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RESEARCH ARTICLE

# Radiographic Evaluation of Neonatal Skeletal Development in *Callimico goeldii* Reveals Closer Similarity to *Callithrix jacchus* Than to *Saguinus oedipus*

MARIA INES HOFMANN[1]*, CARSTEN SCHRADIN[2], AND THOMAS GEISSMANN[3]
[1]*Institute of Anatomy, University of Zurich, Zurich, Switzerland*
[2]*School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa*
[3]*Anthropological Institute, University of Zurich, Zurich, Switzerland*

The phylogenetic affinities of the neotropical Goeldi's monkey (*Callimico goeldii*) have long been a matter of debate. Whereas most morphological evidence appears to place *Callimico* in a sister group position relative to the Callitrichidae, genetic studies place *C. goeldii* within the Callitrichidae and suggest that it is more closely related to marmosets than to tamarins. The present study presents the first radiographic analysis comparing the secondary limb bone ossification of newborn *C. goeldii* with representatives of the marmosets (*Callithrix jacchus*) and tamarins (*Saguinus oedipus*). The state of secondary ossification of the epiphysis and short bones is classified into three different ontogenetic stages. Our results reveal that in terms of the number of ossification centers, *C. goeldii* is significantly closer to *C. jacchus* than to *S. oedipus*. This is the first morphological study to support the findings of molecular studies, and the results suggest that *C. goeldii* is more closely related to marmosets than to tamarins. Am. J. Primatol. 69:420–433, 2007.

**Key words: ossification centers; radiography; Callitrichidae; *Callimico goeldii*; *Callithrix jacchus*; *Saguinus oedipus***

## INTRODUCTION

The New World monkeys (Platyrrhini) traditionally have been divided into two families: the Callitrichidae (including marmosets and tamarins) and the Cebidae. Callitrichids are distinguished from the Cebidae by their small size, the presence of claws rather than nails on all digits except the big toe, and the presence of two molar teeth instead of three in each tooth row [Fiedler, 1956; Fleagle, 1999; Hershkovitz, 1977; Hill, 1957; Martin, 1992]. Although they exhibit

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*Correspondence to: Maria Ines Hofmann, Division of Neuroanatomy and Behavior, Institute of Anatomy, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland.
E-mail: m.hofmann@anatom.unizh.ch

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features that are usually found in single-birth mammals (e.g., a single-chambered uterus and a single pair of teats), marmosets and tamarins typically give birth to twins [Fleagle, 1999; Hershkovitz, 1977; Martin, 1990]. These features have led to the suggestion that marmosets and tamarins are specialized primates that have undergone a secondary reduction in body size (dwarfing) during their evolution [Ford, 1980; Martin, 1992; Rosenberger & Coimbra-Filho, 1984].

Goeldi's monkey (*Callimico goeldii*, the only species of its genus) is also believed to have undergone phyletic dwarfing [Ford, 1980; Martin, 1992] like the callitrichids. Patterns of infant development and ontogenetic trajectories in *Callimico* are similar to those of callitrichids and differ from those of other New World monkeys [Garber & Leigh, 1997; Martin, 1992]. Furthermore, *C. goeldii* resembles Callitrichidae in that it has claws or tegulae on all digits except the hallux [Fleagle, 1999; Ford, 1986], has a relatively small body [Encarnación & Heymann, 1998; Lorenz & Heinemann, 1967], exhibits cooperative infant caregiving, and has a high reproductive output (females are capable of giving birth twice a year) [Garber & Leigh, 1997]. However, this species also shares traits with the Cebidae in that it has a third molar (albeit reduced in size and lacking a distinct hypocone) and produces single offspring [Ford, 1986; Martin, 1992]. Because *C. goeldii* resembles callitrichids in some aspects and cebids in others, it has been a source of curiosity and controversy since it was first discovered about 100 years ago [Ford, 1986; Porter & Garber, 2004]. *Callimico goeldii* has been variously placed in the family Cebidae or ''true monkeys'' [Simons, 1972] (see Tables 1.1 and 3.1 in Martin [1990], in the family Callithrichidae or ''marmoset/tamarin group'' [Groves, 2001; Hill, 1959; Rosenberger, 1981; Rylands et al., 2000], in its own subfamily (Callimiconinae) [Ford, 1986], and even in its own family (Callimiconidae) [Hershkovitz, 1977; Hill, 1957]. Its mosaic of morphological and ontogenetic features has traditionally led many scientists to regard *Callimico* as the most basal group of the callitrichids [Ford, 1980, 1986; Garber & Leigh, 1997; Kay, 1990; Purvis, 1995; Rosenberger, 1981, 1992; Snowdon, 1993].

