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Initiation and early development of the postcanine deciduous dentition in the dasyurid marsupial *Dasyurus viverrinus*

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Abstract

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There has been disagreement for more than 100 years concerning the presence or absence of deciduous and successional third premolars in the dentition of the Australian dasyurid marsupial *Dasyurus viverrinus* as well as in other species of the genus *Dasyurus*. Most authors during the 19th and 20th centuries have considered the missing premolar in *Dasyurus* to be the third premolar family in both jaws, in part because of the reduction in size of the third deciduous premolar in many other genera of dasyurids. While other authors, found "the deciduous premolar to be constantly present in the young mammary foetus as a small and precociously calcified vestigial tooth". However, the fate of this deciduous tooth, and its possible successor in later developmental stages, was never described; and the vestigial dp3 and its possible successor were assumed to undergo absorption during foetal life. With access to later developmental stages of *Dasyurus viverrinus*, via the extensive collections of Professor J.P. Hill, we present new evidence for the later development of dP3 and P3 in both jaws, the probable eruption of the successional P3 in both jaws and evidence that dP2 is the missing tooth in both jaws of this dasyurid species.

Keywords

Dasyurus, deciduous dentition, dental development, dental homologies, pouch young

Introduction

During the years 1895–1905, when he was a Demonstrator of Biology at the University of Sydney, Australia, Professor James P. Hill collected a large sample of juveniles of the dasyurid marsupial *Dasyurus viverrinus*, ranging from newborn young to individuals about four months old. The species was still relatively common in New South Wales at the time and the animals lived relatively well in captivity. Many of these captive-bred dasyurids produced the dated pouch young that are the subject of this paper. Although Hill and colleagues published several papers on the early development, placentation and reproduction in general of *Dasyurus*, only one paper dealt specifically with the development of the pouch young.

An extensive series on the development of the growth stages in the pouch young of *Dasyurus viverrinus* was examined in a monograph by Hill and Osman Hill (1955). The authors presented 16 figures of the pouch young, and they described in detail the external morphology of the developing young in a series of stages labelled A to P. These ranged from unattached newborn young outside and inside the pouch, measuring 5.5–6.0 mm greatest length (GL) and 2.5 mm head length (HL; stage A), up to adolescent young that were four months old (stage P). These oldest young were freely moving about outside the pouch and measured about 60 mm HL. However, no description or figures of the microscopic anatomy of the developing teeth were presented. Unfortunately, Hill passed away in 1954 during the preparation of their manuscript. We suspect that Hill would have published a detailed description of the developing dentition if he had lived longer. After his death, at least a portion of his collections of mammalian embryos and young animals was donated to the Hubrecht Laboratory of Comparative Embryology, Utrecht, Netherlands. These included a series of histological sections of some of the *Dasyurus viverrinus* pouch young described by Hill and Osman Hill (1955) and some older juveniles preserved as alcohol specimens. A few of the alcohol specimens from Hill's collection were borrowed and sectioned by Professor Louis Bolk, University of Amsterdam, Netherlands, and then returned to the Hubrecht Laboratory of Comparative Embryology.

Materials and methods

It is rare to be able to histologically examine closely related stages of early developing pouch young for any marsupial, and we were able to study three unattached intrauterine embryos and 22 early developing stages of pouch young attached to the nipple for *Dasyurus viverrinus* from the Hill collection. The pouch young examined range in age from about 30 hours old, measuring about 6 mm GL, to 40–41 days old, and measuring about 29 mm GL. Given that this species appears to be a useful model for the developmental relationships of the dentition in the extinct dasyuromorphian *Thylacinus cynocephalus* (see Luckett et al., 2019), along with other marsupicarnivore taxa, we present this overview of early dental development in *Dasyurus viverrinus*. These studies were carried out over a period of several years at the Hubrecht Laboratory of Comparative Embryology before the embryological collections were transferred to their present home in the Museum für Naturkunde, Berlin, Germany.

It should be noted that *Dasyurus viverrinus* is probably extinct on mainland Australia, with a last sighting on January 1963 in the suburbs of Sydney (Dickman et al., 2001). The species persists in Tasmania , although it is vulnerable there for several reasons, including climate change and disease, among other possibilities (Fancourt, 2016).

A brief overview of our findings on dental development in *Dasyurus* was presented previously (Luckett, 1989, 1993). We have made new drawings of four of the developing pouch young (fig. 1) examined by us from the Hill collection, ranging from an early attaching pouch young of about 30 hours old to an embryo of about 41 days old, measuring about 29 mm GL and 18 mm HL. Most genera of dasyurids, peramelids and didelphids have three premolars in both jaws of adults. This is presumably the primitive condition for marsupials (Cifelli et al., 1996). Emphasis in our study is given to the evidence for loss of dP2 in this dasyurid with two premolars, and the accelerated development of dP3 and P3, when compared with these features in dasyurids with three premolars. A summary of the major features of early development for the deciduous and successional dentition in marsupials is presented in fig. 2.

Results

Early development of the dental lamina

Hill and Osman Hill (1955) noted that the earliest date of gestation was 16 days in their sample of *Dasyurus viverrinus* embryos. The earliest evidence of a dental lamina that we found was detected in the maxilla of three intrauterine embryonic stages of 5.5–6 mm GL. In the youngest of these embryos, the dental lamina was detected bilaterally in the upper jaw as a localised thickening of the oral epithelium that was associated with a very early differentiation of bone (or prebone) in the distal portion of the developing maxilla. In contrast, the dental lamina and developing bone were not yet detected in the premaxillary region of the upper jaw. The more mature intrauterine young showed dental lamina thickenings in both the premaxilla and maxilla regions of the upper jaw. The dental lamina was not yet evident in the lower jaw of the youngest intrauterine embryo. As explained by Hill and Osman Hill (1955), the newborn young of *Dasyurus viverrinus* are able to find their way to the mother's pouch, unaided by the mother and helped by their own well-developed forelimbs that have very sharp deciduous claws.

In the youngest pouch young attached to the mother's nipple, examined at about 30 hours old and measuring 6 mm GL, a continuous dental lamina was present bilaterally in both the upper and lower jaws. This specimen was illustrated as fig. 5 by Hill and Osman Hill (1955) and we have redrawn this important specimen in our fig. 1a. The HL of this pouch young was 3.25 mm. It should be noted here that all of our measurements from the Hill collection are taken from specimens that had been placed in spirit fixation by Hill. In the upper jaw, three early-bud thickenings are evident on the dental lamina (see fig. 2a for the relations between the dental lamina and an early bud). The most rostral of these is associated with the premaxillary ossification, the next is adjacent to the rostral end of the developing maxillary bone, and the distal bud occurs at the caudal end of the dental lamina and is associated with the distal extent of the maxillary ossification. Based on their bony relationships and comparison with later ontogenetic stages, these tooth buds can be identified as dI2 or dI3 anteriorly, dC and dP3, respectively. The dP3 bud lies beneath the level of the anterior half of the eye. An overview of the major features of dental development for the postcanine dentition in the upper and lower jaws is summarised in Tables 1 and 2.

The bud for the early developing incisors in the upper jaw does not occur at the rostral-most extent of the premaxilla; instead, it is positioned somewhat more distolateral. It is unclear whether this developing tooth germ is dI2 or dI3 at this early stage. The late or retarded development of dI1 in the upper jaw of dasyurids, peramelids and didelphids was noted by Thomas (1887). Later, Guiler and Heddle (1973) suggested that the late development and eruption of dI1 helped the continued suckling of the young. In the lower jaw, a large early bud is evident at the rostral extent of the dentary ossification. Two small bud-like thickenings occur distal to the rostral early bud (presumably di1), but these are not as distinct as the di1. It should be noted here that adult dasyurids possess four upper and three lower incisors, in contrast to the presumably primitive condition in ancestral marsupials and didelphids, which possessed five upper and four lower incisors. It is unclear to us which incisor has been lost in each jaw of *Dasyurus*, so we will simply call them I1-4 above and i1-3 below.

