

Comparative Morphology and Evolution of the Female Reproductive Tract in Macroglossine Bats (Mammalia, Chiroptera)

CRAIG S. HOOD

Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 79409

ABSTRACT Comparative morphological analysis of the female reproductive tract in macroglossine bats was undertaken to test the hypothesis that nectarivory arose at least twice within Old World fruit bats. Given that features of the female reproductive tract are not directly involved in adaptations for feeding, this data set should provide a test of the monophyly of macroglossine bats. A cladistic analysis of variation in the structure of the ovaries, oviducts, uterus, and external genitalia supports the hypothesis that *Megaloglossus* has developed a nectar-feeding habit independent of other macroglossine genera. Most of the variation in female reproductive organs among pteropodids is found in the development of derived external and internal features of the uterus. Fusion of uterine cornua, expansion of the common uterine body, and elaboration of the cervical region are found in a group which includes species of *Pteropus*, *Dobsonia*, *Nyctimene*, and the macroglossines (excluding *Megaloglossus*). Results of this study are concordant with independent data sets, thus providing a phylogenetic framework to evaluate critically structural and functional design in the evolution of pteropodid feeding mechanisms.

One of the most challenging problems in evolutionary biology is the understanding of evolutionary change in the form and function of complex anatomical systems. In recent years, the fields of functional and evolutionary morphology have been redirected by incorporating phylogenetic methods as tools to identify and interpret structural and functional design (Lauder, '81, '82; Liem and Wake, '85). This approach has been successfully applied to the study of feeding mechanisms in actinopterygian fish (e.g., Lauder, '83; Schaefer and Lauder, '86) and plethodontid salamanders (e.g., Lombard and Wake, '86; Wake and Larson, '87).

The chiropteran family Pteropodidae includes 44 genera and about 173 species (Fig. 1; Koopman, '84). Bats of the subfamily Macroglossinae have long been recognized as members of a monophyletic group on the basis of their adaptations to a nectarivorous diet (Dobson, 1875; Andersen, '12; Koopman, '84). Morphological adaptations associated with this highly specialized food habit include an elongated rostrum, modified braincase, reduced dentition, and a highly

elongated and protrusible tongue. However, most of these features (except those of the tongue and hyoid region) are not unique to macroglossine bats, also occur in other pteropodids that do not feed on nectar (Andersen, '12).

Features of the female reproductive system have proven useful in assessing evolutionary relationships within and among bat families (Wimsatt and Enders, '80; Luckett, '80; Hood and Smith, '82, '83). This report describes the system in pteropodid bats, assesses the monophyly of the subfamily Macroglossinae, evaluates the fit of macroglossine bats within the larger context of the family Pteropodidae, and tests of concordance among independent data sets.

MATERIALS AND METHODS

All specimens were collected in the wild (Table 1). The anatomical relationships of female reproductive organs and their asso-

Dr. Craig S. Hood is now at Dept. of Biological Sciences, Loyola University, New Orleans, LA 70118. Address reprint requests there.

