CLADISTICAL ANALYSIS OF G-BANDED CHROMOSOMES OF NECTAR FEEDING BATS (GLOSSOPHAGINAE: PHYLLOSTOMIDAE)

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Abstract

Haiduk, M. W., and R. J. Baker (Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 79409) 1982. Cladistical analysis of G-banded chromosomes in nectar feeding bats (Glossophaginae: Phyllostomidae). Syst. Zool., 31:252-265.—Differentially stained chromosomes, when analyzed in a cladistic framework, provide a systematic hypothesis for ten glossophagine genera. Two separate groups are recognized on the basis of chromosomal data; a chromosomally conservative or plesiomorphic group consisting of Glossophaga, Monophyllus, Leptonycteris, and the brachyphyllines, and a relatively rapidly evolving derived group consisting of Anoura, Lonchophylla, Lionicteris, Choeronycteris, Choeroniscus, Choro- nycteris, Hylonycteris, and Musonycteris. Among the six genera characterized as slowly evolving, only a single rearrangement has been identified, whereas, among the seven genera characterized as rapidly evolving over 100 chromosomal rearrangements are required to explain the observed variation. Such a contrast in rate and type of chromosomal evolution is difficult to explain in terms of most currently accepted theories of chromosomal evolution and the pattern of change is most like "karyotypic megaevolution." Within the derived group, cladistic relationships are resolved to the generic level. Variation in the magnitude of evolution at the morphological and chromosomal levels is such that chromosomal data are useful for the resolution of relationships among genera, whereas, morphological data are more informative at the subfamilial level. A combination of the two data sets is compatible with the hypothesis that the Glossophaginae is monophyletic and provides a better understanding of the nature of evolution within this subfamily. [Glossophagines; chromosomal evolution; phylogeny; cladistics; G-banding.]

The Glossophaginae (Phyllostomidae: Chiroptera) is an assemblage of 13 genera which due to their shared morphological adaptions to a nectarivorous feeding mode has been recognized as a unit since Miller (1907). More recently, however, data from chromosomal (Baker, 1967, 1970; Gardner, 1977), immunological (Gerber and Leone, 1971), and morphological (Phillips, 1971; Griffiths, 1982) studies have led to several alternative proposals indicating a polyphyletic origin of the subfamily.

Baker (1967) recognized two general subgroups within the Glossophaginae on the basis of nondifferentially stained chromosomes. One group was characterized as having diploid numbers (2n) near 32 and fundamental numbers (FN) near 60, and was believed to be closely allied with phyllostomine taxa. The other group consisted of Choeronycteris and Choeronycteris and characteristically possessed reduced diploid and fundamental numbers. Baker (1967) concluded that this group possibly represented an independently derived lineage related to the Carolliniae. Stock (1975), however, studied G-banded chromosomes and demonstrated that little or no chromosomal homology was shared between Choeronycteris and Carollia.

Two subgroups were also recognized within the Glossophaginae by Phillips (1971) and Gerber and Leone (1971). Phillips, based primarily on an analysis of dental characters, suggested that the Glossophaga group was more closely allied with Macrotus and Artibeus, whereas, the Choeronycteris group was possibly derived from the phyllostomines. Gerber and Leone (1971) recognized the same groupings but their analysis of serum immunology suggested that the Glossophaga group was more closely related to the Carolliniae, whereas, the
Choeronycteris group was allied with the Phyllostominae.

Gardner (1977) examined nondifferentially stained chromosomes of additional taxa within the Glossophaginae and recognized essentially the same grouping as that proposed by Phillips (1971). However, Gardner enlarged the Choeronycteris group to include Lionycteris, Lonchophylla, Lichonycteris, Chylonycteris, Platalina, and Scleronycteris, whereas, all of these taxa were included in the Glossophaga group by Phillips (1971). Additionally, Gardner proposed that if the Glossophaginae is monophyletic, then Lonchophylla thomasi represented the probable primitive form chromosomally, but polyphyly was not eliminated as an alternative hypothesis.

Baker et al. (1981) provided data sets based on electrophoretic and immunological studies. These authors concluded that the polyphyletic branching proposed by Baker (1967) was incorrect. The study of Baker et al. (1981) also suggests that the relationship between glossophagines and brachyphyllines is sufficiently close that the subfamilies form a single clade with a shared common ancestry. This is compatible with the conclusion that relative to the primitive karyotype for the phyllostomids, Glossophaga, Monophyllus, Phyllonycteris, Erophylla, and Brachyphylla all share identical derived G- and C-banded karyotypes (Baker and Bass, 1979).

