CLADISTIC ANALYSIS OF FEMALE REPRODUCTIVE HISTOMORPHOLOGY IN PHYLLOSTOMATOID BATS

CRAG S. HOOD AND JAMES DALE SMITH

Abstract

Hood, C. S. (The Museum, Texas Tech University, Lubbock, Texas 79409) and J. D. Smith (Department of Biological Science, California State University, Fullerton, California 92634; and Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007) 1982. Cladistic analysis of female reproductive histomorphology in phyllostomatoid bats. Syst. Zool., 31:241–251.—A cladistic analysis of the neotropical bat families Noctilionidae, Mormoopidae, and Phyllostomatidae is presented utilizing structures of the female reproductive tract. Several shared-derived (synapomorphic) features of the uterus, oviduct, and ovaries were identified within these taxa. These included features of external and internal uterine anatomy, the uterotubal junction, form of oviductal mucosal folds, anatomical relationships between oviduct and uterus, and the position of the ovarian ligament. A cladogram based on these female reproductive histomorphological synapomorphies was constructed and is proposed as a phylogenetic hypothesis. This hypothesis was tested for congruence with independent data sets involving comparative morphological, karyological, and biochemical characteristics. Noctilionids, mormoopids, and phyllostomatids possess synapomorphies that indicate they shared a common ancestor and thereby form a monophyletic group, the Phyllostomatoidea. However, based on features of the female reproductive tract, the neotropical family Thyropteridae (which has been previously assigned to the superfamily Vespertilionoidea) should be included in considering phylogenetic relationships of the Phyllostomatoidea. Familial relationships are somewhat conflicting; some studies (including the present analysis) specify a sister-group relationship between mormoopids and phyllostomatids, whereas others suggest a noctilionid-mormoopid relationship. Relationships within the Phyllostomatidae are resolved at subfamilial levels with female reproductive and independent data sets. The high level of congruence found between the phylogenetic relationships predicted by these data sets is proposed as strong evidence for the phylogenetic resolving power of female reproductive histomorphology. [Reproductive histomorphology; Noctilionidae; Mormoopidae; Phyllostomatidae; Thyropteridae; phylogeny.]

Studies on the phylogenetic relationships of bats (Chiroptera) have been interpreted largely in the context of the classification proposed by G. S. Miller, Jr. (1907), as modified by Simpson (1945) (for a review, see Smith, 1980). Comprehensive studies on various aspects of chiropteran biology have included many ad hoc comments on phylogenetic relationships. However, there are few comparative studies which have critically evaluated kinship relationships among bats.

Evolutionary relationships of the neotropical chiropteran families Noctilionidae, Mormoopidae, and Phyllostomatidae have been debated for many years. Some workers have emphasized primitive features of noctilionids and proposed phylogenetic relationships with the Emballonuridae leading to the placement of noctilionids in the superfamily Emballonuroidea (Dobson, 1875; Trouessart, 1897; Miller, 1907; Simpson, 1945). Other workers have emphasized a close association of noctilionids with mormoopids and phyllostomatids on the basis of shared-derived features and place these three families in a monophyletic superfamily, the Phyllostomatoidea (Winge, 1892; Walton and Walton, 1968; Smith, 1972, 1976; Patton and Baker, 1978; Arnold et al., 1982).

This study presents the first cladistic analysis of noctilionids, mormoopids, and phyllostomatids based on features of the female reproductive tract. Phylogenetic relationships proposed on the basis of synapomorphic features of the female reproductive tract are compared with those found in studies of other, indepen-
Table 1. A List of Phyllostomatoid Taxa Analyzed in This Study. For a Complete List of Outgroup Taxa Examined, See Hood and Smith (1983).