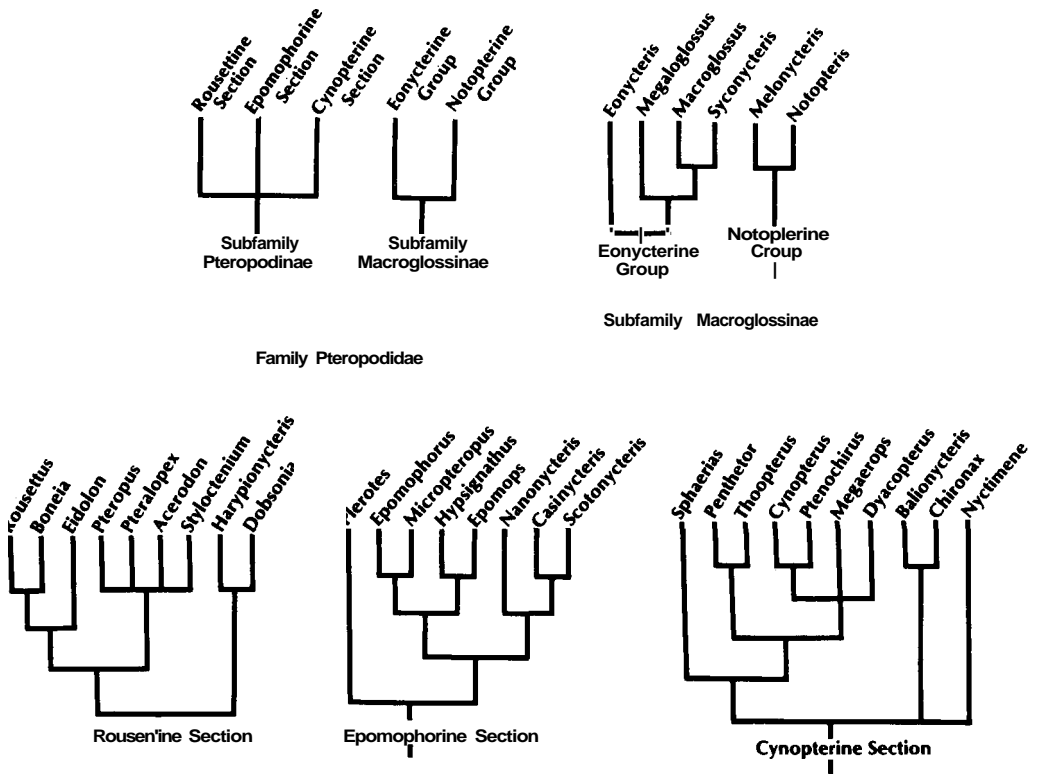


Fig. 1. Phylogenetic relationships of the higher taxonomic groups of pteropodid bats implied by traditional classifications (after Andersen, '12).

ciated supporting membranes were ascertained by gross dissection at the time of capture and excision of tissues, or from dissection of specimens that were collected and preserved intact. Whole reproductive tracts were excised and fixed for gross anatomy, histology, and scanning electron microscopy. Voucher specimens have been deposited in the mammal collections of the American Museum of Natural History; Carnegie Museum of Natural History; Museum of Comparative Zoology, Harvard University; Natural History Museum, Los Angeles County; Thailand Institute of Technology and Research; and The Museum, Texas Tech University.

Tissues were fixed in 10% buffered formalin or Boulin's solution and then processed through paraffin, serially sectioned at 6–10 μ m (Jim, and stained with Mallory's Triple Stain or Gomori's One Step Trichrome Method (Humason, '72; Thompson, '66; Hood and Smith, '83). Selected reproductive tracts

processed for SEM by fixation with 2% glutaraldehyde in 0.1 M phosphate buffer at pH 7.2, dehydration, drying in a Parr 4770 critical-point dryer, and gold-palladium coating at 300 A with a Technics Hummer V Sputter Coater. They were observed with a Hitachi S-570 scanning electron microscope at 20 kV.

Phylogenetic relationships were reconstructed using cladistic methods, with outgroup comparison and parsimony (Kluge and Farris, '69; Watrous and Wheeler, '81; Farris, '82; Maddison et al., '84; Smith and Hood, '84). Outgroups examined included representatives from all bat families except the Craseonycteridae, Furipteridae, and Myzopodidae. Data from the literature were used to determine distribution of character states in other mammalian orders.

RESULTS

Gross morphology and external genitalia

The overall anatomical arrangement of the ovaries, oviducts, and uterus in pteropodid

