Squirrel Monkey (Genus *Saimiri*) Taxonomy

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A Multidisciplinary Study of the Biology of Species

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Introduction

Systematists are more than ever faced with the task of interpreting the biological validity of species from data representing many different biological components. How data, such as molecular, biochemical, chromosomal, behavioral, and morphological, may be interpreted objectively within a consistent paradigm is yet without consensus. Characters have often presided over their interpretation, and it is not unknown for technique to have usurped method. The aim of this study is to assess within a paradigm the contributions of a variety of data toward understanding the species taxonomy of the genus *Saimiri*. This is done under the explicit premises entailed in Mayr's biological species concept (BSC; see Mayr,

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1942, 1963, 1982), and as expanded by Bock (1986; see also Szalay, this volume). A few remarks are made concerning Paterson's (1980, 1985) species recognition concept with regard to *Saimiri* taxonomy.

Seven prominent works have been published this century that have dealt with *Saimiri* taxonomy, including Elliot (1913), Lonnberg (1940), von Pusch (1942), Cabrera (1958), Hill (1960), Hershkovitz (1984), and Thorington (1985). As a result, one to seven species and up to 17 subspecific taxa have been recognized. Constructing testable hypotheses for the species status of one or another group of *Saimiri* is generally arbitrary, that is, whether a single-species hypothesis or a 1000-species hypothesis is used (neither of which may be appropriate) depends largely on preexisting notions formed from reading literature, examining specimens, etc. There is no default null hypothesis for species. Null hypotheses are probablistic and not necessarily biological. For example, Thorington (1985) studied the geographic pattern of coat color variation to construct hypotheses of species that he then tested with a multivariate craniometric analysis. Hershkovitz (1984) alternatively preferred the congruence of karyology and coat color to determine species (hypotheses). The hypotheses considered in this study are similarly treated, that is, a variety of evidence is evaluated for congruence with each species hypothesis. However, species hypotheses need not be constructed *de novo*, as though this is the first look at the genus. The species hypotheses addressed in this study have been advanced by others (most recently, Hershkovitz, 1984; Thorington, 1985; Ayres, 1985), and the ones selected for testing are regarded as those most important to understanding the number of species in the genus.

There are two parts to the approach that follows. The first is a review of literature, by categories of evidence, which is relevant to our current understanding of the number of species of squirrel monkeys, with discussions on the efficacy of the evidence under the BSC paradigm. The second part is an assessment of new evidence, collected in a series of preliminary studies for the determination of species in *Saimiri*. Four species hypotheses are explicitly put to test by the evidence: *S. boliviensis* (Group), *S. ustus*, *S. vanzolinii*, and *S. oerstedii* are each treated as species and tested by the evidence. In light of the new evidence, a fifth hypothesis emerges by default, that South American *Saimiri* is one species.

Review of the Current Status of Saimiri

Geographic Distribution

The geographical distribution of *Saimiri* is basically the Amazon basin, with extensions north into the Guyanas and south into Paraguay. A disjunct population also occurs nearly 1000 km to the north in western Panama and Costa Rica (Fig. 1). The genus is widespread in tropical lowland rainforest along river courses. On the southern continent, collecting localities are densely distributed in an hour-glass-shaped swatch of territory (see Hershkovitz, 1984, Fig. 3), with the major east-west axis situated just below the equator. They are abundant along the Rio Amazonas and its continuation, the Rio Solimões, and for varied distances along many tributaries feeding the great river system. In the west, *Saimiri* fans out to higher latitudes following the central arc of the Andes, reaching as far south as 20°S near the Bolivia–Argentina border and in Paraguay. In the east, more museum specimens come from areas north of the Amazon river, from Guyana, Surinam, and French Guyana. Fewer come from the intervening states of Brazil, and some derive from areas in the east below the Rio Amazonas. Localities also occur north and south of the Rio Amazonas in the central region of the basin, but these are scattered and large areas remain to be sampled. Squirrel monkeys are absent from higher altitudes (above 300 m) and more arid regions surrounding the greater Amazon basin.

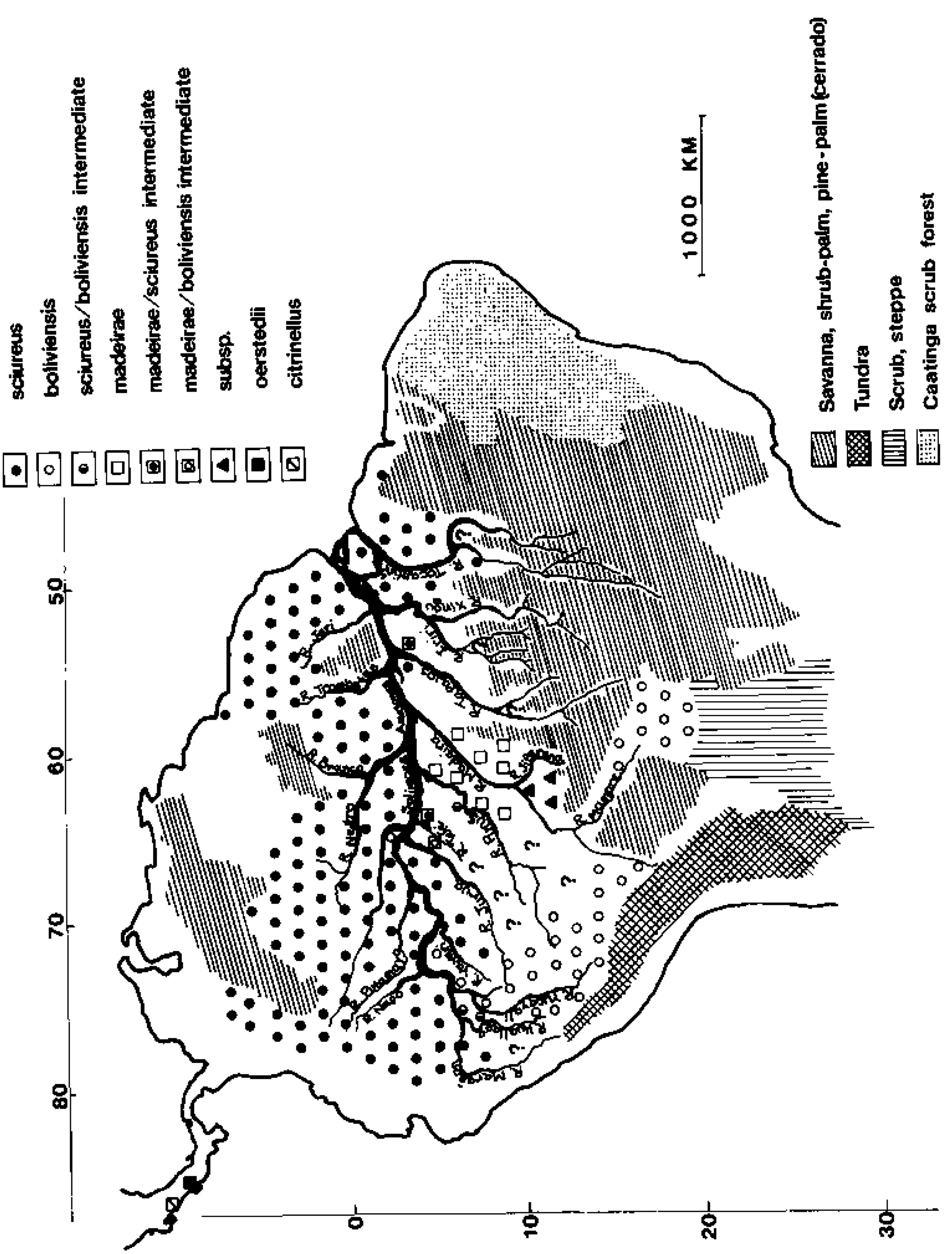
The geographic distribution of South American *Saimiri* appears to consist mainly of parapatric populations, recognized as either species or subspecies. Populations are referred to *sensu lato,* briefly postponing the taxonomic labeling that follows. An exception to parapatry is a single area of (inferred) sympatry involving *sciureus* and *madeirae,* designated by both Hershkovitz (1984) and Thorington (1985), and located between the Rio Madeirae and Rio Tapajós, just south of the Rio Amazonas. Hershkovitz (1984) proposed a second area of sympatry between *boliviensis* and *sciureus* along the Rio Tapiche. According to Thorington (1985) and DaSilva *et al.* (1992), however, the two forms in question intergrade.

As far as (putative) species are concerned, only *sciureus* inhabits the forest on the north side of the Rio Amazonas (following Hershkovitz, 1984; Thorington, 1985), with the exception of the limited north bank distribution of *vanzolinii* (Ayres, 1985) (as shown as an isolated *boliviensis* in Fig. 1). This species (*sciureus*) also inhabits both banks of the Amazon along the eastern and western reaches of that river; thus, with the exception of *vanzolinii,* parapatry of proposed species occurs only along southern tributaries. The distribution of *vanzolinii* is confined to a small string of islands situated within the Rio Solimões and is distributed along its left (north) bank just above Tefé. This region is close to the boundaries of three other *Saimiri* populations, including *madeirae, boliviensis,* and *sciureus.* The *boliviensis* group appears in the upper reaches of the drainage along the Rio Yucayali and Rio Tapiche, and extends south along the Rio Mamoré/Guapore. Parapatry between *boliviensis* and *madeirae* is reported to occur along the Rio Purús and Rio Guapore/Mamoré (Hershkovitz, 1984; Thorington, 1985). The eastern boundary of *madeirae* is not agreed on (see Species Classification, below); therefore, the geographic relationship to *sciureus* cannot be determined from published reports. Very little information is available for the southern ranges and boundaries of groups.

Species Classification

There is no consensus on species or subspecies, partly due to the lack of significant samples from critical geographic areas, and partly to individual differences of interpretation of diverse data. This is likely to be related to different underlying species concepts. Furthermore, with the exception of Hershkovitz (1984) and Thorington (1985), analyses have not been methodologically explained.