<table>
<thead>
<tr>
<th>Noctilionidae</th>
<th>Carolininae</th>
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<tr>
<td>Noctilio albiventris</td>
<td>Carollia castanea</td>
</tr>
<tr>
<td>Noctilio leporinus</td>
<td>Carollia perspicillata</td>
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<tr>
<td>Noctilus parnellii</td>
<td>Carollia subrufa</td>
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<tr>
<td>Noctilus quadridens</td>
<td>Rhinophylla pumilio</td>
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<tr>
<td>Mormoopidae</td>
<td>Stenoderminae</td>
</tr>
<tr>
<td>Pteronotus macleayi</td>
<td>Sturnira lilium</td>
</tr>
<tr>
<td>Pteronotus parnellii</td>
<td>Uroderma bilobatum</td>
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<tr>
<td>Pteronotus quadridens</td>
<td>Vampyrops helleri</td>
</tr>
<tr>
<td>Mormoopus blainvillii</td>
<td>Vampyrophodes carraccioi</td>
</tr>
<tr>
<td>Phyllostomatidae</td>
<td>Vampyressa pusilla</td>
</tr>
<tr>
<td>Phyllostomatinae</td>
<td>Vampyrella alba</td>
</tr>
<tr>
<td>Macrotus californicus</td>
<td>Artibeus jamaicensis</td>
</tr>
<tr>
<td>Micronycteris hirsutus</td>
<td>Enchisthenes hartii</td>
</tr>
<tr>
<td>Micronycteris macrophthalmus</td>
<td>Ariteus flavescens</td>
</tr>
<tr>
<td>Phyllostomus discolor</td>
<td>Ametrina centurio</td>
</tr>
<tr>
<td>Phyllostomus hastatus</td>
<td>Centurio senex</td>
</tr>
<tr>
<td>Phyllostominae</td>
<td>Brachyphyllinae</td>
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<tr>
<td>Trachops cirrhosus</td>
<td>Brachyphylla cavernarum</td>
</tr>
<tr>
<td>Glossophaginae</td>
<td>Phyllonycteris aphylla</td>
</tr>
<tr>
<td>Glossophaga soricina</td>
<td>Desmodontinae</td>
</tr>
<tr>
<td>Monophyllus redmani</td>
<td>Desmodus rotundus</td>
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<tr>
<td>Leptonycteris curasoae</td>
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<tr>
<td>Lonchophylla robusta</td>
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<tr>
<td>Anoura geoffroyi</td>
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Methods

All specimens used in this study were obtained from natural populations. Museum specimens were fixed in formalin, whereas fresh material was fixed in Zenker's or Bouin's solution (Humason, 1972). Whole reproductive tracts were photographed, prepared by standard histological procedures, and stained with Mallory's Trichrome or Gomori's One Step Trichrome Method (Thompson, 1966:788, as modified by Hood and Smith, 1983). The histomorphology of the female reproductive organs was reconstructed by examination of serial sections.

Phylogenetic relationships were assessed following Hennig (1966) as discussed by Smith (1980). Histomorphological features were examined and coded in character transformation series (morphoclines). The polarity of these morphoclines was determined by outgroup comparison. Out-groups used in this study included representatives from the following chiropteran families (genera, species): Pteropodidae (4, 5), Emballonuridae (4, 4), Rhinolophidae (1, 1), Hipposideridae (1, 2), Vespertilionidae (7, 9), Mystacinidae (1, 1), and Molossidae (3, 4). Literature reports were used to determine character distributions in other eutherian orders. A total of 29 genera and 36 species representing the neotropical families Noctilionidae, Mormoopidae, and Phyllostomatidae (including all subfamilies) were examined (Table 1).

The following characters of the female reproductive tract were used to assess phylogenetic relationships among phyllostomatoid bats. The characters as well as the justification of character morphoclines are discussed in detail by Hood and
Smith (1983). Zero states correspond to primitive (plesiomorphic) conditions, numbered states are portrayed in ever increasing, derived (apomorphic) conditions (e.g., 1 \to 1' \to 1'').

Character 1. External uterine fusion (Figs. 1, 2).