However, results from an increasing number of molecular biological studies reveal a different phylogeny. DNA sequences consistently identify *Callimico goeldii* as the sister group of the marmosets (including the genera *Callibella*, *Cebuella*, *Callithrix*, and *Mico*), rather than as a sister group to all Callitrichidae. Instead, tamarins (*Saguinus*) and lion tamarins (*Leontopithecus*) are placed in more basal positions within the phylogeny of the Callitrichidae [Canavez et al., 1999a,b; Chaves et al., 1999; Horovitz et al., 1998; Pastorini et al., 1998; Schneider et al., 2001; Tagliaro et al., 1997; von Dornum & Ruvolo, 1999]. One reason for the apparent incongruence between morphological and molecular data may be that only relatively few morphological characters have been studied so far, and the inclusion of symplesiomorphic and/or convergent morphological characteristics may have cloaked the phylogenetic relationships. Much of the contradiction between the morphological and molecular data is based on the interpretation of dental and reproductive features, especially the lack of dental reduction and twinning in *Callimico*. This is usually interpreted as ancestral callitrichid (and platyrrhine) characteristics, and supports a basal position of *Callimico* among callitrichids. We believe that if the number of morphological features were increased, some characteristics would contradict a basal position of *Callimico* among callitrichids and more closely correspond to the molecular results. Our view appears to be supported by postcranial data obtained by Davis [2002, p. 503]. Although this author did not draw any phylogenetic conclusions, she suggested that increased transverse and sagittal diameters of the distal radial shaft may be ''marmoset morphotypes'' also shared by *Callimico*.

While various aspects of *Callimico* gross anatomy [Hershkovitz, 1977; Hill, 1959; Lorenz & Heinemann, 1967], ecology [Christen & Geissmann, 1994; Ferrari et al., 1999; Masataka, 1981a,b; Porter, 2000], behavior [Porter, 2001; Schradin & Anzenberger, 2001, 2003], and genetics (for references see above) have been documented, details about the skeletal development of *C. goeldii* are lacking. Morphological comparisons of newborns might reveal similarities that are not apparent in adults, because the skeletons of adults become more specialized during development. Thus, while the morphological features of adults do not support genetic data that place *C. goeldii* within the callitrichids between marmosets and tamarins, the pattern might be different if one were to look at morphological features earlier in ontogeny.

Although methodological problems and insufficient sampling have made it difficult to use ontogenetic data to generate phylogenetic hypotheses [Prochel et al., 2004; Sánchez-Villagra, 2002; Schulmeister & Wheeler, 2004], such data are a potentially useful tool for studying phylogeny [Prochel et al., 2004]. Caldwell [1996] found consistent and ordered distributions of mesopodial ossification patterns in mosasauroid reptiles. Within Amphibia, [Yeh, 2002] found that salamanders retain early jaw ossification (the primitive vertebrate condition). Delayed jaw ossification is a synapomorphy of Anura, with a reversal to the primitive vertebrate condition (early ossification) occurring in pipoid frogs [Yeh, 2002]. Postnatal skeletal development has also been identified as a potential source of discrete characters for phylogenetic analysis in mammals [Maisano, 2002]. Data on the relative sequence of ossification of 24 postcranial elements for eight therian mammals and three outgroups were used to create 276 event-pair characters for each species, and revealed that about 50% of these characters could potentially deliver diagnostic features for clades of two or more taxa [Sánchez-Villagra, 2002]. The development of metatarsals was used to elucidate taxonomic relationships among rodent species, and was considered a useful tool for gaining insights into the phylogeny of the Dipodidae family in the order Rodentia [Shahin, 2005].

This paper presents data on neonatal skeletal development in three callitrichid species, including *C. goeldii*, *Saguinus oedipus* (cotton-top tamarin), and *Callithrix jacchus* (common marmoset). Our aim is to test their compatibility with the two conflicting classifications. If the traditional morphological classification is correct, we would expect to find the highest similarity between *S. oedipus* and *C. jacchus*. On the other hand, if the molecular classification is correct, we would expect to find the highest similarity between *C. goeldii* and *C. jacchus*.

