



EXTRAORDINARY DIPHYDONTY-RELATED CHANGE IN DENTAL FUNCTION FOR A TOOTH OF THE EXTINCT MARSUPIAL *EKALTADETA IMA* (PROPLEOPINAE, HYPSPRYMNODONTIDAE)

S. WROE and M. ARCHER

School of Biological Science, University of New South Wales, NSW 2052, Australia

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Summary—A time-dependent, fundamental change in function for a sectorial tooth in a group of extinct, propleopine kangaroos is reported. In juvenile *Ekaltadeta ima* (Marsupialia, Hypsiprymnodontidae, Propleopinae) the second premolar (P_2) functions as a serrated blade at the anterior end of the cheek tooth row. In adults, this tooth drops far below the occlusal plane of the cheek tooth row where it assumes a completely different function, that of a buttress, anterolingual to the base of the crown of the much larger, newly erupted third premolar (P_3). This pattern of diphyodonty-related change in dental function is unique within Mammalia. It also represents an extraordinary example of biological recycling of a normally discarded tooth.

Key words: tooth replacement, *Ekaltadeta ima*, diphyodonty.

INTRODUCTION

In mammals generally, tooth replacement normally involves eviction (shedding) and replacement of a pre-existing deciduous (primary) tooth by a successional tooth in the same tooth family. In marsupials, the only postcanine deciduous tooth is dP_3 which is replaced by P_3 (Flower, 1867; Luckett, 1993). Among marsupials, kangaroos (Macropodoidea) have a uniquely derived tooth replacement condition in which the erupting P_3 evicts P_2 as well as dP_3 . (Dental homology here follows Luckett (1993) for dP_3 and P_3 and Flower (1867) for the rest of the dentition.) Among living macropodoids, the musky rat-kangaroo, *Hypsiprymnodon moschatus* (Hypsiprymnodontidae, Hypsiprymnodontinae), presents a more primitive condition than other kangaroos in that the P_2 persists briefly after the P_3 erupts with loss of dP_3 (Woods, 1960). This condition in *H. moschatus* has been seen as structurally intermediate between the more conventional marsupial condition and the more derived condition of other kangaroos (Flannery, 1987).

The extinct, probably carnivorous (Wroe, 1995) propleopine rat-kangaroos (*Propleopus*, *Jackmahoneya* and *Ekaltadeta*) (Hypsiprymnodontidae, Propleopinae) are regarded to be the sister taxa of the hypsiprymnodontines. Hypsiprymnodontids as a whole are considered to represent the sister taxa to all other kangaroos (Ride, 1993). Following the discovery of abundant remains of the Oligo-Miocene *Ekaltadeta ima* (Archer and Flannery, 1985), it is now evident that this propleopine is unique within Mammalia in its tooth replacement system.

MATERIALS AND METHODS

Observations and conclusions presented in this paper are based on a study of eight juvenile and nine adult maxillae and dentaries of *E. ima* from the Oligo-Miocene deposits of Riversleigh in north-western Queensland. The prefix QMF indicates specimens registered in the fossil collections of the Queensland Museum. The prefix AR indicates specimens held in the research collections of the Vertebrate Palaeontology section of the School of Biological Sciences in the University of New South Wales. Juvenile dentaries include: AR 10899, AR 12116, AR 10561, AR 5247 and QMF 30222. Juvenile maxillae include: AR 17444, AR 12119, AR 16759, AR 13564 and AR 16902. Adult dentaries include: AR 11236, AR 11267, AR 3655, AR 12805, QMF 22761 and QMF 23888. Adult maxillae include: AR 5471, AR 16745 and AR 12837. Comparative material included specimens representing sixteen adult and two juvenile *Hypsiprymnodon* sp. (a new species whose description is in progress) also from the Riversleigh deposits as follows: juvenile dentary, QMF 23652; juvenile maxilla, QMF 11102; adult dentaries, AR 10704, QMF 24621, QMF 23463, AR 10861, AR 11098, AR 14082, AR 15134, AR 10724, AR 10913 and AR 13566; adult maxillae, AR 13569, AR 11075, AR 12087, AR 14826, AR 13394, AR 13998 and AR 10645. Casts of single dentaries of three late Cainozoic propleopines were also available as follows: the late Pleistocene *Propleopus oscillans* (AR 237, cast of holotype), the late Pleistocene *P. wellingtonensis* (AR 110, cast of holotype) and the Pliocene *Jackmahoneya toxoniensis* (AR 17579, cast of holotype). *Jackmahoneya*

toxoniensis was described by Ride (1993); *Propleopus* was reviewed by Archer and Flannery (1985).