TABLE 1. List of specimens examined in this study¹

Family Pteropodidae
Subfamily Pteropodinae
Rousettine-section
<i>Rousettus amplexicaudatus</i> (5)
<i>Pteropus admiratitatum</i> (1)
<i>Pteropus hypomelanus</i> (2)
<i>Pteropus neohibernicus</i> (3)
<i>Pteropus temmincki</i> (1)
<i>Dobsonia moluccensis</i> (2)
<i>Dobsonia praedatrix</i> (2)
Epomorphine-section
<i>Epomops franqueti</i> (3)
<i>Hypsignathus monstrosus</i> (2)
<i>Micropteropus pusillus</i> (4)
Cynopterine-section
<i>Cynopterus sphinx</i> (6)
<i>Cynopterus horsfieldi</i> (1)
<i>Balwyncteris maculata</i> (2)
<i>Nyctimene albiventer</i> (5)
<i>Nyctimene vizzaccia</i> (1)
Subfamily Macroglossinae
<i>Eonycteris spelaea</i> (6)
<i>Megaloglossus woermanni</i> (8)
<i>Macroglossus minimus</i> (24)
<i>Macroglossus sobrinus</i> (3)
<i>Syconycteris australis</i> (1)
<i>Melonycteris melanops</i> (6)
<i>Notopterus macdonaldi</i> (3)

Wos. in parentheses represent sample sizes.

bats is equivalent to that found in other bat families and in eutherians generally. The free uterine horns are long in pteropodids and their ovaries lie more superior than those of emballonurids, rhinolophids, vespertilionids, molossids, and phyllostomoids. The pteropodid arrangement is similar to that found in eutherians that also possess primitive (duplex) uterine morphologies (Dermoptera, Rodentia; Mossman, '77).

A major dichotomy in female external genitalia exists between Megachiroptera and some families of Microchiroptera. In pteropodids, the urogenital orifice is a transverse opening found immediately anterior to the anus. A raised structure, the genital tubercle, is directed caudally over the opening and contains a broad, flattened clitoris. The margins of the urogenital orifice are not raised to form labia majora, but postanal and circumanal folds of unknown homology are present. Pteropodid external genitalia are remarkably similar to that found in *Cynocephalus* (order Dermoptera) and generally like that of many other eutherians (Robin, 1881; Wood Jones, '17).

Within Microchiroptera, variations in these features occur in emballonurids, rhinopomatids, rhinolophids, hipposiderids, nycterids, megadermatids, vespertilionids, mystacin-

ids, and molossids (see also Wood Jones, '17; Matthews, '41; Madkour, '76). Together with pteropodids, these bat families share a broadly flattened genital tubercle and clitoris, and an overall transverse disposition of the vulva. In contrast, the external genitalia of noctilionids, mormoopids, phyllostomids, thyropterids, and natalids are dramatically modified (see also, Wood Jones, '17; Wimsatt and Enders, '80). These bat families show an elongation of the vulva in an anteroposterior direction, an elongate clitoris, prominent labia minora, and poorly developed postanal-circumanal folds. The anteroposterior development of the vulva appears to be a derived feature within eutherian mammals, a similar evolutionary trend being found only in the primates.

Ovarian morphology

The ovaries of pteropodids are either spherical or slightly elongate and their histology is typical of that of other mammals. In all pteropodids examined, both ovaries contain a variety of follicular types and are equally functional, with ovulation alternating between sides. Extensive networks of blood vessels are found in the ovarian hilus, the mesenteries supporting the oviduct, and the cranial end of the uterus in many of the taxa examined. This histological arrangement allows for direct vascular (veno-arterial) shunts between these organs. Such a system occurs in *Pteropus giganteus* and its vascular shunts mediate asymmetrical oviductal and uterine reactions (Marshall, '49; '53). Although the present study was not designed to investigate questions of reproductive function, histological features of ovarian anatomy suggest that vascular shunts occur in a wide variety of pteropodid taxa.

The anatomical relationship of the ovary to the oviduct and uterus in pteropodids has no unusual features compared to those of other mammals. In all pteropodids examined, the ovary and oviduct are enveloped by an ovarian bursa that is composed of a mesovarium and mesosalpinx. Phyllostomid bats demonstrate a tremendous variety of bursal types (Hood and Smith, '83), whereas pteropodids display conservative anatomy. According to the terminology of Mossman and Duke ('73), pteropodids are characterized as having a complete bursa, with a tiny, slitlike peritoneal opening. The oviduct wraps around the lateral and cranial aspects of the ovary (lateral recurve type).