## MATERIALS AND METHODS

A total of eight *C. goeldii*, six *C. jacchus*, and seven *S. oedipus* cadavers were used for this study. All specimens were monkeys born between 1974 and 2000 at the Primate Station of the Anthropological Institute of the University of Zurich, and they were fixed in formalin or frozen until this study was conducted. Apart from three of the *C. goeldii* subjects, all animals used in this study died of natural causes on the first day after birth. Three *C. goeldii* specimens were stillborn but showed no differences in weight or appearance compared to healthy neonates of the same species in their colony. The actual causes of death were unknown. All *Callimico* specimens were single births, three of the six *Callithrix* were triplets, and all other specimens were twins. The numbers of neonates of male, female, and uncertain sex, respectively, were four, three, and one for *Callimico* *goeldii*; two, four, and zero for *Callithrix jacchus*; and three, four, and zero for *Saguinus oedipus*.

All specimens were x-rayed at the Radiological Institute of the University Hospital of the University of Zurich. Because of the small size and density of the animals, we used mammography film (Agfa Mamoray HDR, Germany; 18 × 24 cm), which was originally designed to x-ray human female breasts, to clearly visualize the ossification development. The monkeys were placed on radiographic cassettes in a supine position with their limbs in semiflexion (elbows and knees in 90° flexion). The fingers and toes were extended and taped down with 3 M Transpore. A radiograph was taken using a Philips Medical Systems mammograph (The Netherlands) on Agfa Mamoray HDR film (18 × 24 cm), using 20 mAs (*C. goeldii* and *S. oedipus*) or 16 mAs (*C. jacchus*), 23 kV, and a focal distance of 63 cm. The radiographs were scanned with an Epson Expression 1680 Pro scanner and stored as TIFF files without any editing. Qualitative assessments of the number and degree of development of the ossification centers of the appendicular skeleton were made on all specimens. A total of 66 ossification centers were evaluated in each radiograph. A list of all ossification centers is presented in Table I. The quantity of ossification centers was assessed for each individual, resulting in six values per animal: 1) the overall total, and the number of ossification centers present in the 2) forelimbs (including hands), 3) hands (including carpals and metacarpals), 4) carpals, 5) hindlimbs (including feet), and 6) tarsals.

Special attention was given to the hand/wrist skeleton because this anatomical area contains a large number of developing osseous centers and is commonly used as a general index of skeletal development [Galliari, 1988; Glaser, 1970; Phillips, 1976; Schultea et al., 1983; Tanner et al., 1972; Thurm et al., 1975; Watts, 1971, 1975]. The state of secondary ossification was classified into three stages of development, as shown in Fig. 1. Following Tanner et al. [1972], these stages are defined as follows: short bones: (A) the center is just visible as a single deposit of calcium, or as multiple deposits, without a continuous border; (B) the center is distinct in appearance and oval or round in shape with a smooth continuous border; and (C) adult appearance with visible articular surfaces; and long-bone epiphyses: (A) the center is just visible as a single deposit of calcium, or as multiple deposits, without a continuous border; (B) the maximum diameter of the ossification center is less than the half the width of the end of the diaphysis; and (C) the center's maximum diameter is half or more the width of the end of the diaphysis.

The data were analyzed using the statistical software GraphPad InStat version 3.0b. Because of the small sample sizes and non-normal distribution of the data, we used nonparametric statistics, and present the median values rather than the means. The Kruskal-Wallis test was used for multiple comparisons, followed by Dunn's post-hoc test. A significance criterion of $P \leq 0.05$ was used for all statistical tests.

## RESULTS

Figure 2 shows examples of forelimb and hindlimb radiographs for each of the three study species.

The distribution of three developmental stages among the total number of ossification centers is shown in Table II. The statistical comparison of stages A and B among the three callitrichid species revealed no significant differences (Kruskal-Wallis tests, $P > 0.05$). Stage C was very rare in our samples.

**TABLE I. List of the 66 Secondary Ossification Centers Evaluated in This Study**

| Forelimbs | | Hind limbs | |
|---|---|---|---|
| Humerus | Proximal | Femur | Proximal |
| | Distal | | Distal |
| Radius | Proximal | Tibia | Proximal |
| | Distal | | Distal |
| Ulna | Proximal | Fibula | Proximal |
| | Distal | | Distal |
| Carpal | Scaphoid | Tarsal | Calcaneus |
| | Lunate | | Talus |
| | Triquetral | | Navicular |
| | Pisiform | | Cuboid |
| | Trapezium | | Lateral Cuneiform |
| | Trapezoid | | Intermediate Cuneiform |
| | Os centrale | | Lateral Cuneiform |
| | Capitate | | |
| | Hamate | | |
| Metacarpals | I | Metatarsals | I |
| | II | | II |
| | III | | III |
| | IV | | IV |
| | V | | V |
| Phalanges | | Phalanges | |
| Proximal | I | Proximal | I |
| | II | | II |
| | III | | III |
| | IV | | IV |
| | V | | V |
| Middle | II | Middle | II |
| | III | | III |
| | IV | | IV |
| | V | | V |
| Distal | I | Distal | I |
| | II | | II |
| | III | | III |
| | IV | | IV |
| | V | | V |

Its proportion among the total number of ossification centers amounted to only in two of 95 in *C. goeldii*, zero of 69 in *C. jacchus*, and zero of 23 in *S. oedipus*. Because of the rarity of stage C, its proportion was not tested for differences among species. However, no significant differences were found in our results when we pooled data for stages B and C.

