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Locomotor Behavior and Feeding Ecology of the Panamanian Tamarin (*Saguinus oedipus geoffroyi*, Callitrichidae, Primates)[1]

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The Callitrichidae are a family of New World primates that exhibit a complex of behavioral and morphological characters reputedly similar to those of tree squirrels of the genus Sciurus. *In particular, the locomotor behavior of tamarins and marmosets has been described as "squirrel-like." In this paper I describe a field investigation of the locomotor behavior and ecology of the Panamanian tamarin* (Saguinus oedipus geoffroyi) *and the red-tailed squirrel* (Sciurus granatensis). *From January through August 1978, a total of 1200 hr was spent observing free-ranging populations of tamarins and tree squirrels in an area of secondary forest on the Pacific Coast of Panama. Observations were made using an instantaneous time sampling technique. Individual activity records were collected on focal animals and recorded at 2.5-min intervals throughout the day. The following information was collected: (a) nature and structure of the substrate exploited, (b) activities on these supports and/or types of resources procured, and (c) body posture involved in the use of these supports. Data presented indicate major differences in substrate preference and positional behavior in tamarins and tree squirrels. Unlike squirrels, tamarins avoid vertical and sharply inclined supports during travel. Movements through the canopy is accomplished by a series of long leaps which begin and end on thin terminal supports. However, the Panamanian tamarin spent numerous hours clinging to large vertical trunks while feeding on plant exudate. Gums comprise 23.0% of the noninsect portion of the tamarin diet. The relationships between small body size, claw-like nails, substrate preference, and positional behavior are discussed. Claw-like nails enable this primate to*

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exploit a food resource that would otherwise be inaccessible. The interrelationship between environment, behavior, and morphology provides a framework from which to understand callitrichid adaptations. These adaptations are not convergent with those of the sciurid rodents.

KEY WORDS: Callitrichidae; locomotor behavior; tegulae; gum feeding.

INTRODUCTION

The Callitrichidae are a family of New World primates that exhibit a complex of behavioral and morphological characters rare among primates but reputedly similar to those of tree squirrels of the genus *Sciurus*. Many primatologists have noted this similarity (Le Gros Clark, 1962; Napier and Napier, 1967; Hladik, 1970; Jolly, 1972; Cartmill, 1974; Moynihan, 1976; Dawson, 1976; Hershkovitz, 1972, 1977; Eisenberg, 1977). In particular, the locomotor behavior of tamarins and marmosets has been described as squirrel-like.

Tamarins and marmosets possess "claw-like" nails[3] on all manual and pedal digits with the exception of the hallux, which bears a flattened nail. It has been assumed that the evolution of claw-like nails in the Callitrichidae is directly related to the habitual use of large vertical supports during travel. For example, Hladik states:

> In the tamarin, one finds animals whose appearance is somewhat reminiscent of that of the squirrel. The flattened nails characteristic of the Primates are nearly all replaced by claws, which results in a classical quadrupedal gait. They can quickly run on branches and climb along the trunks of trees by planting their claws in the bark, rather than grabbing the supports in their hands as do other monkeys [translated from Hladik (1970, pp. 1–2)].

Current descriptions of tamarin locomotor behavior are based on random sightings, travelers' reports, and short-term observations. One must be wary of such qualitative accounts of locomotor activity. Often, they tend to overemphasize spectacular behaviors and underestimate the frequency of more prosaic behaviors. To date there has been no quantitative and systematic evaluation of positional behavior and substrate preference in a callitrichid primate. This paper represents the first such study.

[3]The term tegula (Weber, 1928) has been used to characterize the nails of all New World monkeys. This term distinguishes the platyrrhine condition from the true nails (ungula) of catarrhine primates.

SPECIFIC QUESTIONS

Hypotheses focusing on the question of callitrichid–sciurid convergent adaptations have been proposed but not tested. Apparent similarities in the locomotor adaptations of tamarins and tree squirrels stimulate a variety of intriguing questions. For the purposes of this paper, I will explore the following:

(1) Are the behavioral and morphological adaptations of callitrichid primates similar to those of the sciurid rodents?
(2) Is the anatomy of the claw-like tegula in *Saguinus* analogous to that of the true claw of a tree squirrel?
(3) What set of explanations offers the most plausible interpretation regarding the functional significance or biological role of tamarin digital morphology?

