EVOLUTION OF DENTAL REPLACEMENT IN MAMMALS

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ABSTRACT

We provide a review of dental replacement features in stem clades of mammals and an hypothetical outline for the evolution of replacement frequency, mode, and sequence in early mammalian evolution. The origin of mammals is characterized by a shift from a primitive pattern of multiple, alternating replacements of all postcanines in most cynodonts to a derived pattern of single, sequential replacement of postcanines. The stem mammal *Sinoconodon*, however, retained some primitive replacement features of cynodonts. The clade of *Morganucodon* + crown mammals is characterized by the typical mammalian diphyodont replacement in which antemolars are replaced by one generation in antero-posterior sequence, but molars are not replaced. The stem clades of crown mammals including multituberculates and eutriconodonts have an antero-posterior sequential and diphyodont replacement of premolars. By contrast, stem taxa of the trechnotherian clade (*Zhangheotherium*, *Dryolestes*, and *Slaughteria*) are characterized by an alternating (p2 → p4 → p3) and diphyodont replacement, a condition that is shared by basal eutherians. The sequential replacements of premolars in most extant placentals (either antero-posteriorly p2 → p3 → p4 as in ungulates and carnivores, or postero-anteriorly p4 → p3 → p2 as in some insectivores) would represent secondarily derived conditions within eutherians. The single replacement of P3/p3 of metatherians is the most derived for all therian mammals.

INTRODUCTION

Mammals differ from their phylogenetic relatives—nonmammalian cynodonts—in their greatly reduced number of successional teeth per tooth locus. Living mammals have two generations of teeth (diphyodonty) at most, whereas nonmammalian cynodonts had multiple generations of tooth replacement sustained throughout life (polyphyodonty). Mammalian dental replacement is limited partly by a delay in the onset of dental eruption in neonates that nurse on maternal milk. During lactation, the toothless neonates can achieve a considerable amount of cranial growth at a rapid rate before eruption of the first generation of deciduous teeth (Brink, 1956; Hopson, 1973; Pond, 1977; Luckett, 1993). The mammalian dental replacement is also reduced partly by an early termination of dental replacement related to the determinate skull growth in mammals. Prior to weaning, the rate of skull growth exceeds that of the postcranial skeleton. After weaning the rate of skull growth slows down. The termination of the skull growth usually coincides with eruption of the last molar (Pond, 1977).

Diphyodont dental replacement of mammals is a major apomorphy because it is certainly correlated with the determinate growth pattern of the skull, and partly correlated with lactation, which is the most important mammalian characteristic (Pond, 1977; Tyndale-Biscoe and Renfree, 1987; Jenkins, 1990; and Zeller, 1999). Nursing of the neonates by maternal milk has had a profound impact on mammalian growth patterns and on development of numerous apomorphies in dentition and skull, such as: the reduced replacement of the postcanines, development of precise molar occlusion, formation of the dentary-squamosal temporomandibular joint, as first pointed out by Brink (1956) and elaborated by many others (Hopson and Crompton, 1969; Romer, 1970; Ziegler, 1971; Hopson, 1971; Pond, 1977; Kermack and Kermack, 1984; Gow, 1985; Crompton and Hylander, 1986; Luckett, 1993; Luo, 1994; Crompton, 1995).

The complex phenomenon of dental replacement can be broken down to several basic morphological elements. (1) Replacement frequency—number of successional teeth at each tooth locus, especially whether replacement occurred in the posterior molariforms. The rate of dental replacement is directly correlated with the patterns of skull growth. (2) Mode of replacement: alternating *versus* sequential. (3) Direction or sequence of replacement: antero-posterior *versus* postero-anterior. In this study we will attempt to outline these main features of the dental replacement patterns in cynodont-mammal evolution.

DENTAL REPLACEMENT OF EXTANT MAMMALS

Placentals (Fig. 1).—The diphyodont dental replacement in most living placental mammals is characterized by a single replacement of deciduous (''milk'') incisors, canines, and premolars by a second generation of permanent incisors, canines and premolars. Molars are part of the permanent dentition and are never replaced (Ziegler, 1971; Williams et al., 1989; Nowak, 1991; Evans, 1995).

There are several well-known exceptions to this typical diphyodont pattern among the placentals. As the antemolar replacement has some degree of homoplasy, it can vary among genera of the same family. In some very small soricid and talpid insectivores, none of the premolars is replaced and the entire postcanine series is monophyodont (Osborn, 1971; Bloch et al., 1998). The embryonic precursors to the deciduous antemolars in the highly altricial neonates are reabsorbed before eruption (Churchfield, 1990; Nowak, 1991). As a result, these small insectivores have only a one generation of functional postcanine teeth (monophyodonty). The same monophyodont condition appears to be also present in some geolabidid insectivores of the Late Cretaceous and early Tertiary (Lillegraven et al., 1981), although not in others (Bloch et al., 1998). Other exceptions to the typical placental diphyodont dentition can be seen in the anteaters (myrmecophagid xenarthrans) and the pangolins (manid pholidotans). These mammals are toothless and rely on the tongue to feed on ants and other insects. Adult mysticete whales have baleen for filter feeding instead of teeth

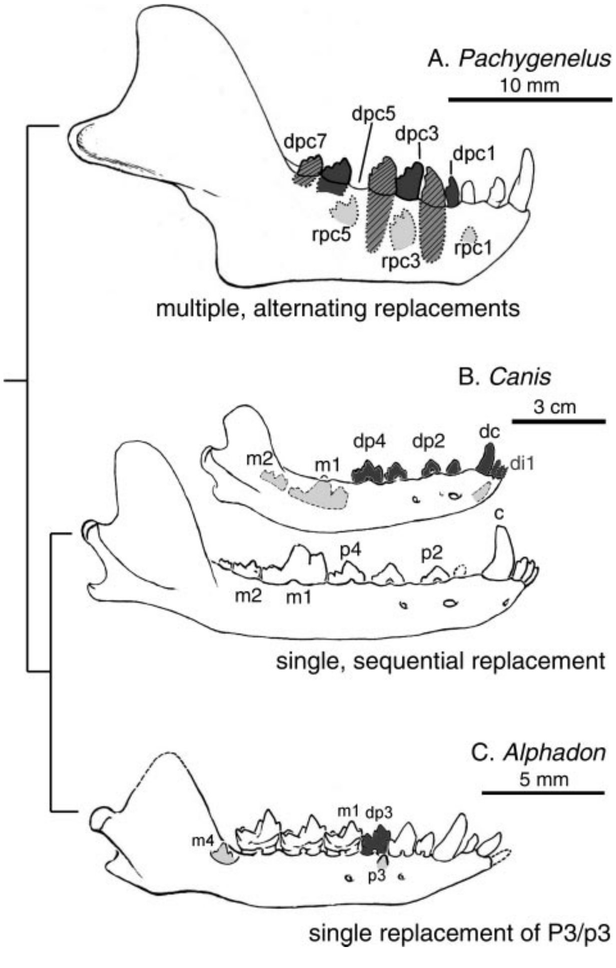

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Fig. 1.—Comparison of dental replacement between nonmammalian cynodonts and extant therian mammals. A. The nonmammalian cynodont *Pachygenelus* (from Crompton and Luo, 1993: fig. 4.14). B. The eutherian *Canis latrans* (coyote): above—deciduous lower dentition of a juvenile (based on Carnegie Museum CM 8653); below—permanent dentition of an adult (CM 7365). C. The metatherians *Alphadon* (modified from Clemens, 1966, and Cifelli et al., 1996). Teeth in light gray: erupting/successor teeth (= permanent teeth after eruption). Dark gray: deciduous predecessor teeth yet to be replaced. Gray/hatched: deciduous predecessor teeth in alternate positions, yet to be replaced. Unshaded: permanent teeth. Abbreviations: di, deciduous incisor; dc, deciduous canine; dp, deciduous premolars; dpc, deciduous postcanines; m, molars; pc, postcanines; rpc, replacing postcanines. Most nonmammalian cynodonts (except gomphodonts and tritylodontids) are characterized by alternating replacements of all teeth for multiple generations, in correlation with indeterminate growth of the jaw. The deciduous postcanines are replaced at every other, or every third tooth position in the same replacement wave (as seen in *Pachygenelus*). As the successor tooth tends to be larger than the predecessor tooth in each tooth position, the jaw had to grow in length to accommodate the larger replacement teeth in cynodonts, as in extant diapsids. In most extant placental mammals, there is only one generation of replacement for the antemolars but no replacement of molars (as seen in *Canis*). Tooth replacement is more reduced in metatherians (as seen in *Alphadon*), postcanine replacement only occurs in the ultimate premolar P3/p3.