- 0 = Uterine horns more than \( \frac{3}{4} \) length of common uterine body.
- 1 = Uterine horns \( \frac{1}{2} \) length of common uterine body.
- 1' = Uterine horns \( \frac{1}{4} \) length of common uterine body.
- 1'' = Fully simplex uterus, uterine horns not distinct from common body.

Character 2. Uterotubal junction.

- 0 = Uterotubal junction with oviductal papilla or complex folds.
- 1 = Uterotubal junction simple, no papilla or complex folds.

Character 3. Internal uterine fusion.

- 0 = Short common uterine lumen, cornual lumina join within the common uterine body.
- 1 = Large common uterine lumen, cornual lumina join immediately within the common uterine body.
- 1' = Large common uterine lumen, cornual lumina reduced to tubular intramural uterine cornua (IUC).

Character 4. Oviductal mucosal folds (Fig. 3).

- 0 = Oviductal folds occur throughout the oviduct.
- 1 = Oviductal folds restricted to extramural oviduct.

Character 5. Relationships between oviduct and uterus.

- 0 = Oviducts enter the lateral border of the uterine horns or body.
- 1 = Oviducts enter the fundic border of the uterine body.
- 1' = Oviducts enter the fundic border of the uterine body near the midsagittal line.

Character 6. Ovarian ligament (Fig. 4).

- 0 = Ovarian ligament extends from ovary to external entry of oviduct.
- 1 = Ovarian ligament extends from ovary to lateral border of common uterine body.

RESULTS

Phyllostomatoid bats have both primitive and derived features of female reproductive histomorphology compared to out-group chiropteran families (Table 2). Because symplesiomorphies do not contribute to resolving phylogenetic rela-
NOCTILIO ALBIVENTRIS

GLOSSOPHAGA SORICINA

Fig. 2.—Semi-diagrammatic, frontal section of the uterus, oviducts, and ovaries in phyllostomatoid bats. Noctilio albiventris represents phyllostomatoids with bicornuate uteri, whereas Glossophaga soricina is representative of phyllostomatoids with a simplex uterus. By referring to Figure 1, fusion of external uterine anatomy is illustrated in Noctilio (Char. 1, state 1). By using the cervix as a marker, the internal uterine lumina are retained as a primitive in Noctilio (Char. 3, state 0). Additionally derived fusion events occur between Noctilio and Glossophaga. Abbreviations: ov, ovary; ovd, oviduct; olp, oviductal lamina propria; utj, uterotubal junction; myo, myometrium; end, endometrium; cs, cervical stroma; cf, cervical folds; va, vagina; cl, common uterine lumen; inc, intramural uterine cornua.

relationships, only synapomorphous features were used in the phylogenetic analysis.

Familial Phylogenetic Relationships

A cladogram that depicts genealogical relationships among phyllostomatoid bats based on the derived states of female reproductive characters is shown in Figure 5. The Noctilionidae, Mormoopidae, and Phyllostomyidae are linked as a monophyletic group by two synapomorphies—fused external uterine anatomy (Char. 1) and simple uterotubal junction (Char. 2, Fig. 5). These synapomorphies distinguish noctilionids, mormoopids, and phyllostomatids from out-groups and support the recognition of the superfamily group Phyllostomatoidea. Inclusion of the chiropteran family Thyropteridae in the cladogram in Figure 5 is based on the results of a recent paper by Wimsatt and Enders (1980) in which they described the uterus and placenta of the Neotropical Disc-winged bat, Thyroptera tricolor. With regards to the features studied in the present work, thyropterids appear to possess a fused external uterine anatomy (Char. 1) and a simple uterotubal junction (Char. 2); proposed synapomorphies linking noctilionids, mormoopids, and phyllostomatids. The phylogenetic position of thyropterids will be discussed below.

