PRIMATES, 22(1): 103–118, January 1981

Sequences of Dental Ontogeny and Callitrichid Taxonomy

KENNETH E. BYRD
University of Washington

ABSTRACT. Sequences of dental development and eruption radiographically determined for 160 immature callitrichids were combined with nonontogenetic criteria in an investigation of callitrichid affinities. Marmosets (*Callithrix* and *Cebuella*) are distinct from tamarins (*Leontopithecus* and *Saguinus*) in both sequences of dental ontogeny and nonontogenetic characters. *Callimico* presents a tamarin-like pattern in its dental ontogeny and overall appearance. A new callitrichid classification which separates marmosets and tamarins into different subfamilies (Callitrichinae, Leontopithecinae and Callimiconinae) is proposed. Dental ontogenetic data suggest that callitrichids are derived platyrrhine taxa.

INTRODUCTION

Clawed members of the Anthropoidea (marmosets and tamarins) have been of interest to naturalists and biologists since the 1500's (HERSHKOVITZ, 1977). Current classifications usually define one (NAPIER & NAPIER, 1967; NAPIER, 1976) or two (HERSHKOVITZ, 1977) callitrichid families. These classifications are based largely on nonontogenetic criteria such as osteology, dental morphology, pelage, etc.

GOULD (1977) has provided persuasive arguments supporting the incorporation of ontogenetic data into taxonomic schema. Recently, SCHWARTZ (1974, 1975) has employed sequences of dental development and eruption in addressing problems of prosimian systematics.

Concerning callitrichids, SCHULTZ (1935) used sequences of dental development and eruption for phylogenetic statements about primate affinities. His study, however, contained observations for only three individual callitrichids. SCHULTZ' study was nonradiographic in nature and dealt only with eruptive sequences. BENNEJEANT (1936) provided an eruptive sequence of M1–I1–I2–P2–P4–M2–C–P3 for "*Hapale*" (= *Callithrix*). His sample consisted of one immature animal. BENNEJEANT did use radiographs for his eruptive sequence determination, however.

STEŚLICKA (1947) determined unusual *Callithrix* eruptive sequences of M1–M2–I1–I2–P4–P2–P3–M3–C (maxillary) and M1–I1–M2–I2–P4–P2–P3–M3–C (mandibular). Her sequences were unusual because they contained third molars. An important radiographic study of ceboid dental development and eruption by SERRA (1952) contained eruptive sequences for *Callithrix*, *Saguinus* and *Leontopithecus*. SERRA made several important observations which will be discussed later.

Prior to eruptive data for *Saguinus nigricollis* provided by CHASE and COOPER (1969), sequences of callithrichid dental ontogeny were nonlongitudinal and based on dried skulls. CHASE and COOPER's study used live animals and concerned itself with sequences of initial gingival eruption. No radiographs were used in their research. The first study to provide both developmental and eruptive sequence data for a callitrichid was by JOHNSTON, DREIZEN and

Levy (1970). Their sample of 40 *Callithrix jacchus* was analyzed cross-sectionally by a series of radiographs.

Tappen and Severson (1971) presented some eruptive sequence information for *Saguinus nigricollis* based on direct observation of dried skulls. No radiographs were taken. Hershkovitz (1977) recorded stages of callitrichid dental eruption based on nonradiographic analysis of dried skulls. His criterion for eruption was apparently the appearance of a tooth in its alveolus.

Recently, Byrd (1978, 1979) has radiographically determined sequences of completed dental development and eruption for all extant platyrrhine genera. A sample of 1,483 immature ceboids contained 160 callitrichids; these 160 callitrichids provide the data for this study.

The purpose of this study is to incorporate dental ontogenetic data with other callitrichid characters and hopefully provide a new, more satisfactory classification of the Callitrichidae.

MATERIALS AND METHODS

Table 1 summarizes the callitrichid sample used in this study. All callitrichid genera were represented with a predominance of *Saguinus* spp. The dried skulls of the 160 callitrichids were radiographed with X-ray units available at museums[1] where the specimens were housed. Anode-skull distance and kilovolt (kv)/milliampere (ma) settings varied depending upon the radiograph facilities. Settings ranged between 25 and 58 kv and 3 to 10 ma. Exposure times were generally short, 2–30 sec. The infant, juvenile and subadult callitrichid skulls were positioned on Kodak X-Omat rapid processing film (5 × 7) with small clay supports. This technique eliminated any shifting of the specimen during X-raying. Crania and mandibulae were oriented on the film in a manner which provided optimum views of maxillary and mandibular dental development and eruption (see Figures). Both left and right sides of the specimen were radiographed.

Table 1. Callitrichids used in this study.

Taxa	Males	Females	Sex unknown	Total
Callithrix jacchus	5	11	3	19
Callithrix argentata	1	2	2	5
Callithrix humeralifer	3	1	0	4
Cebuella pygmaea	1	3	1	5
Callimico goeldii	0	1	0	1
Saguinus fuscicollis	9	13	10	32
Saguinus oedipus	13	22	2	37
Saguinus nigricollis	1	1	14	16
Saguinus midas	1	7	3	11
Saguinus graellsi	2	5	2	9
Saguinus mystax	0	0	6	6
Saguinus bicolor	2	1	1	4
Saguinus leucopus	1	2	0	3
Leontopithecus rosalia	3	4	1	8
Callithrix spp.	9	14	5	28
Saguinus spp.	29	51	38	118
All taxa	42	73	45	160

---

[1] American Museum of Natural History (AMNH), British Museum, (Natural History) (BMNH), National Museum of Natural History (NMNH) and Field Museum of Natural History (FMNH).

Development of exposed radiograph film was done by hand. Development times varied according to darkroom and water temperature. Usually, 5 min in developer and 5 min in fixer provided best results.