We next examined a three-day-old embryo measuring 7 mm GL and 4 mm HL (see fig. 6 in Hill and Osman Hill, 1955). Two small deciduous incisors were in an early-bud stage rostrally in the upper jaw. The moderately sized deciduous canine was in a more distinct early-bud stage. It had a more darkly stained abnormal buccal portion and a more normal pale-stained lingual portion. Based on later developing stages, the darkly stained buccal portion represents the primordium of the rudimentary deciduous canine, and the more normal lingual portion represents the primordium of the successor canine. These modified relationships for the developing deciduous and successional incisors and canines were

Table 1. Development of *Dasyurus viverrinus* upper postcanine dentition

Stage	dP1	dP2	dP3	P3	M1	M2	M3	M4
30 hour PY 6 mm GL (3.25 mm HL)	No trace	No trace	Early bud					
3 day PY 7 mm GL (4 mm HL)	No trace	No trace	Early to middle bud					
5–6 day PY 8 mm GL (4.5 mm HL)	No trace	No trace	Early cap					
7 day PY 9 mm GL (5.5 mm HL)	No trace	No trace	Early cap					
10 day PY 10.5 mm GL (6.5 mm HL)	Slight swelling of lamina	No trace	Early cap					
10 day PY 11 mm GL (7 mm HL)	Very early bud-like thickening	No trace	Middle cap					
14 day PY 13 mm GL (8 mm HL)	Late bud to early cap	No trace	Early to middle bell, flat successional lamina		Late bud			
14 day PY 13.5 mm GL (8 mm HL)	Early cap	Tiny bud-like thickening	Middle to late bell, flat successional lamina		Late bud			
15–16 day PY 14 mm GL (9 mm HL)	Early cap	No trace	Small, late bell, thin dentin, flat successional lamina	Early cap	Middle to late cap			
19 day PY 17 mm GL (10 mm HL)	Early bell	No trace	Moderately developed dentin, successional lamina mesially	Early bud- like swelling	Middle bell			
~19–20 day PY 16–17 mm GL	Early bell	No trace	Moderately developed dentin, successional lamina mesially	Early cap	Middle bell			
~19 day PY 16–18 mm GL	Late cap to early bell	No trace	Moderately thick dentin, thin enamel; successional lamina mesially	Late bud to early cap	Early to middle bell			

Stage	dP1	dP2	dP3	P3	M1	M2	M3	M4
25 day PY 20 mm GL (12.5 mm HL)	Middle to late bell	No trace	thick dentin, thin enamel; lingual successional lamina	Early to middle cap	Late bell, possible odontoblasts	Early cap		
~30–35 day PY ~23 mm GL	Late bell, very early dentin	No trace	Moderately thick dentin, thin enamel; lingual successional lamina	Late bell, early odontoblasts	Moderately developed dentin, thin enamel on metacone	Middle to late bell		
~35 day PY ~23–25 mm GL 13.5 mm HL	moderately thick dentin, moderately developed enamel	No trace	Moderately thick dentin, thin enamel; mesio-lingual successional lamina intact	Late bell, thin dentin	Moderately thick dentin, thin enamel on metacone	Middle to late bell		
~40–41 day PY ~29 mm GL 18 mm HL	Moderately thick dentin, moderately developed enamel	No trace	Moderately thick dentin, thin enamel; incomplete mesio-lingual successional lamina	Late bell, thin dentin	Moderately thick dentin and enamel on metacone	Late bell with thin dentin	Early to middle bud	

Note: GL, greatest length; HL, head length; PY, pouch young

Table 2. Development of *Dasyurus viverrinus* lower postcanine dentition

Stage	dp1	dp2	dp3	p3	m1	m2	m3	m4
30 hour PY 6 mm GL (3.25 mm HL)	No trace	No trace	Early bud-like thickening					
5–6 day PY 8 mm GL (4.5 mm HL)	No trace	No trace	Middle to late bud					
5–6 day PY 8.5 mm GL (4.5 mm HL)	No trace	No trace	Late bud to early cap					
6–7 day PY 9 mm GL (5 mm HL)	No trace	No trace	Late bud					
10 day PY 11 mm GL (7 mm HL)	Flattened early bud	No trace	Early to middle cap					
14 day PY 13 mm GL (8 mm HL)	Flattened late bud to early cap	Possible slight swelling	Middle bell, short flat successional lamina lingually		Early bud			

Stage	dp1	dp2	dp3	p3	m1	m2	m3	m4
~14 day PY 13.5 mm GL (8 mm HL)	Late bud to early cap	Slight swelling of dental lamina	Late bell, no odontoblasts, lingual successional lamina	Possible early bud-like swelling	Middle bud			
~15–16 day PY 14 mm GL (9 mm HL)	Early cap	Slight swelling of dental lamina	Small abnormal bell, moderately developed dentinal cap	No distinct bud-like swelling	Middle bell			
19 day PY 17 mm GL (10 mm HL)	Late cap to early bell	Slight swelling of dental lamina	Moderately developed dentin; mesio-lingual successional lamina	Possible early bud-like swelling	Middle to late bell			
~19–20 day PY 16–18 mm GL Bolk	Early bell	Possible slight swelling	Small, moderately thick dentinal arc, thin enamel	Early bud-like swelling at mesial end of dp3	Middle to late bell	Late cap		
25 day PY 20 mm GL (12.5 mm HL)	Middle bell	No trace	Small, thick dentin, thin enamel	Early bud	Late bell, thin to moderately developed dentin	Middle to late bell		
~30–35 day PY ~23 mm GL Bolk	Late bell, thin dentin	No trace	Small, abnormal dentinal mass, with thin enamel	Moderately sized, middle to late cap, mesial to abnormal dp3	Moderately thick dentin and moderately developed enamel on protoconid	Late bell, moderately developed dentin, thin enamel	Early bell	
~35 day PY 23–25 mm GL Bolk 13.5 mm HL	Late bell, moderately developed dentin, thin enamel	No trace	Abnormal, moderately thick dentinal arc with thin enamel	Moderately large, early to middle bell	Moderately thick dentin, moderately developed enamel on protoconid	Moderately thick dentin, thin enamel	Middle to late bell	
~40–41 day PY ~29 mm GL Bolk 18 mm HL	Moderately thick dentin, moderately developed enamel	No trace	Tiny, solid dentinal mass with thin enamel	Moderately large, late bell, possible odontoblasts	Thick dentin, moderately thick enamel on protoconid	Moderately thick dentin, moderately developed enamel on protoconid	Late bell, moderately developed dentin	Probable early bud