A conflicting result was obtained by Griffiths (1982) from a comparative study of lingual and hyoid musculature. On the basis of his study, Griffiths (1982) split the Brachyphyllinae-Glossophaginae assemblage into four subfamilies. The Glossophaginae was recognized to consist of Glossophaga, Monophyllus, Lichonycteris, Leptonycteris, Anoura, Hylyonycteris, Scleronycteris, Choeronycteris, and Musonycteris. The Lonchophyllinae was established to include Lonchophylla, Lionycteris, and Platalina, and the Brachyphyllinae was split into two subfamilies, the Brachyphyllinae to include only Brachyphylla and the Phyllonycterinae to include Phyllonycteris and Erophylla. Additionally, Griffiths concluded that the Lonchophyllinae was an independent lineage only distantly related to the other three subfamilies.

A review of Systematic Zoology over the past few years reveals that systematic theory has advanced rapidly. However, few papers dealing with hard data sets have maximally utilized these advances to provide a better systematic classification. From the above discussion on the divergent interpretations of data for the nectarivorous leaf-nosed taxa, it is obvious that providing a classification compatible with modern systematic theory will be no small challenge.

In this study, G-banded chromosomal data are presented for nine additional genera of glossophagines representing every major subdivision of the subfamily recognized by previous authors. These data are used in a cladistical framework to assess relationships between genera, and to address the questions of a polyphyletic origin of the Glossophaginae and a workable systematic arrangement for the genera involved.

METHODS

All specimens examined in this study were collected from natural populations and are currently housed as standard museum specimens at The Museum, Texas Tech University, Carnegie Museum of Natural History, or Texas Cooperative Wildlife Collection, Texas A&M Uni-
versity. For most specimens, ear biopsies were taken in the field, returned to the laboratory, and used to establish primary cell cultures. Cultures were maintained and processed according to the procedures described by Baker and Bass (1979). Some animals (Leptonycteris sanborni and Choeronycteris mexicana) were transported alive to the laboratory and bone marrow preparations were made according to the procedure of Lee and Elder (1980). G-bands of Musonycteris harri-soni were obtained from bone marrow processed in the field and frozen in liquid nitrogen as described by Baker et al. (1982). In all cases, banding procedures followed those of Seabright (1971).

Relationships were determined by cladistic methods, using shared, derived chromosomal characters. The families Mormoopidae and Noctilionidae were used as the outgroups. However, the common occurrence of karyotypic mega-evolution (Baker and Bickham, 1980) in
the Glossophaginae and the absence of chromosomal synapomorphies made it necessary to rely on the results of Baker et al. (1981) to unite Glossophaga, Leptonycteris, and Monophyllus with the other glossophagines.

Specimens examined: Anoura caudifer—Suriname: Nickerie; Sipaliwini Airstrip (1♀); Grassalco (1♀); Brokopondo, 1 km N Rudi Kappelvigveld (1♂); Venezuela: Miranda; 25 km N Altagracia de Oríuco (4♀, 1♂). Anoura geoffroyi—Venezuela: Managas; 40 km NW Caripito (1♂). Choeronycteris minor—Suriname: Nickerie; Sipaliwini Airstrip (1♀, 1♂); Grassalco (2♀). Choeronycteris mexicana—Mexico: Sonora; 8 mi S Alamos (8♀). Glossophaga soricina—Mexico: Guerrero; 24.1 mi N La Union (3♀, 2♂); Venezuela: Bolivar; 8 km W El Manteco (1♂). Hylonycteris underwoodi—Mexico: Tabasco; 3 km E Teapa (1♂). Leptonycteris sanborni—Mexico: Sonora; 4 mi NW Alamos (8♀, 4♂). Guerrero; 24.1 mi N La Union (2♀, 2♂). Lionycteris spurrelli—Suriname: Brokopondo; 2 km W, 8 km S Brownsweg (1♀); Saramacca; Bita Gron (2♂); Nickerie, 24 km S, 60 km E Apoera (3♂); Marowijne, 3 km SW Albina (1♀). Musonycteris harrisoni—Mexico: Jalisco, 2 mi NW Tomatlan (2♂).