Radiographs were analyzed by means of a Zeiss dissecting scope (×6–40) and a light box. Developmental and eruptive sequences for each dental quadrant were initially recorded in the format used by SCHULTZ (1935) and SCHWARTZ (1974). This format is shown here in Tables 2 and 3.

Sequences of dental development were determined with the aid of a developmental series modified from GARN and LEWIS (1963) and applied to each tooth: (1) follicle stage; (2) beginning cuspal calcification (the degree of crown calcification relative to crown size: 1/4, 1/3, 1/2, 2/3, etc.); (3) crown completion and beginning of root formation (the degree of root formation relative to completed length); and (4) apical closure of root(s).

Sequences of eruption were determined by eruptive stages modified from KOVACS (1971) and SCHWARTZ (1974): (1) initially erupted (Tip of crown is just protruding above alveolar margin.); (2) noticeably erupted (Tip of crown is definitely above alveolar margin.); (3) 1/4, 1/3, 1/2, 2/3 erupted (proportion of crown relative to total crown height being above alveolar margin); (4) almost fully erupted (Crown is totally above alveolar margin but bone has not yet closed in below crown cervix.); and (5) fully erupted (Alveolar margin closed around base of crown.).

It should be noted here that sequences of dental development and eruption are not necessarily identical (GARN & LEWIS, 1957; SCHWARTZ, 1974). Since dental development and eruption are dynamic processes, the sequences presented here are sequences of completed development and eruption unless otherwise indicated.

Upon determination of developmental and eruptive sequences in the SCHULTZ/SCHWARTZ format, developmental and eruptive sequences for each dental quadrant were ranked. A tooth which demonstrated the greatest degree of development (or eruption) relative to other teeth in that quadrant was ranked "1." A tooth which displayed the lowest degree of development/eruption was given the lowest rank (e.g., "8" if 8 teeth present in quadrant). Teeth which demonstrated identical developmental or eruptive stages were given identical ranks.

Individual developmental and eruptive sequence rankings were compared and then abstracted to create the sequences displayed in Tables 2 and 3. Tables 2 and 3 use the following notations: parentheses enclosing two or more teeth denote sequential variability between those teeth; a dotted line indicates undeveloped or unerupted; a question mark indicates that the developmental/eruptive sequence of two or more teeth could not be ascertained. Dental notation used in this paper follows that presented by SWINDLER (1976).

Since no pronounced sex differences were detected, male and female sequences were pooled. Sequences of dental development and eruption presented here are for the permanent dentition only.

Figures 1–5 were drawn from the original radiographs with the aid of an illuminating box and dissecting scope for the initial tracings. A camera lucida was used for preparation of the final enlarged drawings.

RESULTS

Tables 2 and 3 present the suggested sequences of dental development and eruption. Cur-

Table 2. Sequences of dental development.

Callithrix jacchus									
	M1	I1	M2	I2	P4	P3	P2	C	
	M1	I1	M2	I2	(P3 P4)	P2	C		
Callithrix argentata									
	M1	I1	M2	I2	P4	P3	P2	C	
	M1	I1	M2	I2	P4	P3	P2	C	
Callithrix humeralifer									
	M1	I1	M2	I2	P4	(P3 P2)	C		
	M1	I1	(I2 M2)	P4	P3	P2	C		
Cebuella pygmaea									
	M1	I1	M2	P4	P3	P2	I2	C	
	M1	I1	M2	(I2 P4)	P3	P2	C		
Callimico goeldii									
	M1	I1	I2	M2	(P3 P4)	P2	C	M3	
	M1	I1	I2	M2	P4	P3	P2	C	M3
Saguinus fuscicollis									
	M1	I1	I2	(M2 P4)	P3	P2	C		
	M1	I1	I2	(M2 P4)	P3	P2	C		
Saguinus oedipus									
	M1	I1	I2	M2	(P3 P4)	P2	C		
	M1	I1	I2	M2	P4	(P3 P2)	C		
Saguinus nigricollis									
	M1	I1	I2	(M2 P4)	P3	P2	C		
	M1	I1	I2	M2	P4	P3	P2	C	
Saguinus midas									
	M1	I1	I2	(M2 P4)	P3	P2	C		
	M1	I1	I2	(M2 P4)	(P3 P2)	C			
Saguinus graellsi									
	M1	I1	I2	(M2 P4)	P3	P2	C		
	M1	I1	I2	(M2 P4)	P3	P2	C		
Saguinus mystax									
	M1	I1	I2	(M2 P4)	P3	P2	C		
	M1	I1	I2	M2	(P4 P3)	P2	C		
Saguinus bicolor									
	M1	I1	(I2 M2)	P4	P3	P2	C		
	M1	I1	I2	M2	P4	(P3 P2)	C		
Saguinus leucopus									
	M1	I1	I2	M2	?	?	?	?	
	M1	I1	I2	(M2 P4)	(P2 P3)	C			
Leontopithecus rosalia									
	M1	I1	(I2 M2)	(P3 P4)	P2	C			
	M1	I1	I2	M2	P4	(P3 P2)	C		

Table 3. Sequences of dental eruption.