The numbers of ossification centers found in the various anatomical areas for each individual in the three callitrichid species are listed in Table III, and the variability results are summarized in Fig. 3. The results of the statistical comparison among the species are listed in Table IV. The Kruskal-Wallis test revealed significant species differences for all anatomical areas studied except for the tarsal area, and even in the latter case the error probability ($P = 0.059$) almost reached the significance criterion. Dunn's post-hoc tests revealed no significant differences between *Callimico* and *Callithrix*, but there were always significant

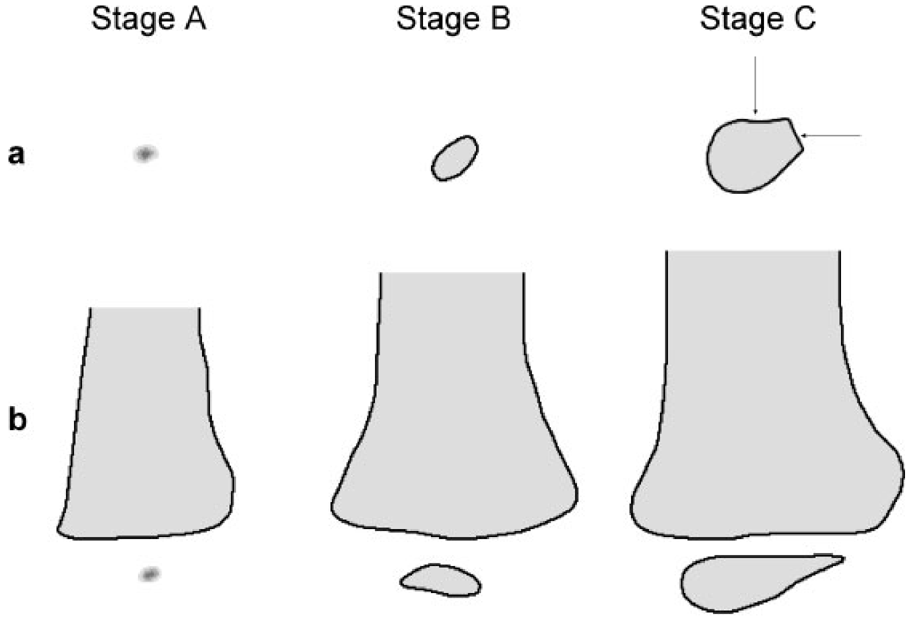

Fig. 1. Diagrams showing ossification stages of carpal and tarsal bones (**a**) and long-bone epiphysis (**b**) (adapted from Tanner et al. [1972]). Arrows indicate visible articular surfaces. Stages: (**A**) amorphous density, (**B**) small but clearly defined borders, and (**C**) short bones with visible articular facets and a maximum diameter of the long-bone epiphyses that is more than half the width of the end of the diaphysis.

differences between *Callimico* and *Saguinus*, and frequently significant differences between *Callithrix* and *Saguinus* (except in the carpal and hindlimb areas; Table IV). In summary, newborns of both *Callimico* and *Callithrix* tend to have higher numbers of ossification centers than newborn *Saguinus*, except in the tarsal area, where the differences are not significant. In most cases (Fig. 3), the variability exhibited by *Callimico* and *Callithrix* does not overlap with that of *Saguinus*, supporting our statistical results.

## DISCUSSION

The proportion of ossification centers that were in stage A (center just barely visible) or B (center clearly visible) did not significantly differ among the species. The absolute numbers of ossification centers per individual, however, exhibited significant differences. Both *C. goeldii* and *C. jacchus* had significantly higher total numbers of ossification centers than *S. oedipus*. As a rule, the difference also remained significant when various limb areas were tested separately. Exceptions include the tarsal samples and the comparison between *Callithrix* and *Saguinus* in carpal and hindlimb samples. We suspect, however, that the results of these comparisons might become significant as well with larger sample sizes, because our *Callithrix* and *Saguinus* samples were smaller than the *Callimico* sample (six, seven, and eight individuals, respectively). In contrast, we found no significant difference between *C. jacchus* and *C. goeldii*. Therefore, *C. jacchus* and *C. goeldii* resemble each other more than each of them resembles *S. oedipus*.