RESULTS

The G-banded karyotypes of Glossophaga soricina and Leptonycteris sanborni (2n = 32, FN = 60) are shown in Figure 1. Within the limits of our methods, no differences exist except that the smallest pair of autosomes is larger in Leptonycteris than in Glossophaga. The G-banded karyotype shared between G. soricina and L. sanborni is also characteristic of Monophyllus and the brachyphylline genera Brachyphylla, Erophylla, and Phyllonycteris (Baker and Bass, 1979).

In Figure 2, the G-banded chromosomal complement of Lonchophylla thomasi (2n = 32, FN = 40) is shown. For the most part, this karyotype is highly derived relative to Glossophaga, or the proposed primitive for the family, with very few homologous arms or arm segments recognizable. Two exceptions are the 13/2 fusion which is identifiable and which also occurs in all the remaining glossophagines, and arm E. Lonchophylla thomasi has a pericentric inversion in the 13/2 chromosome which produced the short arms and serves as an additional autapomorphy for this species. Arm E is found in L. thomasi, Lionycteris, and the taxa of the Choeroniscus group. The G-banded complements of other species of Lonchophylla with a diploid number and a fundamental number more like Glossophaga have not been examined.

The G-banded karyotype of Anoura caudifer (2n = 30, FN = 56) is presented in Figure 3. Both A. caudifer and A. geoffroyi were examined and found to have identical chromosomal complements. Arm 13/2 is present, and makes up one of the arms of the largest chromosomal pair. The other arm is composed of arms 8 and 1 fused in tandem. The remainder of the Anoura karyotype has been sufficiently rearranged that the banding sequences found in Macrotus waterhousii or Glossophaga are not recognizable.

Lionycteris spurrelli (2n = 28, FN = 52) also possesses a highly derived karyotype which is characterized by many autapomorphic arm combinations (Fig. 4). In this species, most of the arms pro-
ANOURA

Fig. 3.—G-banded karyotype of Anoura caudifer. An indistinguishable G-banded karyotype is also found in A. geoffroyi and is autapomorphic for almost every chromosomal pair.

posed as primitive for the family can be identified but they occur in unique combinations and several arms are present which are shared with Choeroniscus, Choeronycteris, Musonycteris, and Hylonycteris (C, D, and E).

The remaining taxa examined (Choeroniscus minor, Choeronycteris mexicana, Musonycteris harrisoni, and Hylonycteris underwoodi) share a high degree of chromosomal homology. In Figure 5, the G-banded karyotype of Choeroniscus minor is shown with each arm designated by a letter. All arms found in C. minor also can be recognized in the other three taxa comprising the Choeroniscus group. Some arms or arm segments shared with Macrotus waterhousii can be recognized, such as the 13/2 which makes up arm A2, but for the most part, the banding sequences of the proposed primitive have not been conserved, suggesting that the ancestor to this clade underwent a radical reorganization of the genome (McClintock, 1978; Baker and Bickham, 1980).
The G-banded karyotypes of *Hylonycteris underwoodi* and *Choeronycteris mexicana* are shown in Figure 6. Variation between these two taxa and *Musonycteris harrisoni* is restricted to 3 chromosomal pairs (C, H, and I). In Figure 7, a composite comparison of all 4 taxa of the *Choeronycteris* group is shown to illustrate this variation and to show that primarily Robertsonian rearrangements have been involved, after the evolution of the *C. minor*-like karyotype.

In part A of Figure 7, the three major centric fusions found in *Choeronycteris*, *Musonycteris*, and *Hylonycteris* are shown. From the *Choeronycteris* karyotype, the others can be derived by the following centric fusions: arm D to A2, arm E to B, and arm J to A1. Additionally, pericentric inversions in chromosome pairs F and G characterize all three derived taxa (Fig. 7B)

Within the three most derived taxa, some chromosomal variation exists. In *Hylonycteris*, chromosome pair C has undergone a pericentric inversion and both *Choeronycteris* and *Musonycteris* share a pericentric inversion in pair I (Fig. 7B). Part C of Figure 7 shows a composite comparison of pair H. *Choeronycteris* and *Choeronycteris* are the same, but *Musonycteris* and *Hylonycteris* share a polymorphic condition for this pair. The cla-
discriminant analysis for these chromosomal data is shown in Figure 8.