Ayres (1985) named a new species of *Saimiri, S. vanzolinii,* based on pelage



sciureus
boliviensis
sciureus/boliviensis intermediate
madeirae
madeirae/sciureus intermediate
madeirae/boliviensis intermediate
subsp.
oerstedii
citrinellus
1000 KM
Savanna, shrub-palm, pine-palm (cerrado)
Tundra
Scrub, steppe
Caatinga scrub forest
50
60
70
80
0
10
20
30
R. Jari
R. Trombetas
R. Branco
R. Negro
R. Xingu
R. Tocantins
R. Madeira
R. Napo
R. Marañon
?

coloration and a restricted geographic distribution covering only young and low flooded forest, that is, the *varzea.* The diagnosis of *vanzolinii* was strengthened by chromosome differences (Yonenaga-Yassuda and Chu, 1985) and the discovery of *sciureus* and *madeirae* populations situated parapatrically to *vanzolinii* without any evidence of intergradation. Hershkovitz (1985) considers *vanzolinii* as a subspecific member of *boliviensis.*

Hershkovitz (1984) focused on developing a key to the species and subspecies, groups based largely on their karyotypes, geographic distribution and pelage coloration, but he also included laboratory hybridization, behavior, and craniodental and body measurement. His scheme recognized four species (*boliviensis, ustus, sciureus,* and *oerstedii*), arranged into two species-groups (the Roman- and Gothic-arch forms). The *S. boliviensis* Group included *boliviensis* only; the *S. sciureus* Group included *sciureus, oerstedii,* and *ustus* (= *madeirae* of Thorington, 1985). He noted (p. 300) that the "true taxonomic status (of *oerstedii*) awaits better knowledge of its karyotype." This reflected Hershkovitz's suspicion that *Saimiri* was introduced by people to Central America in Recent time, and the priority given to karyotype in species discrimination. Hershkovitz's "Group" divisions were originally devised by MacLean (1964) on the basis of facial appearance, especially the shape of the whitish eye patch.

Thorington (1985) provided a detailed assessment of the geographic variation in skins and skulls, including univariate and multivariate analyses of 19 craniodental measurements. He recognized two South American species, *S. sciureus* and *S. madeirae,* lumping Roman-arch *boliviensis* together with Gothic arch *sciureus.* To Thorington, *oerstedii* represents a subspecies of *sciureus.* Although he recognized the strong color differentiation of the red-back *oerstedii,* he found them to be no more different cranially from *S. sciureus sciureus* than the latter is from *boliviensis.* Thorington's second distinct species, *S. madeirae,* refers to the same population that Hershkovitz named *S. ustus* and that he located in central Brazil below the Rio Amazonas, bounded west and east by two major rivers, the Rio Purús/Rio Guapore and Rio Tapajós, respectively. Hershkovitz (1984) recognized the distribution of this population extending further east to the Rio Xingu-Iriri. Thorington considered *Saimiri* from east of the Rio Tapajós to be *sciureus.* Thorington's and Hershkovitz's attribution of species status to the *madeirae* form is based upon several findings: (1) inferred sympatry with other *Saimiri* and (2) a strong phenotypic boundary along the species' southwestern limit at the Bolivia–Brazil border.

Why do Hershkovitz (1984) and Thorington (1985) refer to essentially the same population as *S. ustus* and *S. madeirae,* respectively? *Saimiri ustus* was assigned by Geoffroy (1844) to a specimen obtained in Portugal. Geoffroy's animal is illustrated with an olive crown; burnt-orange dorsum (thus its name, "*Saimiri ustus* a dos brule"); yellow-orange feet, hands, and forearms; and a hairy, not naked, or tufted, ear. The specimen locality is unknown. Hershkovitz (1984)

Fig. 1. The geographic distribution of *Saimiri* in Central and South America. Upper left and clockwise are the two forms of Central American *S. oerstedii, oerstedii,* and *citrinellus.* All South American forms are members of *S. sciureus.* No judgment is made on the subspecific status of these geographic forms. Above the Amazon river is *sciureus;* below the Amazon river, from east to west is *sciureus,* the naked-eared *madeirae,* and the dark skull-capped *boliviensis,* with *peruviensis* directly above.

followed Cabrera (1958) when he accepted *ustus* as a valid name for monkeys with naked ears and fulvous hands, and he restricted the type locality to Humaitá (Thomas, 1908). However, the specimen named by Geoffroy does not fit either Hershkovitz's or Thorington's descriptions and, as Thorington (1985) has suggested, it could not have come from anywhere near the type locality. Thomas (1908) named *S. madeirae* based on five specimens collected along the west bank of the Rio Madeira, at Humayta (= Humaitá). His description agrees perfectly with both Hershkovitz's and Thorington's, though he failed to describe the condition of nearly hairless ears. The name *ustus* is best treated as a junior synonym of *sciureus*, from which Geoffroy's animal is nearly indistinguishable, except for the lack of a tuft of hair on the ear. Naked-ear squirrel monkeys of the type described by both Hershkovitz and Thorington hereafter are referred to as *madeirae*.

The confounding state of taxonomy makes it cumbersome to adopt a neutral, yet useful, nomenclature. We refer to geographic groups throughout this report by the last name of a binomen or trinomen, without any intentions as to the species or subspecies status of the groups. For purposes of style and grammar, genus and species are used to begin sentences. Table 1 and Fig. 1 indicate in detail the geographic groups used and some traits that distinguish those groups from each other.

Pelage Coloration

Saimiri species taxonomy has largely been driven by geographic differences of coat coloration. The taxonomic value of patterns of pelage variation is particularly difficult to interpret in *Saimiri*, an animal that is not known to have geographic variation of premating behaviors (discussed under Behavior, below). Differences of sexual dichromatism between geographic groups that are otherwise similar in coat coloration, and that are undisputed members of the same species, suggest some discontinuity in gene flow, coupled with minor differences in sexual selection, or drift. For example, both male and female *oerstedii* from Costa Rica have black crowns, whereas males and females from the nearest geographic population, *citrinellus* of Panama, have gray and black crowns, respectively (Hershkovitz, 1984). Coat color patterns can be used, however, not only to define sympatry and parapatry, but to infer barriers to the introgression of genes, and alternatively, to recognize intermediates and to infer gene flow. A lack of intermediates from areas of sympatry and parapatry is negative evidence for barriers to gene flow or else may be due to sampling error.

The taxonomic groups deserving closest attention are "*boliviensis*," "*vanzolinii*," "*madeirae*," and "*oerstedii*" (see Table 1). Samples of *boliviensis* (including *peruviensis*) *vanzolinii*, and *oerstedii* are distinguished from *madeirae* and *sciureus* by having black, rather than gray or olive, crowns. *Saimiri boliviensis* and *vanzolinii* are further distinguished by the Roman-arch pattern of supercilliary hairs. This is in contrast to the peaked, Gothic-arch pattern of *oerstedii, madeirae,* and *sciureus*. Of the Roman-arch squirrel monkeys, *vanzolinii* is characterized by a continuous, dark dorsal stripe that runs from crown to tip of tail. *Saimiri oerstedii* is the only group with an entirely red back, and it is the only black-crowned group

Table 1. Pelage Variation and Social Organization

	boliviensis	*madeirae*	*oerstedii*	*sciureus*	*vanzolinii*
Coat color patterns					
Supercilliary Patch	Roman	Gothic	Gothic	Gothic	Roman
Crown	Black, tapers caudally	Bluish-gray	Black	Olive to olive-gray	Black, tapers caudally
Dorsum	Gray, black, orange and agouti	Burnt-orange, black dorsal stripe	Red-orange, long hair	Gray, olive, or burnt-orange	Gray/black, with black stripe
Forelimb	Yellow hand and forearm, gray shoulder	Fulvous hands or hands and forearm, shoulder gray	Orange-yellow hand and forearm, olive-gray shoulder	Orange-yellow hand and forearm, olive-gray shoulder	Yellow hand and forearm, gray shoulder
Behavior					
	Sexually segregated, dominance hierarchy, male emigration	?	Sexually integrated, no dominance hierarchy, female philopatry	Sexually integrated, dominance hierarchy	?

within the Gothic-arch division. *Saimiri madeirae* is distinguished from *sciureus* by a gray crown, naked ears, and fulvous hands, whereas *sciureus* has an olive to olive-gray crown, and the tufted ears and yellow forearms in common with every other group.

Thorington's (1985) analysis of *boliviensis* concluded that there is clinal variation with intergradation between *boliviensis* and *sciureus* in Peru (Fig. 1) and an abrupt western border separating *boliviensis* from *madeirae* along the Rio Guapore/Mamoré and along the Rio Purús. Hershkovitz (1984) does not acknowledge this intergradation.

Specimens of *madeirae* and *sciureus* from around the Rio Tapajós have a mix of traits. Along the east side of the river, naked-ear monkeys share coat color features with *sciureus*. These animals have olive-gray crowns and yellow forearms, in contrast to the gray crown and fulvous hands of *madeirae*, near Humaitá (Thorington, 1985). That this suggests intergradation between *madeirae* and *sciureus* was not overlooked by Thorington (1985), yet the apparent sympatry between them convinced both Thorington and Hershkovitz that the two do not likely interbreed. Thorington also mentioned *madeirae* specimens from Calama (the southern portion of their range) with yellow forearms and gray crowns without suggesting intergradation.

The apparent intergradation along the Tapajós river and on the right (west) bank of the Rio Madeira, at Calama, is equivocal with regard to the species status of *madeirae*. There is inferred sympatry between the Rio Tapajós and Rio Madeira, without intergradation, and there is evidence that may be interpreted as intergradation with *sciureus* east of the Rio Tapajós, and at Calama, in the southwest quadrant of the group's distribution. Either *madeirae* is polytypic, with subspecies located east and south, those enigmatic specimens are intermediates, they represent other species, or the populations are polymorphic.

Cranio-Dental Studies

Niche separation, that is, differential use of the environment, is one common component of species, and species adaptations that vary geographically may reflect differences of the environment, not changes in niche. Cranio-dental features may, therefore, reflect form-functional differences in populations or species-specific adaptations. Establishing such characters in no way implies they are acquired at "speciation," or that they represent species. It only refers to the fact that species' niches evolve, and adaptive, form–function correlates may be discovered.

Dental evidence relevant to the taxonomy of *Saimiri* is limited to a few studies. Orlosky (1973) argued for species status of *oerstedii* based on the presence of statistically significant differences in traditional dental dimensions when compared to a sample of South American *sciureus*. Galliari and Colillas (1985) recorded dental eruption sequences of *boliviensis* and compared their results to those of a similar study of Colombian *sciureus* by Long and Cooper (1968). Their findings reveal significant differences in the sequence and timing of eruption, specifically in the sequences of premolar eruption and the relatively delayed eruption of M_3 in *boliviensis*. Based on this evidence, Galliari and Colillas (1985) suggested that the two groups are separate species. A perfectly valid alternate interpretation of their work suggests the differences are interpopulational, and the notion of species-specific eruption sequences should not be generally applied. Rosenberger *et al.* (1991) showed that standard dimensions of P_4-M_2 did little to segregate the populations recognized by Hershkovitz (1984) and Thorington (1985).

