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TOOTH ERUPTION IN *MONODELPHIS DOMESTICA* AND ITS SIGNIFICANCE FOR PHYLOGENY AND NATURAL HISTORY

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The gray short-tailed opossum (*Monodelphis domestica*) began tooth eruption at 32 days with the deciduous premolars (dp3 and dP3). All but 5 teeth completed eruption by 56 days, with only p3, m4, P3, M3, and M4 unerupted at that age. Eruption was complete by 134 days with eruption of P3 and M4. We found no significant differences between sexes in tooth eruption timing, but significant differences occurred among litters at some tooth positions. Timing and sequence of tooth eruption differed somewhat as seen in live young versus that seen in a series of skulls of known age. Live juveniles can be placed into a series of 6 age classes based on emergence of teeth through the gingiva, whereas juvenile skeletal material is best placed into age classes based solely on eruption of upper molars. Other systems of age classes used in didelphid marsupials that are based on sequence of eruption of P3 and M4 are not generally applicable because of variation in this sequence. In didelphids delayed eruption of I1 may be functionally related to weaning, whereas weaning and 1st reproduction are not obviously correlated with age class based on molar eruption.

Key words: age classes, dentition, development, Didelphidae, *Monodelphis*, tooth eruption, tooth replacement

Timing and sequence of tooth eruption and replacement have been used in population and demographic studies as a method to determine age of juveniles. Knowledge of eruption sequence allows individuals to be placed in relative dental age classes, whereas knowledge of the actual age of tooth eruption allows estimation of the absolute age of juvenile specimens.

A number of studies of the New World marsupial family Didelphidae have used tooth eruption data to assess life history and population parameters. The chronology of tooth eruption and replacement is partially described in *Didelphis* (Atramentowicz 1986; Gardner 1982; Gilmore 1943; McCrady 1938; Petrides 1949; Regidor and Gorostiague 1990, 1996), as are dental age classes based on pattern and sequence of tooth eruption and wear (Atramentowicz 1986; Gardner 1973; Lowrance 1949; Regidor and Gorostiague 1990, 1996; Tyndale-Biscoe and MacKenzie 1976). Dental age classes have been constructed for a variety of other didelphids, including the bare-tailed woolly opossum (*Caluromys philander*—Atramentowicz 1986), little water opossum (*Lutreolina crassicaudata*—Regidor et al. 1999), gray slender mouse opossum (*Marmosops incanus*—Lorini et al. 1994), long-furred woolly mouse opossum (*Micoureus demerarae*—Quental et al. 2001), and gray four-eyed opossum (*Philander opossum*—Atramentowicz 1986; d'Andrea et al. 1994).

Some information on tooth eruption in *Monodelphis* has been reported previously. Ventura et al. (1998) presented age classes and eruption sequence for skeletal material of the red-legged short-tailed opossum (*M. brevicaudata*). Pine et al. (1985) described the state of dental eruption at 2 ages and age classes in the southern short-tailed opossum (*M. dimidiata*). Cifelli and colleagues (Cifelli and Muizon 1998; Cifelli et al. 1996) reported age of canine eruption in osteological specimens of the gray short-tailed opossum (*M. domestica*). Bergallo and Cerqueira (1994) divided a large sample of skulls of wild-caught *M. domestica* into dental age classes of unknown absolute age.

In addition to providing a signal with which to assess age, eruption patterns also may have systematic value. Tribe (1990) noted variability in eruption sequence of P3 and M4 among didelphids and used this character to reassess relationships of the subfamilies. He argued that the relative timing of eruption of P3 and M4 did not support placing *Caluromys* and its close relatives into subfamily Caluromyinae (Tribe 1990).

Finally, the pattern and chronology of tooth eruption and replacement must be related to, and indicative of, other aspects of growth and development in mammals. Smith (1989, 1992, 2000) and Smith et al. (1994) compiled eruption data for

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primates and a few other eutherian orders, and found significant correlations of eruption timing and sequence with maturation rate, brain size, and other life history variables. There is no comparable review of the significance of tooth eruption patterns in marsupials. However, it has been proposed that a functional link exists between tooth eruption and replacement pattern and the extended period of suckling seen in marsupials (Guiler and Heddle 1974; Luckett 1993; Luckett and Woolley 1996; Wilson and Hill 1897; Winge 1941).

This paper reports basic data on tooth eruption and replacement in a small didelphid marsupial, *Monodelphis domestica*. Two sets of eruption sequences and chronologies are presented, the 1st based on a longitudinal study of gingival emergence in individuals from 3 captive litters and the 2nd a study of eruption in a series of skulls of known age. Dental age classes are delineated for materials of both kinds. Variation and significance of eruption sequence and timing also are considered.

Materials and Methods

Study animals.—The study species, *M. domestica*, is native to eastern and central Brazil, Bolivia, and Paraguay (Eisenberg and Redford 1999; Nowak 1991; Streilein 1982a). The life history of gray short-tailed opossums in captivity is well known (Cothran et al. 1985; Fadem and Corbett 1997; Fadem et al. 1982, 1996; Kraus and Fadem 1987; Saunders et al. 1989; VandeBerg 1990). Streilein (1982a, 1982b, 1982c, 1982d, 1982e) and Bergallo and Cerqueira (1994) presented data on life history and natural history based on field studies in Brazil.

