Contributions

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PREMOLAR DEVELOPMENT AND ERUPTION IN THE EARLY EOCENE ADAPOIDS *CANTIUS RALSTONI* AND *CANTIUS ABDITUS* (MAMMALIA, PRIMATES)

BY

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Abstract — New specimens of early Eocene *Cantius ralstoni* and *Cantius abditus* are described that show the sequence of lower premolar development and eruption to have been P2-P4-P3 in early adapoids. This is the sequence documented for living Tupaioidea, some extant Lemuroidea, and living *Tarsius* representing Tarsioidea. It is also the developmental sequence documented for Eocene *Notharctus* and *Darwinius*, and for Miocene *Sivaladapis* within Adapoidea. Broad distribution of a 2-4-3 sequence of premolar development in tree shrews and primitive groups of living primates, and presence of this sequence in early Eocene primates indicates that this is the primitive sequence of development for Primates as an order. *Adapis* and *Leptadapis* have a premolar eruption sequence, 4-(2-3), that differs from the sequence in *Cantius*, *Notharctus*, and other Adapoidea. Eruption of P2 before both P3 and P4 in early Eocene *Cantius* supports interpretation of the small anteriormost upper and lower premolars in *Darwinius masillae* as permanent P^2 and P_2 rather than deciduous teeth.

INTRODUCTION

Dental development, the sequence of tooth eruption, and the timing of tooth eruption are closely correlated with life history in primates and, to a lesser degree, ungulates (Smith, 1989, 2000). For example, fast-growing, short-lived species have permanent incisor, canine, and premolar teeth that develop and replace deciduous precursors late in sequence, after their molars have erupted. In contrast, slow-growing, long-lived species have permanent incisor, canine, and premolar teeth that appear early in sequence. Stated another way, molar teeth form and erupt both relatively and absolutely later in slower-growing, longer-lived species. This tendency is known as 'Schultz's rule' (Schultz, 1935, 1956; Smith, 2000). For smaller groupings of primates, Schultz's rule has explanatory value within Platyrrhini (Henderson, 2007), although some living lemurs show special adaptations of growth and development to the highly seasonal environment of Madagascar (Eaglen, 1985; Godfrey et al., 2005).

Tooth eruption remains poorly documented in fossil primates. Information that is available is generally consistent with Schultz's rule, based on inferred life history. Following Smith (2000: Table 15.4), the presumably faster-growing subfossil lemurs (*Archaeolemur*; Lamberton, 1938) and adapoids (*Notharctus* and *Adapis*; Stehlin, 1912; Gregory, 1920) erupted all of their molars before any deciduous premolars were replaced, while slower-growing parapithecoids (*Apidium*; Kay and Simons, 1983) and hominoids (*Australopithecus*; Smith, 1994) replaced some or all premolars before eruption of M^3/M_3. It is important to distinguish tooth eruption from dental development, but these are themselves correlated, and development of individual teeth relative to each other inevitably influences interpretation of the sequence of tooth eruption in fossils.

This study was undertaken to clarify interpretation of the status of second premolars in the cercamoniine or cercamoniid adapoid *Darwinius masillae* (Franzen et al., 2009). The teeth

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Table 1 — Premolar eruption sequence in living tree shrews and primates that retain three premolars. Eruption sequences P^4-P^3-P^2 in the upper dentition and P_4-P_3-P_2 the lower dentition are represented as 4-3-2, while P^2-P^4-P^3 in the upper dentition and P_2-P_4-P_3 the lower dentition are represented as 2-4-3. Teeth that erupt at the same time or teeth for which the sequence has not been reported are enclosed in parentheses. Presence of the sequence 2-4-3 in taxonomically diverse *Tupaia*, *Eulemur*, *Varecia*, and *Tarsius* suggests that it is the primitive sequence of development and eruption in primates (see Table 3).