**DISCUSSION**

Evolutionary relationships within the Glossophaginae have been highly contested in recent years due to the lack of congruence between the data sets. This lack of congruence is further aggravated by the inability to resolve character states due to the magnitude of variability encompassed within the Glossophaginae. In the following discussion, we describe the relationships of the glossophagine taxa as suggested by chromosomal data and attempt to rectify the issue of incongruence as 1) an unfortunate side effect of highly variable rates of evolution of different clades within the Glossophaginae and 2) as a result of the improper use of cladistic methodologies.

The karyotype like that found in *Macrotus waterhousii* has been proposed as primitive for the family Phyllostomidae (Patton and Baker, 1978; Baker, 1979) with the families Mormoopidae and Noctilionidae representing sister groups to the phyllostomids. Using *Macrotus waterhousii* as the outgroup for the Glossophaginae and Brachyphyllinae, chromosomal character states can be determined for many taxa. Using this approach, Baker and Bass (1979) demonstrated that *Glossophaga* possessed a karyotype in which all the primitive *Macrotus* chromosomal arms could be recognized, although some of these arms were found in unique combinations. Baker and Bass (1979) further showed that the derived condition found in *Glossophaga* was shared with *Monophyllus* and the brachyphyllines (*Brachyphylla, Phyllonycteris, and Erophylla*) and included 10 chromosomal synapomorphies. *Leptonycteris* (Fig. 1) also possesses this derived karyotype and, with the exception of the smallest autosomal pair, is indistinguishable from that found in five other genera. These chromosomal data are compatible with the conclusion of Phillips (1971), Gardner (1977), and Griffiths (1982) that *Glossophaga*, *Monophyllus*, and *Leptonycteris* shared a common ancestry.

The data of Griffiths, however, suggest that *Leptonycteris* subsequently shared a common ancestor with *Anoura* and the *Choeroniscus* group. Since *Leptonycteris* has retained plesiomorphic karyotype, we cannot resolve this question, but if Griffith's conclusions are correct, then the primitive karyotype for the *Anoura* and *Choeroniscus* clade was like that shared by *Leptonycteris* and *Glossophaga*.

Gardner (1977) proposed that if the Glossophaginae represented a monophyletic group, then the karyotype of *Lonchophylla thomasi* would closely resemble the primitive for the Glossophaginae. If the *L. thomasi* karyotype does represent the primitive, then an obvious prediction is that its karyotype would be intermediate between that of *Macrotus waterhousii* (the proposed primitive for the family) and *Glossophaga*, a derived karyotype in which all the primitive chromosomal arms can be recognized. One might also expect that *Lonchophylla* and *Glossophaga* would share one or several derived chromosomal characters relative to *Macrotus*. Our data (Fig. 2) demonstrate that *L. thomasi* possesses a highly derived karyotype in which very few primitive arms can be unequivocally recognized.

If the evolutionary sequence that Gardner (1977) proposes is correct and the primitive karyotype for the family is like that found in *Macrotus waterhousii*, then...
a highly unparsimonious series of rea-
rangements are required. A karyotype like
that of *Macrotus* would have to evolve
into the karyotype seen in *Lonchophylla
thomasi* (where essentially every primi-
tive linkage group banding pattern has
been rearranged) which would then
evolve into a pattern like that seen in
*Glossophaga* (where every linkage group
banding pattern has been reversed to the
primitive condition). We consider this
scenario highly improbable, and agree
with Baker and Bass (1979) that the
karyotype of *Glossophaga* represents the
most likely primitive for the Glossophag-
ae. This is the arrangement we have
shown in Figure 8.

We have not examined other species of
*Lonchophylla* which have been reported
to have a standard karyotype more like
*Glossophaga* (i.e., *L. robusta*, Baker, 1973,
1979) and so cannot rule out the possi-
bility that one of these other taxa has a
more primitive karyotype than *Glossoph-
aga*. However, substantial data suggest
that this also is highly improbable. If the
karyotype of any species of *Lonchophylla*
represents the primitive of the Glossophag-
ae, then, unless it is identical to
that of *Glossophaga*, the karyotype shared
between *Glossophaga, Leptonycteris,
Monophyllus,* and the brachyphyllines
would contain 10 synapomorphies (Baker
and Bass, 1979) uniting all of these taxa
into one clade separate from the other
glossophysines and the Brachyphyllinae
would no longer be a valid subfamily. On
the other hand, if the karyotype like that
found in *Glossophaga* is considered
primitive for the Glossophaginae, then the
brachyphyllines may still be recognized
as a sister taxon in which member taxa
have retained a plesiomorphic karyotype
like that of the ancestor of both clades. It
may be that the brachyphyllines are best
considered glossophysines. This view is
certainly compatible with the chromo-
somal data (Baker and Bass, 1979), elec-
trophoretic and immunologic data (Baker
et al., 1981) and uterine morphological
data (Hood and Smith, 1982) and merits
consideration as a systematic hypothesis.