Gray short-tailed opossums were from a captive breeding colony at Duke University. They were housed in individual plastic cages (48 × 27 × 20.5 cm) with steel lids. An inverted plastic bowl (18.5 cm diameter) served as a nest cavity. Aspen chips served as bedding and shredded newspaper was provided as nest-building material. Opossums received Purina Ferret Diet (Purina Mills, St. Louis, Missouri) and water ad libitum. Diet was supplemented regularly with fruit (bananas, apples, and grapes), canned dog food, and live crickets. Cages were cleaned weekly. Opossums were kept in a 12:12 h light : dark photoperiod at a temperature of 24°C. Males and females were in separate chambers with independent ventilation. Young animals remained with the mother until about 80 days after birth, at which time males and females were divided into separate cages. Young were placed in individual cages at about 100 days or when aggressive interactions began. Animals in this study were treated humanely. Research described here was approved by the institutional animal care and use committee of Duke University and followed the guidelines published by the American Society of Mammalogists (http://www.mammalogy.org/committees/index.asp).

Eight males and 6 females from 3 litters of 3 different sets of parents were examined. Ages of young are given in postnatal days with day of birth designated as day 0. Breeding females were checked once daily for young, so determination of date of birth could be off by up to 1 day. Individuals were marked by selectively clipping small patches of hair or whiskers. At 10–14 days, young *M. domestica* are able to detach and reattach to the nipple and can be temporarily removed from the mother without harm. Most individuals were examined for their state of tooth eruption from 28 to 132 days. Observations were made daily from 28 to $\geq$41 days and every other or every 3rd day afterward. A typical individual was therefore examined about 50 times at an average interval of 2.2 days during the 28- to 132-day observation period.

Monodelphis domestica retains the primitive marsupial dental formula for both adult and deciduous dentition (i 5/4, c 1/1, p 3/3, m 4/4, total 50). We follow the ontogenetically based system of Luckett (1993) in assigning tooth homologies. In this system incisors and canines are considered 2nd-generation (permanent) teeth with no functional predecessors, but 1st and 2nd premolars are thought to be 1st-generation teeth with no successors. We use a prefix of "d" to indicate a 1st-generation ("deciduous") antemolar tooth. The first 2 premolars function in the adult dentition, but are designated dP1–2 and dp1–2. The last premolar positions are the only ones filled by functional teeth from both 1st (dP3 and dp3) and 2nd (P3 and p3) tooth generations, with the 2nd-generation teeth functioning in the adult dentition.

Our terminology for major molar cusps is standard (Vaughan et al. 2000). Lower molars have an anterior trigonid with 3 cusps (protoconid, paraconid, and metaconid). A low talonid basin bordered posteriorly by low cusps is posterior to the trigonid. Upper molars have 3 trigon cusps (protocone, paracone, and metacone) and 4 stylar cusps. Following Clemens (1966), stylar cusps are designated A, B, D, and E, with A being anterior.

Determination of gingival emergence.—A tooth was recorded as having emerged when any part of it had penetrated the gingiva ("standard gingival emergence" of Smith et al. [1994]). On occasion, a tooth was recorded as "emerged" 1 day and as "not emerged" the next. A tooth was only counted as emerged on the date after which it was never scored as "not emerged" again.

State of emergence of individual teeth was determined as follows. Individual young were removed from cages and weighed. They were then handheld by an assistant while the examiner gently wedged the mouth open with a wooden toothpick or applicator stick. All 4 quadrants (left and right, upper, and lower) were then examined visually and by touch. Unemerged teeth are covered by a layer of gingiva that appears opaque and pink where it is thickest and nearly transparent where it is thinnest (i.e., over the tip of a cusp that is about to break through). Emerged portions of teeth can be distinguished by the exposure of bright white enamel. Tactile inspection was performed by gently passing a wooden toothpick over a tooth. A toothpick "catches" on emerged cusp tips. Two females from 1 litter were sacrificed during dental eruption and examined under a dissecting microscope to evaluate the accuracy of the above methods.

Gingival emergence data, statistical methods.—Age when emergence was 1st consistently recorded can overestimate age of 1st emergence, because a tooth could have emerged any time between observations. To compensate for this bias, estimated ages of emergence reported here are ages at which eruption is 1st consistently recorded minus one-half of the period of time elapsed since the previous observations. Data were recorded for both left and right sides, but differences between sides were minor, so all analyses were performed on data from the left side only.

Mixed model, 2-way (3 × 2) analyses of variance (ANOVAs) of emergence age were performed for each tooth position (27 separate ANOVAs). The 2 factors were litter (3 levels) and sex (2 levels). Litter was a random (model II) factor, whereas sex was a fixed treatment effect (model I—Sokal and Rohlf 1981). Because litter sizes were not equal, analyses were unbalanced, so type III sums of squares were calculated (Sokal and Rohlf 1981). Calculation of *F*-statistics and significance testing follow methods of Sokal and Rohlf (1981:337) for mixed models. Statistics were calculated with SuperANOVA (Abacus Concepts 1989) on a Macintosh computer.