Taxon	Upper dentition	Lower dentition	Reference
Tupaioidea			
Tupaia glis	4-3-2	2-4-3	Shigehara (1980)
Lemuroidea			
Eulemur mongoz	2-4-3	2-4-3	Tattersall and Schwartz (1974); Eaglen (1985)
Eulemur fulvus	2-4-3	2-4-3	Tattersall and Schwartz (1974)
Eulemur macaco	2-4-3	2-4-3	Tattersall and Schwartz (1974); Eaglen (1985)
Varecia variegata	2-4-3	2-4-3	Tattersall and Schwartz (1974); Eaglen (1985)
Lemur catta	4-3-2	4-3-2	Tattersall and Schwartz (1974); Eaglen (1985)
Hapalemur griseus	4-3-2	4-3-2	Tattersall and Schwartz (1974)
Lepilemur mustelinus	4-3-2	4-3-2	Tattersall and Schwartz (1974)
Tarsioidea			
Tarsius bancanus	2-4-3	2-4-3	Luckett and Maier (1982)
Ceboidea			
Callithrix jacchus	4-3-2	4-3-2	Johnston et al. (1970); Smith et al. (1994)
Saguinus fuscicollis	4-2-3	4-2-3	Glassman (1983); Smith et al. (1994)
Saguinus nigricollis	4-3-2	4-2-3	Chase and Cooper (1969); Smith et al. (1994)
Cebus capucinus		4-3-2	Henderson (2007)
Saimiri sciureus	4-3-2	4-3-2	Galliari and Colillas (1985); Smith et al. (1994)
Alouatta sp.	2-(4-3)	2-4-3	Henderson (2007)
Ateles sp.	2-4-3	2-4-3	Henderson (2007)
Aotus trivirgatus	4-3-2	4-(3-2)	Hall et al. (1979); Smith et al. (1994)

are small and might reasonably be considered to be deciduous on the basis of their size, although density and the lack of a replacing crown are more in line with permanent teeth. For premolars, however, unless both generations of teeth are present in a single specimen, it takes a developmental sequence to be definitive. And although there is only one specimen of *Darwinius*, we can examine developmental sequences in close relatives. Here we review of the literature on adapoid tooth eruption and describe newly prepared specimens of *Cantius ralstoni* and *Cantius abditus* that preserve erupting teeth.

INSTITUTIONAL ABBREVIATIONS

AMNH — American Museum of Natural History, New York (U.S.A.)
LUVP — Lucknow University Vertebrate Paleontology, Lucknow (India)
MHNL — Muséum d'Histoire Naturelle de Lyon, Lyon (France)
MNHN — Muséum National d'Histoire Naturelle, Paris (France)
NMB — Naturhistorisches Museum Basel, Basel (Switzerland)
PMO — Geological Museum, University of Oslo, Oslo (Norway)
UM — University of Michigan Museum of Paleontology, Ann Arbor, Michigan (U.S.A.)
UMontp. — Université de Montpellier, Montpellier (France)

DENTAL ABBREVIATIONS

dC^1 — Maxillary deciduous canine
dP^2, dP^3, dP^4 — Maxillary deciduous premolars 2, 3, and 4
P^2, P^3, P^4 — Maxillary permanent premolars 2, 3, and 4
M^1, M^2, M^3 — Maxillary permanent molars 1, 2, and 3
dC_1 — Mandibular deciduous canine
dP_2, dP_3, dP_4 — Mandibular deciduous premolars 2, 3, and 4
P_2, P_3, P_4 — Mandibular permanent premolars 2, 3, and 4
M_1, M_2, M_3 — Mandibular permanent molars 1, 2 and 3

FIGURE 1 — Left dentary (reversed) of *Cantius ralstoni*, UM 72167, from University of Michigan locality SC-210 (Wasatchian zone Wa-2) in the Sand Coulee area of the Clarks Fork Basin, Wyoming. Specimen is shown in medial view. This specimen preserves a small alveolus for the dC_1, the erupting crown of P_2, crowns of dP_3 and dP_4, alveoli for fully erupted crowns of M_1 and M_2 (broken away), and the erupting crown of M_3 visible at the surface. Excavation of the medial dentary exposed partially-formed permanent C_1 , P_3 and P_4. See Figure 4 for comparison of stages of tooth eruption.