Thorington (1985) used univariate and multivariate cranial analysis to test species and subspecies hypotheses. When cranial differences were found concordant with pelage differences, taxa were upheld or renamed. Thorington's analysis is not unequivocal, and this is shown in the indeterminancy of the *madeirae–sciureus* comparison. With regard to skull length, the sample he used from the Rio Tapajós is not a cranial intermediate between *madeirae* to the west and *sciureus* to the east. Another sample (*madeirae*) from between the Tapajós and Madeira rivers is more similar to *sciureus* from the same locality than to any other *sciureus* sample, and it falls nearly midway between *sciureus* to the east and *madeirae* from further west. Other "single taxon" samples were separated by skull size, such as a northern sample of *boliviensis* from a southern *boliviensis* group. The deciding principle employed by Thorington to discriminate taxa based on differences of size and proportion is whether there are geographically intermediate samples that are also morphologically intermediate.

Based on the craniodental evidence, a stronger case can be made for the synonymy of *boliviensis* and *sciureus* than for the autonomy of *madeirae*. Cranial evidence for *oerstedii* does not point strongly one way or the other.

Chromosomes

Chromosome studies of squirrel monkeys began in the late 1950s (Bender and Mettler, 1958). While all squirrel monkeys examined to date possess a diploid chromosome number of 44, animals from certain geographic regions have been found to vary in the number of acrocentric (V-shaped) vs. metacentric (X-shaped) chromosomes they possess (Table 2; Jones *et al.*, 1973; Ma *et al.*, 1974; Jones and Ma, 1975; Hershkovitz, 1984; Assis and Barros, 1987; Lacy *et al.*, 1988). This variability has been attributed to pericentric inversions occurring in chromosome pairs 15 and 16 (Ma *et al.*, 1974; Lau and Arrighi, 1976; Moore *et al.*, 1990).

Among captive animals of unknown origin, karyotyping alone is not always a conclusive means of differentiating geographically separated populations within *Saimiri* because certain geographically separated populations possess the same ratio of acrocentric to metacentric chromosomes (e.g., *oerstedii*, *madeirae*, and *peruviensis*) and because this ratio can vary among second and later generation hybrids (Lacy *et al.*, 1988; VandeBerg *et al.*, 1990b). Populations that are generally agreed to belong to the same species show interpopulational variance in acrocentric and biarmed pairs equal to those occurring between groups that are more separated geographically and that show greater differences in other features (e.g., *boliviensis* and *peruviensis* subspecies are as different from one another as, for example, *boliviensis* from *oerstedii*).

Recently, Moore *et al.* (1990) compared several homologous chromosomes among the *boliviensis* Group (*boliviensis* and *peruviensis*) and *sciureus* in order to document differences in the distribution of C-banding patterns and nucleolar organizer regions. Most significant was their finding that only *sciureus* possesses a terminal C-band in chromosome 5.

Chromosomal traits may have causal relevance as postmating isolating *effects*, though there is little evidence to suggest a necessary correlation with speciation (e.g., Sites *et al.*, 1987; Carson, 1987). The number of species documented for intraspecific variation in numbers of chromosomes is steadily increasing (e.g., Hamilton *et al.*, 1980; Rumpler, 1975; Hershkovitz, 1983), and the usefulness of karyotypes in discriminating taxa is not general and remains more of a case-by-case procedure (clusters of Hawaiian *Drosophila* species have identical banding sequences for major chromosomal elements; Carson, 1987). One con-

Table 2. *Saimiri* Chromosome Data

Taxon	2n	Number of acrocentric autosome pairs	Number of biarmed autosome pairs	Terminal C-band in chromosome 5	Ref.[a]
sciureus	44	7	14	Present	1,2,4
macrodon	44	6	15	?	1,2
oerstedii	44	5	16	?	1
madeirae	44	5	16	?	3
boliviensis	44	6	15	Absent	4
peruviensis	44	5	16	Absent	1,2,4

[a] 1, Jones *et al.* (1973); 2, Ma *et al.* (1974); 3, Assis and Barros (1987); 4, Moore *et al.* (1990).

clusion is that inversions are not necessary for speciation. The application of inversions to the taxonomy of groups has been without a thorough understanding of the meiotic effects of inversions on the process of speciation (e.g., Sites *et al.*, 1987) and has resulted in the naming of "chromosomal species." Also the theoretical works of Barton (1979) and Spirito *et al.* (1983) suggest that more than one or two chromosomal rearrangements would be required to effect (reduce) appreciably gene flow in hybrid zones. Until generalizations can be supported on this subject, inversions and other chromosomal polymorphisms should be treated as the symptoms of mating isolation (biological or geographical), not the causes of it.

The notoriously high rates of abortion, stillbirth, and infant mortality among captives (Kaplan, 1977; Wolf *et al.*, 1975; Dukelow, 1982; VandeBerg *et al.*, 1990b) might be indirect evidence that infertile hybrid matings are a more widespread phenomenon than previously recognized (Moore *et al.*, 1990). There are also numerous instances of anomalous karyotypes in the hybrid offspring of parents from geographically separated sources (Moore *et al.*, 1990). To the best of our knowledge, no controlled breeding experiments have been performed to determine the fertility of hybrid crosses between geographically separated *Saimiri* populations. Until *in vitro* cytological studies of meiosis for both sex combinations are executed and establish the frequency of nondisjunction, numbers of chiasmata, and also the degree to which recombination takes place, we cannot say there are genomic postmating isolating mechanisms between parapatric or sympatric samples.

Biochemistry

Protein electrophoresis has played a role in squirrel monkey systematics, and biochemical markers may someday provide an alternative to karyotyping as a means of assessing the affinities of individual animals. Recent studies (DaSilva *et al.*, 1987a,b, 1992; Lacy *et al.*, 1988; VandeBerg *et al.*, 1990a,b) have compared a number of distinct geographic and chromosomal forms using standard electrophoretic methods. VandeBerg *et al.* (1990a,b) describe the first study of biochemical genetic markers in a relatively large number of pedigreed individuals of *boliviensis*, *peruviensis*, and *sciureus*. Twenty-six blood proteins were surveyed, 14 of which were polymorphic. Allelic frequencies at 13 of these variable loci showed statistically significant differences among the three populations and were useful in detecting hybrids. For example, the distribution of two alleles at the *ADA* locus consistently distinguished *sciureus* from *boliviensis* and *peruviensis* samples. Other alleles were restricted to one or two groups.

In a preliminary survey, DaSilva *et al.* (1987b) found genetic distances to be lowest among two geographic samples of *sciureus* from the Rio Jari and the Rio Tocantins, tributaries located on opposite banks of the lower Amazon, and a Peruvian *sciureus* population (*S. s. macrodon* of Hershkovitz)—some of the most widely separated populations within South America. These authors also report low genetic distances between *peruviensis* and *boliviensis*. Finally, they suggest that *madeirae* from central Brazil south of the Rio Amazonas is closer to *sciureus* than to *boliviensis* or *peruviensis*, but their results do not agree with another preliminary study based on karyotyping (Assis and Barros, 1987). In yet another report, Lacy *et al.* (1988) made a preliminary electrophoretic survey of *boliviensis* from Peru and of *sciureus* from Colombia and the Guyanas. Their results did not support any previously proposed classificatory scheme.

One study (DaSilva *et al.*, 1992) sampled 49 animals from Peruvian Amazonia in the area where *macrodon* and *peruviensis* overlap in their distributions. This is in the area where Hershkovitz thought the two groups were sympatric. Along the Rio Ucayali, eight of the animals collected were identified as Roman-arch. Six of those showed biochemical admixture. Another 14 Gothic-arch squirrel monkeys also showed admixture. In all, 22 of the 49 (45%) showed some indication of admixture.

Sampling may play an enormous role in the results gained by electrophoretic studies and many scenarios could be described. If there are hybrid zones, such as the areas described by DaSilva *et al.*, (1992) and Thorington (1985), and one or more exist along the borders of a geographic group, then specimens originating in, near, or away from a zone may effect the results. DaSilva *et al.* (1987b) concluded that *madeirae* is closer to *sciureus* than it is to *boliviensis* or *peruviensis*. Was their *madeirae* sample from near the Rio Tapajós, and thus geographically close to *sciureus* where introgression may be taking place, or was that sample from west of the Rio Purús, in the vicinity of *boliviensis* populations? Lack of specific geographical information for samples used in species-level biochemical studies lessens the usefulness of these contributions for discriminating parapatric species.

Biochemical studies give weak support for a Roman-arch group and a Gothic-arch group, beyond which little can be inferred or taxonomically resolved.

Behavior

Does *Saimiri* exhibit any survival or reproductive behaviors that may function to isolate groups? Three aspects of behavior that may be directly related to (strategies of) reproduction and niche are social organization, vocalization, and feeding behavior (Table 1, Figs. 2 and 3, and Table 3, respectively). Both captive and wild studies provide information on these areas.

Geographic differences of behavior among squirrel monkeys have emerged from observations on captive animals (e.g., Mendoza *et al.*, 1978; Martau *et al.*, 1985). Some of the variations appear to reflect population-specific, and inferred, genotypic differences, such as aspects of social behavior (Mendoza and Mason, 1989), stereotyped displays (Maclean, 1964), and vocalizations (Winter, 1969).

An extensive series of captive studies is available on social behavior and its physiological basis for two forms of *Saimiri: sciureus* and *boliviensis*. Observations indicate (1) *boliviensis* has a sexually segregated social organization in which males and females remain spatially separated outside of the breeding season, whereas *sciureus* males and females are integrated throughout the year. (2) In *boliviensis* social groups, independent linear dominance hierarchies are present within each sex. Among *sciureus* groups, a single linear hierarchy includes both males and females. Male and female social relationships in the two groups ap-