(Nowak, 1991). Nonetheless, most placental mammals have a diphyodont dentition in which all deciduous antemolars (including the premolars or ‘‘milk molars’’) are replaced by the successional and permanent teeth. This generalized placental condition is less specialized than those of extant marsupials and monotremes.

The sequence of replacement of premolars is also variable among various extant placental groups. In the talpid insectivore *Scapanus*, the eruption of deciduous premolars and their replacement occur earlier in the ultimate premolar locus than the more anterior premolar loci (Zielger, 1971). The same postero-anterior sequences of premolar shedding and eruption also occur in the chrysochlorid *Eremitalpa* (Kindahl, 1963), the macroscelidid *Elephantulus* (Kindahl, 1957), and in some lipotyphlans (Luckett, 1993). This postero-anterior sequence of premolar replacement was previously considered to be a general pattern of placental insectivores (Osborn, 1973; Luckett, 1993). Among primates, most non-anthropoid taxa have postero-anterior sequential replacements (Smith, 2000), with the interesting exceptions of the stem anthropoid *Apidium*, in which the upper and lower premolars are replaced alternatingly (P2 → P4 → P3) (Kay and Simons, 1983). Australopithecines shows an alternating pattern of upper premolar replacement (Smith, 1994). Humans at 10 years of age show also an alternating pattern as P2 breaches the gum before P1 and P3 (Williams et al., 1989:fig. 8.84). Primates as a whole have postero-anterior sequential premolar replacements (Smith, 2000).

However, the sequence of premolar replacements in placental ungulates, carnivores, and other placental stem taxa are in the opposite, antero-posterior direction (Schmid, 1972; Smith, 2000). The deciduous premolars are replaced from the anterior to the more posterior positions in horse, sheep, pig, and domestic dog. In cattle (*Bos*), dp2 and dp3 are replaced about the same time (Olsen, pers. comm.) and earlier than dp4. The erupting sequence of p3 erupting before p4 (in an antero-posterior direction) for the premolars is known for the paromomyid *Acidomomys* (Bloch et al., 2002), a stem placental taxon. In the Tertiary stem placental *Microsyops*, p4 erupts before p3 and in *Plesiadapis* p3 and p4 erupt about the same time (Bloch et al., 2002). But the latter two taxa do not seem to represent the generalized condition of most early Tertiary mammals. Given the distribution of these characteristics, it is clear that primitively the placental crown group as a whole has sequential replacement of premolars, but it is not clear whether the antero-posterior direction, or the postero-anterior direction would present the ancestral condition of all extant placentals.

Metatherians (Fig. 1C).—In metatherians including extant marsupials, only the ultimate premolar (P3/p3) has both an erupted deciduous tooth and a successor tooth (Luckett, 1993; Cifelli et al., 1996; Rougier et al., 1998). Other antemolars have only one generation of functional teeth in most marsupials. The first and second premolars have the erupted deciduous teeth retained in adults, without replacing successors. The incisors and canines have rudimentary and nonerupting deciduous predecessors that are lost or reabsorbed, followed by the accelerated development of successional permanent teeth (Luckett, 1993; Luckett and Woolly, 1996; Luckett and Hong, 2000).

The greatly reduced diphyodont replacement of marsupials is correlated with their perinatal specialization for prolonged lactation by fixation on the maternal nipples (Luckett, 1977, 1993; Tyndale-Biscoe and Renfree, 1987; Maier, 1993; Zeller, 1999). This pattern is now traced back to some of the earliest-known stem taxa of metatherians of the Late Cretaceous, by the studies of Clemens (1966), Lillegraven (1969), Cifelli et al. (1996), and Rougier et al. (1998) that shed light on the timing of the evolution of the marsupial developmental specializations.

Monotremes.—The echnidas (Tachyglossidae) have no teeth and rely on the tongue for feeding. The platypus *Ornithorhynchus* (Ornithorhynchidae) has deciduous teeth in early growth stages, but these are replaced by horny dental pads in adults (Simpson, 1929; Green, 1937; Woodburne and Tedford, 1975). Of the two deciduous premolars, dp1 has no replacing successor whereas dp2 has a successional dental lamina (Luckett and Zeller, 1989). In this regard, the premolar replacement in *Ornithorhynchus* retains a vestige of the diphyodont replacement premolar of therian mammals (Green, 1937; Parrington, 1974; Luckett and Zeller, 1989; Archer et al., 1993).