Note: GL, greatest length; HL, head length; PY, pouch young

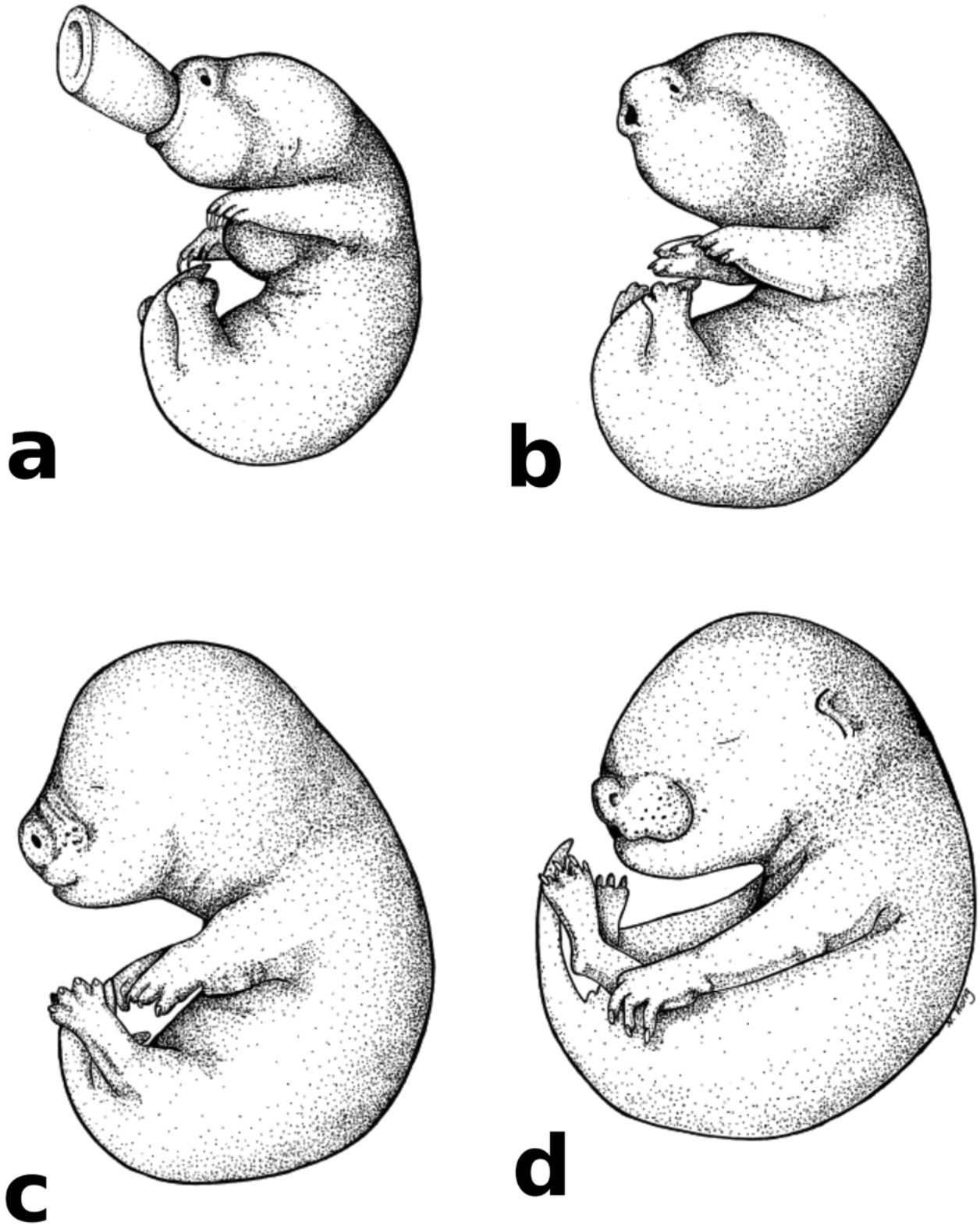

Figure 1. Four early pouch young of *Dasyurus viverrinus*: a, 30 hours old, 3.25 mm head length (HL); b, 5–6 days old, 4.5 mm HL; c, 14 days old, 8 mm HL; d, 25 days old, 12.5 mm HL.

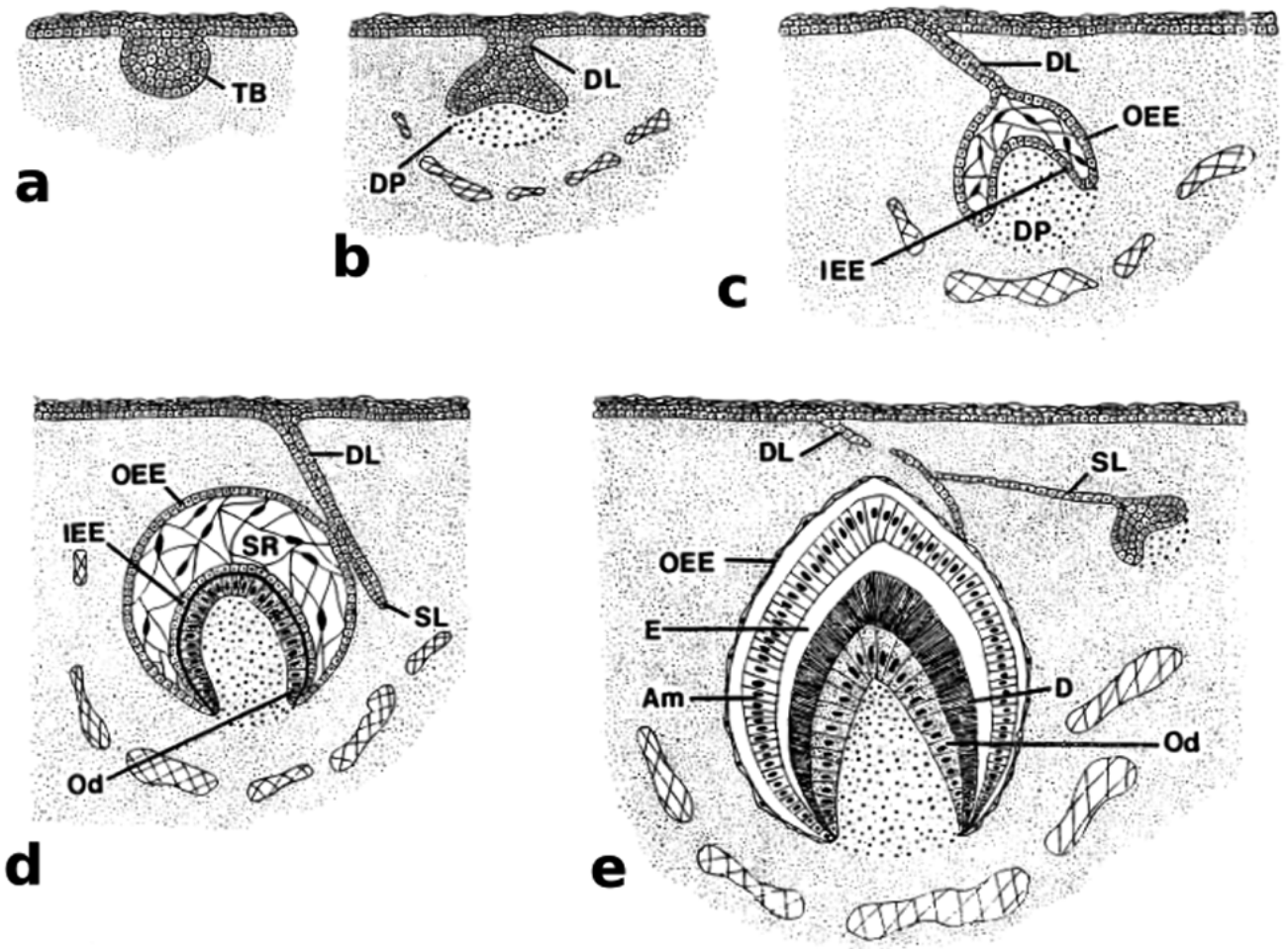

Figure 2. Transverse sections of early developmental stages of the dentition in marsupials: a, early tooth bud forming from the dental lamina; b, early-cap stage; c, middle-bell stage with elongate dental lamina; d, late-bell stage with odontoblasts and early lingual successional lamina; e, well-developed late-bell stage with dentin and enamel. A successional early-cap stage develops from the lingual successional lamina, showing early fragmentation of the dental lamina. Abbreviations: AM, ameloblasts; D, dentin; DL, dental lamina; DP, dental papilla; E, enamel; IEE, inner enamel epithelium; OD, odontoblasts; OEE, outer enamel epithelium; SL, successional lamina; SR, stellate reticulum; TB, tooth bud.

previously described in detail for marsupials (Luckett, 1993). The dental lamina was reduced distal to the developing canine. The lamina became thickened again distally at the level of the rostral end of the developing eye. It then gave rise to a moderate size early- to middle-bud stage dP3. The dental lamina and the maxillary bone disappeared distal to the dP3 bud.

In a slightly older embryo, 5–6 days old and measuring 8 mm GL and 4.5 mm HL (see fig. 7, Hill and Osman Hill, 1955, and our fig. 1b), three early developing incisors are now evident in the premaxillary region of the upper jaw. The anterior two incisors are moderately sized and flattened in the early- to middle-bud stages. The third incisor is moderately large and more spherical in the middle-bud stage, and is located nearer the distal end of the premaxilla. It has a smaller darkly stained buccal portion and a larger lingual lobular portion with lighter, normal-appearing cells. Based on its appearance in later developmental stages, these represent the buccal deciduous incisor and the more normal-appearing lingual successor incisor.

A moderately large late-bud to early-cap stage canine develops at the rostral extent of the maxilla. This also consists of a smaller darker buccal portion and a larger lingual paler-staining portion, representing the future deciduous and successor canines, respectively. The dental lamina is reduced distal to the developing canine and continues distally towards the level of the middle of the eye. At this region, the dental lamina enlarges and gives rise to a moderately large early-cap stage dP3, formed by invagination of the underlying dental papilla cells (see fig. 2b for an example). The dental lamina then disappears a short distance distal to this tooth, near the distal end of the eye.

In the lower jaw, three developing incisors are in early- to late-cap stages at the rostral extent of the dentary. The di1 is in a late-cap stage, with possible odontoblasts buccally and a lingual projection for an early successor bud for i1. The di2 has an early-cap stage buccally and a distolingual projecting lamina for a possible successor i2. The smaller di3 has a less distinct buccal early cap with a relatively indistinct lingual successional lamina. The moderately sized dc is in a late-bud stage with a lingual successional ridge. The dental lamina continues distally as a thin ridge with no suggestion of a dp1 or dp2. The dental lamina then thickens again distally, beneath the level of the distal portion of the eye, and gives rise to a moderately large late-bud to early-cap stage dp3. The dental lamina then ends distal to this developing tooth.

In a 10-day-old pouch young with a 6.5 mm HL and a 10–10.5 mm GL (see fig. 9 in Hill and Osman Hill, 1955), there is little change in the developing incisor and canine regions of the upper jaw. The dental lamina immediately distal to the canine exhibits a somewhat flattened early bud-like thickening for a possible primordium of dP1, but this is not very distinct. The dental lamina is then reduced and extends distally. At the level of the middle portion of the eye, the dental lamina thickens again and gives rise to a moderately large early-cap stage dP3. The dental lamina then ends distal to this tooth. In the lower jaw, there is also a moderately sized early-cap stage dp3 and no trace of a developing dp1.