Above this level of genealogical branching, additionally derived uterine and oviductal morphologies have evolved. Although noctilionids and mormoopids share several features of female reproductive histomorphology, they do not share any derived features to the exclusion of phyllostomatids. However, mor-
moopids do share the derived character—internal uterine anatomy fused (Char. 3, Fig. 5) with phyllostomatids. This synapomorphy scheme implies that moopids share a closer phylogenetic relationship with phyllostomatids than with noctilionids. Little variation in reproductive histomorphology was noted within either the Noctilionidae (1 genus, 2 species), or within the Mormoopidae (2 genera, 4 species examined). No autopomorphic features of the female reproductive tract were discovered for these two families. In contrast, the Phyllostomatiidae is defined as a monophyletic group on the basis of the synapomorphy—restriction of oviductal mucosal folds (Char. 4, Fig. 5). Extensive modification of uterine and oviductal histomorphology has occurred within this family; patterns of variation within and between phyllostomatid subfamilies are considered in detail below.

**Relationships Within the Phyllostomatiidae**

Uterine histomorphology in phyllostomatids is diverse with a trend toward
Table 2. Distribution of character states for female reproductive histomorphological data. Taxa are coded as follows: A, Out-group taxa; B, Thyropteriidae; C, Noctilionidae; D, Mormoopidae; E, Desmodontinae; F, Macrotus-group of Phyllostomatinae; G, Phyllostomus-group of Phyllostomatinae; H, Glossophaginae; I, Brachyphyllinae; J, Carolliinae; K, Stenoderminae. See list of characters in text for explanation of character coding.

<table>
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<tr>
<th>Character number</th>
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A progressive fusion of both the external and internal uterine anatomy. The uterine morphology of Desmodus rotundus (subfamily Desmodontinae) is considered primitive for the family. This phylogenetic position is substantiated by the derived uterine feature—additional external uterine fusion (Char. 1', Fig. 5) which links all phyllostomatid subfamilies to the exclusion of the Desmodontinae.

Based on the reproductive characters presented herein, there are two distinct groups within the subfamily Phyllostomatinae. One of these groups, which has been referred to as the “Macrotus-group” (including Macrotus californicus, Microcycteris hirsutus, M. megalotis, and Trachops cirrhosis) has a relatively primitive uterine form. In contrast, the other group, which has been referred to as the “Phyllostomus-group” (including Phyllostomus discolor, P. hastatus, and Phylloderma stenops) shares two synapomorphies with other phyllostomatid subfamilies—externally simplex uterus (Char. 1") and internal uterine anatomy with IUC’s (Char. 3', Fig. 5).

The Glossophaginae, Brachyphyllinae, Carolliinae, and Stenoderminae are linked as a monophyletic group by the synapomorphy—fundic oviductal entry (Char. 5). The reproductive tracts of glossophagines and brachyphyllines are nearly identical; no qualitative differences could be ascertained. These two subfamilies have been combined on the cladogram as a single group.

Stenodermines and carollines share the derived feature—modified ovarian ligament (Char. 6) that suggests a sister-group relationship between these two subfamilies. All stenodermines possess a similar, derived reproductive morphology with two autapomorphies—internal uterine anatomy fused to a single common lumen (Char. 3") and additionally derived fundic oviductual entry (Char. 5', Fig. 5). These features distinguish stenodermines from all other phyllostomatids and identify this subfamily as possessing the most highly derived reproductive histomorphology among phyllostomatid bats.

DISCUSSION

The phylogenetic relationships predicted by synapomorphous features of female reproductive histomorphology can be most rigorously evaluated by testing for congruence with independent data sets. In this section, we compare the phylogenetic relationships predicted by our data with studies utilizing comparative morphology, karyology, and biochemistry.