It is proposed that claw-like tegulae in *Saguinus* are a specialized adaptation related to food procurement. Specifically, claw-like tegulae enable these small primates to cling to large vertical trunks while feeding on plant exudate. Exudates appear to be an important component of the tamarin diet.

MATERIALS AND METHODS

Behavioral Data

From January through August 1978, I spent a total of 1200 hr studying the ecology and locomotor behavior of free-ranging populations of the Panamanian tamarin (*Saguinus oedipus geoffroyi*) and the red-tailed squirrel (*Sciurus granatensis*) in a dry tropical forest on the Pacific Coast of Panama. Observations were made using an instantaneous time sampling technique (Richard, 1970; Altmann, 1974). Individual activity records (IAR) were collected on focal animals and recorded at 2.5-min intervals throughout the day. The following information was collected on locomotor activity: (1) nature and structure of the substrate exploited; (2) activities on these supports and/or types of resources procured; and (3) body posture involved in the use of these supports.

Anatomical Data

Frozen specimens of *Saguinus oedipus, Sciurus niger* (fox squirrel), and *S. carolinesis* (gray squirrel) were obtained from the Laboratory of

Primate Biology, Department of Anthropology, Washington University. Manual digits were surgically removed, sectioned, and ground on a Beuler rotary grinding apparatus. Thin sections were mounted on slides, examined, and photographed using a Nikon epi-illuminator microscope with photomicrographic attachments.

ANALYSIS: SUBSTRATE PREFERENCE

Data collected in Panama demonstrate that during positional activity, the red-tailed squirrel avoids thin flexible supports. During travel and movement, squirrels habitually employ large trunks as a preferred avenue of travel. An examination of locomotor behavior in the red-tailed squirrel revealed no statistical preference for ascending or descending these supports. *Sciurus granatensis* travel up and down vertical and oblique supports with equal frequency ($P > 0.05$; Tables I and II).

Cartmill (1974) has examined locomotor patterns in various mammalian lineages. He suggests that claws or claw-like nails offer small mammals access to large vertical and/or sharply inclined supports. Once the claw penetrates the substrate, a new interface is created such "that the effective diameter of the support is reduced, the extent of the effective reduction depending on the magnitude of the angle of penetration" (Cartmill, 1974, p. 56). Observations of the locomotor behavior of arboreal squirrels in Missouri (gray squirrel and fox squirrel) and in Panama (red-tailed squirrel) support Cartmill's hypothesis. The ability of tree squirrels to run up and down and rapidly spiral around smooth vertical supports attests to the mechanical advantage of clawed digits.

Table I. Differential Use of Oblique Supports During Travel and Movement

	Branch circumference (cm)					
	0–5	5–10	10–25	25–50	50+	Total
Tamarin						
Up	47	90	190	150	107	584
Down	24	86	123	85	71	389
Total	71	176	313	235	178	973
$\chi^2 = 22.14$, df = 4 $P < 0.001$						
Squirrel						
Up	17	51	62	28	20	178
Down	13	54	61	32	24	184
Total	30	105	123	60	44	362
$\chi^2 = 2.19$, df = 4 $P > 0.05$						

Table II. Differential Use of Vertical Supports During Travel and Movement

	Branch circumference (cm)					
	0–5	5–10	10–25	25–50	50+	Total
Tamarin						
Up	22	31	31	27	36	147
Down	9	10	12	10	13	54
Total	31	41	43	37	49	201
	$\chi^2 = 21.57$, df = 4 $P < 0.001$					
Squirrel						
Up	8	14	43	24	43	132
Down	5	11	44	31	51	142
Total	13	25	87	55	94	274
	$\chi^2 = 1.30$, df = 4 $P > 0.05$					

The extent to which vertical supports are exploited by callitrichid primates is uncertain. Previous reports (Bates, 1854; Enders, 1935; Le Gros Clark, 1962; Thorington, 1968; Hershkovitz, 1972, 1977; Kinzey *et al.*, 1975) have suggested that *Cebuella, Saguinus,* and *Callithrix* habitually travel up and down vertical trunks. This one particular locomotor pattern is primarily responsible for the description of callitrichids as "squirrel-like." Data presented on the Panamanian tamarin suggest an alternative hypothesis.