In a slightly larger 10-day-old pouch young (7 mm HL and 11 mm GL), several distinct changes have occurred compared with the preceding specimen. The developing incisor region remains similar, whereas the deciduous canine has a tiny buccal nodule associated with a large distolingual projecting late-bud to early-cap stage successor canine in the upper jaw. Immediately following the canine is a tiny, somewhat flattened, probable early bud for dP1. The dental lamina is reduced distal to this early bud and extends distally to underlie the eye, where it enlarges to form a moderately sized middle-cap stage dP3. There was no distinct swelling of the dental lamina between the dP3 and the probable early-bud stage dP1. The dental lamina extends slightly distal to dP3 before it disappears.

Note that in the early developing pouch young, there is little space in the jaws for the developing anterior dentition, due in part to the greatly enlarged tongue and its intimate association with the large nipple (fig. 3). This often results in great compression and flattening of the more anterior developing teeth, whereas there is less compression distally in the region of the developing dP3 and molars.

In the lower jaw, there is also a small, flattened early-bud stage for dp1. The dental lamina is then reduced as it extends distally to form a moderately sized early- to middle-cap stage dp3. The dental lamina then ends distal to dp3. As in dasyurids with three premolars, the sequence of early development for the premolars in both jaws is dP3 > dP1 > dP2. As noted in this and later stages, it is the late-developing dP2 that is lost in both jaws of dasyurids with only two premolars.

In an older 14-day-old pouch young, with 8 mm HL and 13 mm GL (see fig. 10 in Hill and Osman Hill, 1955, and our fig. 1c), the developing relationships for dI1 and dI2 in the upper jaw were similar to those of the previous stage. In contrast, dI3 has an early cap knot enclosing a tiny dentinal arc. The small distolingual successional bud for I3 is still relatively small. A small buccal epithelial knot is evident for dC, and there is a large middle-bud stage successor for the canine that is associated with a deep maxillary alveolus. A small, flattened late-bud to early-cap dP1 follows the canine immediately, and then the dental lamina is reduced distal to this. There is a possible slight swelling of the dental lamina beneath the anterior end of the eye, but this is not very distinct. The dental lamina is then reduced distal to this slight swelling. The dental lamina enlarges further distally and gives rise to a moderately sized early- to middle-bell stage dP3 beneath the middle third of the eye (see fig. 2c for a middle-bell stage tooth). This tooth is still intact with its primary dental lamina origin. A flattened lingual successional lamina extends mesial to dP3. Distal to dP3 is a moderately sized late-bud stage M1 underlying the distal end of the large eye. The dental lamina ends distal to this tooth.

In the lower jaw, the di1 is small and cap like, enclosing thin distinct dentin. Distolingual to this is the larger early-bud stage successor i1. The di2 is also a small cap with an irregular dentinal fragment; a slightly larger successor i2 is placed distolingually in a late-bud to early-cap stage. The tiny di3 cap lacks dentin, and its distolingual successor ridge lacks a distinct successor tooth. The small, dark cap for dc lacks dentin and has a distolingual middle-bud stage successor canine. The small, flattened dp1 follows immediately and is in the late-bud to early-cap stage. There is no distinct evidence for a dp2 swelling. Somewhat more distally there is a small middle-bell stage dp3 with a short, flattened lingual successional lamina. Immediately distal to this tooth is a moderately sized early bud for m1. The dental lamina disappears distal to this developing tooth.

In a slightly larger 14-day-old pouch young (13.5 mm GL and 8 mm HL; see fig. 10 in Hill and Osman Hill, 1955), some notable changes are evident in the canine and postcanine dentition. The successor canine is now in the early- to middle-bell stage in the upper jaw. The tiny, flattened dP1 is in the early-cap stage. The dental lamina becomes reduced distal to this tooth and then enlarges slightly to form a possible primordium for a rudimentary dP2. However, the dental lamina is reduced distal to this slight swelling and then enlarges further distally and gives rise to a moderately large middle- to late-bell stage dP3. This tooth has moderately developed stellate reticulum, and a short, slender lingual successional lamina extends mesial to this tooth (see fig. 2d for a late-bell stage with a lingual successional lamina). The dP3 lies beneath the middle region of the eye. The primary dental lamina extends distal to dP3 and gives rise to a moderately large late-bud M1 beneath the distal region of the eye. The dental lamina then disappears distal to this bud.

In the lower jaw, the successor canine is now in the late-bud to early-cap stage. This is followed immediately by the small, elongate late-bud to early-cap stage dp1. The dental lamina is slightly swollen distal to this tooth, but this is not very significant. Further distally, the small dp3 is in the late-bell stage with moderately developed stellate reticulum but no

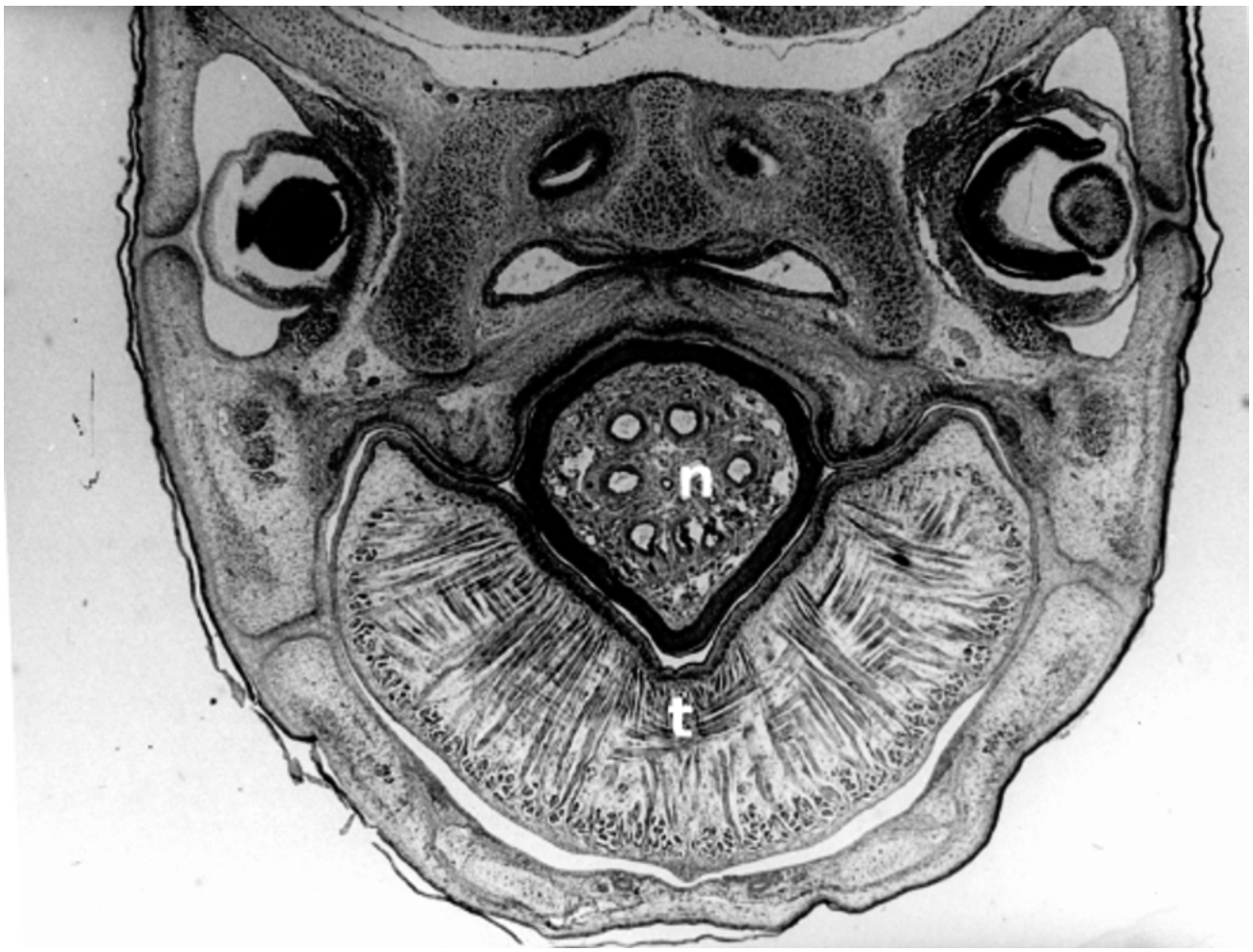

Figure 3. Transverse section through the head at the level of the developing eyes in a 10-day-old *Dasyurus viverrinus* embryo (7 mm head length). Note the close compression between the large tongue (T) and the nipple (N). No developing teeth are evident.

dentin. There is a lingual successional lamina that extends mesial to dp3 and terminates with a slight bud-like swelling. Distal to dp3 is a large middle-bud stage m1, and then the dental lamina disappears distal to this.