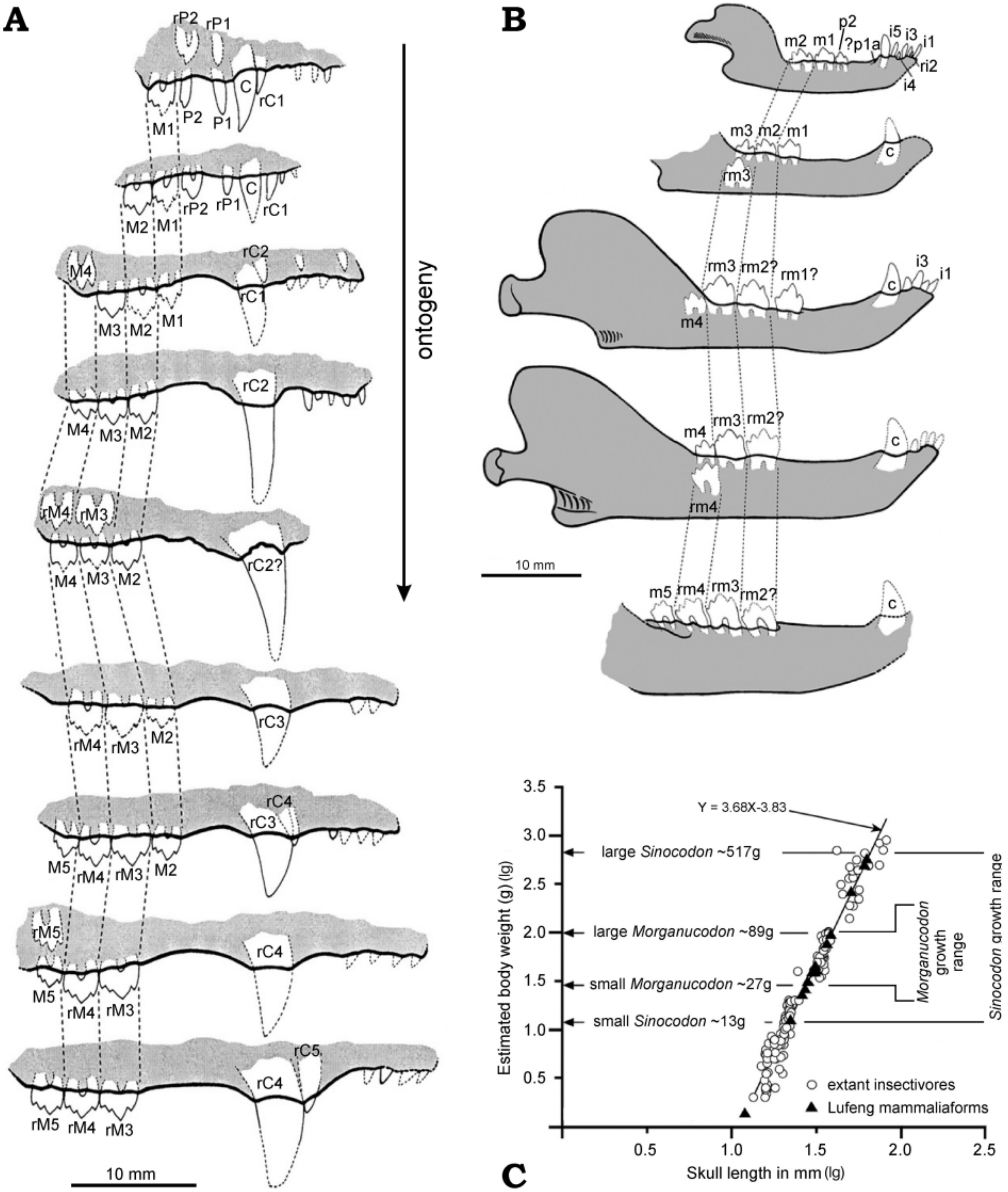


Fig. 2.—Continual dental replacement during cranial and mandibular growth in the stem mammal *Sinoconodon* (from Zhang et al., 1998 and Luo et al., 2001). A. Upper dental replacement. B. Lower dental replacement and growth of mandible. C. Ranges of skull size of currently known specimens in *Sinoconodon* and *Morganucodon*, and estimate of their body mass on the basis of extant insectivore scaling data. At least four generations of replacement canines occurred throughout the entire observed size range of *Sinoconodon* skulls collected from the local Early Jurassic Lower Lufeng Formation. The postcanine replacement shows an antero-posterior sequence: P1 → P2 → ‘‘M3’’ → ‘‘M4’’ → ‘‘M5’’. In correlation with the continuous replacement of smaller predecessor postcanines by larger successors, the jaws and skulls increased in size (the skull length ranging from 22 to 62 mm; estimated body masses ranged from ∼13g to ∼517g) in *Sinoconodon*. By comparison, *Morganucodon* skulls from the same Lufeng fauna have ranged from 27 to 38 mm (with estimated body masses ranging from 27g to 89g). This suggests that *Sinoconodon* had continuous skull growth accompanied by continuous tooth replacement well into late stage of adult life, a characteristic of indeterminate growth pattern of extant nonmammalian amniotes and nonmammalian cynodonts. The narrower range of growth in *Morganucodon* suggests that it is closer to determinate growth of extant mammals than *Sinoconodon* and nonmammalian cynodonts. Solid triangles: *Morganucodon* and *Sinoconodon* skulls; open circles, extant insectivore skull and body mass data in regression of Y=3.68X-3.83 (data from Gingerich and Smith, 1984).

NONMAMMALIAN AMNIOTES

Diapsids.—Most of the toothed diapsid amniotes have multiple generations of teeth, or polyphyodont dental replacements (Edmund, 1960; Hildebrand, 1974). In extant diapsids, such as lizards, hatchlings must be capable of independent feeding with a full set of functional teeth. As demonstrated by Edmund (1960), Osborn (1971, 1973; 1974a), and Westergaard and Ferguson (1986, 1987) the teeth erupt early in growth and are subsequently replaced continuously throughout life. The tooth replacement occurs alternately at every other, or every third tooth position (Edmund, 1960; Osborn, 1971). This continual and alternating dental replacement pattern appears to be primitive for extant tetrapods and amniotes as a whole (Hildebrand, 1974; Berkowitz, 2000). Continual tooth replacement is correlated with indeterminate growth of the jaws, because the continued lengthening of the jaws is required for the smaller predecessor teeth to be replaced by the larger successor teeth that are fixed in size and morphology by enamel on the crown at eruption. The continual replacement by larger teeth in older individuals with simultaneous lengthening of the jaws is characteristic of the indeterminate growth in many diapsids (Osborn, 1971; Westergaard and Ferguson, 1986, 1987) including dinosaurs (Erickson, 1996; Erickson and Tumanova, 2000).

Nonmammalian synapsids (Fig. 1A).—Most cynodonts are characterized by alternate, multiple dental replacements and the related indeterminate jaw growth, as are most extant diapsids. Alternating and continuous dental replacements have been documented for *Thrinaxodon* (Parrington, 1936; Crompton, 1963; Osborn and Crompton, 1973) and *Pachygenelus* (Gow, 1980; Crompton and Luo, 1993), among other nonmammalian cynodonts. Postcanines in *Thrinaxodon* are replaced up to three times at the posterior loci (Osborn and Crompton, 1973). Although lower than those of living diapsids, the number of successional teeth per tooth locus is much higher than for any mammals.

Two well-known exceptions to the general cynodont replacement pattern are diademodontids and tritylodontids. In diademodontids with the ‘‘gomphodont’’ postcanines, and possibly also in related traversodontids, the postcanine replacement is sequential in an antero-posterior direction (Crompton, 1963, 1972; Hopson, 1971; Osborn, 1974b). In tritylodontids, there is no replacement of postcanines. The postcanines erupt by sequential addition at the posterior end of tooth row, and the worn postcanines are shed anteriorly (Kühne, 1956; Hopson, 1965; Cui and Sun, 1987). Nonetheless, the alternating and multiple replacements of *Thrinaxodon* are representative conditions for nonmammalian cynodonts as a whole.

The majority of cynodonts had the reptilian indeterminate growth because their jaws continued to lengthen as smaller predecessor teeth were replaced by larger successor teeth at the posterior loci in large individuals (Osborn and Crompton, 1973). Because dental replacement begins in the smallest known individuals in cynodonts (Crompton, 1963; Hopson, 1971; Osborn, 1973; Osborn and Crompton, 1973; Crompton and Luo, 1993), it is unlikely that nonmammalian cynodonts developed lactation.

STEM CLADES OF MAMMALS

Sinoconodon (Fig. 2).—*Sinoconodon* showed differentiation of premolars from molars and a single replacement of premolars (Zhang et al., 1998; *contra* Crompton and Luo, 1993). Both are derived features of modern mammals. Replacement of the postcanines in *Sinoconodon* followed an antero-posterior sequence. This is a derived character of mammals (defined as common ancestor of *Sinoconodon* and the crown Mammalia; = Mammaliaformes *sensu* Rowe, 1988; McKenna and Bell, 1997), as it differs from the alternating replacement in most nonmammalian cynodonts, although it has some resemblance to the replacement of posterior postcanines in diademodontids.

However, other dental replacement characteristics of *Sinoconodon* are very primitive for mammals. Incisors in *Sinoconodon* show alternate replacement pattern. The canines were replaced at least three times (Crompton and Luo, 1993; Zhang et al., 1998), similar to the multiple alternating replacements of incisors and canines of many nonmammalian cynodonts.

The youngest known specimens of *Sinoconodon* (Fig. 2) have two deciduous premolars. These deciduous premolars were replaced once, but their successor teeth are subsequently lost in the larger (thus older) specimens of their growth series. The anterior molars (M1–M2) of the smaller individuals were probably lost without replacement. The loss of anterior postcanines (premolars and molars) has resulted in a postcanine diastema that is increasingly larger in older individuals. The loss of anterior postcanines, coupled with successive addition of newly erupted molariforms at the posterior end of the tooth row, has resulted in the posterior shift of the functional tooth rows in the jaws. These are primitive features shared by *Thrinaxodon*, *Probainognathus*, diademodontids, and tritylodontids.

This pattern of losing the anterior postcanines is present, although to a lesser extent, in *Morganucodon*, *Hadrocodium*, and possibly also in *Kuehneotherium* (Kermack et al., 1968; Parrington, 1971; Mills, 1971, 1984; Luo et al., 2001a). Few other mammals have this pattern of losing anterior postcanines during growth, except where it presumably was acquired secondarily, as in proboscideans of the Tertiary.