Although our data are not conclusive, they suggest that tamarins, for their body size, are developmentally delayed at birth relative to the marmosets and

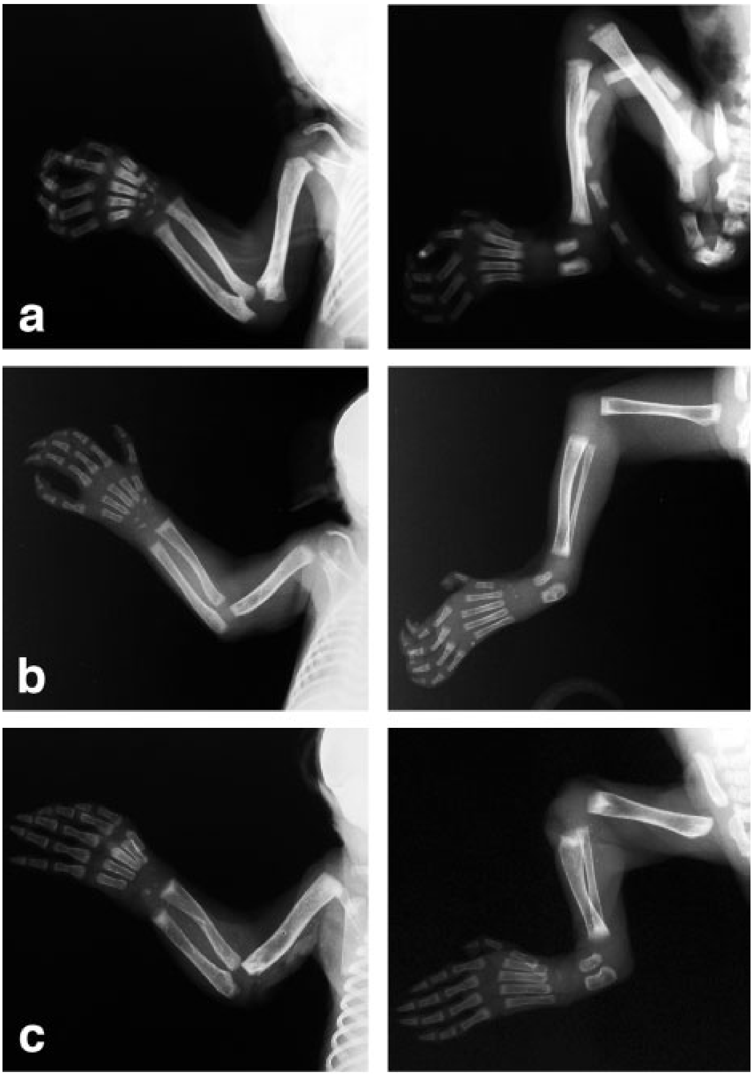

Fig. 2. Examples of radiographs of the forelimb (left) and of the hindlimb (right) of *Callimico goeldii* (**a**), *Callithrix jacchus* (**b**), and *Saguinus oedipus* (**c**).

*Callimico*. If so, tamarins and marmosets may differ in development in general, and possibly in adaptive behavioral aspects of infant dependence.

Three of our six *Callithrix* specimens were triplets. Could this have influenced our findings? Higher litter size may reduce body mass per offspring and affect developmental status [Jen et al., 1978; Koskela, 1998]. If there was any effect of the triplet birth on our results, we would expect to find a lower developmental status in the *Callithrix* sample than in the other samples, but this was not the case.

A comparison of our results with previous studies on skeletal ontogeny and maturation in New World primates is limited because the stages of skeletal development as defined in our study are not applicable to the data published by other authors.

**TABLE II. Numbers of Ossification Centers at Three Stages of Skeletal Development (Median, Range of Second and Third Quartiles, and Absolute range) in Newborn Individuals of Three Callitrichid Species**

| | Total ossification centers | | |
|---|---|---|---|
| Species | Stage A | Stage B | Stage C |
| *Callimico goeldii* | | | |
| Median | 4.5 | 7.0 | 0.0 |
| Interquartile range | 2.0–7.0 | 5.75–8.25 | 0.0–0.0 |
| Absolute range | 2–8 | 4–10 | 0–2 |
| *Callithrix jacchus* | | | |
| Median | 6.5 | 5.5 | 0.0 |
| Interquartile range | 5.25–7.0 | 5.0–6.75 | 0.0–0.0 |
| Absolute range | 2–7 | 4–8 | 0–0 |
| *Saguinus oedipus* | | | |
| Median | 1.0 | 2.0 | 0.0 |
| Interquartile range | 0.5–1.5 | 2.0–2.5 | 0.0–0.0 |
| Absolute range | 0–3 | 1–3 | 0–0 |