In a slightly older pouch young (13–15 mm GL and 9 mm HL) estimated to be 15–16 days old, a significant change has occurred in the postcanine region of the upper jaw. The small dP1 is in the early-cap stage and the dental lamina is greatly reduced distal to this tooth without any suggestion of a swelling for a rudimentary dP2. Further distally, the small to moderate sized dP3 is in the late-bell stage with thin dentin on its apex. The tooth is relatively superficial with a short, intact primary dental lamina stalk to the oral epithelium. The tooth lies beneath the anterior ⅓ of the eye. The slender lingual successional lamina extends mesial to the tooth and then enlarges to form a moderately sized early-cap stage successor P3. The successor P3 extends mesially beneath the anterior margin of the eye. Distal to this, a moderately large middle- to late-cap stage M1 develops beneath the level of the middle of the eye. The dental lamina then disappears distal to this tooth.

In the lower jaw, the dp1 is a moderately sized early-cap stage. The dental lamina is reduced distal to this tooth; there is a slight swelling distally, but this is not very distinct. Further distally, the dental lamina enlarges again and gives rise to a small to moderately sized, somewhat abnormal dp3 with an irregular, moderately developed dentinal cap. There is a short, primary dental lamina stalk to the oral epithelium. The tooth is in a shallow bony alveolus and has a flattened lingual successional lamina. Distal to this tooth is a large middle-bell stage m1. The dental lamina disappears distal to the developing molar. In both jaws, the dP3 appear to be relatively smaller than in earlier stages and they lie closer to the oral epithelium.

In the later developmental stages, we will only discuss the postcanine development of the *Dasyurus* pouch young because there is little controversy concerning the development of the incisor and canine regions. In a 19-day-old pouch young (17 mm GL and 10 mm HL; see fig. 11 in Hill and Osman

Hill, 1955), the small dP1 is somewhat flattened or compressed and has now attained the early-bell stage in the upper jaw. The dental lamina is reduced distal to this tooth and becomes detached from the oral epithelium. The dental lamina becomes reattached further distally and forms an early bud-like swelling; this possibly represents the rudiment of a dP2. The dental lamina is then reduced again and extends further distally; it then enlarges to form a small late-bell stage dP3. There is moderately developed dentin but no enamel on this small tooth. It lies beneath the middle of the eye in a shallow bony alveolus. A lingual successional lamina extends mesially from dP3 and forms a slight bud-like thickening. As noted in the later developmental stages, this thickening is the primordium for the later developing successor P3. The dental lamina extends distal to dP3 and then enlarges to form a moderately large middle-bell stage M1. This tooth lies beneath the distal half of the eye; the dental lamina disappears distal to this tooth.

In the lower jaw, dp1 is a moderately sized, late-cap to early-bell stage tooth with a shallow bony alveolus. The dental lamina is slightly swollen distal to this tooth (possibly representing the site of the lost dp2); then further distally, the dental lamina thickens again and gives rise to a small late-bell stage dp3 with a moderately developed layer of dentin. The lingual successional lamina of this tooth extends mesially, where it is slightly thickened terminally. The dental lamina extends distal to this tooth and gives rise to a large middle- to late-bell stage m1. The dental lamina disappears distal to this tooth.

In a later pouch young of 19–20 days old (16–18 mm GL), sectioned by Dr Louis Bolk, the dP1 is a small tooth in the late-cap to early-bell stage in the upper jaw. The dental lamina distal to this tooth is detached from the oral epithelium. There is no trace of a possible rudimentary dP2. Further distally, the dental lamina reappears and gives rise to a small, late-bell stage dP3 with moderately thick dentin and a thin film of early enamel. The lingual successional lamina of dP3 extends mesially and gives rise to a small late-bud to early-cap stage successor P3, which lies anterior to dP3 (see fig. 2e for a late-bell stage dP3 and its successor early-cap stage P3). Distal to dP3, the dental lamina gives rise to a moderately large early- to middle-bell stage M1. The dental lamina then disappears distal to this tooth.

In the lower jaw, the moderately sized dp1 is in the early-bell stage. The tooth is somewhat compressed and lies in a shallow bony alveolus. There is only a slight possible swelling of the dental lamina distal to this tooth in the region of the missing dp2. Further distally, the dental lamina thickens again and gives rise to a small late-bell stage dp3 with a moderately thick arc of dentin. There is also a thin layer of darkly stained enamel. The slender lingual successional lamina adjacent to dp3 extends mesially and is enlarged as a slight early bud-like swelling for the future successional p3. The dental lamina is reduced distal to dp3 and then enlarges again to form a large middle- to late-bell stage m1. Distal to this tooth is a moderately large late-cap stage for m2. The dental lamina disappears distal to this tooth.

In another 19–20-day-old pouch young (10 mm HL and 16–17 mm GL), there are slight advancements for some of the developing teeth. A moderately sized dP1 is in the early-bell stage in the upper jaw. There is no distinct evidence for a rudimentary dP2 swelling distal to this tooth. The dental lamina thickens further distally and gives rise to a small to moderately sized late-bell stage dP3 with moderately developed dentin on its crown. There is a shallow bony alveolus for the tooth, which lies beneath the anterior third of the eye. The lingual successional lamina of dP3 extends mesially and thickens to give rise to a small early-cap stage successor P3. Distal to the dP3, the dental lamina thickens again and gives rise to a moderately large middle-bell stage M1. This tooth is positioned beneath the middle of the eye. The dental lamina thins and then disappears distal to M1.

In the lower jaw, a moderately sized dp1 is in the late-cap to early-bell stage. There is no distinct evidence for a rudimentary dp2 distal to this tooth. Further distally, there is a small, somewhat abnormal dp3 with a moderately developed dentinal arc but no stellate reticulum. The lingual successional lamina of dp3 is slightly thickened mesially and then gives rise to a small middle-bud stage successor p3 further anteriorly. Distal to dp3, the dental lamina enlarges and gives origin to a large middle- to late-bell stage m1. Distal to this tooth, the dental lamina gives rise to a moderately sized late-cap stage m2. The dental lamina then disappears distal to this tooth. Note that in the 19–20-day-old pouch young, the dentition in the lower jaw is accelerated in its development compared with that in the upper jaw; this trend continues to increase in later developmental stages.

In a later 25-day-old pouch young (20 mm GL and 12.5 mm HL; see fig. 12 in Hill and Osman Hill, 1955, and our fig. 1d) that has been sectioned longitudinally, dP1 is a small to moderately sized tooth in the middle- to late-bell stage in the upper jaw (fig. 4). As in the previous stage, there is no suggestion of a dP2 rudiment. Further distally, the small to moderately sized dP3 has relatively thick dentin and thin enamel. The tooth is located beneath the anterior ⅓ of the eye. The lingual successional lamina of dP3 extends mesially and thickens to form a moderately large early to middle-cap stage successor P3. The deciduous and successor P3 appear to arise from a common primary dental lamina stalk. This is due to the partial fragmentation of the primary dental lamina stalk in later stages of development (compare fig. 4 with 2e). Distal to the developing dP3/P3 complex, the M1 is now in a large late-bell stage with possible early odontoblasts but no dentin. This tooth underlies the middle of the eye. A moderately sized early-cap stage M2 develops distal to M1. The dental lamina then disappears distal to this tooth.

In the lower jaw, dp1 is now a moderately large middle-bell stage tooth, developing immediately distal to the large developing canine. There is no distinct evidence for a rudiment of dp2. Further distally, the small to moderately sized dp3 is partially covered with a thick layer of dentin and a thin layer of enamel. Mesiolingual to the small dp3, the lingual successional lamina gives rise to a larger early-bud stage p3. Further distally is a large late-bell stage m1 with moderately developed dentin on the apex of the tall protoconid. Distal to this tooth, the dental lamina gives rise to a large middle- to late-bell stage m2. A possible early bud for m3 lies distal to this tooth, but problems with the tissue make it difficult to be certain of this.