Two aspects of diphyodonty in *E. ima* were investigated; firstly the persistence of P_2 and secondly the functional value of P_2 in the adult dentition.

Determining the longevity of P_2 in the adult denti-

tion was important both as a possibly unique character among macropodoid marsupials and for its relevance to the second feature examined, that of P_2 function in the adult. To establish the persistence of P_2 , both molar wear and the relative timing of eruption for P_3 and M_4 in *E. ima* were considered as

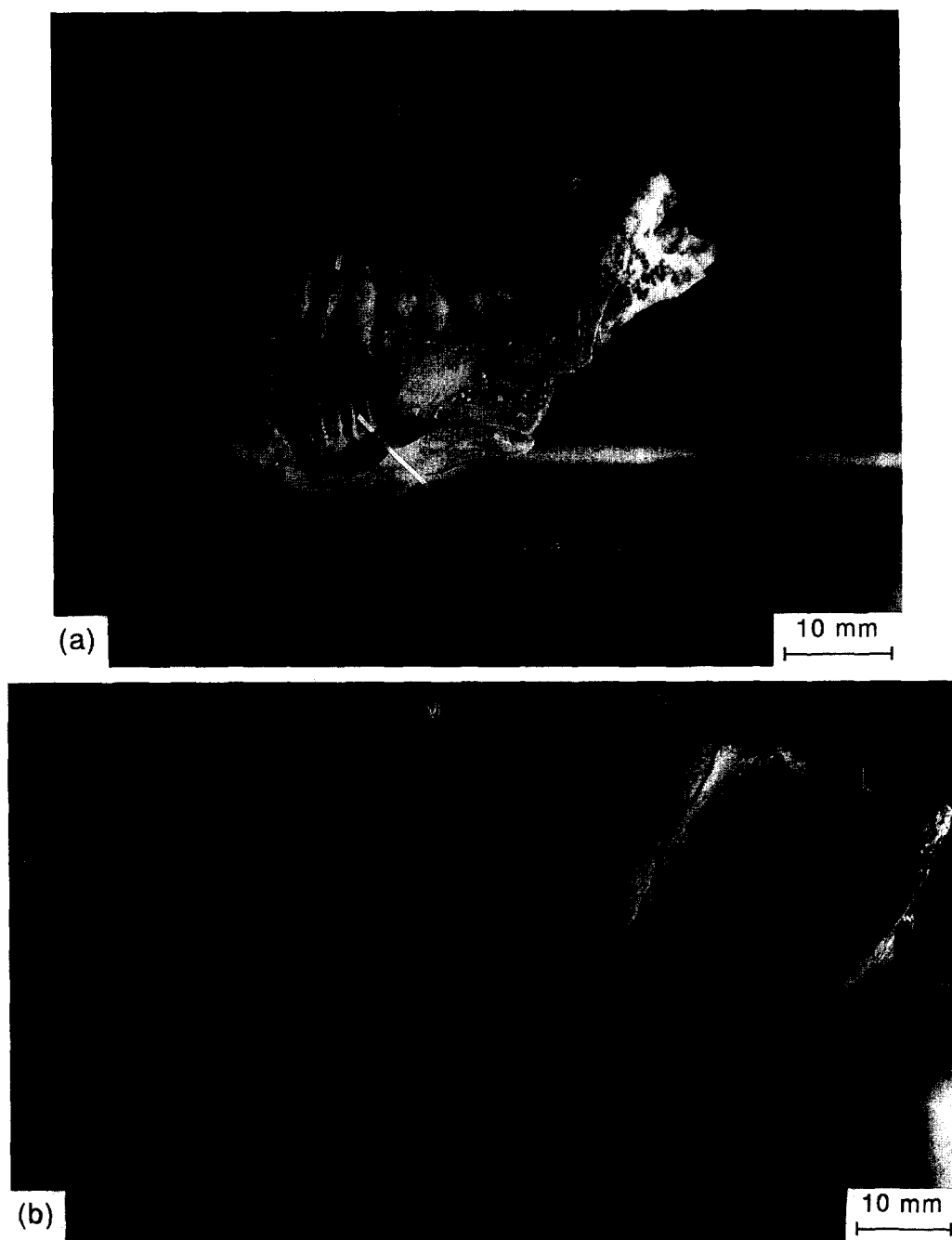


Fig. 1. Juvenile left dentary (top) and adult left dentary (bottom) of the Oligo-Miocene rat-kangaroo, *Ekaltadeta ima*. In the juvenile (AR 5247), P_2 , dP_3 and M_{1-2} are erupted; P_3 is visible in the crypt below dP_3 . In the adult dentary (AR 11267), I_1 , P_3 and M_{1-4} are erupted and in the occlusal plane; following the eruption of P_3 , the P_2 has dropped into its secondary position as a buttressing tooth, ventral and antero-lingual to the P_3 crown. The P_2 undergoes the same age-related change in position and function in the upper tooth row. Magnification $\times 1.89$ (AR 5247) and $\times 1.67$ (AR 11267).