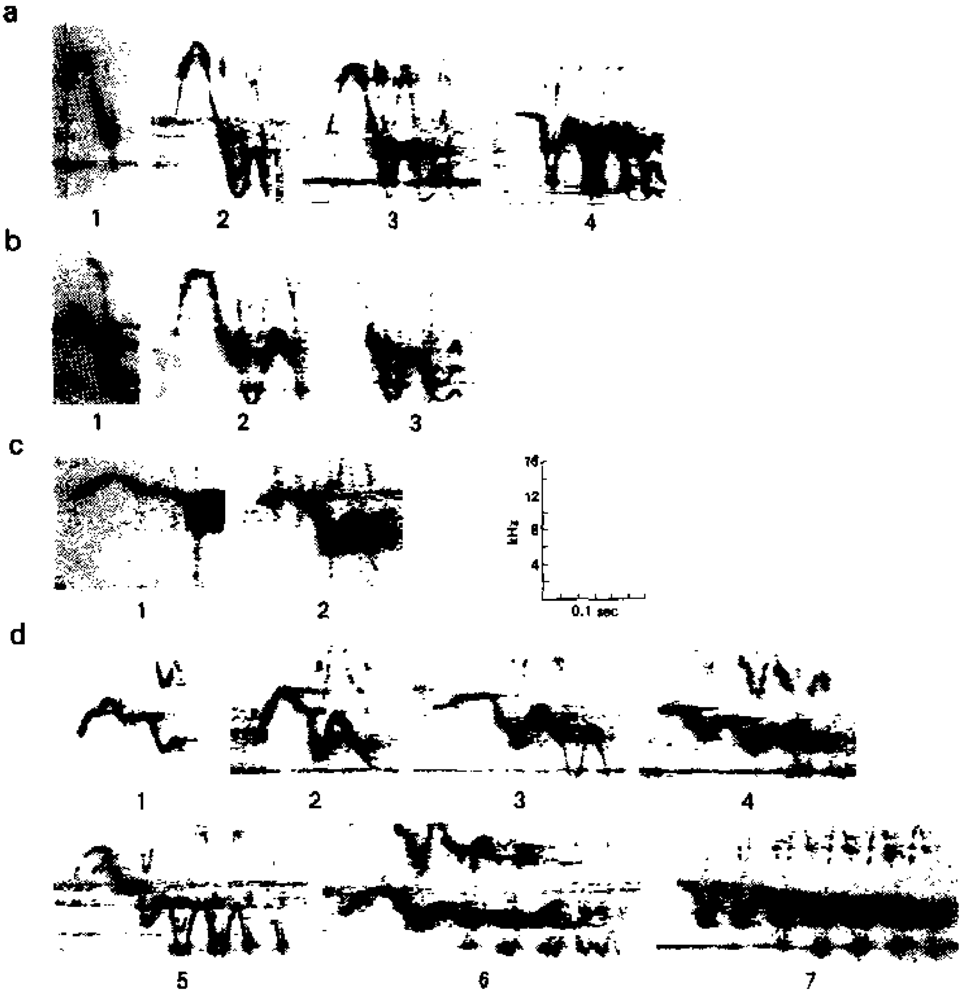


Fig. 2. The major categories of calls produced by *S. oerstedii* in Costa Rica: (a) smooth chuck, (b) bent mast chuck, (c) peep, and (d) twitters. Subtypes within each call category are designated by numbers.

pear to be regulated by two distinct mechanisms, dominance relationships in *sciureus* (Mendoza *et al.*, 1978) and sexual segregation in *boliviensis*. (3) Female *boliviensis* have higher female cortisol titers, longer and more sustained adrenal responses to stress, are dominant over males, and more actively initiate agonistic interactions compared to *sciureus* (Coe *et al.*, 1985).

Unfortunately, the degree to which these data can be applied to the taxonomy of *Saimiri* is limited. Much of the information on *Saimiri* behavior derives from studies in which the exact geographic source of the captive animals is not known.

Field studies of *oerstedii* in Costa Rica and *boliviensis* in Peru reveal strong differences in the social behavior of these groups from each other and particularly among females (Mitchell *et al.*, 1991). In *oerstedii*, female relationships appear to be undifferentiated. There are no female–female alliances and no female dominance hierarchies. Females also disperse from the troop in which they are born. On the other hand, female ***boliviensis*** in Peru exhibit differentiated female relationships, a female dominance hierarchy, and female philopatry. An important evolutionary factor thought to be responsible for the disparity in the social relationships of female squirrel monkeys in Costa Rica and Peru relates to differences in the distribution of fruit resources (Mitchell *et al.*, 1991). In Peru, the fruit patches are large, and it may be advantageous for females to acquire

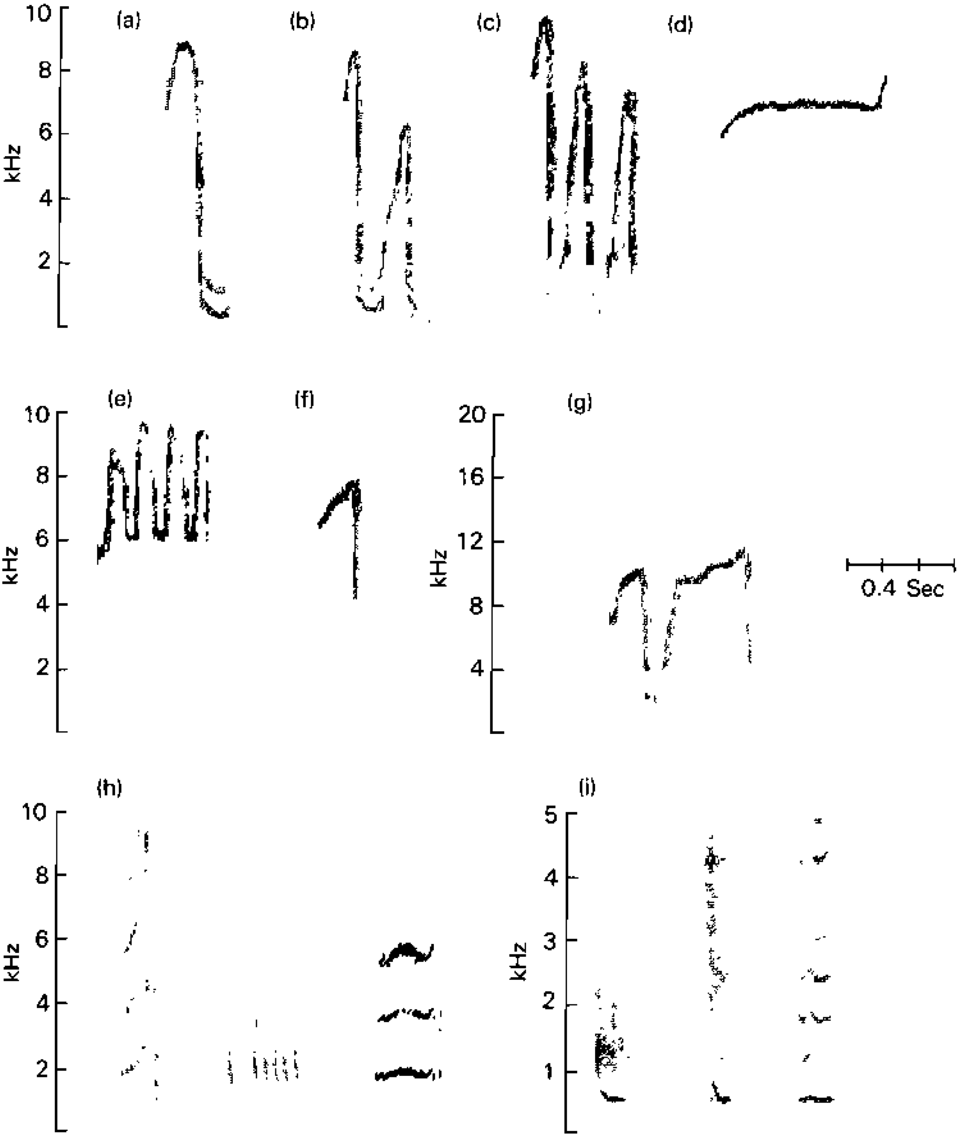


Fig. 3. The major categories of calls produced by *S. sciureus* in Peru: (a) single chuck, (b) double chuck, (c) multiple chuck, (d) peep, (e) tweet, (f) peep-chuck, (g) tweet-chuck, and (h, i) examples of six "mother" calls. Mother calls are vocalizations that appear to be directed exclusively by mothers to their infants and are not found among *S. oerstedii* in Costa Rica.

and to defend them aggressively; hence the dominance hierarchies. In Costa Rica, fruit patches are generally small and unlikely to satiate even one individual. There is no direct competition for food, and dominance hierarchies have not evolved as a consequence of aggressive female interactions.

The limited field information on male squirrel monkey behavior describe differences between *oerstedii* and *boliviensis* (Boinski, 1987b; Mitchell, 1990; Boinski and Mitchell, 1992). Costa Rican *oerstedii* males usually remain in their natal troop until full adulthood. There is only one observed instance of male migration. Aggression among *oerstedii* males within a troop has never been observed, though subadult and young males engage in extensive play and rough play.

S. boliviensis monkeys from Peru emigrate from their natal troop before maturity and form all-male subgroups. The few adult males that remain with the females and young throughout the year have overwhelmingly agonistic interactions with each other and with the females. Aside from the brief mating season, females behave aversively toward males.

Males of the genus, without known exceptions, also undergo annual male fatting (Dumond and Hutchinson, 1967), a reproductive physiology unique among primates.

The vocal behavior of squirrel monkeys has been studied in the laboratory and more recently in the field (Boinski and Newman, 1988; Boinski, 1991; Boinski and Mitchell, 1992). *Saimiri* have easily identifiable calls; nearly all have a simple, pure-tone frequency structure that ranges up to about 12 kHz. Most vocalizations fall into two categories, chucks and peeps (see Figs. 2 and 3), at least based on the phonemic typology of a human scrutinizing a sonogram. Yet contrary to other aspects of their behavior (particularly foraging), vocalizations are geographically differentiated, making it unlikely that geographically separated populations of squirrel monkeys would completely recognize each other's vocal repertoire (Snowdon *et al.*, 1985; Boinski, 1991; Boinski and Mitchell, 1992). Nearly every population of squirrel monkeys studied to date has a set of unique vocalizations, albeit these are not commonly produced (Boinski and Mitchell, 1992). Squirrel monkeys do not produce mating calls, and the likelihood that vocalizations function to preclude hybridization appears to be small (e.g., DaSilva *et al.*, 1992).

However, there are indications that suggest vocalizations may play a role in the postmating success of hybrid individuals. Data from captive animals provide evidence for the genetic basis of the acoustic structure of squirrel monkey vocalizations (Winter *et al.*, 1973; Newman and Symmes, 1982). At least some vocalizations of newborn individuals closely approach adult versions of the same call, indicating that the role of learning is small. The offspring of crosses between *boliviensis* × *sciureus* have structurally intermediate vocalizations. *S. boliviensis* and *sciureus* do not respond to the calls of a separated, distressed infant of the other group but do respond to the "separation peeps" from infants of their own group (Snowdon *et al.*, 1985). Additional differences between the vocal behavior of *sciureus* and *boliviensis* in captivity include the rate at which females exchange chucks and the pattern of extremely slight structural modifications that can occur in these chucks, depending on whether the chucks initiate or end a series (Biben *et al.*, 1986; Masataka and Biben, 1987).