Callithrix jacchus	
	M1 I1 M2 ? ? P2 P3 C
	M1 (I1 M2) I2 ? ? P2 C
Callithrix argentata	
	M1 ? ? ? P4 P3 P2 C
	M1 ? ? (I2 P4) P3 P2 C
Callithrix humeralifer	
	M1 ? ? I2 P4 (P3 P2) C
	M1 ? ? ? P2 P4 P3 C
Cebuella pygmaea	
	M1 I1 M2 (P4 P3) P2 I2 C
	M1 (I1 M2) I2 P4 P2 P3 C
Callimico goeldii	
	M1 I1 (M2 I2) ————————
	M1 I1 (M2 I2) ————————
Saguinus fuscicollis	
	M1 I1 I2 M2 P4 (P3 P2) C
	M1 I1 I2 M2 (P4 P2) P3 C
Saguinus oedipus	
	M1 I1 (I2 M2) P4 (P3 P2) C
	M1 I1 (I2 M2) (P4 P2) P3 C
Saguinus nigricollis	
	M1 I1 I2 M2 P4 ? ? ?
	M1 I1 I2 M2 (P4 P2) ? ?
Saguinus midas	
	M1 I1 I2 ? ? ? P2 C
	M1 I1 I2 M2 P4 P2 P3 C
Saguinus graellsi	
	M1 I1 I2 M2 P4 ? ? ?
	M1 I1 I2 M2 P4 P2 ? ?
Saguinus mystax	
	M1 I1 I2 M2 P4 P3 ? ?
	M1 I1 I2 M2 (P4 P2) ? ?
Saguinus bicolor	
	M1 I1 I2 M2 P4 P3 P2 C
	M1 I1 (I2 M2) P4 P2 P3 C
Saguinus leucopus	
	M1 ————————————
	M1 ————————————
Leontopithecus rosalia	
	M1 ? ? ? P4 (P2 P3) C
	M1 ? ? ? P4 P2 P3 C

sory examination reveals that the developmental and eruptive sequences are not completely similar.

Callithrix jacchus

Callithrix jacchus (Fig. 1) displays slightly different developmental and eruptive sequences. Some eruptive variability exists between I_1 and M_2 while developmental variability occurs for P_3 and P_4. The positions of P^2 and P^3 differ for development and eruption (Tables 2 & 3).

Johnston, Dreizen and Levy (1970) provided a *Callithrix jacchus* developmental sequence of M1–M2–I1–(P3 P4)–I2–(P2 C); this sequence is based upon the "minimum age" of root completion in living animals. They also gave a *Callithrix jacchus* eruptive sequence of M1–M2–I1–(I2 P4)–P3–(P2 C); this sequence is based upon initial gingival eruption of the respective teeth.

Bennejeant's (1936) *Callithrix jacchus* eruptive sequence of M1–I1–I2–P2–P4–M2–C–P3 was apparently based upon an animal which displayed active, unfinished eruption. The *Callithrix jacchus* eruptive sequence given by Hershkovitz (1977) and apparently based on initial tooth appearance, essentially agrees with Johnston, Dreizen and Levy (1970).

Callithrix argentata

The developmental and eruptive sequences of *Callithrix argentata* (Tables 2 & 3) show a basic similarity to those of *Callithrix jacchus*. Some eruptive sequence variability exists between I_2 and P_4. Interestingly, developmental and eruptive sequences of *Callithrix argentata* are almost identical; this may be due to small sample size, however. Hershkovitz (1977) gives a *Callithrix argentata* eruptive sequence which indicates that M1 erupts first and canines erupt last.

Callithrix humeralifer

The sequences of completed dental development and eruption for *Callithrix humeralifer* (Tables 2 & 3) show a fair amount of dissimilarity. Developmental and eruptive sequences of P_2, P_3 and P_4 are very dissimilar. Hershkovitz (1977) presents the only comparative eruptive data for *Callithrix humeralifer*; he notes that M1 and M2 are the first two teeth to appear in their alveoli.

The developmental and eruptive sequences for *Callithrix* presented here show an alternation between incisors and molars in terms of their respective dental ontogenies (Tables 2 & 3). This alternating pattern of incisor-molar ontogeny was recorded for marmoset eruptive patterns by Serra (1952). His *Callithrix* eruptive sequence (Table 4) placed P4 between M2 and I2, however. If one disregards her addition of M_3, Steślicka's (1947) mandibular erup-

Table 4. Callitrichid eruptive sequences determined by Serra (1952).

Callithrix (*N*=93)	M1	I1	M2	P4	I2	P3	P2	C
	M1	I1	M2	P4	I2	P3	P2	C
Saguinus (*N*=12)	M1	I1	I2	M2	P4	P2	P3	C
	M1	I1	I2	M2	P4	P2	P3	C
Leontopithecus (*N*=8)	M1	I1	I2	M2	P4	P2	P3	C
	M1	I1	I2	M2	P4	P2	P3	C

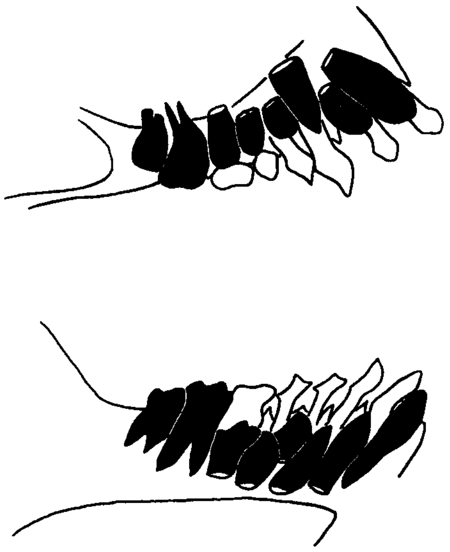

Fig. 1. *Callithrix jacchus jacchus* (BMNH 3.10.1.2). Approximately ×3.0. Compare development and eruption of M2/I2.

Fig. 2. *Cebuella pygmaea* (BMNH 27.3.6.18). Approximately ×4.7. Note the late eruption of I^2.

tive sequence of M_1–I_1–M_2–I_2–P_4–P_2–P_3–C for *Callithrix* also displayed an incisor-molar alternation.

Serra's (1952) large sample of 93 specimens lends credence to his *Callithrix* eruptive sequence, but his lack of sequence polymorphism makes one suspicious. The most parsimonious explanation for differences between *Callithrix* developmental/eruptive sequences presented here and by previous authors is (1) that eruptive sequences of M_2/I_1, I_2/P_4, and $P_2/P_3/P_4$ relative to each other are subject to variation; and/or (2) different investigators use different criteria for assessing dental ontogeny.