Oviductal morphology

The oviducts of pteropodids are relatively short and regionally differentiated into an infundibulum, preampulla, ampulla, isthmus, and junctura. The extramural oviduct, as denned by Hood and Smith ('83), contacts the cranial end of the uterine horn at its apex and traverses the uterine wall until it opens into the uterine lumen. In many of the outgroup taxa, the extramural oviduct and uterine horn have an apical site of contact; examples include emballonurids, rhinolophids, hipposiderids, noctilionids, mormoopids, and some phyllostomids.

Vespertilionids and molossidids possess an uterotubal junction (UTJ) with a prominent colliculus, whereas rhinolophids, hipposiderids, megadennatids, and mystacinids have a small papilla. Phyllostomoids are characterized by having a simple UTJ. Emballonurids do not possess a distinct papilla or colliculus, but have numerous small to medium-sized uterine folds that contribute to form a complicated pocketed region. The UTJ in pteropodids is represented by numerous folds like those found in emballonurids. The number and extent of these folds varies among pteropodid taxa. However, these variations appear to be one of degree. The junction of *Rousettus*, *Hypsignathus*, and *Cynopterus* is least elaborate, with folds that are invested with numerous uterine glands. At the other extreme are species of *Dobsonia*, *Pteropus*, *Eonycteris*, and *Macroglossus*, which are characterized by having fewer, but longer, folds that greatly constrict the cranial end of the uterine cornua. In these taxa, the entire cranial half of the free uterine horns are complicated with endometrial folds and uterine glands.

Uterine morphology

General description and outgroup comparisons

In all chiropteran families examined as outgroups in this study, the free uterine horns are composed of histologically well-defined myometrial and endometrial layers. The common uterine body is often found to consist of two distinct regions: a continuation of the endometrial-lined gestational uterus and the cervix. In phyllostomoids that possess large common uterine bodies, the cervix is limited to the caudal portion of the tract and a single large gestational uterine lumen exists. In contrast, other bat families have

relatively long uterine horns and short common uterine bodies (Fig. 2). In these latter families, the common uterine body is predominantly cervical; thus, the common uterine lumen contributes little to gestation of the developing fetus.

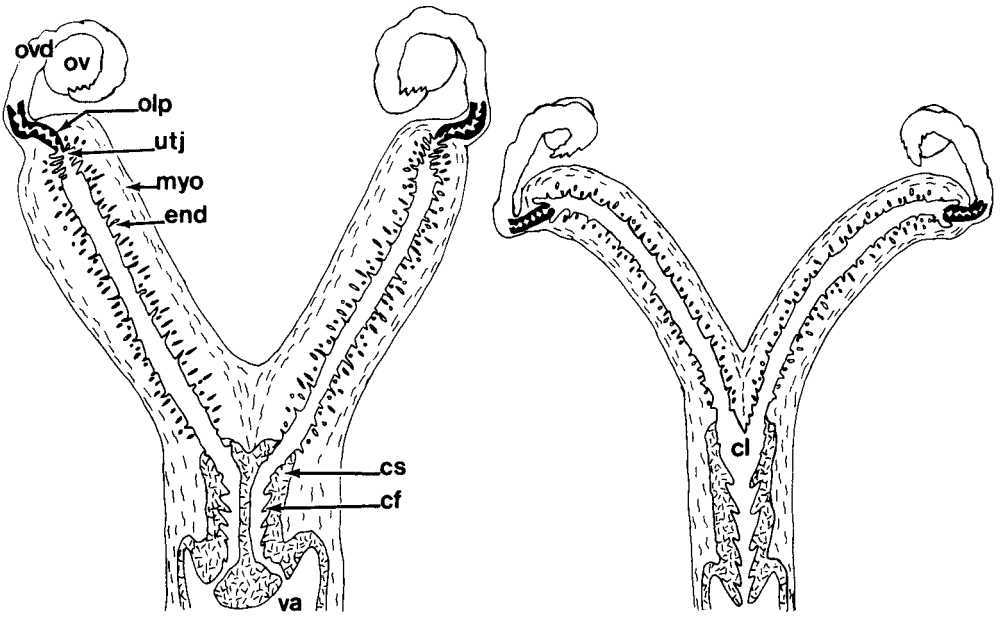
Most families of bats possess histological features of the cervix that are typical by mammalian standards. The length and extent of the cervix is quite variable among bats. In phyllostomoids, emballonurids, rhinopomatids, rhinolophids, hipposiderids, and megadennatids, the cervix constitutes approximately one-third of the total length of the uterus, whereas in vespertilionids and mystacinids, it contributes nearly one-half of the total length. In these microchiropteran families, the portio vaginalis is a low, distinctly rounded or cronical mound. In phyllostomoids, most rhinolophids, and hipposiderids, the portio vaginalis projects centrally into the vagina, whereas in the remaining families it projects from the dorsal wall.