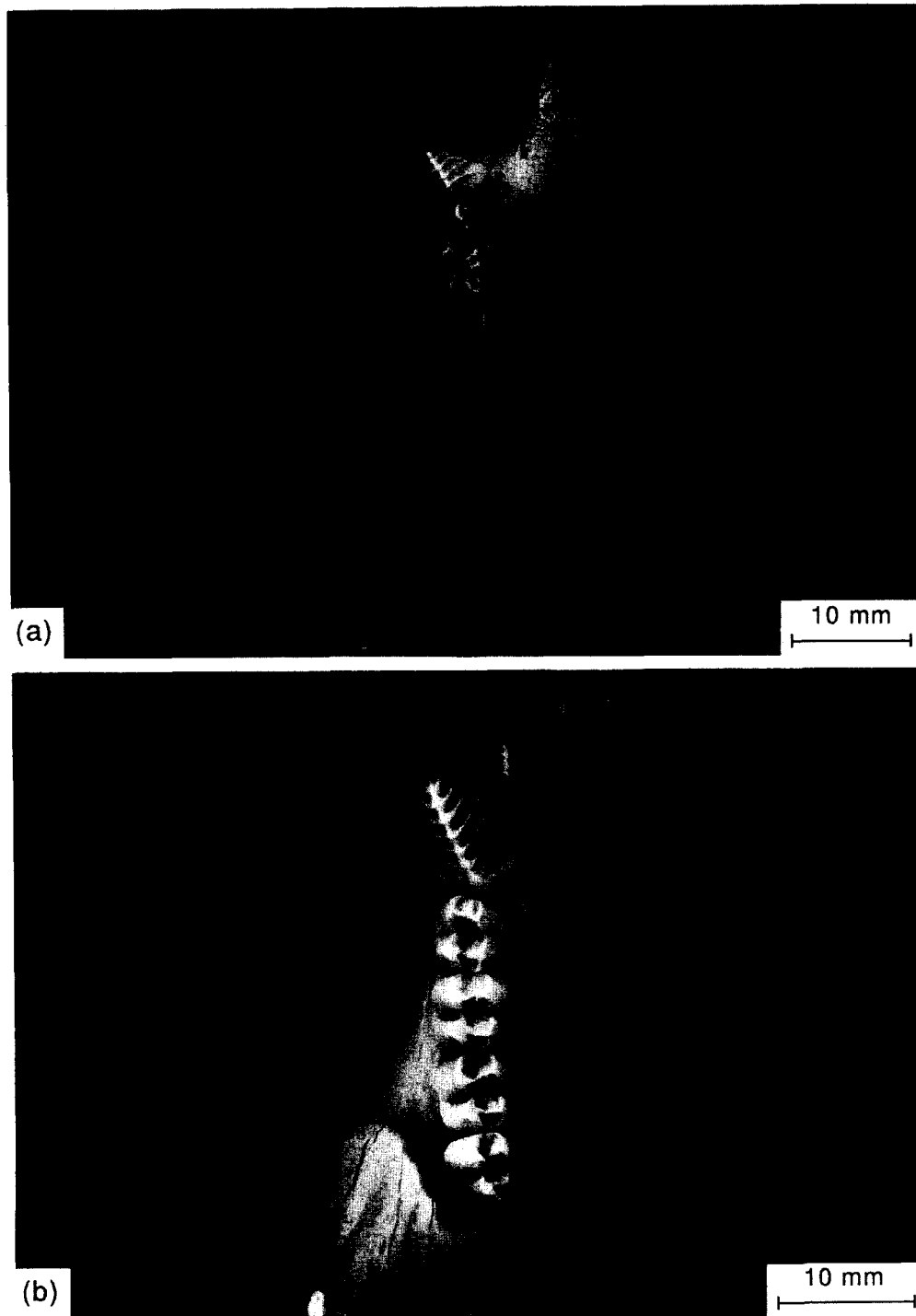


Fig. 2. Occlusal views of juvenile *E. ima* left dentary (AR 5247; top) and adult left dentary (AR 11267, bottom). In the juvenile P_2 is buccally torsioned away from the long axis of the tooth row. This situation is reversed in the adult, with P_2 being realigned with the alveolar row. Magnification $\times 2.15$ (AR 5247) and $\times 2.48$ (AR 11267).

indicators. The degree of wear on the molars is an obvious indicator of age. The stage of development in the eruption sequence has also been used to estimate age in macropodoids (Kirkpatrick, 1964, 1965). Marsupials are considered to be adult with the complete eruption of P_3 and ejection of dP_3 (Thomas, 1888). Among living macropodoids the eruption sequence of

P_3 relative to M_4 is variable (Tate, 1948). In many macropodoids P_3 erupts before M_4 . If this was the case for *E. ima* then the presence of P_2 in specimens containing P_3 and M_4 would have indicated retention of P_2 well into the adult life of the animal. To aid in establishing the eruption programme for *E. ima*, specimens of other hypsiprymnodontids were examined.

Demonstration of a functional role for P_2 in the adult dentition required investigation, as the persistence of P_2 in the adult might alternatively be explained as the retention of a primitive character with no functional value. Subsequently the position and orientation of P_2 in adult and juvenile *E. ima* were compared with those of other hypsiprymnodontids

and considered in terms of possible adaptive significance.

RESULTS

Adult (AR 11627, AR 16745 and QMF 22761) and juvenile (AR 5247) specimens of *E. ima* are shown in Figs 1–4. In six of the nine adult specimens of *E. ima*