Cebuella pygmaea

The smallest living anthropoid, *Cebuella pygmaea* (Fig. 2), displays unusual sequences of dental development and eruption (Tables 2 & 3). The late development and eruption of I^2 is apparently unique among extant primates. Hershkovitz (1977) has also noted the late eruption of I^2 in *Cebuella*. The delayed development and eruption of I^2 has been correlated with its caniniform crown morphology and a postulated developmental/eruptive "canine field overlap" (Byrd, 1978).

The developmental sequence of *Cebuella* presented here is similar to the *Callithrix* eruptive sequence of Serra (Table 4); one exception is the late eruption of I^2. The position of P_2 and P_3 differ between developmental and eruptive sequences of *Cebuella*. The previously mentioned pattern of incisor-molar alternation for development and eruption is present in *Cebuella* (Tables 2 & 3). The overall pattern (excluding I^2) is very similar to *Callithrix*.

Callimico goeldii

The single *Callimico* specimen shown in Figure 3 could not supply enough information

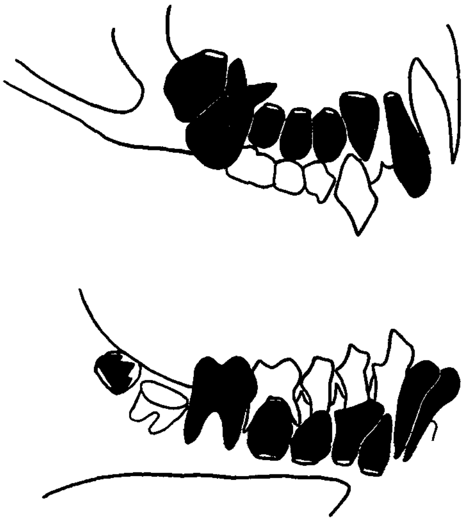

Fig. 3. *Callimico goeldii* (AMNH 98367). Approximately ×3.0. Note the initial calcification of M_3 and the missing M_2 (postmortem).

Fig. 4. *Saguinus mystax mystax* (BMNH 4.7.7.4). Approximately ×2.5. Note late development of canines.

for a complete eruptive sequence (Table 3). The sequence of completed development suggested in Table 2 is based upon two assumptions: (1) the developmental state for a single animal generally reflects the sequence of completed development for a number of *Callimico*; and (2) the bilaterally absent M_2 (postmortem) in the studied animal implies a lesser degree of M_2 root development compared to I_2. The difficulty in obtaining *any* immature *Callimico* made these assumptions necessary.

The partial eruptive sequence data shown in Table 3 agree with that provided by HERSHKOVITZ (1977). The developmental sequence of *Callimico* (Table 2) does not display the incisor-molar alternation shown by *Callithrix* and *Cebuella*. The developmental sequence of *Callimico* is similar to the eruptive sequences of *Saguinus* and *Leontopithecus* presented by SERRA (Table 4). M3 is apparently the last tooth to finish development in *Callimico*.

Saguinus spp.

The developmental sequences for the *Saguinus* species shown in Table 2 are essentially identical. *Saguinus mystax* (Fig. 4), *Saguinus leucopus*, *Saguinus graellsi*, *Saguinus midas*, *Saguinus nigricollis*, and *Saguinus fuscicollis* all show developmental polymorphism for M2 and P4. P_3 and P_2 display developmental sequence variability in *Saguinus midas*, *Saguinus oedipus*, *Saguinus bicolor*, and *Saguinus leucopus*. *Saguinus oedipus* also shows P^3 and P^4 developmental variability (Table 2).

Eruptive sequences (Table 3) differ from developmental sequences in the position of P_2. P_2 tends to finish development seventh and eruption sixth. The eruptive sequences presented here for *Saguinus* agree most with the eruptive sequence of *Saguinus nigricollis* provided by CHASE and COOPER (1969). SERRA's *Saguinus* eruptive sequence differs in the position of P^2 (Table 4). Two *Saguinus midas* (FMNH 46191 and AMNH 77560) displayed unfinished eruptive sequences where I^1 erupted before M^1. HERSHKOVITZ (1977) made similar observations for *Saguinus oedipus* and *Saguinus fuscicollis*.

Fig. 5. *Leontopithecus rosalia* (FMNH 57838). Approximately ×2.7.

The developmental and eruptive sequences of *Saguinus* do not show the incisor-molar alternation seen for *Callithrix* and *Cebuella*. In this regard, *Saguinus* is similar to *Callimico*.

Leontopithecus rosalia

Leontopithecus (Fig. 5) shows developmental and eruptive sequences similar to *Saguinus* (Tables 2 & 3). Developmental sequence polymorphism occurs for I^2/M^2, P^3/P^4 and P_3/P_2. The incomplete eruptive sequence shown here is in agreement with that presented by SERRA (Table 4). The developmental sequence of *Leontopithecus* (Table 2) does not show the incisor-molar alternation of *Callithrix* and *Cebuella*. The *Leontopithecus* eruptive sequence given by SERRA (Table 4) also shows the M1–I1–I2–M2 pattern.

DISCUSSION

In terms of dental ontogeny, there appears to be a basic difference between marmosets (*Callithrix* and *Cebuella*) and tamarins (*Saguinus* and *Leontopithecus*). The marmoset developmental pattern of M1–I1–M2–I2 is also seen in the cebid genera *Saimiri*, *Pithecia* and *Cacajao* (BYRD, 1979). Excluding the presence of M3, *Callimico* presents a tamarin-like pattern of dental ontogeny.