Internally, only some emballonurids (e.g., *Taphozous*) and pteropodids have completely separate uterine lumina that open as independent cervical canals into the vagina (Fig. 2). In all other bat families there is a single common uterine lumen and cervical opening (external os). In most mammals, the cervicovaginal junction is an abrupt and well-defined region located at the external os. However, in some groups, notably Primates and Chiroptera, the cervicovaginal junction is remarkably variable and complex (cf. Hafez and Jaszczak, '72; Hafez, '73; Graham, '73; Kanagawa and Hafez, '73; Hood and Smith, '83).

Variation in external and internal uterine anatomy found in chiropteran families used for outgroup comparisons was described and phylogenetic implications discussed by Hood and Smith ('82, '83). External and internal uterine morphology in pteropodid bats is considered below.

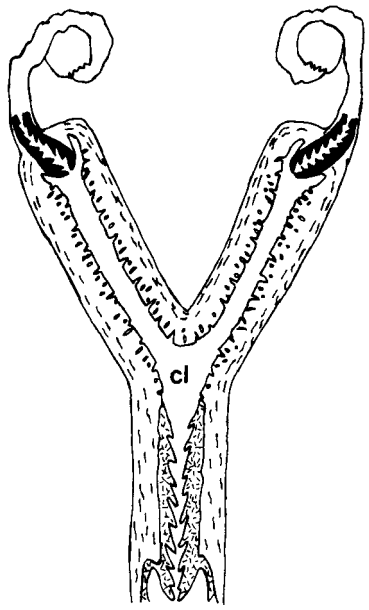
Rousettines

Three genera, *Rousettus*, *Pteropus*, and *Dobsonia*, of Andersen's ('12) Rousettine-section were examined. Externally, the uterus of *Rousettus amplexicaudatus* is distinctly V-shaped, with extremely long uterine horns and a short common uterine body (Fig. 3). The common body constitutes less than one-fourth of the total length of the uterus and consists entirely of the cervix. Cervical ca-

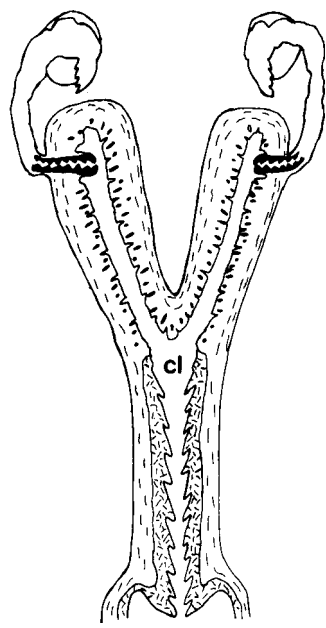


TAPHOZOUS LONGIMANUS

HIPPOSIDEROS DIADEMA



PIPISTRELLUS HESPERUS



TADARIDA PLICATA

Fig. 2. Semidiagrammatic frontal sections of female reproductive tracts in outgroup taxa, including *Taphozous* (Emballonuridae), *Hipposideros* (Hipposideridae), *Pipistrellus* (Vespertilionidae), and *Tadarida* (Molossi-

dae). OV, ovary; OVD, oviduct; OLP, oviductal lamina propria; UTJ, uterotubal jct.; MYO, myometrium; END, endometrium; CS, cervical stroma; CF, cervical folds; CL, common uterine lumen; VA, vagina.