The posterior molars (M3–M5) have one replacement in the larger (presumably older) individuals of *Sinoconodon* (Fig. 2). The replacement of a smaller ultimate molariform by a larger successor followed by eruption of yet another ultimate molar in an older individual occurs only in *Sinoconodon* and diademodontids (Crompton, 1963; Hopson, 1971). *Sinoconodon* also resembles diademodontids in that smaller deciduous postcanines with simpler crowns are replaced by erupting postcanines that are larger and more molariform. By contrast, in the cynodont *Thrinaxodon,* the predecessor postcanine tends to be more molariform and complex and the successive replacing teeth are progressively simpler (Osborn and Crompton, 1973). A convergent pattern can also be found in most mammals (except *Gobiconodon*), in which a deciduous molariform predecessor is usually replaced by a permanent premolar with less molariform crown.

Sinoconodon lacks precise dental occlusion because it does not have the one-to-one opposition between upper and lower molars (Crompton and Sun, 1985). This is correlated with the partial replacement of posterior molariforms and with the successive posterior shift of the functional postcanine row as a part of the indeterminate growth pattern of the skull (Zhang et al., 1998).

The currently available specimens of *Sinoconodon* show a large range of growth from the smallest individual with an estimated body mass of about 13 grams to the largest individual with an estimated body mass of more than 500 grams (Fig. 2C). During this growth, the posterior molariforms were being replaced while the upper and lower jaws continued to lengthen in the older individuals.

From these characteristics of *Sinoconodon* we infer that it experienced indeterminate growth in its skull, accompanied by continual tooth replacement, as in nonmammalian cynodonts (Crompton, 1963; Hopson, 1971; Osborn and Crompton, 1973; Osborn, 1974b) and modern diapsid reptiles (Osborn, 1971, 1974a; Westergaard and Fergusen, 1986, 1987; Berkowitz, 2000). Also it is plausible that *Sinoconodon* did not develop lactation because the polyphyodont replacement of the anterior teeth had already begun with the smallest known individual (Fig. 2A, B) (Zhang et al., 1998).

Sinoconodon is considered to be the sister taxon to all other mammals (Crompton and Sun, 1985; Crompton and Luo, 1993; Rowe, 1993; Luo, 1994; Hopson, 1994; Wible et al., 1995; Rougier et al., 1996; Luo et al., 2001a, b). Given its position in the cynodont-mammal phylogeny, and given its many primitive replacement features of nonmammalian cynodonts, it is parsimonious to regard the dental replacement of *Sinoconodon* as an intermediate stage in the character evolution from the primitive pattern of polyphyodont replacement seen in most cynodonts to the derived diphyodont replacement of mammals. The coexistence of the mammalian dentary/squamosal joint and the cynodont-like multiple replacements of the incisors and canines in *Sinoconodon* indicates that the mammalian temporomandibular joint evolved before the typical mammalian dental replacement pattern (Luo, 1994). The replacement features in *Sinoconodon* also suggest that the reduction in the postcanine replacement preceded the reduction of the replacement of incisors and canines. The suppression of dental replacement had occurred in the postcanines before it did in the anterior dentition.

Morganucodon and Haldanodon.—*Morganucodon* had a single replacement of the posterior premolars (Mills, 1971; Parrington, 1971, 1973, 1978; Clemens and Lillegraven, 1986). Parrington (1971, 1973, 1978) suggested that *Morganucodon* (referred to as ‘‘*Eozostrodon*’’) had a typically mammalian replacement of the incisors and canines. Subsequent observations are consistent with this suggestion (Kermack et al., 1973; 1981; Gow, 1985; Crompton and Luo, 1993). The mode of replacement of premolars is sequential in the antero-posterior direction, similar to that of *Sinoconodon*.

It is more difficult to document the nonreplacement of molariforms in morganucodonts. Gow (1986) suggested that *Megazostrodon*, which is closely related to *Morganucodon*, might have replaced its m2 based on the substantial evidence that this tooth is less worn than the adjacent m1 and m3. Because *Megazostrodon* is represented only by two specimens (Crompton, 1974; Gow, 1986), its sample size is too small to be certain about this. Parrington (1971) described the groove for the replacing dental lamina in some mandibles of *Morganucodon*. This groove is usually present in cynodonts with ongoing postcanine replacement. However, dissecting the posterior mandible did not reveal any replacement teeth, as shown by Parrington (1971, 1973). The ultimate molars in *Morganucodon* are variable in size, which was considered by Parrington (1973) to be due to dimorphic or polymorphic variation.

The consensus of those who studied the dentition of *Morganucodon watsoni* is that the molars were not replaced (Mills, 1971; Crompton, 1972; Parrington, 1973; Crompton and Parker, 1978; Clemens and Lillegraven, 1986; Luo, 1994). There is little evidence for replacement of ultimate molars from the series of complete mandibles of *Morganucodon oehleri* (Young, 1982; Crompton and Luo, 1993) and *Dinnetherium* (Jenkins et al., 1983; Crompton and Luo, 1993). The X-ray of two *Morganucodon oehleri* skulls shows no replacement successors to the ultimate and penultimate functional molars. It is safe to suppose that *Morganucodon* achieved the typical mammalian diphyodont dental replacement both in *antemolars* and the *anterior* molars. It is beyond question that *Morganucodon* has developed the typical diphyodont pattern in all of its *antemolars* and its *anterior molars*. It is reasonable to hypothesize that ultimate molars in morganucodontans were not replaced, until this hypothesis is falsified by additional data from a more complete sampling of skull growth series. If the variation in size and morphology of posterior molars of *Morganucodon* is shown to be correlated with growth stages, then the mode of the skull growth of *Morganucodon* must be reconsidered. With these caveats, we tentatively accept that the ultimate molar was not replaced. This working hypothesis of nonreplacement of ultimate molars (Parrington, 1971; Kermack and Kermack, 1984; Crompton and Luo, 1993; Luo, 1994) is consistent with the skull growth pattern of *Morganucodon* from the currently available (although still small) sample of specimens (Fig. 2C).

Morganucodon shows far smaller size range of the skulls than the contemporary *Sinoconodon* (Fig. 2C). The eight relatively complete skulls of *Morganucodon* discovered so far range in length from 27 to 38 mm (Young, 1982; Crompton and Luo, 1993; Luo et al., 1995; Zhang et al., 1998). This corresponds to a body-size range from 27 grams to 89 grams (Luo et al., 2001b), in strong contrast to a much wider range of variation in the estimated body size of *Sinoconodon* from 13 grams to over 500 grams. This indicates that the adult skulls grew far less in *Morganucodon* than in *Sinoconodon*. Most maxillaries and mandibles of *Morganucodon* from the Rhaeto-Liassic fissure deposits of the Great Britain are adults, and few are juveniles (Kermack et al., 1973, 1981; Parrington, 1971, 1978). Based on this Gow (1985) suggested that *Morganucodon* probably had a very short juvenile stage, a view supported by Luo (1994). The skull growth series and dental replacement indicate that *Morganucodon* had a short growth period to reach its adult size, at least by comparison to *Sinoconodon* (Fig. 2C) and cynodonts. The growth pattern of *Morganucodon* is closer to the determinate growth pattern typical of extant mammals than those of *Sinoconodon* and nonmammalian cynodonts. We hereby hypothesize that *Morganucodon* achieved the determinate growth of the skull characteristics of living mammals.

Dental replacement of the docodonts was studied by various authors since the 1920s (Simpson, 1928; Butler, 1939), but only recently could a definitive replacement pattern be documented in an unambiguous manner by a large sample of juvenile and adult jaws of *Haldanodon* (Krusat, 1980; Lillegraven and Krusat, 1991; Martin and Nowotny, 2000; Nowotny et al., 2001). Molars were not replaced in *Haldanodon*. The incisors, canines and premolars in *Haldanodon* show diphyodont replacement that proceeded from the front to the back in a sequential mode (Martin and Nowotny, 2000; Nowotny et al., 2001). This is an apomorphy in comparison to *Sinoconodon* and cynodonts. *Haldanodon* is more derived than the cynodont *Thrinaxodon*, *Sinoconodon*, *Morganucodon*, *Hadrocodium*, and *Kuehneotherium* in lacking the increasingly large postcanine diastema in the larger and older individuals due to the loss of the anterior premolars.