During travel and movement, only 4.2% of the locomotor behavior of *Saguinus* involves large vertical supports (supports greater than 10 cm in circumference). In the same forest the red-tailed squirrel spent 25.4% of the time traveling on these supports (Table III). Nevertheless, one might assume that *Saguinus* would ascend and descend trunks in equal frequency. The

Table III. Use of Vertical Supports During Travel and Movement

	Branch circumference (cm)						
	0–5	5–10	10–25	25–50	50+	Total	Total travel
Tamarin							
N	31	42	45	38	51	207	3147
%	1.0	1.3	1.4	1.2	1.6	6.6	
	< 4.2% >						
Squirrel							
N	14	26	94	58	111	303	1036
%	1.3	2.5	9.1	5.6	10.7	29.2	
	< 25.4% >						

data indicate that tamarins avoid positional activities involving vertical descent. Tamarins were observed to travel on large vertical supports on 129 occasions. Of these, only 35 involve vertical descent. Similarly, *Saguinus* selectively chose to ascend rather than descend large oblique supports ($P < 0.001$; Tables I and II).

In summary, there are major distinctions in substrate preference and postional behavior in free-ranging populations of *Saguinus* and *Sciurus*. In particular, tamarins avoid vertical supports during travel. However, when exploiting these substrates, *Saguinus* demonstrate a statistically significant preference for travel in an upward direction.

Unlike squirrels, tamarins range through the canopy not by ascending and descending trunks, but rather via a series of long acrobatic leaps. These leaps begin and end on thin fragile branches located on the periphery of the canopy. Claw-like tegulae do not appear to limit movement on these supports. Thus clawed digits alone are not a sufficient condition from which to predict vertical ranging behavior. Perhaps by examining and comparing the structure of the tamarin tegula and tree squirrel claw, we can better understand the functional capabilities of these organs.

STRUCTURE OF THE TAMARIN TEGULA

Much of the confusion concerning the locomotor behavior of the Callitrichidae involves the biological role and anatomy of their claw-like tegulae.

Tamarins possess a set of well-developed apical pads and papillary ridges on the terminal phalanx (Le Gros Clark, 1936; Sonek, 1969; Rosenberger, 1977). Figure 1 illustrates a sagittal section through the middle and terminal phalanges of the fourth manual digit of *Saguinus oedipus* and

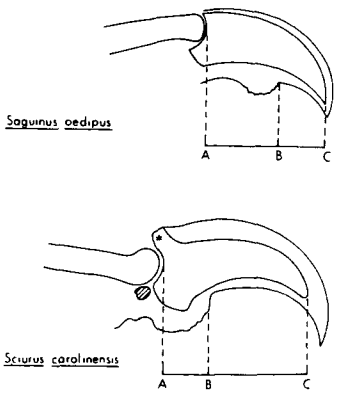

Fig. 1. Sagittal section through the middle and terminal phalanges of *Saguinus* (top) and *Sciurus* (bottom). Note the well-developed extensor process (marked with an asterisk) and the presence of a sesamoid bone (shaded area) in the distal interphalangeal joint in *Sciurus*. Symbols are explained in the text.

Sciurus carolinensis. A corresponds to the beginning of the terminal phalanx, B represents the most distal extension of the apical pad, and C corresponds to the most distal extension of the terminal phalanx. The ratio AB/AC is a measure of the expansion of the terminal pad on the phalanx. In *Saguinus* the digital pad encompasses approximately 60% of the terminal phalanx; in *Sciurus,* barely 40%. The pad functions to increase the sensory contact between the organism and the substrate. The structure and position of the apical pad in the tamarin provide a greater opportunity for prehensile and fine manipulative abilities than is found in the squirrel.