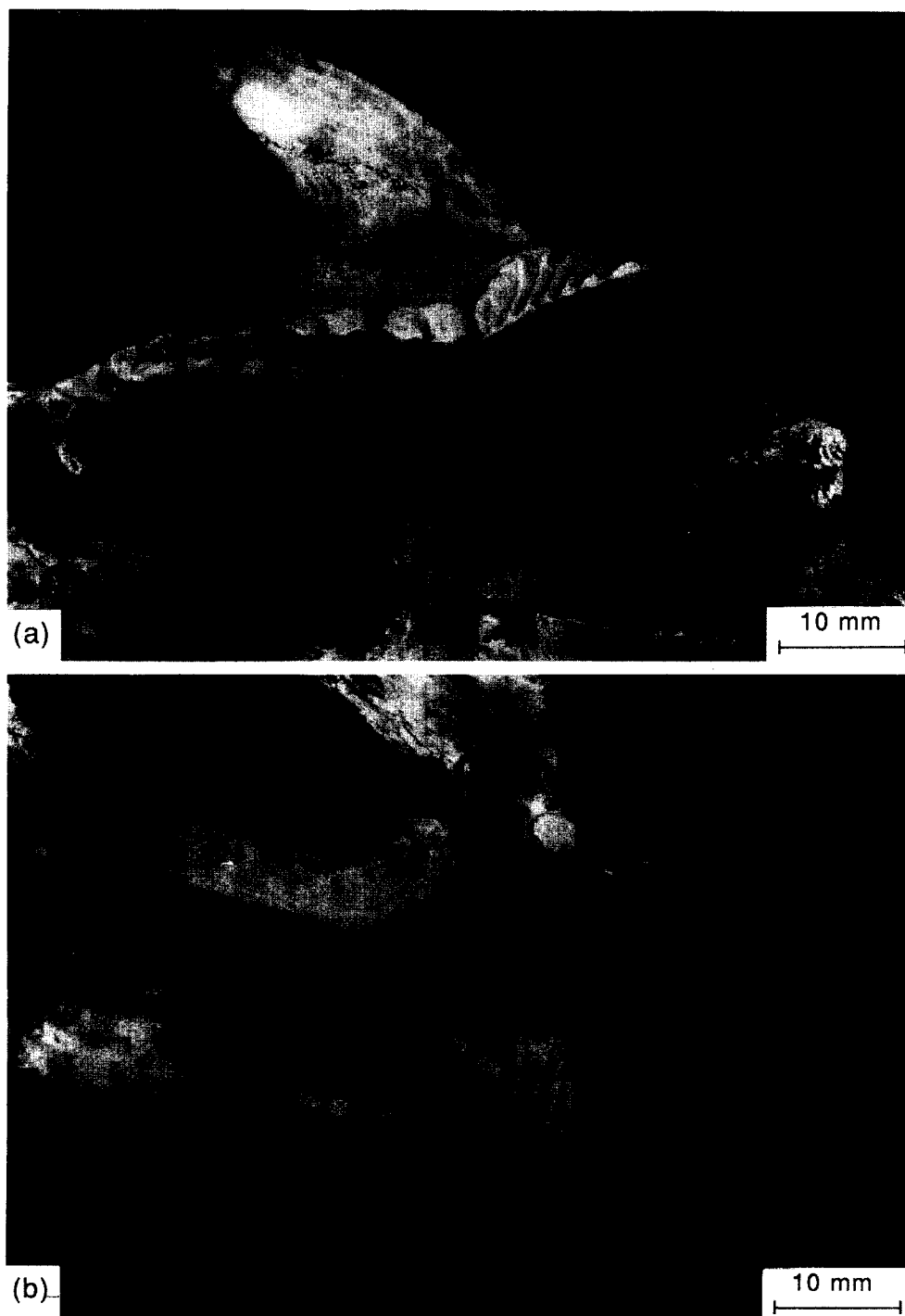


Fig. 3. Adult *E. ima* maxilla (AR 16745) in occlusal view (top) and buccal view (bottom). Magnification $\times 2.26$.