Table 3. Group Feeding Statistics

Trait	*oerstedii* (Costa Rica; Boinski, 1987, 1988)	*boliviensis* (Peru, Terborgh, 1983)	*boliviensis* (Peru, Mitchell *et al.*, 1981)	*sciureus* (Colombia, Klein and Klein, 1975)
Group size	35–65	35	45–75	25–35
Home range	200 ha	>250 ha	250–500 ha	65–130 ha
Density	0.36/ha	0.50/ha	0.60/ha	0.50–0.80/ha
Time allocated to foraging insects	45–65%	50–75%		
Time allocated to rest	5–10%	11%		

Squirrel monkey populations in the wild glean foliage on terminal twigs; forage on soft, berry-like, fruits; and prey on arthropods, particularly caterpillars and grasshoppers (Mitchell *et al.*, 1991; Janson and Boinski, 1992). Occasionally nectar is eaten, but there are no well-documented instances of squirrel monkeys eating nonreproductive plant tissue, such as leaves, bark, or stems. Variations reported from different field studies reflect site differences in the abundance and distribution of food sources, as foraging techniques and food preferences appear identical across sites (Janson and Boinski, 1992). In light of this homogeneity (Table 3), and the close similarity of body size and morphology across populations, it is intriguing to ask whether sympatry could exist in *Saimiri*, as it does in *Cebus* and *Saguinus*, for example. If sympatry does exist, what are the niche differences, if any?

There are no obvious "challenging" behavioral patterns or displays that are likely to inhibit matings between individuals from geographically isolated populations. Wild individuals observed in both Costa Rica and Peru commonly copulate with no evident preparatory interactions, no stereotypical mating displays, and no vocalizations specific to mating (Boinski, 1992; Mitchell, personal communication). In fact, males and females, both in captivity and the wild, typically lack any premating affiliative behaviors apart from the limited association and occasional olfactory investigations that occur just prior to copulation (Mendoza *et al.*, 1991). For squirrel monkeys, it may be extremely difficult to identify even tentatively any effective behavioral reproductive isolating mechanisms. Olfactory signaling may as yet offer an area where barriers can be identified.

The behavioral evidence does show (1) the same feeding behavior is shared by all squirrel monkeys; (2) nontrivial differences in the social organization of three groups, *boliviensis*, *sciureus*, and *oerstedii*, each appearing under different ecological conditions, to optimize their feeding strategy; (3) a genetic basis for the acoustic structure of vocalizations, at the deme or population level, which may act to diminish hybrid viability; and (4) no known premating behaviors that could possibly function in the reproductive isolation of groups.

We cannot say there is more than one mate-recognition system present within the genus. Yet the differences in vocalizations and social behavior, in captivity, suggest a genetic basis for both, a basis that differs between the three groups. Ecological differences may indeed explain why social behaviors differ, and those behaviors may have their bases fixed within the group genomes. All these may well be clinal across territory that is not yet sampled or adequately sampled, where geographic groups come into contact.

Methods and Materials

The "species question" of primary importance with regard to parapatric and sympatric areas in South America is whether there is (indirect) evidence for gene flow across parapatric regions and between forms thought to be sympatric with one another. Character studies are often the basis on which we make inferences about introgression. Each character provides information on the phenotypic differences that have accrued in the forms of *Saimiri*. These may reveal clues about the processes that transform phenetic groups into cladistic ones. The allopatrically distributed Central American *oerstedii* is another matter. We can only assess differences for their significance to the biological validity of the group as a species, knowing there has been geographic separation for some indeterminate amount of time. In this sense, characters are markers that offer indirect evidence of the natural status of a group. To these two ends, we have measured and described characters of *sciureus, boliviensis, madeirae, vanzolinii,* and *oerstedii*. We do not treat the subspecific status of groups.

Geographic Distribution and Pelage Coloration

Skins were examined at three Brazilian museums, Museu Paraense "Emilio Goeldi," Belém (MG); Museu Nacional, Rio de Janeiro (MN); Museu de Zoologia, São Paulo (MZ); and at the American Museum of Natural History, New York (AMNH) and the Field Museum of Natural History, Chicago, to assess coat color variation and patterns of geographic distribution. Specimens from critical areas were recorded on 8-mm videotape and reviewed extensively.

Dentition

A sample of specimens from the American Museum of Natural History was selected to represent as broad a geographic distribution as possible, and to include the major phenetic and taxonomic groups, *boliviensis, sciureus, madeirae,* and *oerstedii*. A minimum of 15 specimens, equally apportioned to sex, when possible, was measured from each major geographic group, for a total of 110 specimens.

We investigated topographic relations of crown morphology and standard tooth-size measures by digitizing the crown surface in two dimensions (see, for example, Fink, 1990; MacLeod, 1990; Rohlf, 1990 for an overview on digitizing). Gathering coordinate data from corresponding landmarks on homologous features allows questions to be asked about topographic regions (O'Higgins, 1989). We do not refer to these landmarks as homologous; they are defined geometrically, by least radius or curvature of a surface or by the intersection of two or more surface features, for example. Traditional maximum and minimum dimensions taken on teeth often do not represent such corresponding points on homologous features, and regardless of the extensive naming of tooth surface features, the actual boundaries of homologous features are undefined. Coordinate data allow exact topographic relations of crown morphology to be quantified. Although not executed for this study, three-dimensional (3-D) digitizing of crown surfaces is feasible and has been done by others (for example, Kanazawa *et al.*, 1983a, 1988; Hartman, 1986, 1989; Richmond, 1987). A significant constraint of 3-D methods is the restriction of samples to nearly unworn teeth and the virtual elimination of M1 from the analysis because of the early eruption of that tooth in the eruption sequence (Hartman, 1989). In two dimensions (2-D), landmark locations may be interpreted on moderately worn teeth without serious compromise of the measure. In 3-D, landmarks must be similarly interpreted on worn teeth; however, 3-D distances are affected by the differential wear of tooth areas or by shape differences (and 3-D metrical analysis is generally one- or two-dimensional).

Landmarks were preassigned to the crown surfaces of all lower first molars before measurement (Fig. 4). The spatial positions of all landmarks were recorded as Cartesian coordinates using a video-digitizing system interfaced with a desktop computer. Linear dimensions were calculated from the X, Y data. Specimens (complete lower jaws) were placed on a stack of flat plastic shims on a stage without further manipulation. The shims were used to maintain the focal distance from the lens by adding or subtracting them, thus avoiding changes in scale with lens adjustments. Any orienting procedure is arbitrary (Ramaekers, 1975; Kanazawa *et al.*, 1988; Hartman, 1989), and this one was selected for ease and repeatibility. A wear-graded series of lower first molars, representing pristine to obliterated crowns with slight increases in wear between adjacent teeth, was studied to determine the effect of wear on the apparent locations of landmarks.

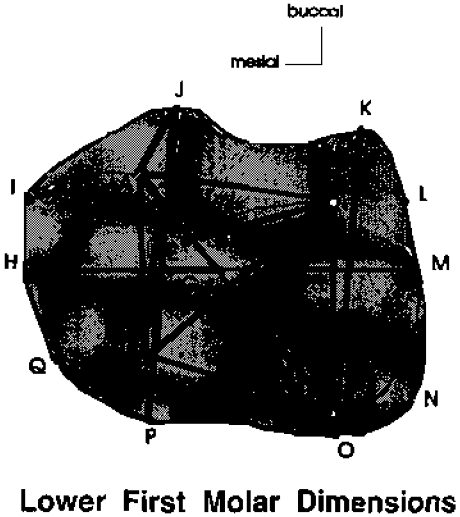


Fig. 4. Landmarks assigned to M_1 and the 11 length variables used for two-dimensional analysis. A, protoconid; B, hypoconid; C, entoconid; D, metaconid; AJ, maximum buccal flare; BE, chord length of cristid obliqua.

A number of specimens were remeasured on different days without reference to the state of wear of those specimens. Coordinates were plotted on graph paper at lens magnification and compared. Differences from day to day were negligible.

Principle components, Pearson correlation coefficients, and t- and f-tests were performed, and simple statistics were calculated using SAS. Frequencies of variables significant at the 0.05 level were determined to assess the relative contribution of variables in the discrimination of groups. In addition, angles between cusps were calculated to compare the topographic relationships of cusps between groups. All variables used in the analysis were checked for approximation to normal distribution. Eleven out of all possible variables were chosen for analysis.

Biochemistry

We have compared squirrel monkeys from four geographic areas using high resolution two-dimensional electrophoresis (2DE; O'Farrell, 1975). This method separates proteins using two independent, intrinsic parameters: protein isoelectric point, a charge parameter, and protein molecular weight. When very sensitive methods are used to stain the proteins separated by the 2DE procedure, hundreds of proteins can be resolved in a single gel, producing tissue-specific patterns that are highly reproducible (Harrison *et al.*, 1992).

Blood samples were studied from six *boliviensis*, four *peruviensis*, and four *sciureus* squirrel monkeys. The majority of these samples were provided by the Department of Comparative Medicine, University of South Alabama College of Medicine; two of the six *boliviensis* were obtained from the Delta Regional Primate Research Center. A single individual in the collection of the Santa Ana Zoo, which we believe represents *oerstedii* on the basis of phenotype, was also examined.

Whole blood was collected in EDTA and the plasma fraction was separated by centrifugation. Plasma proteins were denatured and made soluble in four volumes of a mixture containing 2% sodium dodecyl sulfate (SDS), 1% dithiothreitol (DDT), and 10% glycerol in 40 mM cyclohexylaminoethane sulfonate (CHES, pH 9.5) ("SDS mix" of Tollaksen *et al.*, 1984). Sample aliquots were heated for 5 min in a 95 °C water bath and then stored at −75°C until needed.

High resolution 2DE (O'Farrell, 1975) was performed, with modifications (Daufeldt and Harrison, 1984), using the ISO-DALT™ multiple gel casting and electrophoresis system (N. G. Anderson and N. L. Anderson, 1978; N. L. Anderson and N. G. Anderson, 1978; Tollaksen *et al.*, 1984). Charge (Hickman *et al.*, 1980) and molecular weight standards (Edwards *et al.*, 1982) were added to each gel to facilitate alignment of protein spot patterns between gels. A modification (Harrison *et al.*, 1992) of the ammoniacal silver staining method of Guevara *et al.* (1982) was used to visualize the separated proteins.