STEM CLADES OF MAMMALIAN CROWN GROUP

Gobiconodontids (Fig. 3A).—Gobiconodontids replaced their anterior molariform postcanines (Jenkins and Schaff, 1988; Wang et al., 2001). *Gobiconodon* is unique in that the successor permanent tooth is similar to its deciduous predecessor in the complexity of molariform morphology. In most oth-

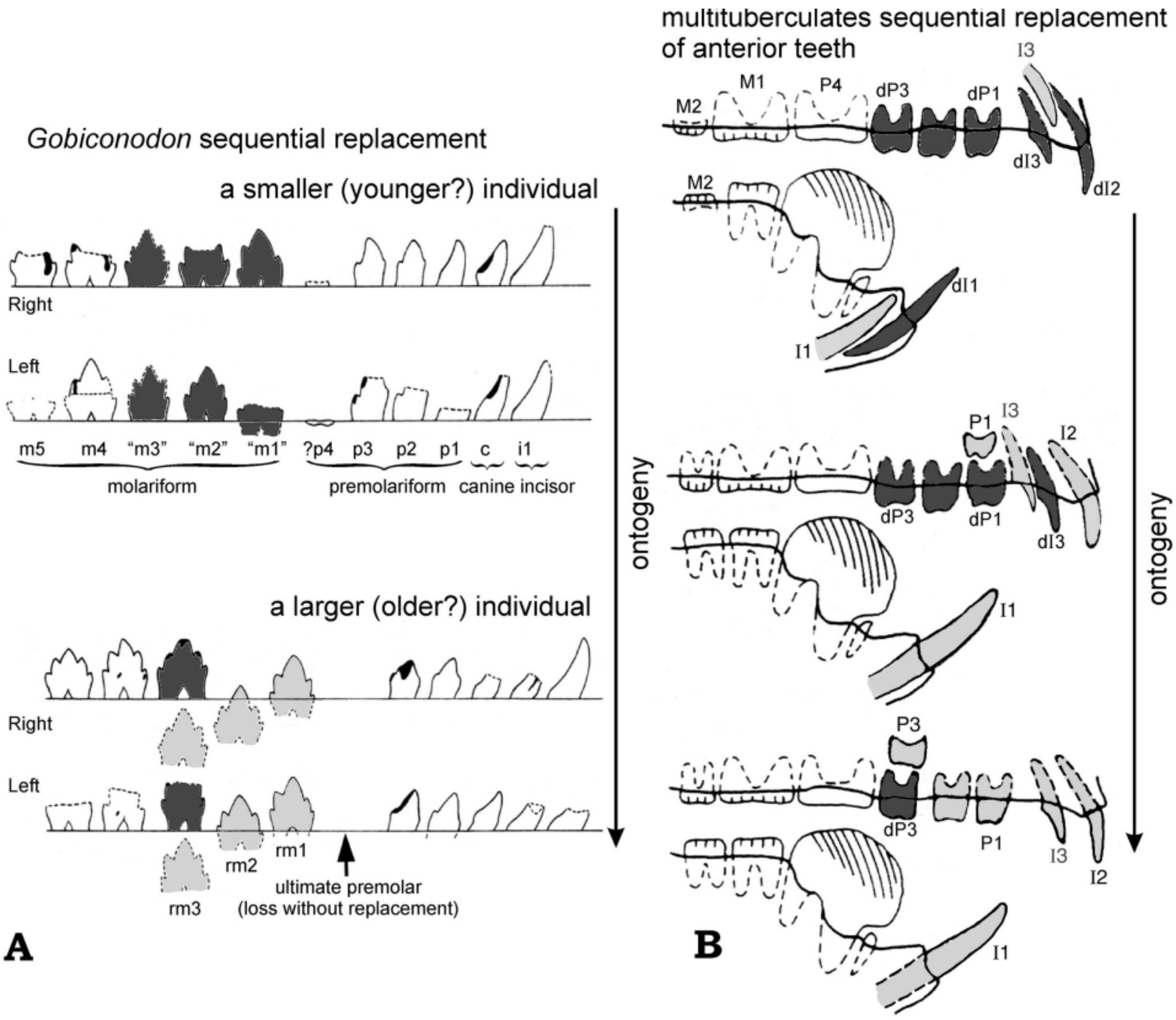


Fig. 3.—Sequential replacement of the anterior postcanines in multituberculates and gobiconodontids. A. Growth series of *Gobiconodon* (adopted from Jenkins and Schaff, 1988). At least two anterior molariform postcanines were replaced each by a molariform successor. The replacement shows an antero-posterior sequence: p4 (only shedding) → ''m1'' → ''m2'' → ''m3''. B. Multituberculate dental replacement shows an antero-posterior sequence (adopted from Greenwald, 1988): i1 → i2 → i3 → p1 → p2 → p3 → p4. Gobiconodontids and the majority of multituberculates and retain the primitive antero-posterior sequence for replacement of premolars. Teeth in light gray: erupting/successor teeth (= permanent teeth after eruption). Dark gray: deciduous predecessor teeth yet to be replaced. Unshaded: permanent teeth.

er mammals, the replacing and successional tooth is simpler in crown morphology than its deciduous predecessor at the same premolar locus. By widely accepted convention for defining molars *versus* premolars (e.g., Romer, 1970; Hildebrand, 1974; Williams et al., 1989; Evans, 1995), the postcanine loci with replacement should be considered to be premolars, regardless whether the permanent tooth of a premolar locus has a molariform crown, or a premolariform crown. The wave of replacement of the anterior postcanines is sequential, continuous from the front to the back, as shown by Jenkins and Schaff (1988), and corroborated by Wang et al. (2001). Based on limited evidence, Simpson (1928) interpreted that, in *Triconodon*, p1–p3 had been replaced before the replacement of dp4 by p4. If this can be corroborated, then *Triconodon* also has antero-posterior sequence of replacement of the premolars, as in gobiconodontids. However, *Triconodon* has a much simpler permanent p4 than its fully molariform dp4, and this differs from gobiconodontids in which both the permanent (successor) and the deciduous (predecessor) teeth at the same locus are equally molariform.

Multituberculates (Fig. 3B).—The incisors and at least some premolars are diphyodont in their replacement (Szalay, 1965; Hahn, 1978; Clemens, 1963; Clemens and Kielan-Jaworowska, 1979; Greenwald, 1988; Hahn and Hahn, 1998). Greenwald (1988) proposed that multituberculates of the North American Tertiary, especially *Taeniolabis*, have a diphyodont replacement similar to that seen in most placental mammals. In these multituberculates, tooth eruption and replacement occurred in an antero-posterior sequence. Hahn and Hahn (1998) believed that the Late Jurassic paulchoffatiid *Kielanodon* is one exception to the typical multituberculate pattern in which the replacement of the premolars could have occurred in an alternating mode, in two waves, and in the postero-anterior direction, as in *Thrinaxodon*.

The differences between the pauchoffatiid *Kielanodon* (Hahn and Hahn, 1998) and Tertiary multituberculates (Greenwald, 1988) can be interpreted by two scenarios. First, the postero-anterior and alternate replacement in paulchoffatiids may be the basal condition of all multituberculates, as proposed by Hahn and Hahn (1998). If so, then multituberculates ancestrally would bear some resemblance to *Thrinaxodon* and to trechnotherians (more discussion below). The antero-posterior and sequential replacement observed in the North American Tertiary multituberculates would therefore represent a secondarily derived condition.