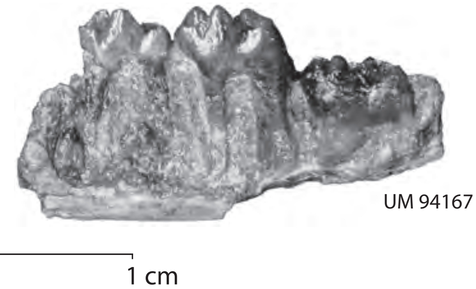

FIGURE 2 — Right dentary of *Cantius abditus*, UM 94167, from University of Michigan locality MP-170 (Wasatchian zone Wa-5) in the McCullough Peaks area of the northern Bighorn Basin, Wyoming. Specimen is shown in medial view. This specimen preserves the root of dP_3, the fully erupted crowns of dP_4 and M_1, and the erupting crown of M_2 visible at the surface. Excavation of the medial side of the dentary exposed the apices of partially-formed crowns of P_3 and P_4. See Figure 4 for comparison of stages of tooth eruption.

PREMOLAR ERUPTION IN LIVING PRIMATES

There are two principal patterns in the development and replacement of premolar teeth in primates (Table 1). The sequence of premolar development and eruption is consistently P2-P4-P3 (or simply 2-4-3) in the lemuroids *Eulemur mongoz*, *E. fulvus*, *E. macaco*, and *Varecia variegata*; but 4-3-2 in living *Lemur catta*, *Hapalemur griseus*, and *Lepilemur mustelinus* (Tattersall and Schwartz, 1974). The tarsioid *Tarsius bancanus* has premolars developing and erupting in the sequence 2-4-3 (Luckett and Maier, 1982).

Anthropoid primates that retain three premolars largely have the sequence 4-3-2 (*Callithrix jacchus*, Johnston et al., 1970; *Saimiri sciureus*, Galliari and Colillas, 1985; and *Aotus trivirgatus*, Hall et al., 1979), or the sequence 4-2-3 (*Saguinus fuscicollis*, Glassman, 1983). One species, *Saguinus nigricollis* has 4-3-2 in the upper dentition and 4-2-3 in the lower dentition (Chase and Cooper, 1969). More recent study by Henderson (2007), however, has identified the 2-4-3 sequence in both *Ateles* and *Alouatta*.

Finally, for comparison, the sequence of premolar eruption in living tree shrew *Tupaia glis* is 4-3-2 in the upper dentition, but 2-4-3 in the lower dentition (Shigehara, 1980). Each of these patterns is relatively common in primates.

We follow Tattersall and Schwartz (1974) and Groves and Eaglen (1988) in inferring that 2-4-3 is the primitive sequence of premolar development and eruption in living primates. The inference is tested here by comparison with premolar eruption in the oldest true primates for which the sequence is known.

PREMOLAR ERUPTION IN *CANTIUS RALSTONI* AND *CANTIUS ABDITUS*

Cantius ralstoni from the early Wasatchian land-mammal age, early Eocene, is one of the oldest true primates known. It is represented here by UM 72167, a left dentary (Fig. 1), from University of Michigan locality SC-210 in the Sand Coulee area of the Clarks Fork Basin, Wyoming. The age is Wasatchian zone Wa-2, or approximately 55.2 Ma (Gingerich, 2010). The specimen preserves a small alveolus for dC_1, the erupting crown of P_2, crowns of dP_3 and dP_4, alveoli for fully erupted crowns of M_1 and M_2, and the erupting crown of M_3 visible at the surface. Excavation of the medial side of the dentary exposed the apex of the partially-formed crown of C_1 and the partially-formed crowns of P_3 and P_4. Here the identification of P_2 as permanent is not in doubt given the confluence of all three premolars in size and developmental stage. Premolars are developing in the sequence P_2-P_4-P_3 (or 2-4-3), which is consistent with the inference from living primates that 2-4-3 is the primitive sequence of premolar development and eruption for the order.

