kielan-Jaworowska 1969).

ence of P/p1-5 is primitive for Eutheria, and that P3 was lost in leptictidans (conceived as including both *Kennalestes* and *Gypsonictops*). Support for this view came with the long-awaited publication of *Prokennalestes*, from the Aptian-Albian of Mongolia. *Prokennalestes* is the earliest well known eutherian, and specimens clearly demonstrate the presence of five premolar positions (Kielan-Jaworowska & Dashzeveg 1989; Sigogneau-Russell *et al.* 1992, see Fig. 1). Based on McKenna's (1975), hypothesis, these teeth have been termed P/p1-5, and this has become established practice for early eutherians in which five premolars are known or inferred (e.g., Archibald 1996; Nessov *et al.* 1998; Cifelli 1999).

Luckett (1993) noted that phylogenetic loss of premolars usually proceeds posteriorly from the canine, and that loss in the middle of the series is unusual[2]. He proposed an alternative interpretation (earlier suggested by Clemens 1973) for the presence of a supernumerary tooth in the middle of the premolar series of some Cretaceous eutherians: that it is a retained deciduous premolar, probably dP/p2, that was not immediately (or, in some cases, ever) displaced ontogenetically by eruption of the successor P/p2. There exists little fossil evidence to test this hypothesis. However, it is consistent with ontogenetic loss of this tooth in *Gypsonictops* and *Kennalestes*, mentioned above. In addition, a recently described specimen belonging to the Coniacian eutherian *Daulestes* (Fig. 1B) represents an immature that is interpreted to have retained dp2 after eruption of the successor though, like *Kennalestes*, the deciduous tooth was probably lost in adults (McKenna *et al.* 2000).

Whether loss of a tooth at the third position was phylogenetic or ontogenetic (see Archibald & Averianov 1997), however, a common tooth formula, implying homology at the respective loci, should be employed. It is generally agreed that P/p1-2 and P/p3-4 (of four-premolared eutherians) are, respectively, homologous with P/p1-2 and P/p4-5 (of those having five). Given the long, well established tradition for numbering premolars in 'conventional' primitive Eutheria, which have four premolars, considerable confusion would arise from referring to the four premolars as P/p1-2, 4-5. In view of this, and the fact that neither the phylogenetic nor ontogenetic hypothesis can be adequately tested with data at hand, I suggest adoption of a numbering system that is both neutral, in terms of the identity of the middle premolar in five-premolared taxa, and that implies homologies for the remaining four premolars. Two such schemes have been used (Lillegraven 1969; Clemens 1973; Kielan-Jaworowska 1981); perhaps the one least susceptible to misinterpration, advocated herein, is: P/p1-4 for eutherians with four premolars; and P/p1-2, P/pX, and P/p3-4 for those with five.

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[2] Loss in the middle of the series is not, however, unprecedented. In the djadochtatheriid multituberculates *Catopsbaatar* and *Tombaatar*, reduction to three upper premolars was accomplished through loss of P2 (see Kielan-Jaworowska 1974; Rougier *et al.* 1997).

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