Features of the female reproductive tract analyzed in the present study demonstrate two synapomorphies that predict a common ancestor for noctilionids, mormoopids, and phyllostomatids. Previous studies using comparative morphology (Walton and Walton, 1968; Smith, 1972,
1976) and karyology (Patton and Baker, 1978) are corroborated and support the recognition of the superfamily Phyllostomatoidea. At this point, the phylogenetic position of the Thyropteridae needs to be discussed. Thyropterids have been considered as allied with two other neotropical families, the Natalidae and Furipteridae; these three families have been placed in the superfamily Vespertilionoidea (also including the Vespertilionidae, Mystacinidae, Myzopodidae, and Molossidae). The association of thyropterids with natalids and furipterids in the context of the Vespertilionoidea has been based primarily on general similarities of cranial morphology and osteology (Winge, 1892; Miller, 1899, 1907). However, Smith (1972:21) noted a similarity in the structure of the distal articulation of the humerus in thyropterids, natalids, furipterids, and phyllostomatids. Other comparative data sets (e.g., chromosomal morphology, Baker et al., 1982) have yet to reveal synapomorphies that establish a relationship between thyropterids and other families of bats. The discovery that *Thyroptera tricolor* shares derived reproductive features with phyllostomatoid bats (including the two synapomorphies defined in this study) suggests that the Thyropteridae be included in the monophyletic superfamily Phyllostomatoidea, though, of course, information on the conditions found in the Natalidae and Furipteridae would be highly desirable.

Familial relationships among phyllostomatoxid bats are somewhat less problematical. For many years, systematists considered the Mormoopidae as a primitive subfamily (=Chilonycterinae) of the Phyllostomatidae. However, Smith’s (1972) review and comparative analysis demonstrated that mormoopids deserve familial status and are aligned with noctilionids and phyllostomatids. Smith (1972) suggested a closer sister-group relationship between mormoopids and noctilionids than between mormoopids and phyllostomatids. Patton and Baker (1978), Baker and Bickham (1980), and Sites et al. (1981) have presented chromosomal data suggesting that mormoopids and noctilionids share five chromosomal rearrangements. These rearrangements were assessed as synapomorphic features relative to the proposed primitive karyotype for the superfamily which was supposed to be like that found in *Macrotus waterhousii*. Patton and Baker (1978) acknowledged that the noctilionid-mormoopid karyotype might be primitive for the superfamily, but noted that this would re-
quire several additional rearrangement events. However, it should be noted that, at present, no other bat family (including the Thyropteridae) can be related karyotypically to the Phyllostomatoidea; so that out-group comparison cannot corroborate the proposed primitive karyotype. Arnold et al. (1982) reviewed the resolving power of independent data sets for phyllostomatoid bats and noted that familial relationships are confounded with contradictory synapomorphies existing among the three families.

The monophyly of the biologically diverse family Phyllostomatidae has been supported by numerous studies (Walton and Walton, 1968; Smith, 1972; Baker et al., 1976, 1977, 1979a); the present study corroborates this monophyly with an oviductal synapomorphy. The systematic position of vampire bats (subfamily Desmodontinae) has been a much-contested issue. Many researchers regard the specializations for sanguivory (blood-feeding) in these bats as being sufficiently unique to merit familial status. For example, Van Valen (1979:108) says, “I do not accept placement of the Desmodontidae in the Phyllostomatidae mainly because of a large adaptive shift of each family.” However, recent studies have proposed that desmodontines be included as a subfamily of the Phyllostomatidae on the basis of shared-derived characteristics (ectoparasitic data, Machado-Allison, 1967; stomach morphology, serology, and karyology, Forman et al., 1968; post-cranial osteology, Smith, 1972). This phylogenetic position is corroborated by the reproductive synapomorphy scheme.

The existence of a major dichotomy within the subfamily Phyllostomatinae has been proposed by several authors (Walton and Walton, 1968; Smith, 1972, 1976). The “Macrotus- and Phyllostomus-groups” recognized on the basis of female reproductive histomorphology correspond to similar groups proposed on the basis of exomorphology, dentition, osteology, and karyology. The congruence among these data sets strongly sug-

gests that the Phyllostomatinae is a paraphyletic group.