An average gingival emergence sequence was generated by assigning each tooth from an individual (i.e., 25 teeth from adult dentition plus dP3 and dp3) a numerical sequence rank (1–27), averaging these ranks over all 14 individuals and then ordering the teeth by average rank.

Determination of eruption in defleshed and cleaned skulls.—A series of known-age skeletal specimens was produced to assess progression of dental eruption as observed on defleshed and cleaned skulls. This sample of individuals represents part of the normal culling of excess healthy animals from the colony. Animals were euthanized in a chamber filled with carbon dioxide. The series consists of 48 skulls (41 males and 7 females) representing 38 ages from 30 to 150 days. No age gaps >5 days occur in the series. Individuals were from many different litters produced by multiple sets of parents. Some litters have several siblings represented in the series. The series includes 5 males and 2 females from the gingival emergence study. The series is housed in the laboratory of KKS.

The dentition of each skull was examined and each tooth was scored as "unerupted" or "erupted." A tooth was scored as "erupted" if it had fully erupted into occlusion. (We use the term "eruption into occlusion" even though upper and lower premolariform teeth of this species do not technically occlude with each other. Also, even if a tooth erupts into position, it will not actually occlude until its opposite number has erupted into occlusion.) Incisors were considered to be erupted when their crowns were fully exposed above alveolar bone and their tips reached the same height as any previously erupted incisors. Previous studies (Cifelli and Muizon 1998; Cifelli et al. 1996) found that canines in *M. domestica* have an extended period of eruption, about 19 days from early eruption to completion for the lower canine. Here, a canine was considered to have erupted when its tip projected beyond the line formed by tips of erupted incisors and premolars, which is approximately equivalent to "early eruption" of Cifelli et al. (1996:717, figure 3). The premolariform teeth and initial molariform teeth (dP3 and dp3) were deemed to have erupted when their crowns were fully exposed. Molars erupt in front to back sequence behind these teeth. An upper molar was considered erupted when stylar cusp A aligned with stylar cusp E of the molar just anterior. Lowers had erupted when the paraconid was higher than hypoconid of the molar just anterior.

An estimate of age at which a tooth erupts into occlusion was made by taking the average of age of oldest specimen in which the tooth is unerupted and youngest age at which the tooth is recorded as fully erupted. In some cases a tooth was recorded as fully erupted in a specimen of a given age and as unerupted in a different specimen of same age. In this case, age of eruption was deemed to be that particular age. In the case where specimens of sequential age were recorded as "unerupted," "erupted," "unerupted," "erupted," and "erupted" thereafter, an estimate of eruption age was made by averaging ages of the 1st and 4th specimens in the series. An approximate sequence of eruption into occlusion was produced by ordering teeth on the basis of their estimated age of eruption.

RESULTS

Gingival emergence.—The 1st tooth (usually dP3) emerges on average at 32 days, with a number of other teeth emerging in the next several days (Table 1; Appendix I). Most of the remaining teeth have emerged by 54 days, with only 3 molars and the 3rd permanent premolars yet to emerge. The 1st upper incisor emerges at 53 days, well after I2–4, which erupt in sequence between 39 and 45 days.

The molar teeth emerge in sequence from front to back, with m4 emerging at 83 days on average and M4 at 127 days. The p3 is the last tooth to emerge in the lower jaw, at 109 days. P3 emerges before M4 in the upper jaw at 111 days. In several cases P3 showed gingival emergence of its highest cusp before dP3 was shed (i.e., both teeth occupying the 3rd upper premolar position were recorded as "emerged" at the same time.)

TABLE 1.—Dental age classes for fleshy (live) specimens of *Monodelphis domestica*.

Dental age class and approximate ages	Average gingival emergence sequence	Average age of gingival emergence
Class G0: 0–31 days	No teeth erupted.	
Class G1: 32–48 days	dP3	32.0
	dp3	32.4
	i1	33.5
	m1	33.1
	i2	34.2
	i3	34.4
	dP2	34.5
	i4	35.1
	M1	35.8
	dp2	36.4
	dP1	37.8
	dp1	38.1
	I2	39.2
	m2[a]	39.9
	I3[a]	40.1
	c	40.1
	I4	42.3
	C	41.8
	I5	44.5
Class G2: 49–81 days	M2	49.0
	m3[a]	53.4
	I1[a]	53.3
Class G3a: 82–107 days	m4	82.8
	M3	83.5
Class G3b: 108–125 days	p3	108.8
	P3	111.2
Class G4: >125 days	M4	126.5

[a] These pairs were equal in sequence.

Among the animals monitored for gingival emergence, 4 individuals (representing 2 litters and both sexes) lost 1 of the last 4 upper incisors (I2–5). Three cases involved loss of a left incisor and 1 case was bilateral. In all cases the teeth were recorded as emerged and subsequently disappeared. There were no obvious oral pathologies that would account for these losses.