Returning to Fig. 1, we observe further distinctions in the anatomy of the tamarin tegula and the squirrel claw. In contract to the condition observed in clawed mammals, the tamarin tegula is conspicuous in the absence of a sesamoid in the joint between the terminal and middle phalanges. The presence of a sesamoid in *Sciurus* indicates that a major component of body weight is actively transmitted through this joint.

Calhoun (1977) has conducted an extensive analysis of the distribution and function of sesamoid bones in the primate hand. During locomotion, specific areas of the hands (and feet) are subject to large and potentially damaging tensile and compressive forces. These forces threaten the integrity of the joint by causing damage to both the articular cartilage and the synovial membrane. Calhoun (1977) therefore concludes that the function of the sesamoid lies in its ability to dissipate large compressive forces by increasing the surface area over which these forces are transmitted. The absence of a sesamoid at the distal interphalangeal joint in tamarins and marmosets suggests that this joint plays only a minor role in weight bearing during locomotion.

In addition, tamarins lack a definite bony process on the terminal phalanx to accommodate the insertion of the extensor tendor (Le Gros Clark, 1936). In tree squirrels the extensor process is well developed. The development of an extensor process, coupled with a well-defined concavity immediately proximal to the head of the middle phalanx (Fig. 1), enables *Sciurus* to hyperextend the phalanx and claw. The distal interphalangeal joint of *Saguinus* is incapable of such movement.

Thorndike (1968) has conducted a histological analysis of the microstructure of the tegula and nail in various species of primates (*Saguinus oedipus, S. nigricollis, Cebus albifrons,* and *Cercopithecus aethiops*). Histologically, the tamarin "claw" possesses a deep stratum and terminal matrix, both elements of the typical mammalian claw (Le Gros Clark, 1936). The deep stratum runs along the midline axis of the claw and provides strong support. However, in tamarins and marmosets this stratum is extremely thin. Concomitant with this, the terminal matrix is significantly reduced and "comprises a correspondingly small proportion of the total

matrix" (Thorndike, 1968, p. 250). In *Phalanger,* a clawed marsupial, the terminal matrix accounts for 73% of the length of the germinal layer (Le Gros Clark, 1936); in *Saguinus* it represents merely 19% (Thorndike, 1968).

The most significant contribution of Thorndike's analysis is the discovery that the hallucial and digital nails of *Saguinus* and the nails of *Cebus albifrons* exhibit a rudimentary deep layer and terminal matrix. Therefore both platyrrhine families (Cebidae and Callitrichidae) possess nails that are histologically similar. This character state has been termed tegula (Weber, 1928) and is distinguished from true claws (falcula) and from the nails (ungula) of all catarrhine primates.

Thus, the tegula complex in *Saguinus* is enigmatic in that it bears structural similarities to a true claw (elongated, laterally compressed and pointed nails, deep stratum) while retaining the general morphology of a cebid-like state. This condition is somewhat analogous but certainly not homologous to that of the claw of a tree squirrel. Tamarin tegulae possess elements that increase the leverage and support capabilities of the digits. This is accomplished while retaining a fair degree of prehensility. However, the relatively limited flexion and extension of the tegulae imply a circumscribed and perhaps specialized adaptation. The question remains: What is the nature of this adaptation?

As previously stated, observations on tamarin locomotor behavior indicate that very little travel activity involves the use of the claw-like tegulae. However, during feeding, tamarins exhibit a very different set of positional behaviors. Over 67% of all activity on vertical supports greater than 25 cm in circumference involved vertically oriented clinging while feeding on plant exudate. It is during this activity that claw-like tegulae play a critical role in providing access to a set of resources that would otherwise be unavailable. Previous reports and qualitative accounts of tamarin positional behavior have overlooked the importance of vertical clinging as a feeding posture [Kinzey *et al.* (1975) have discussed this behavior in *Cebuella*].