Chromosomal evolution in the Gloss-
ophysinae has ranged from highly con-
servative to rapid and extreme and this is
reflected in the fact that only one chro-
mosomal synapomorphy can be found
which unites those genera that do not
possess the plesiomorphic karyotype. This
synapomorphy, the tandem fusion of
primitive arms 13 and 2, is found in all of
the chromosomally "nonprimitive" taxa, but
represents a relatively weak point in
the cladogram. The relationship between
*Anoura* and the remaining taxa is not re-
solvable because this genus is character-
ized by an autapomorphic karyotype. The
autapomorphic condition is the result of
a high rate of chromosomal evolution and
the karyotype of *Anoura* requires a min-
imum of 30 rearrangements to so radically
reorganize its banding pattern.

The relationships between *Loncho-
phylla, Leptonycteris, Choeroniscus, Choe-
ronycteris, Hylonycteris,* and *Musonycte-
ris* are more easily resolved. All of these
genera share one chromosomal synapo-
morphy (arm E), but have experienced
different sequences of chromosomal rear-
rangement after sharing a common ances-
tor.

*Lonchophylla thomasi* possesses a
highly derived karyotype in which all
arms have been rearranged. This has re-
sulted in an essentially autapomorphic
karyotype unique to this species. *L. ro-
busta* on the other hand, may not possess
such a highly derived karyotype but may
in fact share an identical (or essentially
so) karyotype with *Leptonycteris spurrelli.*
Baker (1979) reported data for *Loncho-
phylla robusta* and *Leptonycteris spurrelli,*
and both share identical standard karyo-
types (2n = 28, FN = 50). Standard
karyotypic data are by no means defini-
tive, but the possibility exists that band-
ing data will confirm this hypothesis.
Should this be the case, then the resolu-
tion of relationships will be further im-
proved. A derived karyotype shared be-
tween *Lonchophylla robusta* and *Leptonycteris* would indicate that these two
genera shared a common ancestor after
diverging from the *Choeroniscus* line and
that the extensive chromosomal evolution that has occurred in the Lonchophylla thomasi lineage has taken place after L. thomasi and L. robusta shared a common ancestry.

The Choeroniscus group represents the most well defined clade (9 synapomorphies), with seven highly rearranged chromosomal arms plus two other rearrangements (Pa A2, SA on C). Choeroniscus minor probably retains the primitive for this clade. Three centric fusions (D/A2, E/B, A1/J) and pericentric inversions in two chromosome pairs (F and G)
are synapomorphies for Hylonycteris, Choeronycteris, and Musonycteris. Hylonycteris retains a primitive condition for pair I but possesses an autapomorphic pericentric inversion in pair C. Choeronycteris and Musonycteris possess a synapomorphic pericentric inversion in pair I, but can be distinguished from each other by the presence of a polymorphism in pair H of Musonycteris. This polymorphism is either a convergent character found in Hylonycteris and Musonycteris or the polymorphism was found in the ancestor for all three genera.

The chromosomal data summarized in Figure 8 do not differ radically from the results of other authors (Phillips, 1971; Gardner, 1977). A different level of resolution is obtained with chromosomes, however, and a close association of Lonchophylla, Hylonycteris, and Lionycteris with Choeroniscus is strongly documented by chromosomal synapomorphies. This is in contrast to Phillips (1971), Gardner (1977) and Griffiths (1982). Both Phillips and Gardner placed Hylonycteris in clades distinct from the Choeroniscus clade and associated Lionycteris with Lonchophylla. Griffiths placed Hylonycteris in a clade only distantly related to the Choeroniscus clade. Griffiths (1982) differs with these authors by associating Hylonycteris closely with the Choeroniscus group but recognizes the Lonchophylla-Lionycteris clade as a distantly related clade worthy of subfamilial status. Our data agree with his inclusion of Hylonycteris in the Choeroniscus group but stand in opposition to the recognition of the Lonchophyllinae (Griffiths, 1982).