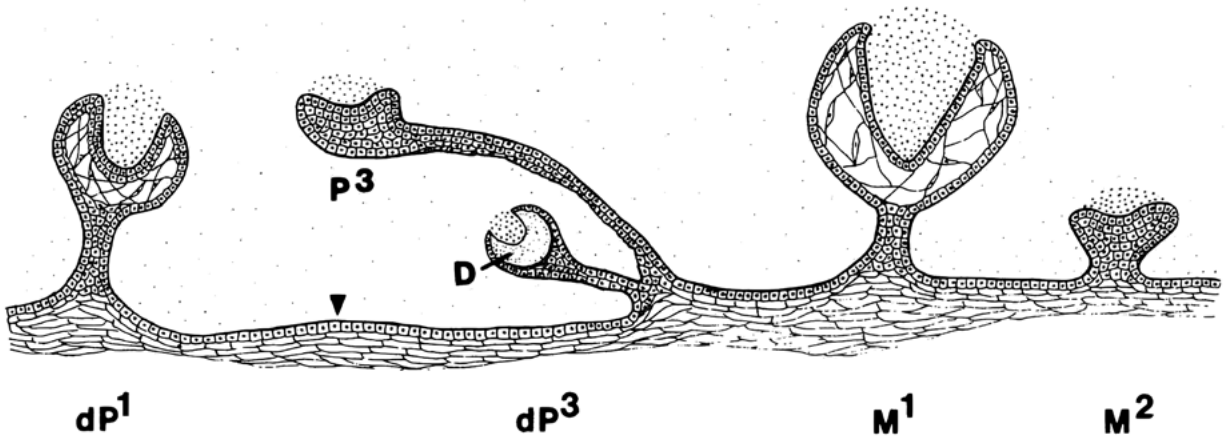

Figure 4. Parasagittal section through the dentition in a 25-day-old pouch young (12.5 mm head length) showing the developing teeth between dP1 and M2 in the upper jaw. Arrowhead refers to the site of the missing dP2. Abbreviation: D, location of developing dP3 follicle.

In a 30–35-day-old pouch young (23–24 mm GL and 13.5 mm HL; see fig. 13 in Hill and Osman Hill, 1955), the dP1 is now a moderately sized tooth with moderately thick dentin and thin to moderately developed enamel on its crown in the upper jaw. The tooth lies in a shallow bony alveolus, just below the oral epithelium. This is related in part due to the large canine that partially underlies the smaller dP1 throughout its length. There is no trace of a rudimentary dP2. Further distally, the dental lamina thickens and gives rise to a small, somewhat elongate dP3 with moderately thick dentin and a partially disrupted layer of enamel. The tooth lies anterior to the developing eye. The lingual successional lamina of dP3 extends mesially and gives rise to a larger moderately sized late-bell stage successor P3 with odontoblasts and a thin layer of predentin on its crown. The P3 extends both anterior and posterior to dP3 because of its larger size. There is a normally sized developing bony alveolus for P3, whereas a distinct bony alveolus is lacking for the small dP3. Instead, the small deciduous tooth lies more superficially, in the apex of the deeper alveolus for the larger P3. Distal to the dP3/P3 complex, the large M1 has moderately thick dentin and thin enamel on its elevated metacone. There is a flattened residual lingual lamina along the extent of the tooth. This tooth lies beneath the anterior half of the eye. A moderately large middle- to late-bell stage M2 lies beneath the distal half of the eye. The dental lamina disappears distal to this tooth.

In the lower jaw, dp1 is a relatively large tooth with moderately developed dentin and thin enamel on its apex. There is no suggestion of a rudimentary dp2. Further distally, the small dp3 has a relatively thick dentinal arc overlain by a thin film of enamel. The enamel is covered by inactive cuboidal ameloblasts. Lingual to the small abnormal dp3 is a thin successional lamina; this extends further mesially and gives rise to a moderately large early- to middle-bell stage p3 with a loosening of its stellate reticulum. Distal to the dp3/p3 complex, the m1 is a large tooth with moderately thick dentin and thin to moderately developed enamel on the apex of its tall protoconid. The tooth has a short, flat residual lamina. Distal to this tooth is a large m2, also with moderately developed to moderately thick dentin and thin enamel on its tall protoconid. The m2 also has a short, flat residual lamina. A moderately large m3 lies distal to m2 and is in the middle- to late-bell stage. The dental lamina disappears distal to this tooth.

Another pouch young 30–35 days old (23 mm GL) was sectioned by Louis Bolk and showed some small differences with the previous specimen. The dP1 is small to moderately sized and is in the late-bell stage with early odontoblasts and thin predentin in the upper jaw. The dp1 has a short, flat lingual successional lamina. Again, there is no suggestion of a rudimentary dP2. The small, somewhat abnormal dP3 has moderately thick dentin and possibly a thin film of enamel. Mesio-lingual to dP3 is a moderately sized late-bell stage P3 with very early odontoblasts. The elongate lingual successional lamina is fragmented in places and it is not clearly connected to dP3, in contrast to earlier stages. Distal to dP3 is a large late-bell stage M1 with moderately developed dentin and thin enamel on the tall metacone. A prominent, flattened residual lamina is present lingually. Distal to this tooth is a moderately large middle- to late-bell stage M2. The dental lamina disappears distal to this tooth.

In the lower jaw, the moderately large late-bell stage dp1 has thin predentin on the apex of its single cusp; it immediately follows the large canine. There is no suggestion of a rudimentary dp2. Further distally is a small, abnormal dentinal mass for the rudimentary dp3 with a thin layer of enamel on the surface of the dentin. The primary dental lamina connection to the oral epithelium persists. Anterior to the abnormal dp3 is a moderately sized middle- to late-cap stage p3. Only a few fragmented epithelial nodules represent

the earlier remnants of the lingual successional lamina from dp3. Distal to dp3 is the large m1 with moderately thick dentin and thin to moderately developed enamel on the apex of its tall protoconid. A thin, flattened residual lamina is evident mesially. Distal to this is a large late-bell stage m2 with moderately developed dentin and thin enamel on the apex of the tall protoconid. There is also a prominent, short residual lamina lingually. Distal to this tooth is a moderately sized early-bell stage m3; the dental lamina then disappears distal to this tooth.

In a later pouch young of about 41 days old (29 mm GL and 18 mm HL; see fig. 14 in Hill and Osman Hill, 1955), also sectioned by Louis Bolk, further changes occurred, especially with regards to the dP3 and P3 in both jaws. In the upper jaw, the small dP1 now has moderately thick dentin and moderately developed enamel on the apex of the unicuspid tooth. There is a short, flattened lingual successional lamina, and again no trace of a rudimentary dP2. Further distally, there is a small dP3 with moderately thick dentin and moderately developed enamel. Ameloblasts are low cuboidal and probably are no longer functional. Fragmented strands of the lingual successional lamina extend anteriorly and give rise to a moderately sized late-bell stage successor P3 with thin early predentin on its apex. Further distally, the large M1 appears; it has moderately thick dentin and enamel on its tall disto-buccal metacone. Distal to this tooth is a large late-bell stage M2. This tooth also has an elevated disto-buccal cusp that has odontoblasts and a very thin layer of predentin. Following this tooth is a moderately sized early to middle-bud stage M3. The dental lamina then disappears distal to this developing tooth.

In the lower jaw, dp1 is a moderately sized tooth with a relatively thick layer of dentin and a moderately developed layer of enamel (partially disrupted). Its primary dental lamina stalk is still attached to the oral epithelium. Only a slight suggestion of the thin lingual successional lamina is evident mesially. There is no trace of a rudimentary dp2. Distal to dp1 is a very small, abnormal dp3 with a prominent dentinal mass. There is also a very thin film of enamel, although there are no distinct remnants of ameloblasts. The tooth is considerably reduced in size compared with earlier developmental stages. The primary dental lamina connection of dp3 with the oral epithelium and its lingual successional lamina are also broken in places. Nevertheless, the fragmented lingual successional lamina extends mesially and gives rise to a moderately large late-bell stage successor p3. The p3 has well-developed stellate reticulum and possibly early odontoblasts, although this is not clear. The tiny dp3 lies more superficial than its larger successor and lacks a distinct bony alveolus.

Distal to dp3 is a large m1 with thick dentin and moderately thick enamel on its tall, mesio to buccal protoconid. The tooth lies in a deep bony alveolus. Distal to m1 is a large m2 with moderately thick dentin and moderately developed enamel on its tall protoconid. Further distally, m3 is a moderately large tooth in the late-bell stage with a moderately developed layer of dentin on its tall protoconid. There are also early ameloblasts on the tooth cusp, but no enamel. There is a well-developed lingual residual lamina mesially on the tooth. Distal to this tooth is a possible early bud for m4 developing on both sides of the jaw, but tissue disruption makes this difficult to confirm. The dental lamina disappears distal to this region.