FEEDING BEHAVIOR: AN ALTERNATIVE HYPOTHESIS

The feeding ecology of the Panamanian tamarin is characterized by three distinct types of food resources: (1) insects, 40%; (2) small fruits, 38.4%; and (3) exudate, 14.4%. These resources are located in different parts of the canopy, and access to them involves distinct sets of locomotor and postural activities.

Table IV. Support Preference During Insect Foraging in the Panamanian Tamarin

	Branch circumference (cm)						
	< 2.5	2.5–5	5–10	10–25	25–50	50+	Total
N	248	175	148	46	14	40	671
%	36.9	26.0	22.0	6.8	2.0	5.9	100
			< 84.9% >				

The primary component of the tamarin diet is insect protein. Foraging and capturing insect prey involve cautious and rapid movement on thin flexible supports in dense vine tangles in the forest understory. Eighty-four and nine-tenths percent of the insect predation occurred on supports less than 10 cm in circumference (Table IV).

The Panamanian tamarin exhibits a distinct preference for feeding on thin supports (Fig. 2). Once supports reach 5.0–10.0 cm, there is a significant decline in feeding behavior. In the subsequent size class (supports 10–25 cm), only 7.4% of the feeding occurs. A cross-tabulation of activity and support circumference demonstrates that tamarins exploit supports of 10–25 cm with a greater frequency than any other. However, during the maintenance activities of feeding and foraging, supports of this size are utilized infrequently (Fig. 3). Thus, like many other primates, *Saguinus oedipus* feeds in a terminal-branch setting (Grand, 1972). The only apparent contradiction to small-branch feeding is observed on supports greater than 100 cm. Twenty and two-tenths percent of all feeding bouts occur on these supports. This disparity is easily explained.

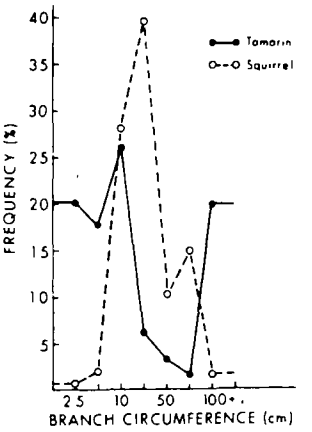

Fig. 2. Comparison of support preference in *Saguinus* and *Sciurus* during feeding.

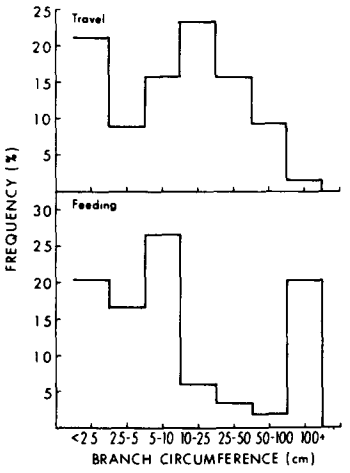

Fig. 3. This figure illustrates the support preference during travel (top) and feeding (bottom) in the Panamanian tamarin.

GUM FEEDING

Figure 3 illustrates the relationship between support size and feeding activity in *Saguinus oedipus.* Ninety-five and six-tenths percent of the cases recorded as large-branch feeding (supports greater than 50 cm in circumference) involve the postural act of clinging to vertical trunks while feeding on plant exudate. During no other activity does the use of large vertical supports constitute a critical factor in the positional repertoire of *Saguinus.* Exudate, principally from one species of tree, *Anacardium excelsum* (espave), accounts for 23.0% of the noninsect portion of the tamarin diet. This resource "provides these small primates with a high-energy, carbohydrate source not utilized to any great extent by larger primate species and other mammals and birds" (Coimbra-Filho and Mittermeier, 1977, p. 109). It is possible that exudates provide some essential minerals or amino acids vital to the diet of this primate.