The results of 27 ANOVAs that were performed on age of gingival emergence at each tooth position (Appendix I) can be summarized as follows. No significant differences ($P < 0.05$) were found between sexes at any tooth position. Significant differences were found among the 3 litters at 11 tooth positions (values in parentheses are F-statistic followed by P-value): I1 ($F = 20.89$, $P = 0.001$), I3 (7.01, 0.02), I4 (48.01, 0.0001), I5 (34.77, 0.0002), C (12.38, 0.004), M1 (28.27, 0.0002), M2 (81.94, 0.0001), M3 (9.25, 0.01), dp2 (11.31, 0.005), m2 (4.87, 0.04), m3 (9.69, 0.01). At 1 tooth position (p3), a significant interaction effect of litter and sex was found ($F = 6.43$, $P = 0.04$).

The sequence of gingival emergence differed slightly in all 14 individuals examined. Average emergence sequence was dP3, dp3, i1, m1, i2, i3, P2, i4, M1, p2, P1, p1, I2, (m2, I3), c, I4, C, I5, M2, (m3, I1), m4, M3, p3, P3, M4 (parentheses enclose teeth of equal rank in the sequence.) Only 1 tooth position had the same rank in all individuals: M4 was the last tooth to emerge (number 27) in all cases. Seven different teeth

Table 2.—Dental age classes for defleshed and cleaned skulls of *Monodelphis domestica*.

Age class and approximate ages	Eruption sequence[a]	Estimated day of eruption
Class 0: <46 days	i1, i2, i3, i4, dP3, dp3	33
	I2, I3, I4, m1	44
Class 1: 46−55 days	I5, C, c, dP1, dp1, dp2, **M1**, m2	46
	dP2	52
Class 2: 56−97 days	**M2**	56
	I1, m3	56
	m4	93
Class 3: 98−133 days	**M3**	98
	dp3 shed	107
	dP3 shed	110
	p3	127
Class 4 and later: >133 days	**M4**, P3	134

[a] Teeth on same line are equal in sequence. Teeth used in setting age class boundaries are in boldface.

were recorded as 1st (either alone or simultaneous with another tooth): dP3 (13 times), dp3 (7 times), i1 (3 times), m1 (2 times), i2 (1 time), i3 (1 time), and dp2 (1 time).

Two female young (44 and 57 days old) from 1 litter were sacrificed and differences in the state of emergence, as recorded on the same individual on the same day, while alive and later during dissection, were noted. In the younger specimen upper canines and lower 2nd molars (m2) were coded as erupted by tactile and gross visual criteria, but were in fact covered by a very thin, transparent layer of gingiva. Upper 1st incisors (I1) had barely broken through the gum, but had not been recorded as erupted on the older specimen.

Examination of these individuals also allowed the sequence of molar cusp emergence to be determined. For upper molars it is trigon cusps (protocone, metacone, and paracone), then stylar cusps B and D, then A and E. For lower molars it is trigonid cusps (protoconid, metaconid, and paraconid), then talonid cusps and basin. The talonid of a lower molar does not emerge until about the time the upper molar situated above and behind that lower molar emerges. For example, the talonid of m2 would not emerge until M3 emerges. Therefore, there may be a considerable lag (e.g., about 47 days in the case of m4) between the time that anterior and posterior ends of a lower molar emerge.

Eruption in defleshed and cleaned skulls.—Six teeth have completed eruption by 33 days: dp3, dP3, and i1–4 (Table 2; Fig. 1). Here, too, I1 at 56 days was delayed compared to I2–5 (44–46 days). By 56 days all teeth have erupted, except for the following 5: in the lower jaw, m4 at 93 days and p3 at 127 days; in the upper jaw, M3 at 98 days, and M4 and P3 both at 134 days. The approximate eruption sequence is (i1, i2, i3, i4, dP3, dp3), (I2, I3, I4, m1), (I5, C, c, dP1, dp1, dp2, M1, m2), dP2, M2, (I1, m3), m4, M3, p3, (P3, M4).