The sequence of premolar development can also be determined in a second slightly younger species, *Cantius abditus*, represented by two specimens. UM 94167 (Fig. 2) is a right dentary of *C. abditus* from University of Michigan locality MP-170 in the McCullough Peaks area of the northern Bighorn Basin, Wyoming. UM 86931 (Fig. 3), is a right dentary of *C. abditus* from locality MP-16, also in the McCullough Peaks area of the northern Bighorn Basin, Wyoming. Both are from Wasatchian zone Wa-5 and have an age of about 53.8 Ma (Gingerich, 2010).

UM 94167 (Fig. 2) preserves the root of dP_3, the fully erupted crowns of dP_4 and M_1, and the erupting crown of M_2, which were all visible at the surface before preparation. Excavation of the medial side of the dentary exposed the apices of partially-formed crowns of P_3 and P_4. UM 86931 has a fully erupted crown of P_2, partially-erupted crowns of P_3 and P_4, crowns of M_1 and M_2, and alveoli for M_3, which were again visible at the surface before preparation. Excavation of the medial side of the dentary exposed the fully-formed crowns of P_3 and P_4. The first

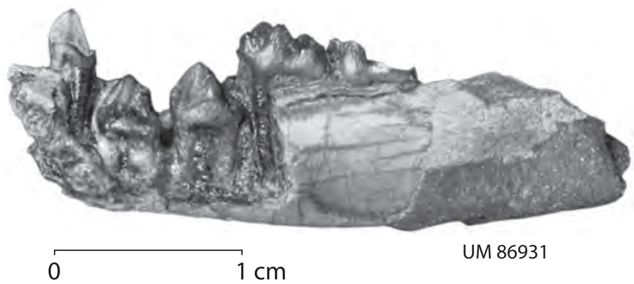

FIGURE 3 — Right dentary of *Cantius abditus*, UM 86931, from University of Michigan locality MP-16 (Wasatchian zone Wa-5) in the McCullough Peaks area of the northern Bighorn Basin, Wyoming. Specimen is shown in medial view. This specimen has a fully erupted crown of P_2, partially-erupted crowns of P_3 and P_4, crowns of M_1 and M_2, and alveoli for M_3 visible at the surface. Excavation of the medial side of the dentary exposed the fully-formed crowns of P_3 and P_4. See Figure 4 for comparison of stages of tooth eruption.

of the specimens is not informative regarding the sequence of premolar development and eruption, but the second specimen, UM 86931 (Fig. 3), shows that P_2 erupted first. The crown of P_4 is positioned a little higher in the dentary than that of P_3. Thus it is reasonable to infer that the sequence of premolar development and eruption in *Cantius abditus* was P_2-P_4-P_3 (or 2-4-3), which is consistent with the sequence in *Cantius ralstoni* and consistent with the sequence inferred to be primitive for living primates.

All three specimens are compared in Figure 4, which shows UM 72167 (*Cantius ralstoni*) to be intermediate in stage of development compared to UM 94167 and 86931 (the two specimens of *Cantius abditus*). P_2 is erupting or erupted in UM 72167 and 86931, and P_4 has a crown more developed than P_3 or higher in the dentary in both specimens. The two species are consistent in having a 2-4-3 sequence of premolar development and eruption.