DISCUSSION

Previous reports have suggested that plant gums play a relatively insignificant role in the diet of *Saguinus.* For example, Hladik and Hladik (1969) found only minor amounts of exudate in the stomachs of a small number of wild-shot tamarins in Panama. Similarly, Dawson (1976) failed to report any instances of gum feeding in an 18-month study of *S. oedipus* in the Panama Canal Zone. However, it should be pointed out that most of Dawson's behavioral data were collected over a relatively limited period of

time. In fact many of his observations occurred during the process of radiotracking two tamarin groups, one for 29 days and the other for 31 days. Given the fact that gum feeding is both an apparently seasonal activity and exceedingly difficult to observe in the field, it is not surprising that such behavior may frequently go unnoticed and thus underestimated in its importance.

Recent studies of tamarin behavior and ecology indicate that the use of plant exudate is more widespread than previously imagined. Neyman (1977) describes a number of feeding bouts characteristic of *Saguinus oedipus* in Columbia that appear to involve the ingestion of plant exudate. She states, "They extracted unidentifiable material from the surfaces of the branches and trunk of some trees by pressing the mouth to the surface and possibly pulling. In some trees the same sites were visited by a succession of individuals" Neyman, 1977, p. 61). Although Neyman was unable to ascertain the exact nature of the resource in question, she suggests that exudate is a likely possibility. The description provided by Neyman (1977) is in exact accord with the set of activities which typify gum feeding in *S. oedipus* in Panama. Furthermore, observations of gum feeding have now been reported for *S. fuscicollis* (Izawa, 1976) and *S. mystax* (Castro and Soini, 1977) in Peru. In light of these data and the information presented in this article, it may be necessary to reassess the role of plant gums in the tamarin diet. Exudates appear to be an important dietary resource for a number of tamarin species.

This paper describes the most extensive observations of exudativory in the genus *Saguinus*. Particularly during the months of May and June, 1978, the Panamanian tamarin spent numerous hours clinging to trunks of *Anacardium excelsum* feeding on plant exudate (Fig. 4). The interrelationship between claw-like tegulae, small body size, and gum feeding on vertical trunks appears to be fairly direct. This specialized form-function complex involves a postural adaptation related to food procurement. Claw-like tegulae enable this primate to exploit a food resource that would otherwise be inaccessible.

Plant exudate is an important component in the diet of certain other primate species as well. Extensive observations of gum feeding have been reported in *Cebuella pygmaea* (pygmy marmoset), *Callithrix jacchus* (white tufted-ear marmoset), *Phaner furcifer* (forked lemur), and *Euoticus elegantulus* (needle-clawed galago). Each of these forms exhibits a complex of characters remarkably similar to those observed in *Saguinus*. *Phaner, Euoticus, Cebuella,* and *Callithrix* are small-bodied, insect exudate-feeding primates which exhibit keeled or claw-like nails on nearly all manual and pedal digits (Ramirez *et al.,* 1977). Modified nails in these forms provide access to large vertical trunks and plant exudate. These resources are inaccessible to other primate species exploiting the same habitat (Charles-Dominique, 1974, 1977).