CRITERIA AND CLASSIFICATIONS

Recent callitrichid classifications have placed both marmosets and tamarins into one subfamily, the Callitrichinae (NAPIER, 1976), or one family, the Callitrichidae (HERSHKOVITZ, 1977). In HERSHKOVITZ' (1977) classification, *Callimico* was given its own family, the Callimiconidae. HERSHKOVITZ apparently felt that the presence of M3 placed *Callimico* between callitrichids and cebids. The diagnostic character for the Callitrichidae *must* be the presence of claws on all digits except the hallux (NAPIER & NAPIER, 1967; NAPIER, 1976). This condition in an anthropoid primate neatly separates callitrichids from all other extant primates. In ad-

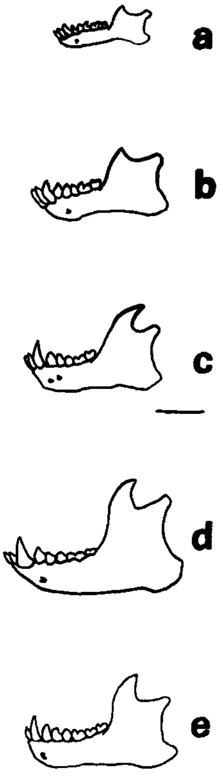

Fig. 6. Lateral aspect of callitrichid mandibulae drawn from HERSHKOVITZ (1977). Horizontal bar represents 10 mm. Contrast coronoid processes and canines of *Cebuella* (a) and *Callithrix* (b) with those of *Saguinus* (c), *Leontopithecus* (d) and *Callimico* (e).

dition, third molars have been recorded for *Callithrix* and *Saguinus* (HERSHKOVITZ, 1970a). HILL's (1959) monograph clearly defines the callitrichid status of *Callimico*.

Other criteria beside dental development and eruption suggest that marmosets and tamarins should be accorded separate family rank. Figure 6 shows mandibulae of *Cebuella*, *Callithrix*, *Saguinus*, *Leontopithecus*, and *Callimico*. The coronoid processes of *Cebuella* and *Callithrix* are much shorter and smaller than those displayed by *Saguinus*, *Leontopithecus*, and *Callimico*. In tamarins, the coronoid process is somewhat "hook-shaped" in appearance (Fig. 6). The "long-tusked" condition of tamarins (SWINDLER, 1976) is another diagnostic which refers to the extension of the mandibular canine beyond the apices of the lower incisors. In marmosets, the mandibular canine barely projects above the lower incisors (Fig. 6). *Callimico*'s large mandibular canine and coronoid process suggest tamarin affinities.

Another view of the difference between marmoset and tamarin mandibular canines is shown in Figure 7. An additional distinction between marmosets and tamarins is the shape of their respective mandibular dental arcades (Fig. 7). *Callithrix* and *Cebuella* display triangular, pointed arcades while tamarins show more rounded arcades.

Marmosets and tamarins are further distinguished by the thickness of enamel on the lingual surfaces of their mandibular incisors (ROSENBERGER, 1978). *Cebuella* and *Callithrix* apparently lack lingual enamel while *Saguinus* does not. This difference between marmosets and tamarins apparently reflects their respective feeding habits (KINZEY, ROSENBERGER & RAMIREZ, 1975; COIMBRA-FILHO & MITTERMEIER, 1976). Dental cingula further separate

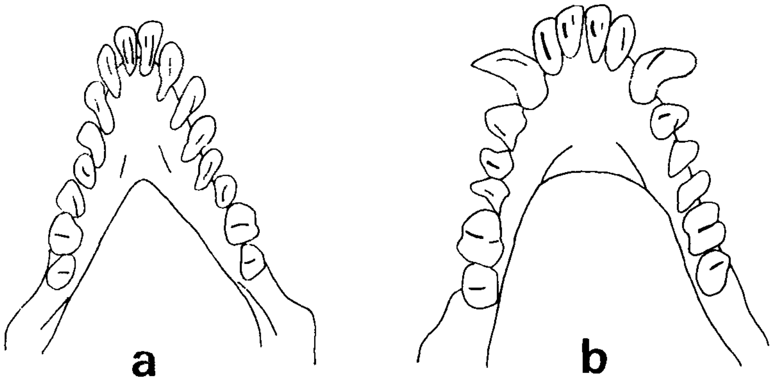

Fig. 7. Occlusal view of callitrichid dental arcades drawn from Hershkovitz (1977). Compare arcade shape of *Callithrix* and *Cebuella* (a) with that of *Saguinus*, *Leontopithecus* and *Callimico* (b). Horizontal bar represents 10 mm.

marmosets and tamarins. The maxillary molars of *Saguinus* usually display an enlarged distolingual cingulum while *Callithrix* maxillary molars do not (Kinzey, 1973).

In a morphometric study of platyrrhine femora, Ciochon and Corruccini (1975) presented a plot of ceboid femoral size distances based upon raw measurements. Although their plot reflected body size differences, tamarins (*Callimico*, *Leontopithecus* and *Saguinus*) were clearly separated from marmosets (*Callithrix* and *Cebuella*).

Karyotypes do not separate marmosets and tamarins (Egozcue, Perkins & Hagemenas, 1968; Hershkovitz, 1977). Immunological data, however, do discriminate between the two groups (Cronin & Sarich, 1975, 1978). Interestingly, Cronin and Sarich place *Callimico* closer to *Cebuella* and *Callithrix* while "*Leontideus*" (= *Leontopithecus*) is not aligned with either marmosets or tamarins.

Discrepancies between different criteria for callitrichid classification are to be expected. Different biological systems evolve at varying rates (Le Gros Clark, 1959; King & Wilson, 1975; Cherry, Case & Wilson, 1978). Given this situation, it is advantageous to compare many biological systems prior to proposing new classifications. Hopefully, the classification outlined in Table 5 reflects this philosophy and portrays a more accurate phylogenetic picture of the callitrichids.