A close phylogenetic relationship between the subfamilies Glossophaginae and Brachyphyllinae has been proposed by chromosomal and biochemical studies (Baker and Bass, 1979; Baker et al., 1981; Haiduk and Baker, 1982). The results of the present study are consistent with this proposal as the two subfamilies have qualitatively identical reproductive features. Further study may justify combining these two subfamilies. At present, independent data sets do not refute a sister-group relationship. It should be noted that several authors have suggested polyphyletic (or paraphyletic) origins for the Glossophaginae (Baker, 1967; Phillips, 1971; Smith, 1972, 1976). Although this problem is not resolved by the reproductive data, it is quite possible that some glossophagine taxa may be more closely related to brachyphyllines than to other glossophagines (Baker et al., 1981). In a recent study, Griffiths (1982) examined this question using morphology of the hyoid and lingual region. Unfortunately, this paper, which claims to be a “cladistic” analysis, falls short of its goals. Griffiths’ character analysis and outgroup comparison is weak and, worse, inconsistent. In spite of this, he did detect a brachyphylline/glossophagine relationship. His conclusion that the Glossophaginae is “polyphyletic” is flawed by the lack of proper outgroup comparison (see also Haiduk and Baker, 1982).

A sister-group relationship between Stenoderminae and Carolliinae has not been strongly supported by previous work. In fact, no consistent phylogeny has been revealed by morphology (Walton and Walton, 1968; Smith, 1972), karyology (Gardner, 1977; Baker, 1979), or biochemistry (Straney et al., 1979). Most authors have associated stenodermines with glossophagines (in part), and/or the “Phyllostomus-group,” whereas carollines have been aligned with glossophagines (in part), brachyphyllines, desmodontines, and/or the “Macrotus-group”
(for a review see Smith, 1976). However, Smith and Starrett (1979) noted that the architecture of the wing of stenodermines and carollines were generally similar. The present study supports a sister-group relationship between these two subfamilies.

Bats of the genus Sturnira have been considered by some authors as meriting a subfamilial status separate from the Stenodermatinae. However, recent workers (De La Torre, 1961; Baker, 1967; Jones and Carter, 1976; Baker et al., 1979b; Smith and Starrett, 1979) have argued against this proposal and regarded them as members of the Stenodermatinae. Reproductive synapomorphies presented in this study support this arrangement.

Evolution of Bat Reproductive Tracts

Compared to the general conservatism found in most eutherian orders, it is remarkable that extensive evolution of uterine morphology has apparently occurred within the Chiroptera, and in particular within phyllostomatoid bats (Robin, 1881; Wood Jones, 1917; Matthews, 1942; Mossman, 1977). The evolution of the mammalian female reproductive tract has been discussed by many authors (Wood Jones, 1923; Mossman, 1953, 1977; Le Gros Clark, 1959; Lilliegraven, 1969, 1976; Luckett, 1980a). By considering uterine morphology in monotremes and marsupials together with available ontogenetic data, the primitive eutherian uterus is hypothesized to have consisted of two separate uterine horns; these opened independently into the vagina (Mossman, 1977). Derived morphologies apparently have developed by progressive caudal to cranial fusion of the uterine horns, resulting in the formation of a median, common uterine body. This “fusion hypothesis” for the evolution of the mammalian uterus has received a great deal of support from comparative anatomists and embryologists. However, there have been few studies that evaluate the phylogenetic implications of this notion. The present study has shown the value of using histomorphological techniques (see also, Hood and Smith, 1983) and a phylogenetic approach to evaluate this hypothesis and to assess the evolution of uterine morphology in phyllostomatoid bats. The high degree of congruence found between the histomorphology of the female reproductive tract and independent data sets stands as strong evidence for the phylogenetic resolving power of this form/function complex. Like other data used in phylogenetic analysis, the possibility of convergent evolution must be considered. Derived uterine morphologies have apparently evolved convergently in several eutherian orders; for example, the simplex uterus is found in anthropoid primates, edentates, and phyllostomatid bats (Le Gros Clark, 1959; Mossman, 1977; Luckett, 1980b). However, analysis of synapomorphy allows recognition of such events as convergent through congruence testing of independent data sets (Eldredge and Cracraft, 1980; Wiley, 1981).

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