Later development and eruption of the dentition in *Dasyurus viverrinus*

We would like to have been able to microscopically examine later developmental stages of the dentition in *Dasyurus viverrinus*, but at the time we were working at the Hubrecht Laboratory of Comparative Embryology, later stages were not available. Many older specimens, from 46 days old to about 120 days old, were described by Hill and Osman Hill (1955), but only a few brief comments were provided by them concerning the early eruption of a few teeth. Presumably, these later stages of alcohol specimens were included in the Hill collection when it was moved with the Hubrecht collection to the Museum für Naturkunde.

Concerning the later development and eruption of teeth in *Dasyurus viverrinus*, Hill and Osman Hill (1955) cited the earlier studies by Thomas (1887) and especially Woodward (1896), and accepted their beliefs that P3 is the tooth that has been suppressed in this species with two premolars. They all agreed that a vestigial dP3 developed in the jaws and that the lingual successional lamina of this tooth was much swollen and probably represented a rudiment for the successor P3, although it probably does not develop much further. All agreed that the vestigial dP3 is present but does not erupt and that the swollen primordium of P3 does not differentiate much further or erupt.

It seems clear to us that none of these authors microscopically examined later developmental stages of *Dasyurus viverrinus* beyond the “much swollen” stage of P3. In our studies, this stage occurred at 15–20 days of development. Indeed, in some 19–20-day-old pouch young, the successor P3 was already in the late-bud to early-cap stage. Between 20 and 41 days of development in our study, the P3 developed normally in both jaws, attaining the late-bell stage. In contrast, the dP3 in both jaws became relatively smaller and more abnormal in these later developmental stages; this would be consistent with continued reduction and non-eruption of dP3 in later stages.

The absence of a developing dP2 and the normal development of the successor P3 in the 25–41-day-old pouch young in our study provide a strong basis for our belief that dP1 and P3 are the two erupting premolars in both jaws of later developmental stages in *Dasyurus viverrinus*. Hopefully, future investigators will microscopically examine the later developmental stages and early eruption of the jaws in *Dasyurus viverrinus* to corroborate (or refute) our hypothesis of dental homologies.

Comparison of *Dasyurus viverrinus* with the three-premolared dasyurids *Sminthopsis virginiae* (Luckett and Woolley, 1996) and *Antechinus stuartii* (Luckett and Hong Luckett, pers obs) shows that there is a similar pattern in the early postcanine development of the premolars in these two groups, despite the loss of one deciduous premolar in the *Dasyurus* species. While the deciduous premolars differentiate

and develop in a posterior to anterior series (dP3 > dP2 > dP1) in both jaws of the didelphids *Didelphis* and *Monodelphis*, the dasyurids show a different developmental sequence of dP3 > dP1 > dP2. In *Sminthopsis virginiae*, a previous study showed that dP2 was relatively late in its initiation, not appearing until about 20 days of pouch young development (Luckett and Woolley, 1996). The same is true for *Antechinus stuartii*. As shown in our developmental series of *Dasyurus viverrinus*, it is this later developing dP2 that has been lost in this species with only two premolars. In our *Dasyurus viverrinus* series, it was during the 15 to 20 days of development that there was a slight suggestion of thickening of the dental lamina between dP1 and dP3; this probably represented a rudimentary attempt to develop a dP2. In the later stages of development, from 25 to 41 days, there was no longer any sign of a rudimentary dP2.

Another interesting and unusual condition in *Dasyurus viverrinus*, when compared with the dasyurids with three premolars, is the nature of the development of dP3 in both jaws. The dP3 is the first postcanine tooth to initiate differentiation in both jaws, as also occurs in all three-premolared dasyurids examined, as well as in didelphids. In contrast with these marsupials with three premolars, however, the dP3 in *Dasyurus* undergoes an abnormal state of development in later stages in both jaws, including a relative reduction in size and having a relative superficial position in the jaw with only minimal development of a bony alveolus. This abnormal development of dP3 is even more noticeable in the lower jaw. There is a large amount of dentin but only minimal amounts of enamel. In contrast, the successional P3 is developing normally in both jaws and it is quickly larger in size and deeper in the jaw than its deciduous predecessor. Although we could not follow later stages histologically, it is the normal developing successor P3 that erupts adjacent to dP1 in both jaws. In contrast, we are unaware of any evidence for eruption of the small, abnormal dP3 in *Dasyurus viverrinus.*

Another significant difference between *Dasyurus viverrinus* and the dasyurids with three premolars is the accelerated rate of development and eruption of P3 in *Dasyurus*, when compared with these other dasyurids and with didelphids. In the 97-day-old *Sminthopsis virginiae* examined by us (see Luckett and Woolley, 1996), M1-2 are erupted in both jaws and M3 is partially (⅓) erupted in the upper jaw. In the lower jaw, m3 is almost completely erupted and the protoconid of m4 is in an early stage of eruption. The dP1 to dP3 are erupted in both jaws, whereas the moderately large and well-developed successor P3 is still unerupted in both jaws.

In contrast, there is no sign of an erupted or unerupted dP3 in either jaw of *Dasyurus viverrinus* at about 95 days old, and dP1 is in early eruption. The successor P3 is in early eruption at about 98 days old; this is about the same time as the early eruption of M1. These data on *Dasyurus viverrinus* eruption are from the study by Merchant et al. (1984), although we have changed the names of their premolars ("first and second upper premolars") to correspond to our more precise and correct terminology because they considered dP2 to be present and P3 to be lost. As with most other studies on *Dasyurus viverrinus*, Merchant et al. (1984) did not microscopically examine any of their extensive series of developing pouch young. We also note that these authors found no trace of an erupted dP3 in earlier or later stages of development; this is consistent with our findings of abnormal development of dP3 in later stages of development.

Variation in the fate of dP3 within *Dasyurus*

Neither Hill and Osman Hill (1955) nor Merchant et al. (1984) could detect any evidence for the eruption of a rudimentary dP3 in *Dasyurus viverrinus*, and we have not seen such a tooth in any of the juvenile or subadult skulls that we have examined. However, in another *Dasyurus* species that we have studied, *Dasyurus albopunctatus*, we have noted similar developmental stages to those of *Dasyurus viverrinus*, as well as an unusual condition during later developmental stages and early eruption (Luckett pers obs). Our specimens of *Dasyurus albopunctatus* consist of microscopic sections of two early pouch young and a larger number (26) of skulls of juvenile and subadult specimens with erupting postcanine dentitions.

In the youngest specimen (fig. 5) that we examined microscopically (AMNH 195149; 12 mm HL), the postcanine region contained a moderately large late-bell stage dP1 with no

Figure 5. *Dasyurus albopunctatus* pouch young (AMNH 195149, 12 mm head length). Scale bar is 5 mm.

odontoblasts in the upper jaw. There was a diastema for the missing dP2 with no swelling of the dental lamina. Further distally was a moderately sized dP3 with moderately thick dentin and moderately developed enamel. Extending mesially from the dP3 was a lingual successional lamina that gave rise to an early- to middle-bud stage successional P3. Further distally was a large M1 with moderately developed dentin but no enamel. Distal to this was an early- to middle-cap stage for M2; the dental lamina ended distal to this tooth. This specimen is very similar in its developmental features to that of our *Dasyurus viverrinus* 25-day-old pouch young (12.5 mm HL). A later developmental stage of *Dasyurus albopunctatus* (AMNH 193967; 32 mm HL) was considerably advanced. The dP1 had thick dentin and enamel, and again, there was no trace of a rudimentary dP2 in the upper jaw. The now tiny calcified dP3 was elongate and slender, considerably reduced in relative size compared with the previous specimen; it was very close to the overlying alveolar margins. Deeper in the jaw and lingual to this was a moderately large successor P3, with thick dentin and enamel. This specimen was considerably more advanced in its development compared with our 41-day-old *Dasyurus viverrinus*.

In a slightly later juvenile skull of *Dasyurus albopunctatus* (AM M24313; skull damaged; not measured), the second to fourth incisors were in early eruption in the upper jaw and the canine was in an earlier stage of eruption. The dP1 was ½–⅔ erupted and there was no trace of a dP2. Immediately distal to this, the moderately sized successor P3 was in very early eruption, less than that of dP1. Lying on the apex of the P3 crown was a tiny, elongate and pearl-shaped dP3 on both sides of the jaw. The tiny dP3 had a crown height of 1.3 mm on the right side and 1.4 mm on the left side. The M1 was almost completely erupted and M2 was in early eruption. In comparison with the data on *Dasyurus viverrinus* from Merchant et al. (1984), this specimen would be 95–98 days old. In the lower jaw, the incisors are almost completely erupted, as is the canine. The dp1 is also almost completely erupted. The successor p3 is about ⅔ erupted and there is no trace of a tiny dp3. The m1 is almost completely erupted and m2 is about ½ erupted.