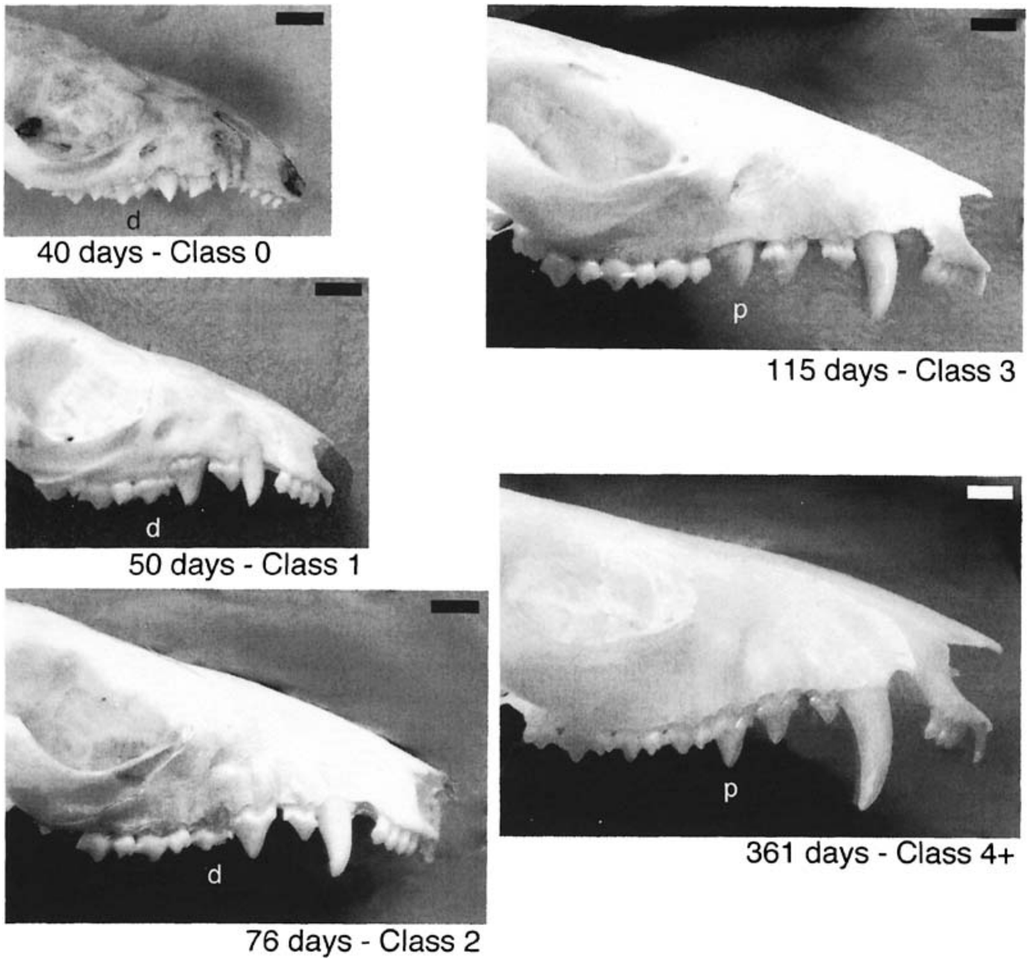
Discussion

Dental age classes for fleshy specimens.—We have designated 6 different juvenile age classes based on gingival emergence with approximate age ranges: G0 (0–31 days), G1 (32–48 days), G2 (49–81 days), G3a (82–107 days), G3b (108–125 days), and G4 (>125 days; Table 1). Age class boundaries correspond to times when there were larger time gaps in eruptive activity. The numeral in the class name refers to the upper molar that emerges during that class (because upper molars emerge in order of numerical sequence). Class G0 contains animals in which no teeth have emerged. G1 represents a 17-day period in which 19 teeth emerge. It begins with the emergence of the 1st tooth and ends before the emergence of M2. G2 begins with the emergence of M2. G3 begins with the nearly simultaneous emergence of m4 and M3 and can be subdivided into G3a and G3b, representing periods before and after emergence of p3. G4 begins with the emergence of M4. The small number of errors that were discovered upon dissection indicates that our methods are basically sound. We estimate that all errors occurred in teeth within 3 days of actual emergence. Our technique does not seem to introduce a consistent bias, because 2 errors were underestimates and 1 was an overestimate of age of emergence.

Use of these age classes to determine approximate ages of wild *M. domestica* requires the assumption that tooth eruption in captive animals is similar to that in wild populations. Dental development is relatively resistant to nutritional extremes and systemic developmental defects (Garn et al. 1965a, 1965b) and, therefore, should be a consistent system for estimating ages. We know of no other data on emergence variability or the effects of captivity in *M. domestica*. Offspring of wild-caught *M. dimidiata* were close to dental eruption at approximately 28 days of age and had erupted most anterior teeth by approximately 35 days (Pine et al. 1985). The dentitions of *M. domestica* from this study were in a similar state at 28 days and most anterior teeth on the lower jaw had emerged by 35 days.

Proposed age classes for defleshed and cleaned didelphid specimens.—One previous study has defined dental age classes for *M. domestica* (Bergallo and Cerqueira 1994). In that study, defleshed and cleaned skulls of wild-trapped animals were placed into age classes based on eruption and wear of the upper posterior cheek teeth (P3–M4), by following the system devised by Tyndale-Biscoe and MacKenzie (1976) for skeletal material of *Didelphis*. The eruption sequence for *Didelphis* found by Tyndale-Biscoe and MacKenzie (1976) was M1, M2, M3, P3, M4. This differs from the sequence that we found in *M. domestica* of M1, M2, M3, (M4, P3). In the system of Tyndale-Biscoe and MacKenzie (1976), class 1 is defined as the period between full eruption of M1 and full eruption of M2. Class 2 is between eruption of M2 and M3. Class 3 is between eruption of M3 and P3. Class 4 is defined as the period between eruption of P3 and eruption of M4. Class 5 is defined as the period after full eruption of M4, but before significant wear of the molars. Classes 6 and 7 are based on patterns of molar wear.

Bergallo and Cerqueira (1994) report trapping of *M. domestica* of age classes 2–7, including class 4, implying that at least part of their sample shows the P3–M4 sequence. Based on our series of skulls, we found P3 and M4 to erupt at the same age (134 days). This has the result of collapsing classes 3 and 4 into a single class. This contradictory finding could be



40 days - Class 0

115 days - Class 3

50 days - Class 1

361 days - Class 4+

76 days - Class 2

Fig. 1.—Dental age classes in *Monodelphis domestica*. The progression of age classes is characterized by the sequential eruption of the molariform teeth from the deciduous 3rd premolar (dP3) to the last molar (M4). Also note the delayed eruption of 1st incisor, the loss of dP3 by class 3, and the extended period of eruption of the canine. All specimens are male. Scale bars are 2 mm. The tooth in the last premolar position (P3) is labeled as deciduous (d) or permanent (p).

attributable to individual variation, population-level variation, or both, in eruption sequence or different definitions of "eruption" (see below). Unfortunately, neither Bergallo and Cerqueira (1994) nor Tyndale-Biscoe and MacKenzie (1976) present detailed eruption criteria that can be used for comparison.