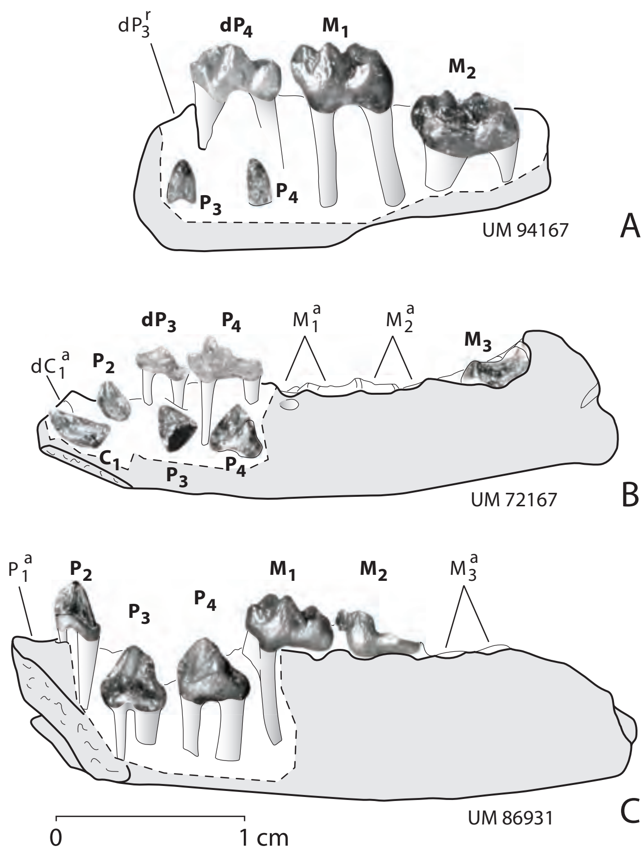

FIGURE 4 — Composite drawing showing the dentaries of *Cantius ralstoni* and *C. abditus* arranged in order of dental maturation. A, UM 94167, right dentary of *Cantius abditus* illustrated in Figure 2. B, UM 72167, left dentary of *Cantius ralstoni* (reversed) illustrated in Figure 1. C, UM 86931, right dentary of *Cantius abditus* shown in Figure 3. All specimens are shown in medial view, with the medial surface of the dentary cut away to show developing crowns and roots. Together these document a 2-4-3 sequence of premolar eruption in the lower dentition of *Cantius*.

PREMOLAR ERUPTION IN *ADAPIS PARISIENSIS* AND *LEPTADAPIS MAGNUS*

Stehlin (1912) was the first to consider tooth eruption in a fossil primate, for the two middle and late Eocene species *Adapis parisiensis* and *Adapis* (now *Leptadapis*) *magnus*. Stehlin's treatment is complicated by use of an unconventional numbering system: he numbered deciduous and permanent premolars 1 to 4 from back to front instead of the usual system of numbering premolars 1 to 4 from front to back. Here we have translated Stehlin's numbering into the conventional system. *Adapis parisiensis* has four premolars, and following Stehlin (1912: 1185), P_1 erupted first, with M_1; then somewhat later P_3 and P_4 erupted, seemingly together according to Stehlin; and finally P_2 erupted. Thus, according to Stehlin, the sequence for premolars P_2, P_3, and P_4 was (P_3-P_4)-P_2, or (3-4)-2. Stehlin's sequence is based on eruption of lower premolars, but he implies that this represents the sequence for upper premolars as well. Stehlin (1912: 1246) further stated that tooth development in *Leptadapis magnus* follows the pattern for *Adapis parisiensis*.

Our observations, based on comparison of a larger number of specimens (Table 2), indicate a different sequence of tooth eruption from that reported by Stehlin. The premolar eruption sequence in *Adapis parisiensis* and in *Leptadapis magnus* is 4-(3-2) — or the equivalent 4-(2-3). This differs from Stehlin's interpretation in that, for both genera and species: (1) P_4 is consistently the first premolar to erupt; and (2) P_2 is not necessarily the last tooth to erupt as Stehlin claimed. As before, this is a distinctly different sequence from the 2-4-3 sequence of *Cantius ralstoni* and in *C. abditus*. The *Adapis*-*Leptadapis* sequence is unusual for adapoids, although some later lemuroids converge to it. We need more examples of early primates that retained all four premolars to fully understand the evolution of premolar sequences.

Table 2 — Specimens clarifying premolar tooth eruption in *Adapis parisiensis* and *Leptadapis magnus*. Tooth positions are scored based on the presence of an alveolus only, a tooth in a crypt, a tooth erupting, or a tooth crown present. Premolar eruption sequence is 4-(3-2) or the equivalent 4-(2-3) in both species.