**TABLE III. Numbers of Ossification Centers Per Region for Each Individual of Three Callitrichid Species**

| | Forelimb | Hand | Carpal | Hind limb | Tarsal |
|---|---|---|---|---|---|
| *Callimico goeldii* | 8 | 7 | 7 | 1 | 0 |
| | 5 | 5 | 5 | 3 | 2 |
| | 6 | 6 | 6 | 3 | 2 |
| | 8 | 8 | 8 | 3 | 2 |
| | 7 | 7 | 7 | 5 | 4 |
| | 9 | 8 | 8 | 6 | 5 |
| | 8 | 8 | 8 | 7 | 5 |
| | 8 | 7 | 7 | 8 | 7 |
| *Callithrix jacchus* | 7 | 6 | 5 | 2 | 2 |
| | 10 | 10 | 6 | 3 | 3 |
| | 5 | 5 | 5 | 4 | 4 |
| | 7 | 7 | 6 | 4 | 4 |
| | 11 | 11 | 7 | 4 | 4 |
| | 7 | 7 | 6 | 5 | 5 |
| *Saguinus oedipus* | 0 | 0 | 0 | 2 | 2 |
| | 0 | 0 | 0 | 2 | 2 |
| | 0 | 0 | 0 | 2 | 2 |
| | 2 | 2 | 2 | 2 | 2 |
| | 3 | 3 | 3 | 2 | 2 |
| | 2 | 2 | 2 | 2 | 2 |
| | 2 | 2 | 2 | 2 | 2 |

The numbers of hand and foot ossification centers in newborn primates have been published for a few species. In most cases, however, data are available for very few individuals, and frequently only for the hand. The data available from published studies of ossification centers in other primate species at birth are summarized in Table V. The few previously published data for callitrichids

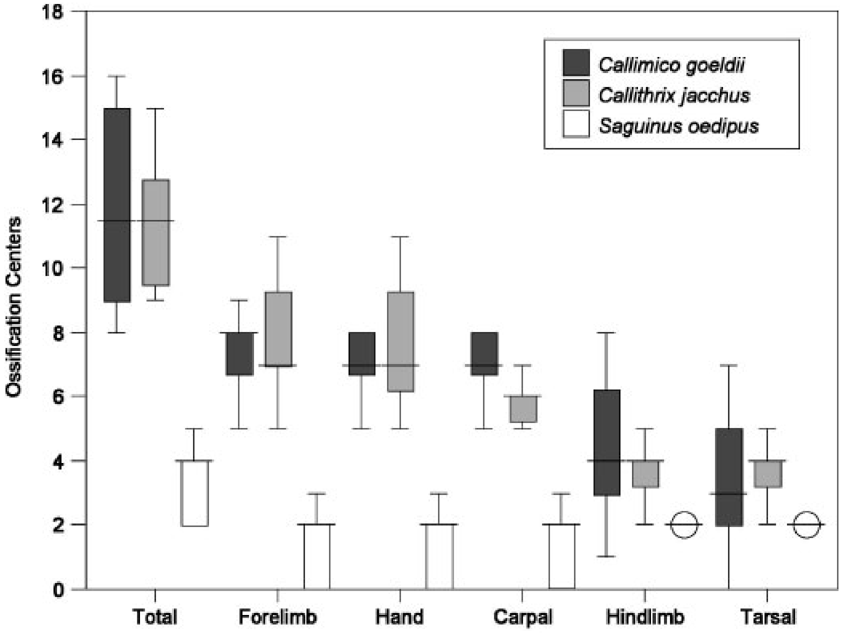

Fig. 3. Numbers of the ossification centers of three callitrichid species. The box plots show median values, second and third quartiles, and maximum and minimum values. If these values are identical for all individuals, circles indicate the number of ossification centers of that species.