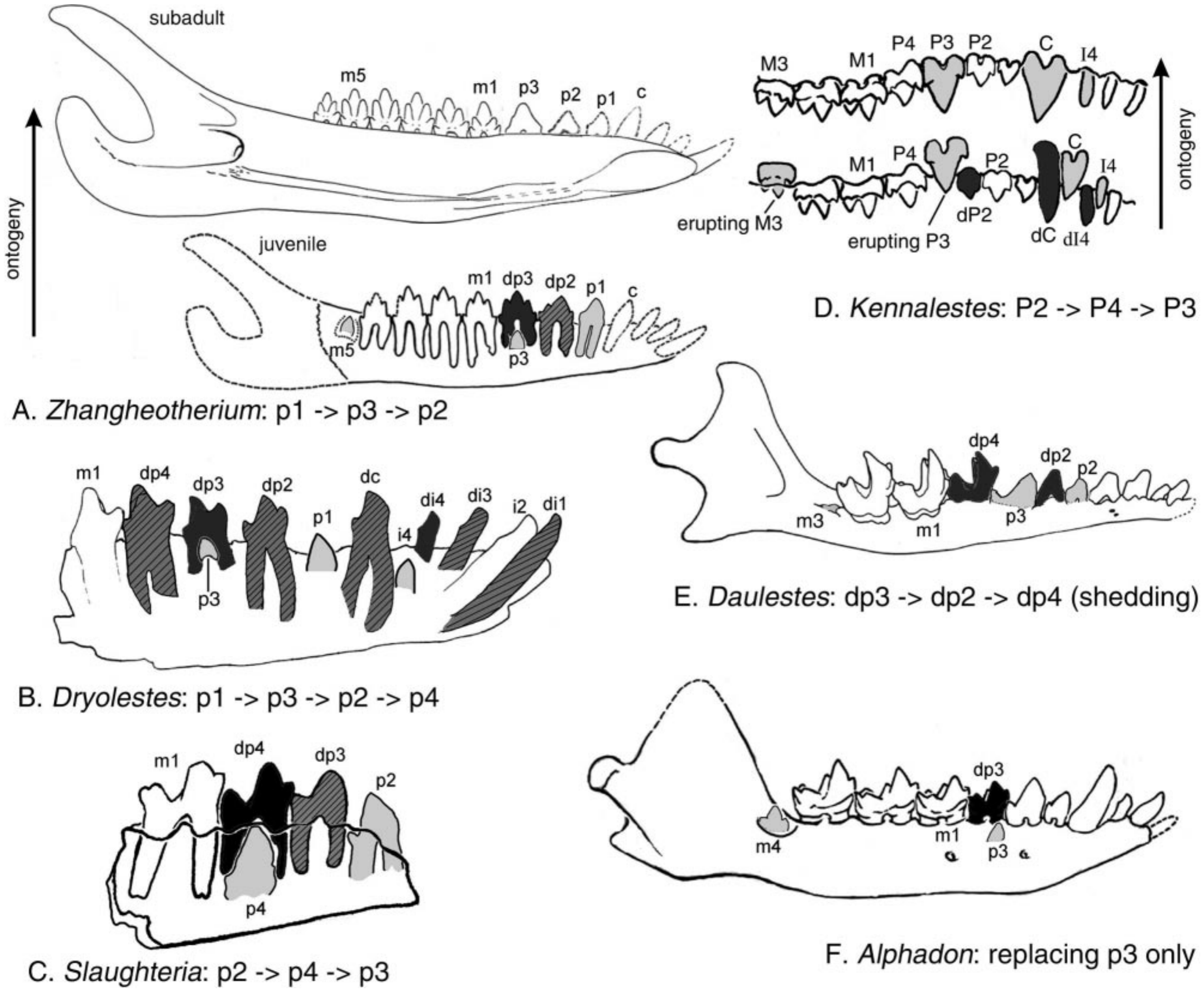
The second possible interpretation is that the antero-posterior sequential replacement is primitive for multituberculates as a group as proposed by Greenwald (1988), and the alternating replacement of paulchoffatiids is not only atavistic to the distant cynodonts, but also convergent to that of trechnotherians (to be described below). According to Greenwald's (1988) interpretation, multituberculates would be more similar to *Sinoconodon, Morganucodon, Haldanodon* and eutriconodonts, than to trechnotherians, in the replacement sequence. Which of these conditions is basal to multituberculates as a whole depends on the position of multituberculates on the mammalian phylogenetic tree (see the recent reviews on multituberculate relationships by Butler, 2000 and Luo et al., 2002). Greenwald's (1988) interpretation is consistent with a more parsimonious explanation of evolution of dental replacement among major clades of mammals. Here we tentatively accept that antero-posterior sequential replacement of antemolars is characteristic of multituberculates as a whole (*sensu* Greenwald, 1988).

Trechnotherians (*sensu* McKenna, 1975; McKenna and Bell, 1997).—The majority of stem therians has an alternating pattern in an antero-posterior sequence for their diphyodont premolar replacement (Fig. 4). The alternating replacement in trechnotherians is limited to only one generation of successor per tooth locus. By contrast, the alternating replacement in many cynodonts is in the postero-anterior direction and with multiple generations of successors.

The spalacotheriid ‘‘symmetrodont'' *Zhangheotherium* has an alternate diphyodont replacement in an antero-posterior sequence in the lower jaws (Fig. 4A). The currently available juvenile and subadult specimens show that permanent p1 erupted first, followed then by shedding of dp3 and eruption of permanent p3, and lastly by replacement at the p2 locus. The replacement at the p3 locus occurs around the time of eruption of m5. The replacement at the p2 locus occurs around the time of eruption of m6. Thus the sequence of replacement is: p1 → p3 → p2, both for the shedding of deciduous teeth and for eruption of permanent teeth. We suggest that this alternate premolar replacement in *Zhangheotherium* could be applicable to other spalacotheriids for which replacement of premolars is known (Cifelli, 1999). In all premolar loci, the deciduous predecessor tooth is more ‘‘molariform'' than its permanent successor. There is no evidence that molars are replaced in any spalacotheriids.

Dental replacement in the ‘‘eupantothere'' *Dryolestes* is documented with extensive data (Martin, 1997, 1999). Deciduous teeth have long been recognized in dryolestids (Butler, 1939; Butler and Krebs, 1973). Martin (1997, 1999) further demonstrated that all antemolar teeth are replaced in *Dryolestes*. The diphyodont replacement, at least in the lower jaw, occurs in the antero-posterior sequence by two waves. The first replacing wave consists of i2, i4, p1, p3, which are followed by the second wave of i1, i3, c, p2, p4. p4 is the last premolar to erupt, just prior to eruption of the sixth molar (m6). The premolar replacement (both shedding of deciduous teeth and eruption of permanent teeth) is characterized as: p1 → p3 → p2 → p4 (Martin, 1997).

The stem boreosphenidan *Slaughteria* (referred to as a ‘‘tribothere'' by many previous authors) also has a similar replacement sequence of premolars: p3 → p2 → p4 (Kobayashi et al., 2002). Therefore, the alternating sequence of premolar replacement (p3 → p2 → p4) is consistently present from spalacotheriids through dryolestids to stem northern tri-