The classification proposed here agrees with Pocock (1925), Wood-Jones (1929), Cabrera and Yepes (1940), Hill (1959) and the Napiers (Napier & Napier, 1967; Napier, 1976) in the inclusion of *Callimico* within the Callitrichidae (Table 5). The tamarin subfamily proposed here, Leontopithecinae, was initially defined as "Saguininae" (Gray, 1825) by Byrd (1979). Since Gray (1825) included noncallitrichid taxa in his original subfamily, the subfamily name "Saguininae" cannot be used to refer to the tamarins. Hill (1959) also saw fit to separate tamarins from marmosets as the callitrichid subfamily "Leontocebinae."

CALLITRICHID PHYLOGENY

No fossil callitrichids have yet been described. With this fact in mind, a survey of the literature reveals that there are two basic schools of thought concerning callitrichid evolution.

Table 5. Diagnostic characters of proposed callitrichid taxa.

Callitrichidae (THOMAS, 1903):	1. Modified claws on all digits except hallux which bears a flat nail. 2. Size small (total length: $\leq$ 650 mm). 3. Tail nonprehensile. 4. Diploid number = 44–48.
Callitrichinae (THOMAS, 1903): (genera: *Callithrix*, *Cebuella*)	1. Dental formula $\frac{2\cdot1\cdot3\cdot2}{2\cdot1\cdot3\cdot2}\times2=32$ 2. Mandibular dental arcade triangular and narrow. 3. Coronoid process of mandible small. 4. Mandibular incisors elongated. 5. Mandibular canines barely project above occlusal plane. 6. M2 third tooth to complete development and eruption. 7. Diploid number = 44–46.
Leontopithecinae (new subfamily): (genera: *Leontopithecus*, *Saguinus*)	1. Dental formula $\frac{2\cdot1\cdot3\cdot2}{2\cdot1\cdot3\cdot2}\times2=32$ 2. Mandibular dental arcade rounded and moderate in width. 3. Coronoid process of mandible large and hook-shaped. 4. Mandibular canines project well above occlusal plane. 5. M2 fourth tooth to complete development and eruption. 6. Diploid number = 46.
Callimiconinae (THOMAS, 1913): (genus: *Callimico*)	1. Dental formula $\frac{2\cdot1\cdot3\cdot3}{2\cdot1\cdot3\cdot3}\times2=36$ 2. Mandibular dental arcade rounded and moderate in width. 3. Coronoid process of mandible large and hook-shaped. 4. Mandibular canines project well above occlusal plane. 5. M2 fourth tooth to complete development (eruption also?). 6. Diploid number = 48.

The first, espoused by ELLIOT (1913), WOOD-JONES (1929), LE GROS CLARK (1959), and lately HERSHKOVITZ (1970b, 1977), states that callitrichids represent remnants of the basal ceboid stock. In other words, callitrichids are viewed as the most primitive living platyrrhines. The second school of callitrichid evolution deems marmosets and tamarins advanced, specialized members of the Ceboidea. This school derives callitrichids from a platyrrhine stock similar to *Aotus* or *Callicebus*. Members of this school include POCOCK (1917, 1920, 1925), GREGORY (1920), HILL (1959) and HOFFSTETTER (1969). Recently, ROSENBERGER (1977) and CRONIN and SARICH (1978) have stated that the callitrichid morphological pattern is a derived condition.

It is somewhat amusing that the same callitrichid characters are used by both the "primitive" and "derived" schools as evidence supporting their respective views. For example, both groups have used small size, variable/absent hypocones, and claws as criteria proving the primitive/derived nature of callitrichids. Which view is supported by sequences of callitrichid dental development and eruption?

If one assumes that the *zahnreihen* concept of dental development and eruption (EDMUND,

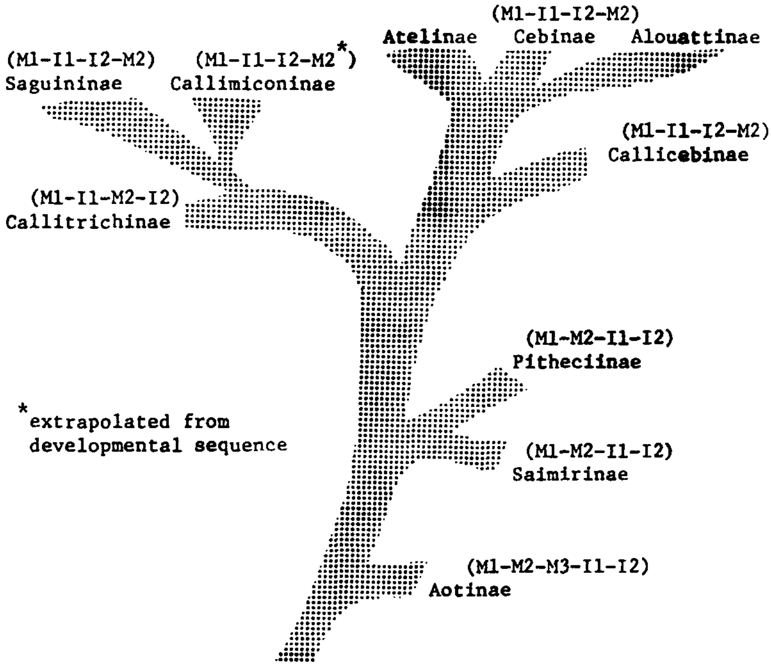

Fig. 8. Model of callitrichid phylogeny based upon incisor-molar eruptive sequences (Byrd, 1979). In this model, delayed molar eruption denotes more advanced/derived platyrrhine taxa. "Saguininae" = Leontopithecinae.