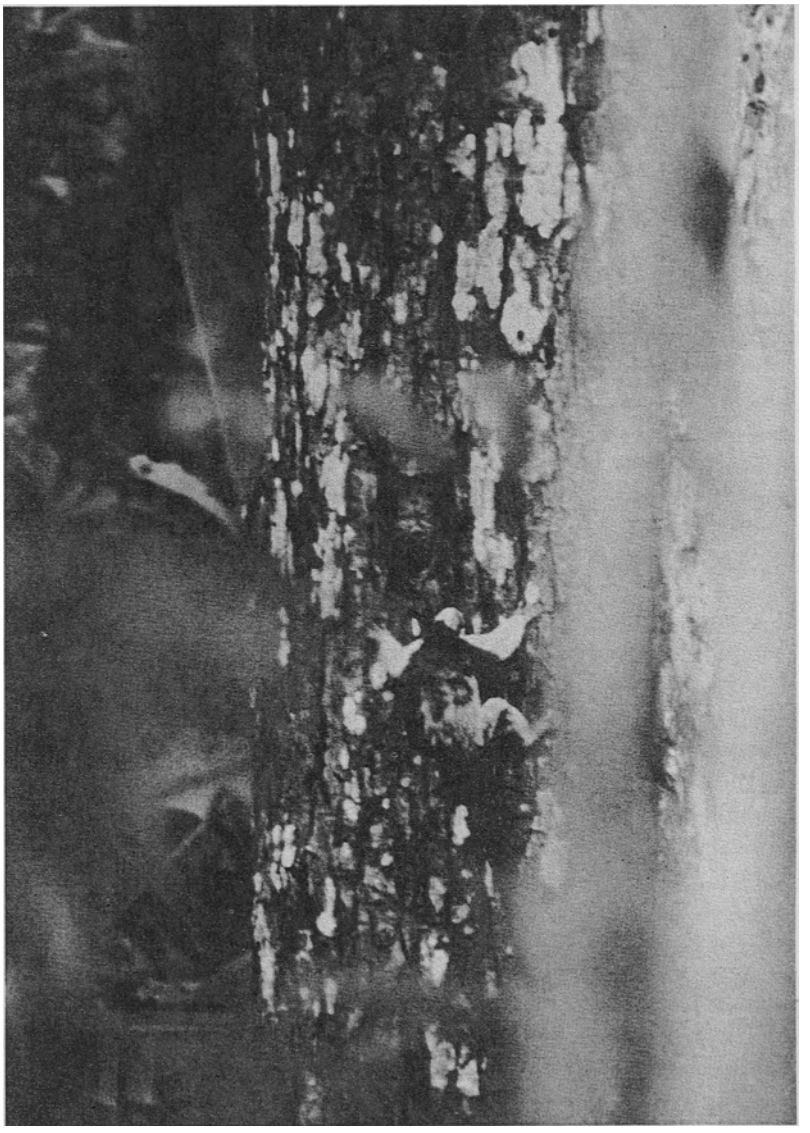

Fig. 4. *Saguinus oedipus geoffroyi* clinging to the trunk of *Anacardium excelsum*, feeding on plant exudate.

Thus, in Africa, Madagascar, and Central and South America, there appears to have been a parallel radiation of exudativorous primate forms. Each of the species in question exhibits a number of behavioral and morphological characters in common. They are as follows:

(1) diminutive body size,
(2) procumbent or specialized incisors,[4]
(3) claw-like tegulae or pointed nails,
(4) ability to cling to large vertical trunks,
(5) insect protein a significant part of the diet, and
(6) plant exudates a critical component of the diet.

CONCLUSION

Numerous accounts of callitrichid ecology and behavior have mentioned the similarity between tamarins and tree squirrels. The use of such an analogy must be exercised with extreme caution, particularly in the absence of supporting data. Sympatric populations of tamarins and tree squirrels in Panama exhibit marked differences in locomotor behavior, substrate preference, and habitat utilization.

As noted in the introduction, many authors have felt that the evolution of claw-like tegulae in the Callitrichidae reflects a locomotor adaptation involving the habitual use of large vertical and sharply inclined supports. In this paper I have attempted to demonstrate that during travel, the Panamanian tamarin avoids such supports and restricts most of its activity to small and medium-sized branches. Similarly, much of the feeding and foraging behavior of this primate occur on dense vine tangles and fragile interlacing foliage. Movement in this milieu is dependent upon the ability to grasp and climb on thin flexible supports. This necessitates a very specific locomotor morphology. Claw-like tegulae in the tamarin do not appear to hinder movement on these branches. In contrast, tree squirrels habitually feed and travel on larger, more stable supports. Their general avoidance of thin supports is noteworthy and at a variance with the patterns of substrate preference observed in *Saguinus oedipus*. Thus, the existence of claw-like tegulae in the callitrichids is not in itself a sufficient condition from which to predict vertical ranging behavior.