A. *Zhangheotherium*: p1 -> p3 -> p2

B. *Dryolestes*: p1 -> p3 -> p2 -> p4

C. *Slaughteria*: p2 -> p4 -> p3

D. *Kennalestes*: P2 -> P4 -> P3

E. *Daulestes*: dp3 -> dp2 -> dp4 (shedding)

F. *Alphadon*: replacing p3 only

Fig. 4.—Alternating premolar replacement in stem therians and some eutherian mammals. A. The ‘‘symmetrodont’’ (stem technotherian) *Zhangheotherium* (subadult adopted from Hu et al., 1997, 1998; juvenile is based on National Geological Museum of China, NGMC 352, from Luo et al., 2001c). B. The ‘‘eupantothere’’ (stem cladotherian) *Dryolestes* (adopted from Martin, 1999). C. The stem boreosphenidan (a ‘‘tribothere’’) *Slaughteria* (adopted from Kobayashi et al., 2002). D. The eutherian *Kennalestes* (modified from Kielan-Jaworowska, 1981). E. The eutherian *Daulestes* (from McKenna et al., 2000). F. The metatherian *Alphadon* (modified from Clemens, 1966, and Cifelli et al., 1996). Teeth in light gray: erupting/successor teeth (= permanent teeth after eruption). Dark gray: deciduous predecessor teeth yet to be replaced. Gray/hatched: deciduous predecessor teeth in alternate positions, yet to be replaced. Unshaded: permanent teeth. By comparison to the antero-posterior sequential replacement of premolars gobiconodontids, multituberculates and *Sinoconodon*, the premolar replacement in trechnotherians (clade of *Zhangheotherium* and extant therians) occurred alternately, characterized by P1 → P3 → P2 → P4. This pattern was retained in basal eutherians (*Kennalestes* and *Daulestes*). It is only in the placental crown group (such as in carnivores, ungulates and primates) that the premolar replacement occurs sequentially, which must be considered to be a secondarily derived condition.

bosphenic mammals in three different hierarchies of therian mammal phylogeny, making a compelling case that this is a widespread condition for all basal trechnotherian lineages (including the basal eutherians) for which the replacements have been known (Fig. 5). This is different from the primitive pattern of the antero-posterior sequential replacement of postcanines in all mammal groups outside the trechnotherian clade, such as multituberculates (except *Kielanodon*), *Gobiconodon*, *Haldanodon*, *Morganucodon*, *Sinoconodon*, and possibly triconodontids. We regard the alternating replacement of premolars (at least for p3 → p2 → p4) to be a synapomorphy of the trechnotherian clade.

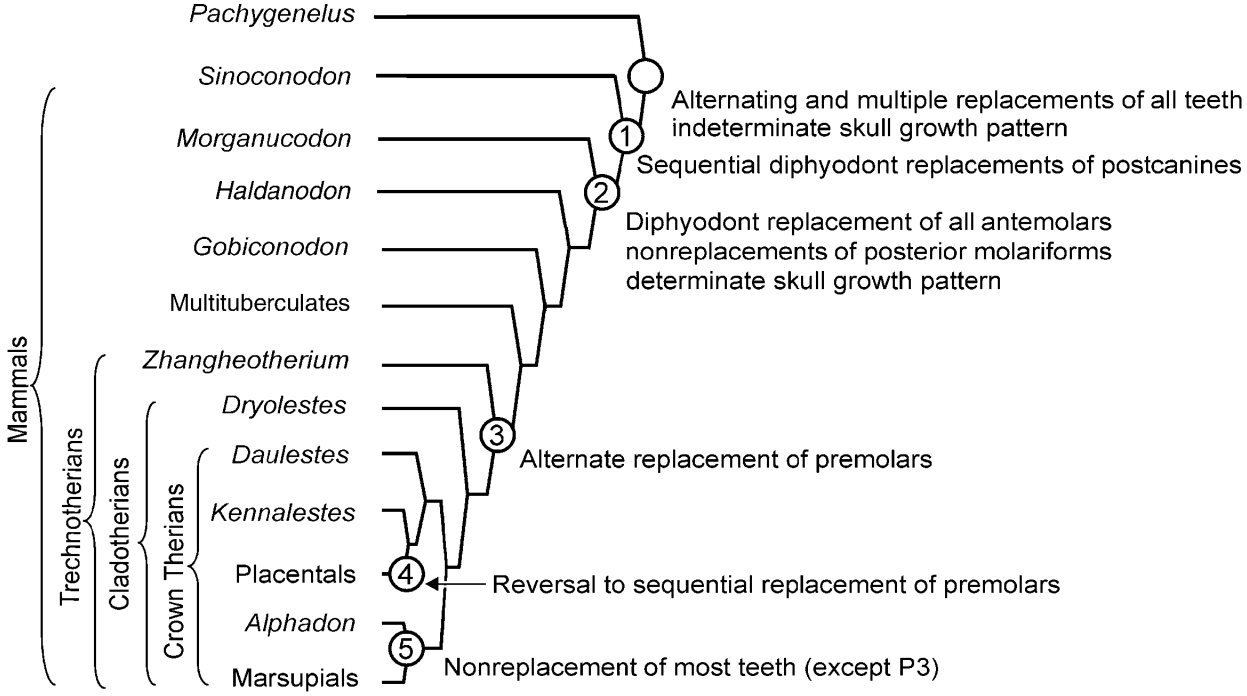


Fig. 5.—Acquisition of apomorphies in dental replacement and skull growth pattern in early evolution of mammals. The plesiomorphic condition of primitive nonmammalian cynodonts: multiple (polyphyodont) and alternate replacements of all teeth. Acquisition of apomorphies: Node 1 (mammals = mammaliaforms of Rowe, 1988; McKenna and Bell, 1997): Differentiation of premolars and molars, a single replacement of premolars, a single replacement of some posterior molariforms in antero-posterior sequence. Node 2 (clade of *Morganucodon* and crown mammals): single replacement of incisors and canines, antero-posterior sequence for a single replacement of premolars, molars without replacement; determinate skull growth pattern; the diphyodont replacement of incisors and canines is possibly associated with lactation. Node 3 (trechnotherian): alternating single replacement of premolars, a pattern that is shared by the known stem eutherians. Node 4 (extant placentals): reversal to the antero-posterior sequential replacement of premolars. Node 5 (metatherians): nonreplacement of most teeth (except P3/p3), which represents the most derived feature of dental replacement among mammals.

STEM CLADES OF EUTHERIANS AND METATHERIANS

Stem Eutherians (Fig. 4D, E).—The most primitive eutherians known for their full dentition, *Prokennalestes* and *Eomaia*, have five premolars (Kielan-Jaworowska and Dashzeveg, 1989; Sigogneau-Russell et al., 1992; Ji et al., 2002). The more derived zhelestids also have five premolars (Archibald and Averianov, 1997; Nessov et al., 1998; Cifelli, 2000). But the replacement pattern is unknown in these taxa. The more derived eutherians have four premolars, and it is generally accepted that the homolog of the third premolar (P3/p3) of *Prokennalestes* was lost in the Late Cretaceous eutherians with four premolars (McKenna, 1975; Novacek, 1986; Cifelli, 2000).

Replacement of anterior dentition is known for three Late Cretaceous eutherians that have four permanent premolars: *Daulestes* (McKenna et al., 2000), *Kennalestes* (Kielan-Jaworowska, 1975, 1981) and *Gypsonictops* (Lillegraven, 1969; Clemens, 1973; Novacek, 1986). Among these, *Daulestes* and *Kennalestes* have preserved evidence for an alternate replacement of premolars in an antero-posterior sequence as in the stem ‘‘therians’’ *Zhangheotherium*, *Dryolestes* and *Slaughteria*.

The juvenile specimen of *Daulestes* has four premolar loci, permanent p2 has erupted before permanent p3, which in turn erupts before p4 (Fig. 4E). The sequence of eruption of the permanent teeth in *Daulestes* is consistent with an antero-posterior sequential replacement. However, if taking into account that permanent p2 and deciduous dp2 co-exist with each other because permanent p2 failed to dislodge dp2 (also see discussion by Luckett, 1993 on *Kennalestes*), then there would be a different characterization of the replacement. The shedding of dp3 occurs before the shedding of dp2, forming a shedding sequence of dp3 → dp2 → dp4.

McKenna (1975) considered that the Cretaceous eutherian *Kennalestes* had five premolars in juveniles and four in adults (also see Bown and Kraus, 1979). But Luckett (1993) reinterpreted that one of the five premolars in the *Kennalestes* juvenile is a retained dp2, and that *Kennalestes* should have only four premolars in both juvenile and adult. This interpretation was accepted by McKenna et al. (2000) and by Cifelli (2000), and it will be followed here (Fig. 4D).