1960) is a correct one, those mammals with teeth that develop/erupt in waves [M1–M2–M3–I1–I2– (P2 P3 P4) –C] are, in terms of dental ontogeny, more primitive than those with teeth that do not. Schultz (1935) asserted that early molar eruption is a primitive trait among primates. Conversely, he stated that any sequence of dental ontogeny which shows a delay of molar development/eruption is an advanced (derived) condition.

Serra (1952) took Schultz' concept and applied it to platyrrhine dental eruption. Serra stated that *Aotus*, with its eruptive sequence of M1–M2–M3–I1–I2–P4–P3–P2–C, is the most primitive living ceboid in terms of dental eruption. In Serra's scheme, callitrichids are considered specialized (derived) when compared to the cebids *Cacajao*, *Pithecia*, *Saimiri*, and *Aotus*.

Byrd (1979) used the ideas of Schultz (1935) and Serra (1952) and presented a ceboid phylogeny based on eruptive sequences of incisors and molars. In this model (Fig. 8), callitrichids are derived from the cebid lineage sometime between differentiation of the callicebines and pithecines/saimirines. This event may have occurred sometime after the Colhuehuapian (Late Oligocene). The eruptive sequences of molars and incisors suggest that the Leontopithecinae and Callimiconinae are more advanced (delay of molar eruption) than the Callitrichinae. In this model, then, marmosets serve as the callitrichid stock from which tamarins evolved.

The phylogenetic relationships between callitrichid subfamilies proposed in Figure 8 are, of course, very tentative. Any phylogeny based upon neontological data eagerly awaits testing by fossil evidence. Sequences of dental development and eruption do suggest that callitrichids are derived platyrrhines, however.

CONCLUSIONS

The classification presented here incorporates nonontogenetic and dental ontogenetic data. It relies heavily on criteria which may be detected in callitrichid fossils yet to be described. I suggest that this division of the family Callitrichidae into three subfamilies accurately reflects the overall pattern of callitrichid diversity. Classifications based upon biological systems which are not preserved in fossils are of less value than those which are. Dental ontogenetic data can be used in primate paleontology as recently demonstrated by CONROY, SCHWARTZ and SIMONS (1975). Hopefully, the information presented here will prove useful in future studies of callitrichid evolution.

Sequences of dental development and eruption suggest that marmosets and tamarins are indeed derived platyrrhine taxa; marmosets are suggested to be more primitive than tamarins. How callitrichids attained their specialized appearance is still unresolved.

Acknowledgements. I would like to thank the following people for their assistance during my collection of data: Drs. SYDNEY ANDERSON, C. LAVETT SMITH, RICHARD G. VAN GELDER, Mrs. NORMA FEINBERG and Mr. PHILIP GOLDSTEIN of the American Museum of Natural History; Drs. LUCILE E. ST. HOYME, DOUGLAS H. UBELAKER, RICHARD W. THORINGTON, JR. and Mr. DWIGHT SCHMIDT of the National Museum of Natural History; Drs. PHILIP HERSHKOVITZ, ROBERT E. MARTIN, EDWARD J. OLSEN, WILLIAM D. TURNBULL and RAINIER ZANGERL of the Field Museum of Natural History; and Mrs. PRUDENCE H. NAPIER of the British Museum (Natural History).

In addition, I would like to thank Dr. WARREN G. KINZEY for providing access to the *Callimico* specimen, Dr. ALFRED L. ROSENBERGER for his comments on the subfamily "Saguininae," and Dr. DARIS R. SWINDLER for advice and suggestions. This research was supported in part by NIDR grant 1 F32 DE05198-01.

REFERENCES

BENNEJEANT, C., 1936. *Anomalies et Variations Dentaires chez les Primates.* Clermont-Ferrand, Paris.

BYRD, K. E., 1978. Radiographic analysis of dental development and eruption sequences in the pygmy marmoset, *Cebuella pygmaea* (SPIX, 1823). *Amer. J. Phys. Anthropol.*, 48: 384.

———, 1979. Sequences and asymmetries of dental development and eruption in the Ceboidea. Ph.D. Dissertation, Univ. of Washington, Univ. Microfilms, Ann Arbor.

CABRERA, A. & J. YEPES, 1940. *Mammiferos Sub-Americanos* (*Vida, Costumbres y Description*). Compañia Argentina de Editores, Buenos Aires.

CHASE, J. E. & R. W. COOPER, 1969. *Saguinus nigricollis*—physical growth and dental eruption in a small population of captive-born individuals. *Amer. J. Phys. Anthropol.*, 30: 111–116.

CHERRY, L. M., S. M. CASE & A. C. WILSON, 1978. Frog perspective on the morphological difference between humans and chimpanzees. *Science*, 200: 209–211.

CIOCHON, R. L. & R. S. CORRUCCINI, 1975. Morphometric analysis of platyrrhine femora with taxonomic implications and notes on two fossil forms. *J. Human Evol.*, 4: 193–217.

COIMBRA-FILHO, A. F. & R. A. MITTERMEIER, 1976. Exudate eating and tree-gouging in marmosets. *Nature*, 262: 630.

CONROY, G. C., J. H. SCHWARTZ & E. L. SIMONS, 1975. Dental eruption patterns in Parapithecidae (Primates, Anthropoidea). *Folia Primatol.*, 24: 275–281.

CRONIN, J. E. & V. M. SARICH, 1975. Molecular systematics of the New World monkeys. *J. Human Evol.*, 4: 357–375.

——— & ———, 1978. Marmoset evolution: the molecular evidence. *Prim. Med.*, 10: 12–19.

EDMUND, A. G., 1960. Tooth replacement phenomena in the lower vertebrates. *Contrib. Life Sci. Div. R. Ont. Mus.*, 52: 1–90.

EGOZCUE, J., E. M. PERKINS & F. HAGEMENAS, 1968. Chromosomal evolution in marmosets, tamarins and pinchés. *Folia Primatol.*, 9: 81–94.