**TABLE IV. Multiple Statistical Comparisons of the Numbers of Ossification Centers Among Three Callitrichid Species**

| | | Dunn post-hoc test | | |
|---|---|---|---|---|
| Ossification centers per individual | Kruskal-Wallis test | *Callimico*/ *Callithrix* | *Callimico*/ *Saguinus* | *Callithrix*/ *Saguinus* |
| Total | $P = 0.0011$ | $P > 0.05$ | $P < 0.01$ | $P < 0.01$ |
| Forelimb | $P = 0.0011$ | $P > 0.05$ | $P < 0.01$ | $P < 0.01$ |
| Hand | $P = 0.0011$ | $P > 0.05$ | $P < 0.01$ | $P < 0.01$ |
| Carpal | $P = 0.0004$ | $P > 0.05$ | $P < 0.001$ | $P > 0.05$ |
| Hind limb | $P = 0.0117$ | $P > 0.05$ | $P < 0.05$ | $P > 0.05$ |
| Tarsal | $P \geq 0.0595$ | n.t. | n.t. | n.t. |

n.t., post-hoc tests were not calculated because the *P* value of the Kruskal-Wallis test was greater than 0.05.

appear to support our results. *Cebuella*, which is closely related to *Callithrix*, also exhibits a relatively high number of ossification centers in the hand, whereas *Saguinus niger* exhibits much lower values, similar to those we found in *S. oedipus*.

In an extensive review and analysis of neonatal and infant/juvenile growth in several callitrichid species, Garber and Leigh [1997] were unable to show any significant differences with respect to patterns of relative growth in body mass, either pre- or postnatally. Thus, their body mass data are not consistent with the current ossification data, which indicate a significant difference between tamarins

**TABLE V. Number of Hand and Foot Ossification Centers at Birth in Various Primate and One Non-Primate Species**

| | Mean number of ossification centers | | | | | | |
|---|---|---|---|---|---|---|---|
| | Hand | | | Foot | | | |
| Species | n | Mean | Range | n | Mean | Range | References |
| *Tupaia belangeri* | 3 | 0 | 0–0 | 3 | 1 | | Glaser [1970] |
| *Lemur catta* | 2 | 0 | 0–0 | 2 | 2 | | Glaser [1970] |
| *Eulemur fulvus* | 1 | 0 | | 1 | 2 | | Glaser [1970] |
| *Nycticebus coucang* | 1 | 1 | | 1 | 2 | | Glaser [1970] |
| *Galago senegalensis* | 1 | 0 | | 2 | 3 | | Glaser [1970] |
| *Cebuella pygmaea* | 3 | 4.67 | 1–8 | 3 | 3 | | Glaser [1970] |
| *Cebuella pygmaea* | ? | 9–10 | 9–10 | ? | 3 | | Christen [1974] |
| *Callithrix jacchus* | 1(?) | 5 | | 1(?) | 5 | | Wettstein [1963] |
| *Callithrix jacchus* | 6 | 7.7 | 5–11 | 6 | 3.7 | 2–5 | This study |
| *Callimico goeldii* | 8 | 7.0 | 5–8 | 8 | 3.375 | 0–7 | This study |
| *Saguinus oedipus* | 8 | 1.3 | 0–3 | 8 | 2.0 | 2–2 | This study |
| *Saguinus niger* | ? | 1 | | ? | 3 | | Christen [1974] |
| *Saguinus niger* | 2 | 2 | | 2 | 2.5 | 2–3 | Glaser [1970] |
| *Cebus apella* | 1 | 1 | | 1 | 2 | | Glaser [1970] |
| *Cebus apella* | 4 | 2.5 | 2–3 | | | | Watts [1990] |
| *Cebus albifrons & apella combined* | (14+4) | 4.3 | | | | | Watts [1990] |
| *Cebus capucinus* | 1 | 3 | | 1 | 2 | | Glaser [1970] |
| *Saimiri boliviensis* | 9 | 8.0 | x–10 | | | | Watts [1990] |
| *Lagothrix lagotricha* | 1 | 2 | | 1 | 3 | | Glaser [1970] |
| *Cercopithecus nictitans* | 2 | 24.5 | 24–25 | 2 | 22 | 21–23 | Glaser [1970] |
| *Macaca mulatta* | 14[a] | 16.4 | 11–23 | | | | Michejda [1987] |
| *Macaca mulatta* | 63 | 23.7 | 14–29 | | | | Watts [1990] |
| *Macaca mulatta* | 1 | 19 | | 1 | 19 | | Schultz [1937] |
| *Macaca nemestrina* | 33 | ~20.0 | | 33 | ~23.0 | | Newell-Morris & Tarrant [1978] |
| *Nasalis larvatus "newborn"* | 1 | 6 | | 1 | 6 | | Schultz [1942, 1956] |
| *Hylobates lar* | 1 | 8 | | 1 | 5 | | Schultz [1944, 1956] |
| *Pongo* | 2 | 2.5 | 2–3 | 2 | 3.5 | 3–4 | Schultz [1941, 1956] |
| *Gorilla* | 1 | 2 | | | | | Schultz [1956] |
| *Pongo* | 1 | 2 | | 1 | 2 | | Winkler [1996] |
| *Pan troglodytes* | 1 | 3 | | 1 | 4 | | Schultz [1937, 1956] |
| *Pan troglodytes* | 10 | 3.3 | | | | | Watts [1990] |
| *Pan troglodytes* | 6 | 1.67 | 1–2 | 6 | 3.17 | 2–5 | Winkler [1996] |
| *Homo sapiens* | ? | 0 | | | | | Michejda [1987] |
| *Homo sapiens* | ? | 0 | | | | | Greulich & Pyle [1959] |
| *Homo* | 228 | 0 | | 228 | 0 | | Vogt & Vickers [1938] |