A 2DE gel was run for each of the 15 individual squirrel monkeys in our sample (e.g., Fig. 5). In addition, each possible pair-wise combination of the four taxonomic samples was run together on a single gel (termed *coelectrophoresis*), using one individual to represent each group. Forty-eight of the best resolved

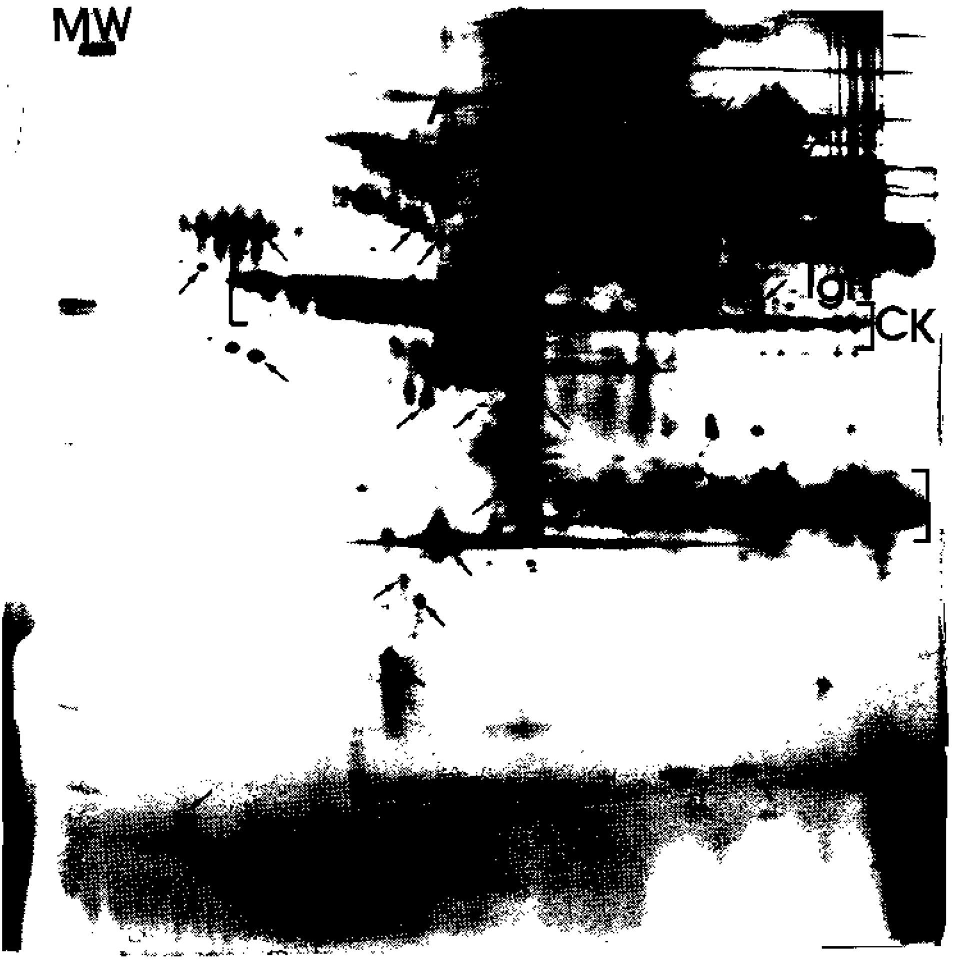


Fig. 5. Two-dimensional gel of *S. oerstedii* blood plasma proteins. Small arrows indicate the proteins (n = 48) compared among squirrel monkey populations for differences in electrophoretic mobility. A, albumin; MW, molecular weight standards; CK, creatine kinase charge standards; IgH, immunoglobulin heavy chains region; IgL, immunoglobulin and light chains region; H, hemoglobin chain.

proteins (Fig. 5) were surveyed for differences in electrophoretic mobility among the 15 squirrel monkeys in our sample. The 2DE gels, and the archival "XRD images" (Harrison, 1984) made from them, were scored manually over a light box. Protein spot patterns were aligned using the internal charge and weight standards and the constellation of invariant proteins in the immediate vicinity of the proteins being compared. Reference was made to the co-electrophoresis gel patterns in an effort to verify or to rule out apparent mobility differences initially detected during gel-to-gel comparisons.

Genotypic data (not shown) were analyzed with the help of the BIOSYS-1 (Swofford and Selander, 1989) and NTSYS-pc (Rohlf, 1988) software packages. A contingency chi-square test was performed to test the significance of interpopulational differences in allelic frequency values (Workman and Niswander, 1970; Swofford and Selander, 1981). A number of similarity and distance coefficients were applied to the gene frequency data, including Nei's (1978) unbiased genetic identity and genetic distance, and a modified Roger's distance (Wright, 1978). Coefficients were clustered using the UPGMA algorithm of Sneath and Sokal (1973).

New Evidence Bearing on Species of Saimiri: Data and Discussion

Geographic Distribution and Pelage Coloration

Specimens collected since 1984 from Brazilian Amazonia provide important information from "species" boundary areas south of the Rio Amazonas. These specimens are from (1) the area of Tefé, where *vanzolinii*, *sciureus*, and *madeirae* occur (Ayres, 1985) and (2) the left and right banks of the Rio Jiparaná, a tributary of the Rio Madeirae, near the probable southern extent of *madeirae's* distribution. Additional comments are given to specimens collected from complicated areas bearing on the validity of *Saimiri madeirae*, the area of inferred sympatry, and the eastern border of that group along the Rio Tapajós.

Two specimens from Tefé labeled *S. ustus*, collected in 1985, are in the "Emilio Goeldi" collection and are of interest for their mix of traits. One, MG13210 (male), is from the left bank of the Rio Tefé, at the mouth of the Rio Bauana (Ponta da Castanha: see Ayres, 1985, Map 1). This specimen has the burnt-orange dorsum and fulvous hands typical of *madeirae*, a grayish preauricular patch typical of *sciureus*, but unknown in *madeirae* specimens from near Humaitá, and ear hair intermediate between naked and tufted (Fig. 6).

The second specimen, MG13209 (female), also from the west bank of the river, at Lago Boia, does not have an equivalently burnt-orange dorsum as the first, and is more evenly gray/black and orange, similar to some *boliviensis*, but with a darker gray tail, approximating a condition intermediate between *vanzolinii* and other *Saimiri*. The hands are fulvous and the forearms have slightly

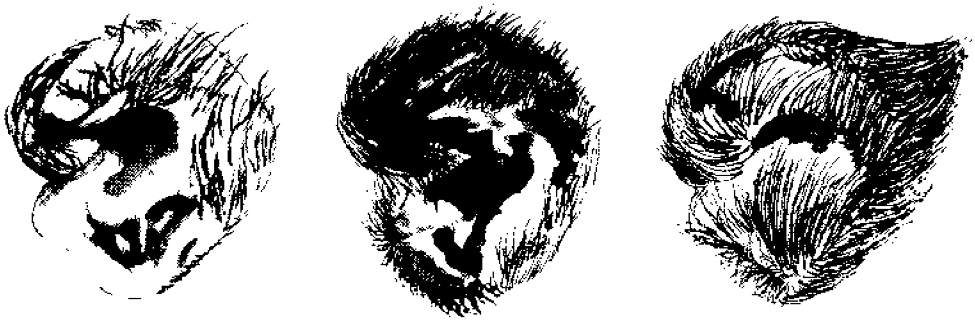


Fig. 6. Expressions of the variation of ear hair: from left to right: naked-eared squirrel monkey c.f. *madeirae;* intermediate expression of hair typical of samples from the border areas of *madeirae;* tufted ear typical of all South American *Saimiri* except *madeirae*.

more of this color, but are not covered with orange or yellow, like all other *Saimiri*. The crown is mottled olive and dark gray to black, with black bars along the margin near the ears and black on the forehead, with a nearly complete Roman-arch pattern. The preauricular patch is uncharacteristically mottled for *Saimiri*, and ear hair is even greater than the first specimen, although not tufted.

MG13210 is likely a hybrid, or a generation or two removed from a hybrid parent, of *sciureus* and *madeirae*. MG13209 is probably the offspring of *madeirae* crossed with *vanzolinii* or *boliviensis*. We have seen only one other specimen, from Fordlândia, that has a mottled crown, mostly black with less olive. That specimen is an interesting mix of *sciureus* and *madeirae* features, and mottling may occur in some specimens as a result of hybridization. The geographic proximity to *vanzolinii* and the darker tail may implicate *vanzolinii* admixture; however, the distribution of *boliviensis* in the region is unknown. Neither specimen can be neatly pigeon-holed into any taxon, unless one arbitrarily selects a single character for that purpose.

A few more specimens from Tefé are in the collection of the Museu de Zoologia (MZ19013, MZ19014, MZ19015, collected in 1984). These are all right bank (east) collections from Vila Vale, near the confluence of the Rio Tefé with the Rio Solimões. These specimens more closely approximate *madeirae* from Humaitá, with a few exceptions. The skull cap is not the consistent bluish-gray found in *madeirae* from Humaitá and the ears show more hair. These specimens may be viewed as weak indicators of gene exchange with *sciureus* from the left bank of the Rio Tefé, and perhaps from small groups of *sciureus* that have crossed the river. A similar situation may occur with *sciureus* having crossed the Rio Solimões. Alternatively, there may be an east-west cline, without intergradation, where central populations of *madeirae* with naked ears, fulvous hands, and blue-gray crowns shift toward olive-gray crowns and hairier ears as they approach the eastern and western boundaries. To accept the latter, one must also accept that the morphological direction of the cline is twice toward the condition of *madeirae's* neighbors.

There was extensive collecting recently at a number of sites along the upper reaches of the Rio Madeira, including the hydroelectric site of Samuel on the Rio Jamari, Rondônia ("Emilio Goeldi," Museu Nacional, 1988), the Rio Madeirae at Humaitá, and a Madeira tributary, the Rio Jiparaná (Ferrari and Lopes, 1992). Opposite Humaitá, on the right bank of the Rio Madeirae, specimens are typical *madeirae* as described by Thomas (1908). The same is true of specimens taken on the right bank of the Rio Jiparaná. No monkeys were collected on the left bank of the Rio Madeirae, but a household pet squirrel monkey from that side is reported to be identical to right bank monkeys (Ferrari and Lopes, 1992). However, specimens from the left bank of the Rio Jiparaná and from Samuel, which is situated between the Rio Jiparaná and the Rio Madeirae, differ in some features. Most striking is the combination of all golden hands and forearms, together with naked ears. All specimens examined are consistent for these features, and none have exclusively fulvous hands. Features are so consistent that we consider this form to be a new subspecies. There is yet no information on the southern boundary of this phenotype and whether or not it is contiguous with *boliviensis*.

Between the Rio Madeira and Rio Tapajós, some specimens have a mix of traits and others are either *sciureus* or *madeirae*. Three specimens from the Rio Arapiuns (MG), are *sciureus* without any *madeirae*-like states of coat color characters; additionally, the orange-yellow on the feet extends onto the leg. We know of no new specimens that can shed light on the area of inferred sympatry.