Specimen	P2	P3	P4	Eruption sequence
***Adapis parisiensis* upper dentition**				
--	--	--	--	--
***Adapis parisiensis* lower dentition**				
NMB Basel QD100	--	--	erupt	--
NMB Basel QW1599	crypt	crypt	--	--
MHNL Lyon 8079	crypt	crypt	erupt	P3 ahead of P2
MHNL Lyon PQ 655	--	--	erupt	--
MNHN Paris 10966	crypt	crypt	erupt	P4-P3-P2 sequence
MNHN Paris 10964	crypt	crypt	erupt	P4-P2-P3 sequence
MNHN Paris 10936	crypt	crypt	erupt	--
UMontp. unnumbered	--	--	erupt	--
NMB Basel QJ11	erupt	erupt	alveolus	P2-P3 at same stage
NMB Basel QD60	alveolus	erupt	alveolus	P3 after P2
NMB Basel QD72	tooth	tooth	tooth	Fig. by Stehlin: fig 265; P2 last
MNHN Paris 11111	erupt	erupt	alveolus	P2 before P3
UMontp. unnumbered	erupt	erupt	tooth	P2 before P3
***Leptadapis magnus* upper dentition**				
NMB Basel QV368/401	--	--	crypt	--
NMB Basel QD3 Max.	crypt	erupt	erupt	P4-P3-P2
***Leptadapis magnus* lower dentition**				
NMB Basel QD28 Dent.	crypt	crypt	crypt	P4-P2-P3; crypt for P3 lowest

PREMOLAR ERUPTION IN *NOTHARCTUS TENEBROSUS* AND OTHER FOSSIL PRIMATES

Fossil primates with three or more premolars and known premolar eruption sequences are listed in Table 3, which includes results reported here, and sequences for a number of additional Eocene and Miocene adapoids, several Recent subfossil lemuroids, and finally two Oligocene parapithecoids.

Gregory (1920: 152) wrote "The evidence is incomplete in the case of *Notharctus*, especially with regard to the incisors and canines, but so far as it goes it indicates that the order of [tooth] replacement was not dissimilar to that of *Adapis*." He based his inference about premolar eruption in middle Eocene *Notharctus tenebrosus* ('*N. tyrannus*') on a single specimen, AMNH 13029, which has unerupted P_2, P_3, and P_4. Gregory observed that P_2 lies nearer to the surface than P_3 or P_4, indicating that it would have erupted before them, which is a clear difference from *Adapis*. Further, his Plate XLII, Fig. 9, appears to show P_4 positioned higher in the dentary than P_3. Thus AMNH 13029 resembles UM 86931 described here, and it is reasonable to interpret the lower premolar eruption sequence in *Notharctus* to be 2-4-3, as it is in *Cantius*. The sequence of eruption of upper premolars is not known in *Notharctus*.

Franzen et al. (2009) described the upper and lower premolar eruption sequence as 2-4-3 in PMO 214.214, the type specimen of middle Eocene *Darwinius masillae*. There is a very small maxillary tooth interpreted as P^2 on plate B of the specimen, and a small mandibular tooth interpreted as P_2 present on both plates A and B. All are fully erupted. The mandibular tooth has a more densely mineralized crown than deciduous teeth in the same specimen, casting a denser shadow on radiographs. Roots are long on these teeth, and they are clearly advanced in development over the remaining permanent premolars. The crown of P_4 is less than half formed, but nevertheless noticeably advanced over the crown development of P_3.

Sivaladapis nagrii is a late-surviving Miocene adapoid nearing the age of extinction of the whole superfamily. One specimen, LUVP 14505, was prepared by cutting away the side of the dentary to expose crowns of developing teeth beneath the deciduous premolars (Gingerich and Sahni, 1984). The cut revealed P_2 to have a large complete crown with some root formation; P_4 to have a complete crown with no roots, lying in a crypt deeper in the dentary; and P_3 to be in an initial stage of crown formation — so here again the sequence of development and eruption of lower premolars was 2-4-3.