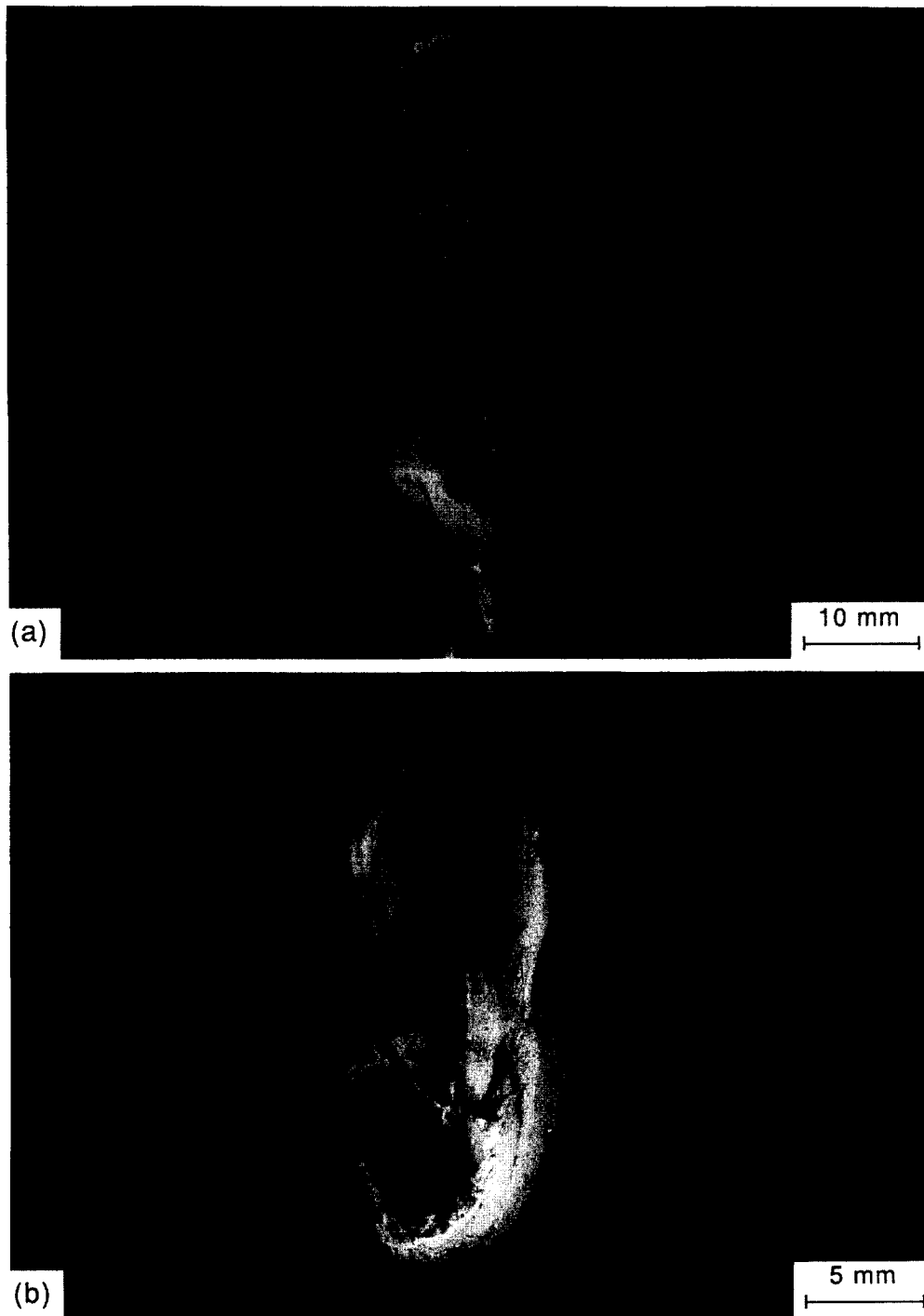


Fig. 4. Adult left dentary (QMF 22671). Occlusal view (top) with P_2 persisting in clearly aged specimen with well worn dentition and M_4 erupted. Anterior view (bottom) showing position of P_2 relative to P_3 . P_2 closely abuts the P_3 antero-lingually beneath the bulbous P_3 crown. Anteriorly directed dislodging forces acting on P_3 would have depressed the P_2 crown into its alveolus and surrounding dentary. Magnification $\times 2.04$ (top) and $\times 4.22$ (bottom).

(four dentaries and two maxillae), P_2 was firmly fixed in alveolus (AR 11267, AR 5471, AR 16745, AR 3655, AR 12805 and QMF 22761). In the remaining three adult specimens (AR 11236, AR 12837 and QMF 23888), although P_2 was missing the alveolus was open with no evidence of ossification, suggesting

that in these individuals P_2 was lost before fossilization. In five adult *E. ima* specimens (AR 11267, AR 5471, AR 16745, AR 3655 and QMF 22761) possessing complete cheek-tooth rows, P_2 persisted with a completely formed but unerupted P_3 , although M_4 had fully erupted. In two adult *Ekaltadeta ima*

specimens containing P_2 and P_3 (QMF 22761, Fig. 4; and AR 3655) the molar rows were well worn. Juvenile *E. ima* dentary (QMF 30222) had a completely formed P_3 but unerupted P_3 in its crypt. In this same specimen the M_3 crown had only partially formed whilst the M_4 crown had not yet begun to calcify. In contrast, among the 13 adult *Hypsiprymnodon* sp. examined the P_2 alveolus was gone having been clearly ossified/filled with secondary bone. The only exception was dentary fragment AR 10861, which retained an open alveolus. Similarly, in the adult *Propleopus oscillans* (AR 237), *P. wellingtonensis* (AR 110) and *Jackmahoneya toxoniensis* dentaries, P_2 had been shed and no evidence remained of an alveolus for P_2 . For two of the *Hypsiprymnodon* sp. specimens from Riversleigh the P_2 was lost and its alveolus completely filled, although M_4 had not yet erupted (AR 11098 and AR 13566). In a single *Hypsiprymnodon* sp. adult the alveolus for the erupted P_2 had not completely ossified (AR 10861); the posterior portion of the dentary, including the region of M_4 , was missing.