A number of specimens are known from east of the Rio Tapajós. Three specimens from Fordlândia (MZ) are remarkable in having very little hair on their ears, fulvous hands and forearms, and olive crowns, with the crown color extending onto the dorsum in a broad stripe, specimens that in every way except the ears, are like *sciureus*. One specimen, a female, has the black and olive mottled crown mentioned above. From Bom Jardim (MZ) are specimens intermediate for hand-forearm color, the orange being restricted to the distal portion of the forearm above the hand. Ears are variable for hair, some completely denuded, others intermediate (e.g., Fig. 6). The next major river to the east is the Rio Iriri/Xingú, and *Saimiri* reported from along the Iriri are referred to as *sciureus* (Martins *et al.*, 1986). Because of the mosaic nature of characters where *sciureus* and *madeirae* occur, however, survey observations without specimen samples are not the strongest evidence for the recognition of boundaries.

Pelage variation and zoogeography are still equivocal. New specimens from the western range of *madeirae* weaken the hypothesis that *madeirae* and *sciureus* are separate species. Other specimens weaken the species status of *vanzolinii*; they include one probable hybrid from Tefé, samples that bear remarkable resemblance to *vanzolinii* from the nearest *boliviensis* sample along the Rio Jurua and its tributary the Rio Eiru, and nearly identical *boliviensis* from around Envira. *Saimiri vanzolinii*, as remarked by Hershkovitz (1985), is best considered a member of *boliviensis* until further evidence indicates otherwise.

Pelage variation is distributed in zoogeographic patterns, with South American groups of *Saimiri* distributed along and between the major rivers. All groups, though, are not contained by river boundaries, such as *sciureus* north and south of the Rio Amazonas. The parapatric distribution of populations may indeed indicate either insufficient niche differences for the successful coexistence of those groups or nonadaptive stochastic differences between them. Traits may have accumulated through episodic periods of isolation.

Dental

Table 4 lists Pearson correlation coefficients (and the significance probabilities calculated for N = 111 under the null hypothesis that the correlation is zero) of 11 variable means (listed in Table 5) for the total *Saimiri* sample. Some variables with high correlation values are easily understood as the alternate sides of the same triangle (Fig. 4). The variable pairs AD/AC, BC/AC, CD/AC, AB/BD, AD/BD, BC/BD, and CD/BD are of this type and range from 0.45 to 0.71 (R = 0.0001). The two diagonals, AC and BD, also have a high correlation (0.44). Variable BE, the chord measure of the cristid obliqua, has higher correlation coefficients with AB and BD. That crest is anchored anteriorly near the protoconid base (near landmark A) and distally at the hypoconid (landmark B). Thus BE is the alternate side of triangles ABE and DBE. AD/BC (0.48) refer to the distances between the anterior trigonid cusps (protoconid-metaconid) and

Table 4. Pearson Correlation Coefficients

PROB > |R| UNDER HO: RHO = 0 N = 111

	AB	AC	AD	AJ	BC	BD	BE	CD	HM	JP	KO
AB	1.00										
AC	0.38 *.0001*	1.00									
AD	0.05 *.6102*	0.66 *.0001*	1.00								
AJ	0.23 *.0145*	−.021 *.0290*	−0.32 *.0005*	1.00							
BC	0.18 *.0586*	0.60 *.0001*	0.48 *.0001*	0.09 *.3256*	1.00						
BD	0.46 *.0001*	0.44 *.0001*	0.46 *.0001*	0.24 *.0119*	0.71 *.0001*	1.00					
BE	0.67 *.0001*	0.39 *.0001*	0.19 *.0490*	0.04 *.7139*	0.37 *.0001*	0.50 *.0001*	1.00				
CD	0.31 *.0010*	0.59 *.0001*	0.05 *.5828*	0.07 *.4505*	0.23 *.0171*	0.45 *.0001*	0.27 *.0040*	1.00			
HM	0.35 *.0001*	0.35 *.0002*	0.04 *.6739*	0.06 *.5282*	0.21 *.0259*	0.20 *.0396*	0.39 *.0001*	0.33 *.0003*	1.00		
JP	0.36 *.0001*	0.41 *.0001*	0.32 *.0006*	0.34 *.0003*	0.49 *.0001*	0.48 *.0001*	0.30 *.0014*	0.21 *.0289*	0.28 *.0025*	1.00	
KO	0.31 *.0010*	0.33 *.0004*	0.22 *.0198*	0.31 *.0009*	0.59 *.0001*	0.55 *.0001*	0.34 *.0003*	0.19 *.0480*	0.24 *.0119*	0.65 *.0001*	1.00

the posterior talonid cusps (hypoconulid-entoconid). The relatively high correlation coefficients that remain to be accounted for relate maximum buccolingual dimensions of the tooth, JP, KO, to each other, and to the talonid cusps, AD, BC, and the diagonal BD. Notably, the trigonid cusps dimension, AD, is not as highly correlated (although highly significant) with the maximum trigonid width, JP (0.32), as it is with the talonid cusps, BC (0.48). This appears related to the fact that there is an inverse correlation between AJ, the distance from the protoconid, A, to the maximum buccal flare of the tooth, J (an indirect measure of

Table 5. Variable Means

Variable	*oerstedii*	*sciureus*	*madeirae*	*boliviensis*	*peruviensis*
AB	1.42	1.51	1.44	1.50	1.43
AC	2.25	2.30	2.25	2.29	2.21
AD	1.58	1.54	1.53	1.53	1.49
AJ	0.68	0.77	0.74	0.82	0.82
BC	1.62	1.74	1.72	1.78	1.75
BD	1.82	1.95	1.90	1.99	1.97
BE	1.03	1.09	1.03	1.10	1.03
CD	1.23	1.28	1.20	1.36	1.26
HM	2.83	2.73	2.65	2.74	2.73
JP	2.61	2.73	2.73	2.71	2.72
KO	2.42	2.58	2.56	2.58	2.74

cingulum development), and AD, the trigonid cusp distance, and AC, the diagonal. There is a very slight tendency for tooth width to be maintained independent of intercusp spread.

T- and f-tests were performed for the 11 variables (Fig. 7A) with representative samples of the geographical groups. The inset box shows the order of placement of variables being compared. More variables were significant for *oerstedii* ($p > 0.05$), 24, compared to all other groups. *Oerstedii* also registered the greatest number of significantly different variables (nine) when compared to just one other group, *sciureus*. *Sciureus* follows with a total of 18, seven of which result from the comparison with *madeirae*. *Madeirae* has 17 total significant variables; *peruviensis* has 12, and *boliviensis* has 9. The groups showing fewest significant variables are *boliviensis* and *peruviensis* when each are compared to *sciureus*. A histogram (Fig. 7B) shows the frequencies at which variables were involved in discriminating groups. The three highest variable frequencies—JP, BD, and KO—reflecting trigonid width, hypoconid-metaconid distance, and talonid breadth, respectively, also have relatively high correlation values to each other (0.48–0.65). Variable AD, the protoconid-metaconid distance, does not discriminate.

Figure 8 shows the mean topographic positions of cusps and Table 6 is a list of the mean angles formed between cusps. In Fig. 8, all lengths between cusps are scaled to the longest base line, BC, which is made equal for all groups. Notable differences between group patterns in Fig. 8 are dependent on two variables: size and shape, and the distance between cusps and their angles. Because all group means for variables are scaled to an equal baseline BC, any other lengths that are equal between two groups will not appear equal on the diagram if their lengths for BC are not also equal. The diagram is used only to depict angular, and not length, relationships.

From Fig. 8, we see that in *peruviensis* the protoconid (A) and metaconid (B) are shifted lingually relative to other topographies. The relations between cusps

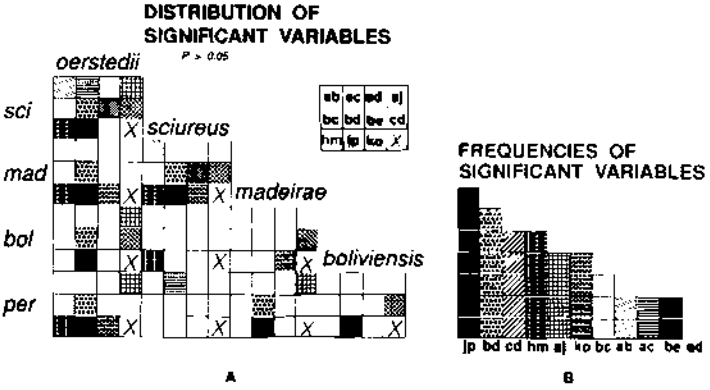


Fig. 7. (A) Distribution of significant variables calculated from the t-test, $p < 0.05$. The box with variables ab - ko shows the order of variables that correspond to patterns within the matrix. X fills an empty box. Samples of taxa are compared two by two. (B) The histogram shows the frequencies for each variable in the discrimination of all pair-wise samples.

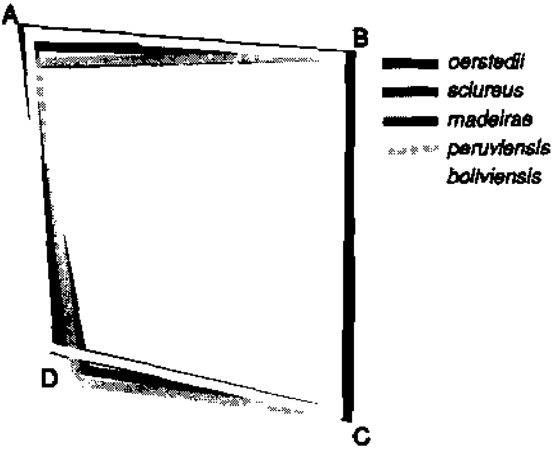


Fig. 8. Mean topographic relations of cusps among samples scaled to the longest base (BC) and superimposed.

approach a rhombus in shape, with alternating acute and oblique angles. A shift of the angles of the rhombus, without changing distances between cups, will not affect the statistical analysis of lengths. Thus, *sciureus* and *peruviensis* forms appear visually different, yet may be discriminated by only one distance, the diagonal AC.

The two forms considered sympatric in their distributions south of the Rio Amazonas, *madeirae* and *sciureus*, were similarly compared. The specimens used were collected from the area along the Rio Madeira, at Borba and Rosarinho. These samples compared more closely than any other two. This may, however, be due to sampling error, since samples were $n = 3$ for *madeirae* and $n = 5$ for *sciureus*. Figure 7A shows seven variables that discriminate these two forms. The sample used for Fig. 7A included localities where the two forms are not known to be sympatric.

This 2-D study of *Saimiri* M_1 reveals that two molar patterns are differentiable. One is found in the Central American *oerstedii* and the other in South American *Saimiri*, with differential expression among geographic groups of the latter. The Central American molar pattern is distinguished from the South American pattern by (1) less buccal flare (and less buccal cingulum) at the trigonid, resulting in a narrower tooth anteriorly without reduction of protoconid-metaconid distance; (2) a narrower talonid basin with hypoconid-entoconid distance reduced; (3) a reduced posterior tooth width; and (4) greater molar length.