This situation also points to a more general problem. A system of age classes will not work if the sequence of eruption of tooth positions important in defining age classes varies. The sequence of P3 and M4 eruption is known to vary among and within species of didelphids (Tribe 1990), so any system that assumes a particular P3–M4 sequence will not be generally applicable. Instead, we propose a system of dental age classes based on eruption of upper molars (Table 2; Fig. 1). Upper molars of didelphids always erupt in sequence M1 to M4, so this system should be valid for the entire family. The first 4 classes (0–3) are defined by the state of eruption of the upper molars. Subsequent classes (4 and higher) could be defined by progression of tooth wear as in Tyndale-Biscoe and MacKenzie (1976) or Gardner (1973, 1982). In our proposed system, class 1 is defined as the period between full eruption into occlusion of M1 and M2. Classes 2 and 3 are defined similarly with respect to M2–M3 and M3–M4. Class 4 is defined as the period between full eruption of M4 and accumulation of significant tooth wear. Class 0 is the period preceding full eruption of M1. Conversion from the system of Tyndale-Biscoe and Mackenzie (1976) is simple (assuming a similar definition of eruption). Classes 1 and 2 are the same in both systems. Their classes 3 and 4 are both considered class 3 in our system. Their class 5 is equivalent to our class 4.

Comparison of gingival and occlusal eruption.—Very little is known about the rate of progression of eruption from gingival emergence to occlusion in mammals. This rate can be quantified by using our data if average age at gingival emergence is subtracted from estimated age of eruption into occlusion. At most tooth loci, eruption proceeds from gingival emergence to eruption into occlusion. The average length of this eruptive period is 5 days for canines, 14 days for premolariform teeth, and 7 days for molariform teeth. Upper incisors have an average eruptive period of 3 days, but lower incisors actually achieve eruption into occlusion about 2 days before they pierce the gums.

The fact that eruptive periods vary means that different teeth erupt at different rates and that there will be different sequences for gingival emergence and eruption into occlusion (Tables 1 and 2). Two salient differences in *M. domestica* are relatively early eruption of I2–5, compared to emergence, and change from emergence sequence dP3–dP2–dP1 to eruption sequence dP3–dP1–dP2. The difference in P3–M4 sequence was mentioned above. A similar variation of P3–M4 sequence was found in *M. demerarae*, with the sequence P3–M4 seen in living animals (Quental et al. 2001) and M4–P3 in osteological material (M. R. Sánchez-Villagra, pers. comm.; Tribe 1990). This finding is important because it shows that age classes based on eruption sequences determined by using different sets of eruption criteria may not be comparable.

Despite differences in detail, the general pattern of both sorts of eruption is very similar in *M. domestica*. No teeth erupt before 32 days, and then all but 5 teeth erupt in the period from about 32 to 56 days of age. Next, m4 and M3 erupt in the range of 82–98 days of age. The last teeth (p3, P3, and M4) erupt after 108 but before 135 days of age.

Systematic value of didelphid eruption sequences.—Tribe (1990) examined the sequence of eruption of upper cheek teeth in didelphids and found that the sequence always began dP3–M1–M2–M3, but that there was variability in the sequence of the remaining 2 teeth (P3 and M4). He found that, in general, *Chironectes*, *Didelphis*, *Lutreolina*, and *Philander* show the P3–M4 sequence, whereas *Caluromys*, *Glironia*, *Gracilinanus*, *Marmosa*, *Marmosops*, *Micoureus*, and *Monodelphis* show the M4–P3 sequence (Tribe 1990). He argued further that this character-state distribution might be evidence for 2 monophyletic groups within the Didelphidae and did not support placing *Caluromys* and its close relatives into the subfamily Caluromyinae. However, Tribe (1990) found the sequence of eruption of M4 and P3 to be variable within these groups, with some species showing both sequences or an intermediate condition (M4 and P3 erupting simultaneously). Tribe (1990) and our study both determined that defleshed and cleaned skulls of *M. domestica* show the intermediate condition.

The value of this eruption sequence character must be reconsidered in light of several issues. Tribe (1990) considers only 2 states of this character, when there is a 3rd, fairly common, intermediate state (M. R. Sánchez-Villagra, pers. comm.; Tribe 1990). Also, the way this character is defined does not take into account that species with different sequences may differ in eruption timing by only a matter of days.

Lastly, Tribe (1990) uses the microbiotheriid *Dromiciops gliroides* (monito del monte) as an outgroup for the Didelphidae, making eruption of P3 before M4 the primitive condition, but *D. gliroides* is not an appropriate outgroup (Horovitz and Sánchez-Villagra 2003). Fortunately, there is a relevant fossil record of tooth eruption sequence. Two Late Paleocene taxa that are appropriate outgroups for the Didelphimorphia (Horovitz and Sánchez-Villagra 2003) are *Mayulestes ferox* and *Pucadelphys andinus*, in both of which P3 erupts before M4 (Cifelli and Muizon 1998). Therefore, fossil evidence indicates that the P3–M4 sequence is probably primitive for didelphids.