The position of P_2 relative to P_3 showed no variation between any of the six *E. ima* specimens which contained both teeth in either the upper or lower dentitions. In *Ekaltadeta ima*, as for all hypsiprymnodontids, P_3 was angled obliquely away from the long axis of the alveolar row of the dentary or maxilla (Figs 2–4). This was also the case for P_2 in juveniles (i.e. where P_3 had not erupted). In the six adult *Ekaltadeta ima* specimens containing both P_2 and P_3 , the P_2 sat below the occlusal plane in the dentary, or above in the maxillae, with the posterior part of the P_2 shearing crest contacting P_3 below the bulbous base of the P_3 crown. This point of contact was about half-way along the lingual face of P_3 (Fig. 4). The buccal torsion observed in the P_2 of juveniles was not evident in any of the adult specimens examined, P_2 being oriented instead in line with the molars. Among *E. ima* juveniles, P_2 was a tri-rooted tooth. In adult *E. ima* the P_2 posterior roots were almost completely resorbed, but the anterior root was only partly resorbed. The length of the P_2 anterior root could not be determined in most specimens where the tooth remained *in situ*, with the exception of AR 11267 (Figs 1 and 2) and AR 5247 (Figs 1 and 2) where the anterior root was exposed. An estimate for P_2 anterior root length was found by measuring the depth of the root's alveolus in specimens where P_2 was missing (AR 11236, QMF 23888 and AR 12873). The anterior root measured 8.15 mm in the juvenile dentary AR 5247 and 6.41 mm in juvenile maxillae AR 13564. The measurements of P_2 anterior root length in adult *E. ima* were as follows: AR 11267 (dentary), 5.03 mm; QMF 23888 (dentary), 5.35 mm; AR 11236 (dentary), 5.22 mm; AR 12873 (maxilla), 4.95 mm. Our interpretation of these data is presented below.

DISCUSSION

The persistence of P_2 in *Ekaltadeta ima* into adulthood is supported by the presence of this tooth in six adult specimens (i.e. with P_3 erupted), including two with well-worn dentitions, and by the lack of ossification in the P_2 alveolus of the three adult specimens

where P_2 is missing. Longevity of P_2 in the adult dentition of *E. ima* is further supported by the presence of P_2 in tooth rows that also contain an erupted M_4 . Although the timing of eruption for P_3 relative to M_4 is variable among living macropodoids, there are no known macropodoids contemporaneous with *E. ima* in which M_4 erupts before P_3 (B. Cooke, personal communication). The P_2 of *H. moschatus* may persist for a short period after the eruption of P_3 (upper and lower dentitions), but is lost before the eruption of M_4 (Woods, 1960; Ride, 1961). In two of the *Hypsiprymnodon* sp. specimens from Riversleigh the P_2 is lost and its alveolus completely filled, although M_4 is not yet erupted (AR 11098 and AR 13566). This demonstrates that the eruption sequence of *H. moschatus* is also common to the Riversleigh species of *Hypsiprymnodon*. In a single *Hypsiprymnodon* sp. adult, the alveolus for the ejected P_2 has not completely ossified (AR 10861). Precise determination of this animal's age is impossible, though a lack of wear on the two preserved molars ($M_{1,2}$, the rest having been lost in fossilization) suggests that this is a young adult. In the other hypsiprymnodontid taxa (*Propleopus*, *Jackmahoneya*) there is no evidence for persistence of P_2 beyond early adulthood, with the P_2 shed and its alveolus completely ossified in every known specimen. In *E. ima* all specimens with P_3 also contain M_4 , or lack the posterior portion of the dentary. However, in juvenile dentary QMF 30222, the P_3 crown has completely formed in its crypt, although it has not yet erupted, whilst the M_3 crown has only partially formed and the M_4 crown is clearly uncalcified. We consider this convincing evidence that the eruption programme in *E. ima* resembles that of the species of *Hypsiprymnodon*, with P_3 erupting before M_4 . Subsequently we regard the presence of P_2 and M_4 together in *E. ima* as indicative of persistence of P_2 in the dentition beyond early adulthood.