The only known juvenile specimen of *Kennalestes* also has the dP3 → dP2 → dP4 shedding sequence of the deciduous teeth (Fig. 4D), as revealed by the comparison of the juvenile skull to the adult skull (Kielan-Jaworowska, 1975; Kielan-Jaworowska, 1981; Luckett, 1993). The permanent P3 erupted long after the permanent P2 and P4 had become fully functioning (Fig. 4). So the erupting sequence of these permanent molars is likely to be: P2 → P4 → P3. Luckett (1993) interpreted that the premolar before the erupting successional P3 was a deciduous dp2 in the *Kennalestes* juvenile specimen (Fig. 4), and this was accepted by McKenna et al. (2000) and Cifelli (2000). Following Luckett's interpretation, the sequence for shedding deciduous teeth in *Kennalestes* was dp3 → dp2 → dp4. Therefore the replacement sequence, both for shedding deciduous teeth and for erupting permanent teeth, was identical to the alternating antero-posterior replacement in *Slaughteria* (Kobayashi et al., 2002), *Dryolestes* (Martin, 1997), and *Zhangheotherium* (Luo et al., 2001c).

The alternating, antero-posterior eruption of permanent teeth in *Kennalestes*, as well as the antero-posterior alternate shedding of deciduous teeth for both *Daulestes* and *Kennalestes* are different from the pattern in extant placentals. In extant placental insectivores, the development of the precursor dental lamina (Luckett, 1993) and the eruption of the deciduous premolars occur first in the ultimate premolar and then proceed anteriorly in talpids (Ziegler, 1971; Osborn, 1971, 1973; Osborn and Crompton, 1973), chrysochlorids (Kendahl, 1963; Osborn, 1973), macroscelidids (Kadahl, 1957), some lipotyphlans (Luckett, 1993) and fossil non-anthropoid primates (Smith, 2000). Most eutherian carnivores and ungulates have an antero-posterior sequence for eruption of permanent premolars (Schmid, 1972; Smith, 2000). However, from the currently available fossil evidence of the stem eutherians, this sequential premolar replacement in extant placentals is secondarily derived. The alternating, antero-posterior replacement of antemolars of Cretaceous eutherians is the primitive condition for eutherians as a whole.

Metatherians (Fig. 1C).—The perinatal adaptation in marsupial neonates by fixation of the mouth to the maternal nipple for prolonged lactation (Tyndale-Biscoe and Renfree, 1987; Maier, 1993; Zeller and Freyer, 2001) is directly correlated to the accelerated growth of the skeletomuscular system of the skull (Maier, 1993) relative to the brain (Smith, 1996, 1997). This is also correlated with the highly transformed diphyodont replacement of marsupials that is limited to a single replacement of the ultimate premolar P3/p3 (Luckett, 1977; 1993). Dental replacement in marsupials is the most derived of all mammalian tooth replacement patterns. It can be traced to the stem taxa of metatherians of the Late Cretaceous (Clemens, 1966; Lillegraven, 1969; Cifelli et al., 1996; Rougier et al., 1998).

EVOLUTION OF DENTAL REPLACEMENT FROM CYNODONTS TO MAMMALS

Diphyodont dental replacement among extant therian mammals is characterized by several features, including two generations of ante-molars and deciduous predecessor being more complex (''molariform'') than the permanent successor at the same premolar locus, and replacement of premolars proceeding either in postero-anterior direction (small placental insectivores), or in antero-posterior direction (placental ungulates and carnivores). It has been widely accepted that the diphyodont replacement in therians probably was derived from the ancestrally polyphyodont replacement of cynodonts by slowing down of the tooth replacements (see the historical reviews by Kermack, 1963, 1967; Osborn, 1971, 1973; Hopson, 1971; Crompton and Parker, 1978; Kermack and Kermack, 1984; Berkowitz, 2000). However, before the late 1980s, the detailed information on the number of successional teeth per premolar loci, mode, and direction of premolar replacement waves was not available for a wide diversity of Mesozoic mammals, thus limiting our previous understanding about the evolutionary patterns of these replacement features.

Since the late 1980s, especially since the startling discovery of the molariform replacements in *Gobiconodon* (Jenkins and Schaff, 1988), a series of new fossils have revealed some crucial pieces of information in all morphological elements of dental replacements in various stem mammal groups including the fossil taxa of crown mammals: (1) the replacement frequency: number of replacements per tooth locus; (2) the replacement mode: alternating *versus* sequential; and (3) the direction: antero-posterior *versus* postero-anterior replacement sequence. The new data, as summarized here, have shown a much greater degree of homoplasy in the modes and sequences of dental replacement than in the change of replacement frequency.

Frequency of replacement (number of succesional teeth per locus) through the cynodont-mammal transition shows a two-step reduction, firstly in the premolars of *Sinoconodon* (Fig. 5:node 1), then in the incisors, canines and posterior molariforms (= molars) of *Morganucodon* and *Haldanodon* (Fig. 5: node 2). The incisors and canines are also limited to one replacement as in most extant therians, instead of multiple replacements as in *Sinoconodon* (Crompton and Luo, 1993; Zhang et al., 1998) and cynodonts. Once the apomorphic diphyodont replacement and determinate skull growth occurred in the stem mammals of the Early Jurassic, there have been no documented cases of derived mammalian group reversing to the polyphyodont replacements and the indeterminate skull growth. This is the most fundamental transformation in mammalian biological adaptation as this significant shift in skull growth pattern is probably correlated with the origin of lactation (Brink, 1956; Hopson, 1973; Pond, 1977; Gow, 1985; Luo, 1994; Zhang et al., 1998).

The mode and direction of the replacement waves have some degree of homoplasy in cynodont-mammal evolution. The alternating mode of replacement is a general pattern for many cynodonts including tritheledontids (again, except for diademodontids and tritylodontids). If tritheledontids are the sister-taxon to mammals, as is preferred by the majority of workers, then the mammalian origin can be characterized by a shift from primitive multiple, antero-posterior and alternating replacements of all postcanines in most cynodonts to a derived pattern of single, and antero-posterior sequential replacement of postcanines in the clade of *Sinoconodon* and living mammals (Fig. 5:node 1). In a more derived clade of *Morganucodon*, *Haldanodon*, and mammalian crown group, the antero-posterior sequential replacement only occurred in premolars, but not in posterior molariforms (molars) (Fig. 5:node 2). Gobiconodontids have antero-posterior sequential replacement for anterior molariform postcanines (‘‘molars’’) but not for the posterior molars (Jenkins and Schaff, 1988). This is consistent with the replacement pattern of *Morganucodon*, *Haldanodon*, and most multituberculates.

The antero-posterior sequential replacement of premolars is a predominating pattern widespread among early divergent clades of the mammalian crown group (possibly including triconodontids) and in many (but not all) placental groups (Schmid, 1972; Smith, 2000). However, the trechnotherian clade (Fig. 5:node 3) is characterized by an alternating, diphyodont sequence (p2 → p4 → p3) as evidenced by most stem taxa of this clade (*Zhangheotherium*, *Dryolestes*, and *Slaughteria*). The basal eutherians retained the primitive condition of an alternate, antero-posterior replacement of premolars (p2 → p4 → p3). The sequential replacement characteristics in the majority of extant placentals (Fig. 5:node 4) is a secondarily derived condition within eutherians. Among the crown placentals, the replacement sequence is in the antero-posterior direction (p2 → p3 → p4) for most groups including ungulates and carnivores (Schmid, 1972; Smith, 2000). The postero-anterior sequential replacement (p4 → p3 → p2) occurs in various insectivores, and the majority of the prosimian primates (Smith, 2000) may not represent a generalized condition for extant placentals as a whole, in contrast to a previous belief. The single replacement of P3/p3 of metatherians (Fig. 5:node 5) is the most derived dental replacement pattern of all therian mammals. This metatherian dental replacement is correlated with the high specialized reproduction seen in extant marsupials.

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