If the P3–M4 sequence is primitive and the intermediate character state is recognized, distribution of intermediate and M4–P3 sequences indicates that there must have been many independent derivations of either one or both of these derived patterns. This weakens Tribe's (1990) argument that delayed eruption of P3 (the pattern of *M. incanus*) is a shared, derived character linking *Monodelphis*, *Marmosa*, *Gracilinanus*, *Marmosops*, *Micoureus*, *Thylamys*, *Caluromys*, *Caluromysiops*, and *Glironia* into a monophyletic group.

Life history and tooth eruption in M. domestica.—Reduction of tooth replacement to at most the P3/p3 loci has been functionally linked to the period of attachment of marsupial young to the nipple (Luckett 1993; Wilson and Hill 1897; Winge 1941). The present data do not allow us to comment on this hypothesis (see van Nievelt and Smith 2005), but we can comment on a more specific hypothesis linking suckling and tooth eruption. Thomas (1887) noted that eruption of I1 is delayed relative to other upper incisors in a number of polyprotodont marsupials from the families Didelphidae, Dasyuridae, and Peramelidae. Subsequent authors (Guiler and Heddle 1974; Luckett and Woolley 1996; Winge 1941) confirmed this observation and hypothesized that eruption of I1 is delayed to allow for a gap in the middle of the upper incisors for the nipple to fit into, facilitating continued suckling after tooth eruption had begun. This gap might be expected to be filled by the erupting I1 around time of weaning.

The 1st upper incisor, I1, in *M. domestica* erupts into occlusion at 56 days, well after the other upper incisors (Fig. 1) and at time of weaning (van Nievelt and Smith 2005). Eruption of I1 also occurs at age of weaning in *Sarcophilus laniarius* (Tasmanian devil—Guiler and Heddle 1974) and *Didelphis virginiana* (Virginia opossum—McCrady 1938). This agrees with the prediction that eruption of I1 would be delayed until completion of suckling. The proposed functional explanation for the delayed eruption of I1 is reasonable, but further research on the function and distribution of this phenomenon in both marsupial and placental mammals is needed.

Weaning and 1st reproduction of females are 2 major life history events. The ages at which these events occur have been shown to be strongly correlated with age at which molars erupt in primates (Smith 1989; Smith et al. 1994). If molar eruption is closely tied to life history in didelphids, one might expect weaning and 1st reproduction to be coincident with a particular dental age class. Dental age class at weaning, 1st reproduction, or both has been reported for 8 didelphid species (*C. philander*—Atramentowicz 1986; *Didelphis albiventris*—Cerqueira 1984; Regidor and Gorostiague 1990, 1996; *Didelphis aurita*—Tribe 1990; *Didelphis marsupialis*—Atramentowicz 1986; Tyndale-Biscoe and MacKenzie 1976; *D. virginiana*—Gardner 1982; McCrady 1938; *M. incanus*—Lorini et al. 1994; *M. domestica*—this study; Bergallo and Cerqueira 1994; and *P. opossum*—Atramentowicz 1986; Hingst et al. 1998). After converting to the system of age classes for defleshed and cleaned material recommended above, we found that there is interspecific variation in the age classes at which didelphids are weaned (classes 0–2) and begin reproduction (classes 3 to >4). We believe that these ranges of variation are large enough to indicate actual variation in age classes at weaning and 1st reproduction, but an unknown portion of variation is attributable to differing methods and samples of the various studies.

Monodelphis domestica is dimorphic in body size, with adult males in our colony typically weighing about 50% more than adult females. However, this dimorphism is not reflected in timing of tooth emergence. This is despite the fact that sexual dimorphism becomes significant before completion of eruption, even in less dimorphic wild populations (Bergallo and Cerqueira 1994). This lack of differences between sexes increases our confidence in the reliability of using tooth eruption as a means of age determination.

RESUMEN

La zarigüeya colocorto gris (*Monodelphis domestica*) comienza su erupción dentaria a los 32 dias con los premolars deciduos dp3 y dP3. Con solo 5 excepciones (p3, m4, P3, M3 y M4), los dientes estan completamente salidos a los 56 dias. El proceso de la erupción termina a los 134 dias con la erupción de los ultimos dientes, P3 y M4. No se manifiestan diferencias sexuales en la cronometria de la erupción, pero se registraron diferencias significativas en algunas posiciones dentarias entre distintas crias. Comparando juveniles vivientes con una serie de craneos de edad conocida, se establece diferencias tanto en la cronometria como también en la secuencia. Juveniles vivientes pueden clasificarse en una serie de 6 estados distintos en base a la salida de los dientes através de la encía, mientras se clasifica material esqueletal juvenil en base a la erupción de los molares superiores. Otros sistemas de clasificación por edad en marsupiales didélfidos basados en la secuencia de erupción de P3 y M4 no resultan tan útiles debido a la variación observada. In didélfidos, el retroceso de la erupción del I1 puede relacionarse funcionalmente al destete, mientras el destete y la edad del primer parto no estan corelacionados con la clase de edad determinada por la erupción de los molares.