The South American molar pattern is simply a broader and shorter tooth

Table 6. Molar Cusp Angles

Taxon	A	B	C	D
oerstedii	78.0	94.6	76.0	111.4
sciureus	84.8	91.2	77.0	107.0
madeirae	80.6	88.9	80.0	110.5
boliviensis	82.1	94.7	76.4	106.8
peruviensis	85.3	88.9	82.8	103.0

that has greater buccal flare and talonid cusps spread farther apart. This pattern is expressed least in *sciureus*, to an intermediate extent in *boliviensis*, and is greatest in the *peruviensis*. Whether or not molar differences and the grading of this tooth have adaptive significance, are the result of genetic drift, or represent a cline without interruption is presently a matter of speculation. Ecological differences in the habitat structure do occur (Mitchell *et al.*, 1991), and they may reflect selective variables driving regional adaptive, not niche, differences (*sensu* Bock and von Wahlert, 1965).

The dental evidence may not be appropriate for the discrimination of species in *Saimiri*. These data are limited and quite preliminary. However, they do suggest that *oerstedii* is more distinct, thus more distant, from any South American form of the genus than any of these are from each other. In addition, they do not support any multiple species hypotheses within South America.

Biochemical

Twelve of the 48 proteins surveyed showed evidence of polymorphism. Gene frequency data for *boliviensis, peruviensis,* and *sciureus*, along with the genotype of the single *oerstedii* we studied, are presented in Table 7. Unbiased average heterozygosity values (Nei, 1978) were 3.3% in *boliviensis*, 4.5% in *peruviensis*, and 5.3% in *sciureus*.

The contingency chi-square analysis suggests statistically discernible differences in gene frequencies between the sample populations we examined exist in only 5 of 12 variant proteins at the 5% error level (Table 8). Genetic identity and distance coefficients are presented in Table 9.

The main relevance of the protein data is with the genetic distances inferred from it. The genetic distances are so close between the groups that only *oerstedii* may approach a minimum distance adequate for the recognition of species [see VandeBerg (1990b) for species and subspecies comparisons]. These results, though plagued by an inadequate sample, indicate that *oerstedii* has undergone genome evolution to a greater extent than any other group. What amount of time is involved is an open question, but the suggestion by Hershkovitz (1984) that these animals were introduced by humans in Recent time is not supported.

We hope to have compensated for the small sample to some extent by examining a fairly large number of genetic loci (n = 48) (Nei and Roychoudhury, 1973; Nei, 1978; Gorman and Renzi, 1979; but see Archie *et al.*, 1989). However, there are serious problems other than sample size that render these findings tentative. (1) The autosomal codominant nature of the apparently polymorphic proteins we examined has yet to be confirmed; such confirmation will require study of a much larger sample of pedigreed individuals. (2) Due to the nature of the staining technique, the assessment of homology for the 48 proteins identified for study is tentative. (3) These data do not objectively identify the groups as "real."

Few biochemical markers have been found that fit preconceived notions of the number of taxa thought to exist. There are many alleles shared between two or more geographic groups. Who is to say which markers define groups and

Table 7. Gene Frequencies at 12 Variable Loci for Four Squirrel Monkey Samples

Locus and alleles	*boliviensis* N = 6	*peruviensis* N = 4	*sciureus* N = 4	*oerstedii* N = 1
1A	0.083	0.000	0.000	0.000
1B	0.917	1.000	1.000	1.000
7A	0.000	0.000	0.250	0.000
7B	1.000	1.000	0.750	1.000
8A	1.000	1.000	0.750	1.000
8B	0.000	0.000	0.250	0.000
9A	0.000	0.000	0.000	1.000
9B	1.000	1.000	1.000	0.000
10A	0.000	0.125	0.000	0.000
10B	1.000	0.875	1.000	1.000
15A	1.000	1.000	0.750	1.000
15B	0.000	0.000	0.250	0.000
17A	0.500	0.875	0.875	0.000
17B	0.500	0.125	0.125	1.000
18A	0.083	0.500	1.000	0.000
18B	0.000	0.000	0.000	1.000
18C	0.750	0.000	0.000	0.000
18D	0.000	0.125	0.000	0.000
18E	0.000	0.375	0.000	0.000
18F	0.167	0.000	0.000	0.000
19A	1.000	0.750	1.000	1.000
19B	0.000	0.125	0.000	0.000
19C	0.000	0.125	0.000	0.000
43A	0.250	0.625	0.000	0.000
43B	0.750	0.000	0.000	0.000
43C	0.000	0.375	1.000	1.000
44A	1.000	1.000	0.500	1.000
44B	0.000	0.000	0.500	0.000
46A	1.000	1.000	0.750	1.000
46B	0.000	0.000	0.250	0.000

which play an important role in isolating species? We performed the protein study by grouping specimens into taxonomic categories and then tested for significant differences between categories. Essentially, this begs the questions of species. By contrast, the dental data were treated locality by locality before any localities were combined, though circularity may still creep into the testing of groups. We do not know if, for example, all the *boliviensis* or *sciureus* samples would have clustered together if a discriminant function analysis were performed on all the individual animals comprising the groups. We have completed some work along this line and the groups mostly hold together, but there were aberrant individuals.

Table 8. Contingency Chi-squared Analysis at 12 Polymorphic Loci

Locus	Number of Alleles	Chi square	D.F.	p
1	2	1.552	3	0.67038
7	2	5.893	3	0.11694
8	2	5.893	3	0.11694
9	2	30.000	3	0.00001
10	2	2.845	3	0.41617
15	2	5.893	3	0.11694
17	2	8.625	3	0.03474
18	6	65.769	15	0.00001
19	3	5.893	6	0.43530
43	3	32.704	6	0.00001
44	2	12.692	3	0.00535
46	2	5.893	3	0.11694

Animals originating from between the Rio Tapajós and Rio Xingú, for example, are considered to belong to *madeirae* by Hershkovitz (1984) and *sciureus* by Thorington (1985). Depending on which author is followed, comparisons of animals from between the Tapajos and Xingu with other taxa of *Saimiri* will be interpreted differently.

A conservative conclusion of this and other studies (e.g., VandeBerg *et al.*, 1987, 1988, 1990a,b) is only that differences between squirrel monkeys from different geographic localities have been detected. Our electrophoretic study does not support species differences between South American groups, and it minimally supports species distinction of *oerstedii*. Results from different electrophoretic studies do not all give a consistent picture. Again, sampling error may be at work here; the geographic origin of specimens will likely effect results, even though specimens used from study to study appear to be members of the same taxonomic group. Not only would large samples of a group be desirable, so would samples over the range of the group.

Table 9. Genetic Identity and Distance Coefficients Derived from 2DE Analysis of 48 Plasma Proteins in Four Samples of *Saimiri*

	Squirrel Monkeys			
Sample	*boliviensis*	*sciureus*	*peruviensis*	*oerstedii*
boliviensis	*****	0.958	0.981	0.941
sciureus	0.213	*****	0.981	0.934
peruviensis	0.151	0.155	*****	0.941
oerstedii	0.244	0.261	0.247	*****

Above diagonal: Nei's (1978) unbiased genetic identity.
Below diagonal: Modified Rogers distance (Wright, 1978).

Conclusions

Patterns of pelage variation, geographic distribution, and survival and reproductive behaviors, together with the biochemical and dental evidence reported here, consistently indicate there are few differences between samples of South American *Saimiri* that support multiple species hypotheses. The evidence is similarly concordant in showing greater differences between Central and South American *Saimiri* than exist between South American groups. Based on this evidence, we consider the genus *Saimiri* to contain two nominal species, the Central American *S. oerstedii* Reinhardt, 1872, and the South American *S. sciureus* Linnaeus, 1758. Thorington (1985, p. 21) postulated, "it is not obvious that *oerstedii* is sufficiently different from the South American squirrel monkeys to be considered a distinct species," and "that it is no more distinct in other ways from *Saimiri sciureus sciureus* than the latter is from *Saimiri sciureus boliviensis*, and that by analogy, it, too, should be considered a subspecies of *Saimiri sciureus*." The data we provide on blood proteins and molar patterns demonstrate greater differences than previously reported. Although this study is preliminary, we are encouraged by the consistency with which the various data direct us to our conclusions, and we regard this as a strength of the biological species concept. Not one of the preliminary studies is convincing on its own; together, however, they each corroborate the hypotheses we have accepted.

Under Paterson's (1980, 1985) species recognition concept, we must conclude that one, rather than two, species of *Saimiri* exists. We were unable to find any significant differences in the mate-recognition system (as defined by Patterson) of *S. oerstedii* and *S. sciureus*. Yet appreciable genomic, behavioral, pelage, and dental differences have accrued with *extensive* isolation of *S. oerstedii*. The apparently gradual buildup of differences in multiple systems, without a "niche shift," appears to be the effect of random genetic change or assortative mating (e.g., see Froehlich *et al.*, 1991, on species of *Ateles*). Some threshold must finally be reached where these differences have an irreversible effect on the outcome of mating. Such studies are not available for *Saimiri*.

Summary

Two species taxa are recognized, the Central American *S. oerstedii* and the South American *S. sciureus*. The previously named *S. madeirae* and *S. boliviensis* are regarded as geographic forms of *S. sciureus*.

Two molar patterns distinguish South and Central American *Saimiri*. The molar pattern shared by South American squirrel monkeys appears to grade clinally ("*sciureus*" → "*boliviensis*" → "*peruviensis*"). Samples of sympatrically distributed "*madeirae*" and "*sciureus*" are compared and found closer morphologically than any samples compared between parapatric groups.

Genetic distances computed from protein frequency data show (1) slight differences between South American geographic groups and (2) a greater dis-

tance between Central American monkeys and any of those groups. The degree to which *S. oerstedii* may be genetically distinct is minimal for species recognition. Karyology is so far minimally informative at the species level.

Patterns of pelage variation and geographic distribution indicate hybridization where groups meet. There is evidence to suggest intergradation between "*madeirae*" and "*sciureus*," "*vanzolinii*" and "*madeirae*" (this report), and "*boliviensis*" and "*sciureus*" (Thorington, 1985; DaSilva *et al.*, 1992). Populations of "*boliviensis*" geographically near to "*vanzolinii*" share coat patterns with the former.

Behavioral evidence does not identify any premating behaviors that could function to isolate any one group of *Saimiri* from any other. All squirrel monkeys share the same feeding strategy, diet, and breeding systems, and differ in social organization only in conjunction with changes in forest structure and the distribution of food resources.

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