The conclusions of Griffiths concerning the Lonchophylla clade are so divergent from our results and those of previous authors that we felt compelled to look at his character analysis. We present our cladistic analysis of his data (from Table 1, p. 39, Griffiths, 1982) in Figure 9. Although there may be good reasons for his weighting of characters, his resulting cladogram clearly does not follow the rule of parsimony. As a result, the cladistic analysis of Griffiths (his Fig. 33) results in three synapomorphies which unite the Lonchophyllinae and seven convergent events which occur both in the Lonchophylla clade and the glossophagine clade. If Griffiths' characters are given equal weighting and analyzed parsimoniously, a different perspective is obtained (Fig. 9). The clad consisting of Lonchophylla, Lionycteris, and Platalina can be included in the glossophagine clade at the same level as Leptonycteris and Anoura on the basis of seven synapomorphies (his characters 2, 3, 4, 5, 8, 9, and 15). When these data are interpreted this way, the Lonchophylla clade can be distinguished on the basis of three synapomorphies (in characters 11, 12, and 13) but five reversals are necessary (characters 6, 7, 14, 17, and 18). No matter which way the data are analyzed, the Lonchophylla clade is unusual in that it is characterized by a high level of convergence.

The critical point of our reanalysis is that when Griffiths' (1982) data are placed into a cladogram with the same branching sequences resulting from a cladistical analysis of G-banded chromosomes, fewer reversals or convergent events are required to explain his data. Considering that 1) in our opinion, Griffiths did not use a proper sister group analysis, 2) his data are more parsimoniously explained by the branching pattern resulting from chromosomal data, and 3) when his data are applied to the branching patterns suggested by chromosomal data, six synapomorphies can be recognized to document the shared common ancestry of glossophagine taxa, we conclude that his division of the Glossophaginae-Brachyphyllinae into four subfamilies was premature. It is our conclusion that the results of Baker et al. (1981), Hood and Smith (1982), and Griffiths (1982) are compatible with a monophyletic glossophagine clade hypothesis (Figs. 8 and 9). We also conclude that the morphological and chromosomal data sets are congruent but offer resolution at different levels. Morphological data provide resolution of relationships close to the base of the cladogram, whereas, chromosomal data allow reso-
volution of relationships in the upper portions of the cladograms. We feel that if the results of the two data sets are combined, a more accurate assessment of the relationships of glossophagine taxa can be determined.

Chromosomal evolution in the Glossophaginae and Brachyphyllinae has proceeded at highly differential rates. Glossophaga, Leptonycteris, Monophyllus, Brachyphylla, Erophylla, and Phyllonycteris all have essentially the same karyotype (only Leptonycteris has a single unique rearrangement). On one hand, we observe six genera that classical systematists have divided into two subfamilies (Glossophaga, Leptonycteris, and Monophyllus in the Glossophaginae and Brachyphylla, Erophylla, and Phyllonycteris in the Brachyphyllinae) giving a total of one chromosomal rearrangement in six genera examined. On the other hand, the chromosomal diversity in seven genera (Lonchophylla, Anoura, Lionycteris, ...
Choeronycteris, Choeroniscus, and Museronycteris) requires a minimum of 120 rearrangements and possibly a much higher number to explain the variation. In the glossophagine taxa with derived karyotypes, chromosomal evolution has involved numerous rearrangements so that few primitive chromosomal arms can be recognized, but all these taxa share the tandem fusion of arms 13 and 2 (13/2). Lionycteris spurrelli is an exception in that essentially all of the primitive arms can be recognized, but they have been considerably rearranged so that all arms except 13/2 are in unique combinations for the family.

Several points relative to the contrast in rate and magnitude of chromosomal evolution are worthy of note. 1) Such a contrast is difficult to explain in terms of most currently accepted theories of chromosomal evolution and fixation of chromosomal morphs by random processes (Lande, 1979); 2) Chromosomal evolution does not behave in a clocklike fashion and the mode and tempo of chromosomal evolution for some taxa appears somewhat similar to a pattern proposed as punctuated equilibrium (Gould and Eldredge, 1977); 3) Baker and Bickham (1980) documented a pattern where some species experienced a radical reorganization of the chromosomal banding pattern (karyotypic megaevolution) while other closely related species retained the primitive condition. A relatively large number of the nectar feeding species appear to have undergone this highly accelerated rate of chromosomal evolution; and 4) Wilson et al. (1975) hypothesized a relationship between extent of chromosomal evolution and magnitude of morphological evolution. We find no clear cut support for this hypothesis in the glossophagine data set.

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