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APPENDIX I

Statistics for age of gingival emergence (in days) for the teeth of *Monodelphis domestica*.

				By sex						By litter									
	All specimens			Male			Female			9A			7A			4D			
Tooth	Mean	*SD*	*n*	Mean	*SD*	*n*	Mean	*SD*	*n*	Mean	*SD*	*n*	Mean	*SD*	*n*	Mean	*SD*	*n*	Significant differences[a]
I1	53.3	4.0	13	54.0	4.7	8	52.2	2.5	5	59.3	2.9	3	50.3	1.5	4	52.3	1.8	6	L**
I2	39.2	1.7	14	39.7	2.1	8	38.7	0.8	6	40.6	2.3	4	38.8	0.5	4	38.7	1.5	6	
I3	40.1	2.1	14	40.5	2.3	8	39.7	1.8	6	42.5	1.0	4	38.8	0.5	4	39.5	2.0	6	L*
I4	42.3	2.3	13	42.6	2.3	8	41.8	2.4	5	43.3	1.2	3	39.3	1.0	4	43.8	0.5	6	L***
I5	44.5	2.8	13	45.1	2.4	8	43.4	3.3	5	46.7	1.2	3	40.8	1.5	4	45.8	0.5	6	L***
C	41.8	1.8	14	42.5	1.9	8	40.8	1.3	6	42.0	0.0	4	39.8	1.0	4	43.0	1.8	6	L**
dP1	37.8	1.5	14	37.7	1.7	8	37.8	1.5	6	39.4	1.0	4	37.3	0.5	4	37.0	1.5	6	
dP2	34.5	1.1	14	34.1	1.1	8	35.0	1.1	6	34.8	1.3	4	35.0	0.6	4	34.0	1.2	6	
dP3	32.0	1.4	11	31.9	1.7	7	32.3	1.0	4	29.5	N.A.	1	33.0	0.6	4	31.8	1.4	6	
P3	111.2	7.6	12	108.8	7.3	8	116.3	6.2	4	109.5	0.0	2	115.5	6.9	4	109.0	8.8	6	
M1	35.8	2.6	14	36.0	2.8	8	35.5	2.5	6	32.5	0.8	4	38.5	0.0	4	36.2	1.6	6	L***
M2	49.0	3.9	13	48.8	4.0	8	49.5	4.1	5	54.5	0.0	3	50.3	1.5	4	45.5	0.6	6	L***
M3	83.5	3.5	12	83.6	3.9	8	83.3	2.9	4	88.5	4.2	2	84.8	1.5	4	81.0	1.6	6	L*
M4	126.5	3.9	12	124.9	3.7	8	129.8	1.5	4	127.5	4.2	2	129.0	3.0	4	124.5	3.8	6	
i1	33.5	1.2	14	33.6	1.6	8	33.3	0.8	6	34.0	1.0	4	33.0	0.6	4	33.5	1.7	6	
i2	34.2	1.0	14	34.4	1.1	8	34.0	0.8	6	34.8	1.0	4	33.5	0.0	4	34.3	1.2	6	
i3	34.4	1.1	14	34.6	1.4	8	34.2	0.8	6	34.8	1.0	4	33.5	0.0	4	34.8	1.4	6	
i4	35.1	1.4	14	35.5	1.7	8	34.5	0.6	6	34.8	1.0	4	34.3	0.5	4	35.8	1.8	6	
C	40.1	1.5	14	40.6	1.9	8	39.5	0.6	6	41.0	1.2	4	38.8	0.5	4	40.5	1.7	6	
dp1	38.1	1.1	14	38.1	1.1	8	38.3	1.2	6	38.8	0.9	4	37.5	1.4	4	38.2	0.8	6	
dp2	36.4	1.6	14	36.7	1.6	8	36.0	1.7	6	37.6	0.8	4	34.5	1.2	4	36.8	1.2	6	L***
dp3	32.4	1.0	13	32.3	1.2	8	32.7	0.8	5	31.8	0.6	3	33.3	0.5	4	32.2	1.2	6	
p3	108.8	5.9	12	106.1	4.9	8	114.0	3.9	4	111.0	2.1	2	109.5	4.2	4	107.5	7.8	6	(L × S)*
m1	33.1	1.5	14	33.1	1.8	8	33.2	1.2	6	32.3	1.0	4	34.5	0.0	4	32.8	1.8	6	
m2	39.9	3.1	14	40.4	3.3	8	39.2	2.9	6	41.9	2.8	4	41.3	1.0	4	37.7	3.1	6	L*
m3	53.4	2.1	13	54.1	1.4	8	52.3	2.8	5	54.5	0.0	3	51.0	1.7	4	54.5	1.6	6	L**
m4	82.8	3.3	12	83.6	3.6	8	81.0	1.7	4	85.5	0.0	2	84.0	3.9	4	81.0	2.5	6	

[a] L indicates a significant difference between litters. (L × S) indicates a significant interaction effect of litter and sex. * $0.05 > P > 0.01$; ** $0.01 > P > 0.001$; *** $0.001 > P$.