Most remarkable in *E. ima* is not the persistence of P_2 , but its time-dependent dual function. Support for a successional dual function of P_2 rests on two premises: (1) the clear change of position for P_2 from juvenile to adult; (2) demonstration of an adaptive advantage imparted by this change. The change in position of P_2 is clearly documented. In adult *E. ima* when P_3 erupts P_2 is lowered (Fig. 3) to sit well below the occlusal plane, and the buccal torsion in P_2 evident in the juvenile is reversed in the adult (Fig. 2). In the species of *Hypsiprymnodon*, the closest relatives of *E. ima* in which the process of P_3 eruption can be observed, P_2 sometimes remains for a short period but it does not drop below the occlusal plane, nor is the buccal torsion observed in the juvenile reversed in the adult. The adaptive advantage in retaining and repositioning P_2 is best explained in terms of the value of buttressing for P_3 . The large size and marked buccal torsion of P_3 in *E. ima* renders the tooth susceptible to anteriorly directed dislodging forces during mastication. Buccal torsion of P_3 diverts these dislodging forces away from the region of greatest support in the dentary or maxilla (S. Wroe, unpublished observation). The repositioned P_2 in the adult is well situated to counter these forces, being tucked anteriorly under the lingual face of the P_3 crown and realigned to follow the long axis of the dentary or maxillary. The P_2 may not be strongly

anchored in the adult *E. ima* dentary, being secured only by the single, diminished anterior root. Data available suggest that the anterior root length is not greatly reduced in the adult. In juvenile *E. ima* the P_2 anterior root length is 8.15 mm in the dentary (AR 5247) and 6.41 mm in the maxilla (AR 13564); this compares with adult measurements ranging from 5.03 to 5.35 mm in three dentaries (AR 11267, QMF 23888, AR 11236 and AR 12873) and 4.95 mm in a single maxilla (AR 11236). We believe this reduction in root length does not significantly detract from the tooth's role as a buttress because the primary supporting function of P_2 is provided by the P_2 crown. Depression or anteriorly directed force on P_3 would push the P_2 crown deeper into its alveolus or against the surrounding dentary or maxilla into which the tooth is already partly recessed.

In conclusion, our understanding of this situation is as follows, focusing on circumstances in the lower dentition of *E. ima* which mirror similar events in the upper dentition. The crown of P_2 in juveniles functioned as part of the cheek-tooth row. Its blade formed the anterior half of a longitudinal shearing unit whose posterior half was the laterally compressed trigonid of dP_3 . In adults, the much larger P_3 evicted dP_3 and fixed in position adjacent to the anterior flank of M_1 . The erupting P_3 of *E. ima* did not, however, evict P_2 . Instead, almost complete resorption of the posterior roots of P_2 and partial resorption of the anterior root, which occurred as the P_3 crown developed in its crypt, enabled P_2 to drop deeply into its alveolus and realign with the long axis of the dentary. In this new position P_2 was established well below the level of the adult tooth row (Fig. 1). Anchorage for P_2 at this point was provided by the remaining anterior root. In its new position it abutted P_3 , anterolingually just below the base of the P_3 crown, providing basal support for this large sectorial tooth. P_2 evidently persisted as part of the adult dentition, unlike the condition of any other kangaroo.

The way in which this dual-function system evolved is enigmatic. How the P_2 was physically depressed (or withdrawn) into and subsequently fixed within the anterior recess of the eruption alveolus of P_3 is unclear. We assume that the primary selective pressure controlling crown shape in P_2 is the need for a minimum absolute length of sectorial blade in juveniles as well as adults. This need is served by having the combined lengths of the P_2 blade plus the trigonid of dP_3 closely approximate that of the blade length of P_3 (the tooth that normally displaces both the P_2 and dP_3 in adults; Wroe, 1995), a pattern common among diprotodontian marsupials (Archer, 1984).

We are unaware of any other group of mammals in which a tooth, or for that matter any organ, comes to serve such a profoundly different function at different stages in the animal's post-embryonic life. In the extinct multituberculates and some marsupials (the extinct polydolopids, burramyids) with serrated anterior cheek teeth, diminutive premolars sometimes provide basal crown support for the primary sectorial blade (Marshall, 1982) but in these groups the buttressing crowns never serve a prior purpose of the

kind that P_2 did in *Ekaltadeta ima*. Evolutionary opportunism of this kind, involving recycling of a normally discarded organ for an entirely different purpose, may be unique to these kangaroos.

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