[a] 14 drawings (pp. 5, 9, 12 and 13).
n, sample size.

and marmosets, including *Callimico*. Tappen and Severson [1971] compared the sequence of eruption of permanent teeth and epiphyseal union in three species of New World monkeys, but found no significant differences in maturation among the study species, which included *Saimiri sciureus*, *Saguinus nigricollis*, and *Cebus albifrons*. In a comparison of the skeletal age changes between *Saguinus* *fuscicollis* and *S. oedipus*, Glassman [1982, p. 141f] found ‘‘an overall similarity in sequence and timing’’ of dental eruption for the permanent teeth, but a slight difference in sequence and timing of epiphyseal union in long bones: ‘‘*S. oedipus* began fusion later than *S. fuscicollis*, although the difference in most cases does not exceed six months.’’ This finding, together with ours, suggests that *S. oedipus* may exhibit a slower development than other callitrichids. A comparison of gestation lengths provides further support for this hypothesis. The average gestation period in most callitrichid species ranges from 131 to 150 days, whereas ‘‘*S. oedipus* has a uniquely long gestation length of 184 days, the reasons for which are not yet understood’’ [Hartwig, 1996].

Our findings can be interpreted as providing morphological support for the molecular-based classification, according to which *C. goeldii* is more closely related to marmosets than to tamarins. To date, this morphological support has been missing, because traditional morphological data tend to identify *Callimico* as the most basal group of the callitrichids. Because our data suggest that marmosets are developmentally advanced over tamarins, we interpret the similar ‘‘advanced’’ developmental status of *Callimico* as an indicator of taxonomic affinity to marmosets. Although our taxonomic interpretation is consistent with recent studies on callitrichid phylogeny [e.g., Porter and Garber, 2004], there may be alternative explanations.

For instance, we compared *C. goeldii* with only one species each of the tamarins and the marmosets. It remains unknown to which degree the selected species are truly representative of their respective genera in the characters we studied. Given that *Saguinus* and *Callithrix* are each among the most speciose of primates, it may be that there is no representative species for either. The comparison of gestational lengths appears to indicate that *S. oedipus* may develop more slowly than other callitrichids, and may be a particularly untypical representative of its genus (see above). Future studies should not only include additional species of the genera *Callithrix* and *Saguinus*, but also members of the other callitrichid genera, such as *Callibella*, *Cebuella*, *Mico*, and *Leontopithecus*. If all genera that are deemed most closely related to *Callimico* also shared similar ossification center numbers, our conclusion as stated would be much stronger. It should be noted that the few previously published numbers of ossification centers for callitrichids (Table V) appear to support our results, especially for the hand region. It is unknown, however, whether these numbers are based on representative samples.

Furthermore, the developmental status of *Callimico* may reflect a singleton fetus and greater pre- and postnatal body mass. Body mass often appears to be correlated with maturation status [Hayakawa et al., 2003] and ossification status [Leshem et al., 2002].

Our results must also be regarded with caution because we studied just two characters (i.e., the number of ossification centers and the stage of ossification), and only one of these showed significant differences. Studies on other, unrelated characters may reveal different results.

Finally, our results are based on the concept that a phenetic similarity indicates a phylogenetic relationship. Although similarity often correlates with relationship, this link can be misleading. If organisms that appear to be more similar are grouped together, the results of parallel or convergent evolution are overlooked and the risk of identifying relatives based on primitive traits is increased, which may lead to the creation of artificial groups [Bininda-Emonds, 2000; Geissmann, 2003; Hull, 1998; Wiley et al., 1991]. It would be interesting to further evaluate our findings in a cladistic study that includes an outgroup consisting of neotropical primates other than the callitrichids.

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