Lamberton (1938) made a thorough study of juvenile specimens of large subfossil lemurs from Madagascar. He showed that *Megaladapis edwardsi*, *Archaeolemur majori*, and *Hadropithecus stenognathus* all had premolar eruption sequences of 4-3-2, as seen in some *Adapis parisiensis* and some *Leptadapis magnus* among Eocene primates, and in *Lemur catta*, *Hapalemur griseus*, and *Lepilemur mustelinus* among living lemurs.

The premolar eruption sequence is known for two Oligocene parapithecoids: *Apidium phiomense* and *Simonsius grangeri*

Table 3 — Premolar eruption sequence in fossil primates that retain three premolars, with sequence abbreviations as in Table 1. Teeth that erupt at the same time or teeth for which the sequence is variable are enclosed in parentheses. Eruption of premolars in the sequence 2-4-3 in *Cantius* and *Notharctus*, the oldest primates for which sequences are available, suggests that this as the primitive development and eruption sequence in primates (see Table 1).

Taxon	Upper dentition	Lower dentition	Reference
Adapoidea			
Cantius ralstoni	--	2-4-3	This study
Cantius abditus	--	2-4-3	This study
Notharctus tenebrosus	--	2-4-3	Gregory (1920); this study
Darwinius masillae	2-4-3	2-4-3	Franzen et al. (2009)
Sivaladapis nagrii	--	2-4-3	Gingerich and Sahni (1984)
Adapis parisiensis	--	4-(3-2)	Stehlin (1912); see Table 2 above
Leptadapis magnus	4-3-2	4-(2-3)	Stehlin (1912); see Table 2 above
Lemuroidea			
Megaladapis edwardsi	4-3-2	--	Lamberton (1938)
Archaeolemur majori	4-3-2	4-3-2	Lamberton (1938)
Hadropithecus stenognathus	4-3-2	4-3-2	Lamberton (1938)
Parapithecoidea			
Apidium phiomense	--	2-4-3	Conroy et al. (1975), Kay and Simons (1983)
Simonsius grangeri	--	2-(4-3)	Kay and Simons (1983)

(Conroy et al., 1975; Kay and Simons, 1983). *Apidium* shares the sequence 2-4-3 found in *Cantius*, *Notharctus*, *Darwinius*, and *Sivaladapis*. *Simonsius* also has P_2 erupting first, as in *Apidium*, but the development and eruption of P_3 and P_4 are tied in *Simonsius* (which may reflect the smaller number of specimens known for this taxon).

DISCUSSION

This study was undertaken to clarify interpretation of the status of premolars P^2 and P_2 in the cercamoniine or cercamoniid adapoid *Darwinius masillae* (Franzen et al., 2009). The teeth at these positions are small and might reasonably be considered to be deciduous on the basis of size alone. In *Darwinius*, the mandibular tooth, P_2, has a more densely mineralized crown like that of developing permanent teeth, casting a denser shadow on radiographs; further, there is no sign of a replacing tooth, and on this basis of these observations it was considered to be a permanent tooth (Franzen et al., 2009).

If P^2 or P_2 could be shown to erupt late in the premolar series in adapoids, then an argument could be made that small upper and lower teeth at these positions in *Darwinius* and related primates might be retained deciduous teeth. However, our finding that P_2 erupts before P_3 and P_4 in the early and primitive adapoid *Cantius*, combined with evidence that the same is true in *Notharctus* and *Sivaladapis*, reinforces interpretation of small upper and lower teeth at the P^2 or P_2 positions in *Darwinius* as reduced teeth of the permanent dental series. Interpretation of P^2 and P_2 as permanent premolars in *Darwinius* makes the observed eruption sequence 2-4-3, which is the sequence expected in an early primate.

Sequences of dental development and eruption can help in identifying homologous teeth in closely related taxa. However, dental development is also related to life history (Schultz, 1935, 1956; Smith, 1989, 2000). We do not have a good understanding of the evolution of dental development through primate history, which will require investigation of more juveniles in the primate fossil record. Differences in life history may explain differences in eruption pattern, like those distinguishing *Cantius* and *Notharctus* on one hand from *Adapis* and *Leptadapis* on the other. A better understanding of the evolution of dental development will also clarify how consistently developmental sequences in primates reflect relatedness.

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