Recently, studies concerned with the systematics of platyrrhine evolution have suggested that a number of callitrichid adaptations (i.e., small

[4]Compared to the callitrichid genera *Callithrix* and *Cebuella*, tamarins of the the genus *Saguinus* possess relatively diminutive incisors. In this respect, they appear to be dentally primitive. Tamarins do not gouge holes in the trunks to elicit the flow of exudate. Instead, they appear to feed opportunistically on exudate that is stimulated by injury to the tree. Such injuries may be the result of insect predation.

body size, insectivorous diet, tendency toward multiple births, claw-like tegulae, loss of third maxillary molars) represent a set of derived character states related to phyletic dwarfing. Rosenberger (1977), Leutenegger (1979), and Ford (1980) provide weighty evidence in support of this hypothesis. However, a reduction in body size over time still fails to explain satisfactorily the origin and evolution of claw-like tegulae in the Callitrichidae. Many primate lineages are characterized by body weights of 900 g or less (Napier and Napier, 1967; Kay, 1973), and yet the majority of these taxa does not exhibit a claw-like digital morphology. Furthermore, there is no evidence at present to indicate that during travel and movement, the so-called "clawed" primates exploit their habitat in a manner significantly different from that of small-bodied "clawless" primates. For example, in Charles-Dominique's (1977) study of positional behavior in five sympatric species of lorisids, *Galago demidovii, G. alleni,* and *Arctocebus calabarensis* all exploit vertical supports at a far greater frequency than *Euoticus elegantulus,* the needle-clawed galago. Table V contains field data on substrate preference in a number of species of small-bodied primates. In examining these data, there is no indication of any overall relationship between the use of vertical supports and the existence of claw-like nails. However, in *Euoticus,* as in *Saguinus oedipus,* the use of large vertical supports does appear to be specifically associated with the procurement of plant exudates. In this regard, Charles-Dominique states, "The search for gums constrains the needle-clawed bushbaby to explore particular large-

Table V. Support Preference – Orientations of Supports Utilized During All Sets of Activities[a]

	Support orientation[b]		
	Horizontal	Oblique	Vertical
Galago demidovii (61 g)	18.5	40.0	41.5
Galago alleni (260 g)	7.1	19.8	73.0
Euoticus elegantulus (300 g)	17.9	48.2	34.0
Perodicticus potto (1100 g)	32.4	35.3	32.4
Arctocebus calabarensis (210 g)	25.0	30.0	45.0
Saguinus oedipus (508 g)	36.0	50.8	13.1

[a]The information presented on the lorisid species can be found in Charles-Dominique (1977).
[b]Support orientations: horizontal, 0–15°; oblique, 15–75°; vertical, 75–90°.

calibre lianes and certain trees, particularly large trunks and branches which are inaccessible to the other prosimian species" (Charles-Dominique, 1977, p. 65). Petter *et al.* (1975) have reached a similar set of conclusions in their study of gum feeding in *Phaner furcifer.* A comparable adaptive pattern has been observed in *Cebuella* and *Callithrix* as well.

The modified tegulae exhibited in *Saguinus* are not truly analogous to the claws of a tree squirrel. Structural distinctions, coupled with relatively limited flexion–extension capabilities of the terminal phalanx, prohibit "squirrel-like" locomotor activity on large vertical and sharply inclined supports. The anatomical structure of the tamarin tegula suggests a fairly specific and circumscribed adaptation. It is proposed that this adaptation involves a complex of behavioral and morphological characters related to the procurement of plant exudates. When available, exudates appear to be a preferred item in the diet of this primate.

There is very little quantitative information on substrate preference and positional behavior in any callitrichid primate. Thus, conclusions drawn from the study of a single species (*Saguinus oedipus*) must be viewed with extreme caution. This is particularly true in regard to the Callitrichidae, for one would anticipate a great deal of variation in the locomotor activity of forms such as *Cebuella, Callithrix*, and *Saguinus* which differ so markedly in body weight. Nonetheless, it does appear that exudates are an important dietary resource for many callitrichids and that exudativory in these small-bodied primates is associated with the postural adaptation of vertical clinging. I suggest, therefore, that at present there is evidence to support the contention that claw-like tegulae in *Saguinus* represent a specialized feeding adaptation and not simply a primitive primate character.

The interrelationship between environment, behavior, and morphology provides a framework from which to understand callitrichid adaptations. These adaptations are not convergent with those of the sciurid rodents.

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