Elliot, D. G., 1913. *A Review of the Primates. Vols. 1 & 2.* American Museum Natural History, New York.

Garn, S. M. & A. B. Lewis, 1957. Relationship between the sequence of calcification and the sequence of eruption of the mandibular molar and premolar teeth. *J. Dent. Res.*, 36: 992–995.

——— & ———, 1963. Phylogenetic and intra-specific variations in tooth sequence polymorphism. In: *Dental Anthropology*, D. R. Brothwell (ed.), Pergamon, New York, pp. 53–73.

Gould, S. J., 1977. *Ontogeny and Phylogeny.* Harvard Univ. Press, Cambridge.

Gray, J. E., 1825. An outline of an attempt at the disposition of Mammalia into tribes and families, with a list of the genera apparently appertaining to each tribe. *Ann. Philos.*, 10: 337–344.

Gregory, W. K., 1920. The origin and evolution of the human dentition. Part III. *J. Dent. Res.*, 2: 357–426.

Hershkovitz, P., 1970a. Dental and periodontal diseases and abnormalities in wild-caught marmosets (Primates—Callitricidae). *Amer. J. Phys. Anthropol.*, 32: 377–394.

———, 1970b. Notes on Tertiary platyrrhine monkeys and description of a new genus from the late Miocene of Colombia. *Folia Primatol.*, 12: 1–37.

———, 1977. *Living New World Monkeys. Vol. 1.* Univ. of Chicago Press, Chicago.

Hill, W. C. O., 1959. The anatomy of *Callimico goeldii* (Thomas). A primitive American primate. *Trans. Amer. Philos. Soc.*, 49: 1–116.

Hoffstetter, M. R., 1969. Un primate de L'Oligocene Inférieur Sud-Américain: *Branisella boliviana* gen. et sp. nov. *Comp. Ren. Séan. Acad. Sci.*, 269: 434–437.

Johnston, G. W., S. Dreizen & B. M. Levy, 1970. Dental development in the cotton ear marmoset (*Callithrix jacchus*). *Amer. J. Phys. Anthropol.*, 33: 41–48.

King, M. & A. C. Wilson, 1975. Evolution at two levels in humans and chimpanzees. *Science*, 188: 107–116.

Kinzey, W. G., 1973. Reduction of the cingulum in Ceboidea. In: *Symp. 4th Int. Congr. Primatol., Vol. 3*, W. Montagna & M. R. Zingeser (eds.), S. Karger, Basel, pp. 101–127.

———, A. L. Rosenberger & M. Ramirez, 1975. Vertical clinging and leaping in a neotropical anthropoid. *Nature*, 225: 327–328.

Kovacs, I., 1971. A systematic description of dental roots. In: *Dental Morphology and Evolution.* A. A. Dahlberg (ed.), Univ. of Chicago Press, Chicago, pp. 211–256.

Le Gros Clark, W. E., 1959. *Antecedents of Man.* Edinburgh Univ. Press, Edinburgh.

Napier, J. R. & P. H. Napier, 1967. *A Handbook of Living Primates.* Academic Press, London.

Napier, P. H., 1976. *Catalogue of Primates in the British Museum (Natural History). Part I: Families Callitrichidae and Cebidae.* British Museum (Natural History), London.

Pocock, R. I., 1917. The external characters of the Hapalidae. *Ann. Mag. Nat. Hist.*, 20: 247–258.

———, 1920. On the external characters of the South American monkeys. *Proc. Zool. Soc. London*, 1: 91–113.

———, 1925. Additional notes on the external characters of some platyrrhine monkeys. *Proc. Zool. Soc. London*, 1: 27–47.

Rosenberger, A. L., 1977. *Xenothrix* and ceboid phylogeny. *J. Human. Evol.*, 6: 461–481.

———, 1978. Loss of incisor enamel in marmosets. *J. Mammal.*, 59: 207–208.

Schultz, A. H., 1935. Eruption and decay of the permanent teeth in primates. *Amer. J. Phys. Anthropol.*, 19: 489–581.

Schwartz, J. H., 1974. *Dental Development and Eruption in the Prosimians and Its Bearing on Their Evolution.* Ph.D. Dissertation, Columbia Univ., Univ. Microfilms, Ann Arbor.

———, 1975. Re-evaluation of the morphocline of molar appearance in the primates. *Folia Primatol.*, 23: 290–307.

Serra, O. D., 1952. A seqüencia eruptiva dos dentes definitivos nos símios Platyrrhina e sua interpretação filogenética. *Anais Fac. Farm. Odont. Univ. São Paulo*, 10: 215–296.

Steślicka, W., 1947. Uzbienie naczelnych (The dentition of primates). *Ann. Univ. Mariae Curie-Sklodowska*, 1: 183–276. (in Polish with English summary)

Swindler, D. R., 1976. *Dentition of Living Primates.* Academic Press, London.

Tappen, N. C. & A. Severson, 1971. Sequence of eruption of permanent teeth and epiphyseal union in New World monkeys. *Folia Primatol.*, 15: 293–312.

Thomas, O., 1903. Notes on South American monkeys, bats, carnivores and rodents, with descriptions of new species. *Ann. Mag. Nat. Hist.*, 12: 455–464.

———, 1913. On some rare Amazonian mammals from the collection of the Para Museum. *Ann. Mag. Nat. Hist.*, 11: 130–136.
WOOD-JONES, F., 1929. *Man's Place Among the Mammals.* Arnold, London.

—Received *April 11, 1980*; Accepted *June 25, 1980*

Author's Name and Address: KENNETH E. BYRD, *Department of Biological Structure and Physiology and Biophysics, University of Washington School of Medicine, Seattle, Washington 98195, U.S.A.*