In nine juvenile skulls of *Dasyurus albopunctatus* from later developmental stages that we examined, we could see the tiny dP3 lying adjacent to the erupting P3 in the upper jaw in skulls where the P3 was not completely erupted (see fig 6a–d). It would be incorrect to say that the tiny dP3 were erupted, and we prefer to consider them to be *displaced* during the eruption of P3. The oldest specimen that we examined with the tiny dP3 was a partially damaged juvenile skull (AMNH 151980; 43.51 mm Skull Length). The dP1 was erupted and P3 was almost completely erupted on the right side of the upper jaw. The M1 was erupted and M2 was almost completely erupted. In the lower jaw, dp1, p3 m1 and m2 were erupted and m3 was about ¾ erupted. As in all the juvenile specimens examined by us for this species, there was no trace of a dp3 in the lower jaw. This specimen was briefly noted by Tate (1947, p. 142) who stated that the "upper and lower fourth premolars are absent. The milk P4, however, can still be detected". As we have shown in this and earlier developmental stages, it is dP2 that is the missing tooth in both jaws, and P3 (his fourth premolars) is developed in both jaws. It was the tiny dP3 (his "milk P4") that he detected in the upper jaw.

In later developmental stages of *Dasyurus albopunctatus*, in which P3 was completely or almost completely erupted in the upper jaw, the tiny dP3 was absent in most cases. However, in a few instances of some specimens with P3 erupted, tiny tooth-like fragments of a probable apical or basal remnant of dP3 were found unilaterally (AMNH 151973, 151971). The oldest juvenile that we found with a slender root remnant of dP3 unilaterally (fig. 6d) was in a male (BBM-NG 97868; 47.25 mm Skull Length) with dP1, P3, M1 and M2 erupted in the upper jaw, and M3 was about ½ erupted.

We suggest that the pattern of dental development and eruption in *Dasyurus albopunctatus* is an intermediate condition between that of the dasyurids with three premolars that we have examined and *Dasyurus viverrinus*. Both of our species of *Dasyurus* have a similar accelerated rate of development for the eruption of P3 at about the same time as M1 and M2, compared with that for the dasyurid species *Sminthopsis* and *Antechinus* with three premolars. The greatly reduced dP3 adjacent to the erupting P3 in the upper jaw of *Dasyurus albopunctatus* is an intermediate condition between the presence of an erupted dP3 in the dasyurids with three premolars and its absence in *Dasyurus viverrinus*.

Although we have not made an extensive search for rudimentary dP3 remnants in other species of *Dasyurus*, we suspect that they can and will be found in some of these species. We have seen one such probable tiny dP3 in *Dasyurus geoffroii* and *Dasyurus hallucatus*, and we have seen a similar condition of accelerated eruption of P3 in these two species. We also note that Archer (1975, p. 255) reported the presence of a rudimentary spicule-like tooth in the position of the "normally absent" dP3 in *Dasyurus geoffroii* (WAM M6370); we suspect this was also a dP3 fragment.

A final thought. Although *Dasyurus viverrinus* is considered to be extinct on mainland Australia, we hope that investigators in Tasmania will help complete our studies on the later development and eruption of the dentition in this species, which still exists there but is threatened. Investigators there have studied many other aspects of the biology of this interesting species, and we hope that this paper will stimulate some to further support or challenge our findings on dental development.

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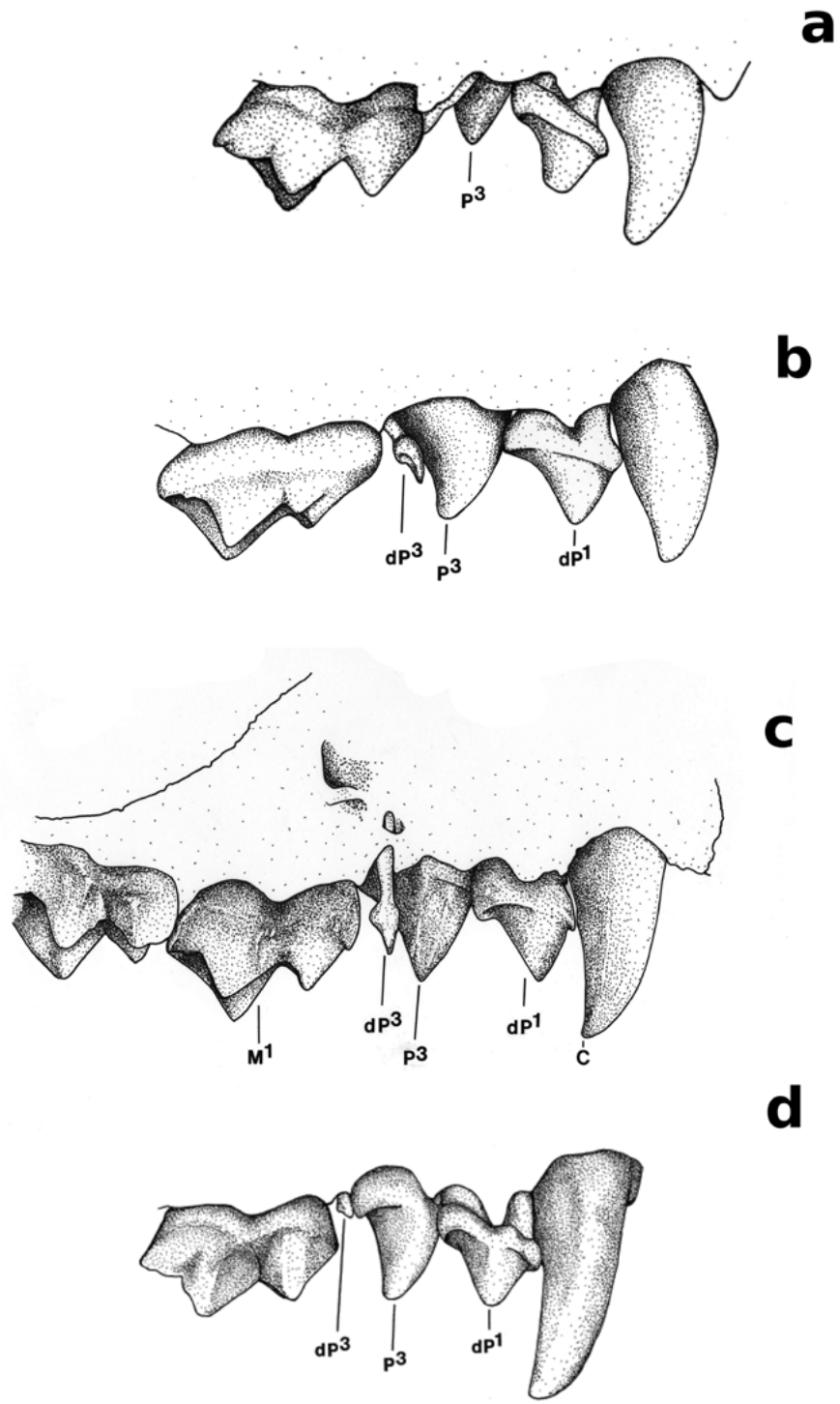

Figure 6. *Dasyurus albopunctatus* pouch young: a, (AMNH 190927; 36.64 mm skull length). Erupting teeth in the upper jaw with canine about ½ erupted. The dP1 is almost completely erupted and P3 is in early eruption. A tiny, slender dP3 is lying on the distal margins of the erupting P3, pointing posteriorly; its apex is not evident. M1 is erupted and the M2 is about ¾ erupting (not shown); b, (AMNH 221650; 37.53 mm skull length) slightly older than the preceding. The dP1 is erupted in the upper jaw and P3 is erupting (½–⅔). A tiny, elongate dP3 is evident along the posterior margins of the erupting P3; c, (BBM – NG 28247; 37.89 mm skull length). The dP1 is erupted, and the P3 is almost completely erupted in the upper jaw. A tiny, slender and elongate dP3 is evident along the distal margin of P3 and its root extends distally beneath the anterior opening of the infraorbital canal; d, (BBM – NG 97868; 47.25 mm skull length). In this older young, the P3 is almost completely erupted in the upper jaw. A tiny, slender root remnant of dP3 is evident, distal to the buccal end of P3.

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