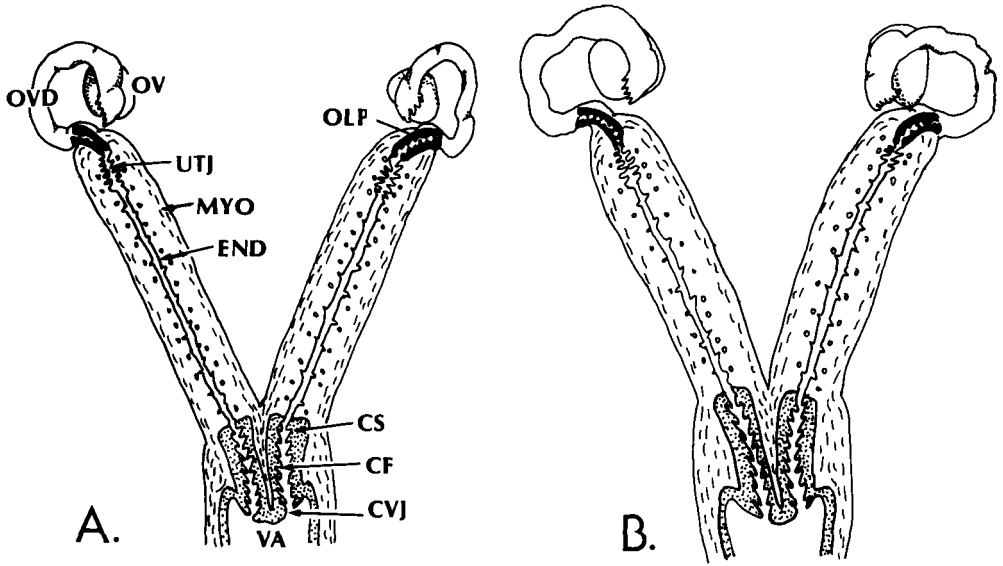


Fig. 3. Semidiagrammatic frontal sections of female reproductive tracts in the pteropodid genera *Roussettus*

(A) and *Hypsignathus* (B). Abbreviations as in Figure 2.

nals open into the vagina independently through a short, centrally projecting portio vaginalis.

Observations on *Roussettus leschenauiti* confirm those previously reported (Gopalakrishna and Choudhari, '77; Karim et al., '79), but contradict the report by Karim ('75) that the portio vaginalis is a hemispherical bulb. In specimens examined in the present study, the portio is a short, centrally projecting structure.

The form of the uterus varies considerably among species of *Pteropus*. The uterus of *P. neohibernicus* is Y-shaped, has a long comua, and a short common uterine body (Fig. 4) which constitutes nearly one-third of the total length of the uterus and consists only of cervical tissue. The lumina of its cervical canals are narrow and open into the vagina independently. The portio vaginalis is a scarcely detectable rounded mound. In contrast to all other pteropodids examined, the vagina of *P. neohibernicus* has a muscular median septum that divides it into two canals for about one-third of its length. This septum is composed of striated muscle that also invests the vaginal wall.

The cervixes of *Pteropus hypomelanus* and *P. temmincki* do not differ (Fig. 4). In these two species, the uterine horns are long but

constitute slightly less of the total length of the uterus compared with that of *P. neohibernicus*. The common body is short and broad and possesses a distinct myometrial layer. Cervical canals are narrow and open independently into the vagina by way of a low, rounded portio vaginalis. No median vaginal septum is present.

The uterus of one specimen of *Pteropus admiralitatum* examined presented a somewhat different form. In this species, the uterine horns taper distinctly, being broadest at their bases (Fig. 4). The common uterine body is slightly longer than that observed in other species of *Pteropus*, and the uterine horns appear shorter. The anatomical relationship of the cervical canals to the vagina is similar to that found in *P. hypomelanus* and *P. temmincki*.

The uteri of *Dobsonia moluccensis* and *Z. praedatrix* do not differ; *D. moluccensis* is described (Fig. 4). The uterus of *D. moluccensis* is Y-shaped, with long uterine horns and a short, broad, common uterine body that represents about one-third to nearly one-half of the total length of the uterus. Uterine lumina within the common body are entirely cervical. The two cervical canals are flattened in transverse section, and open independently into the vagina through a low,

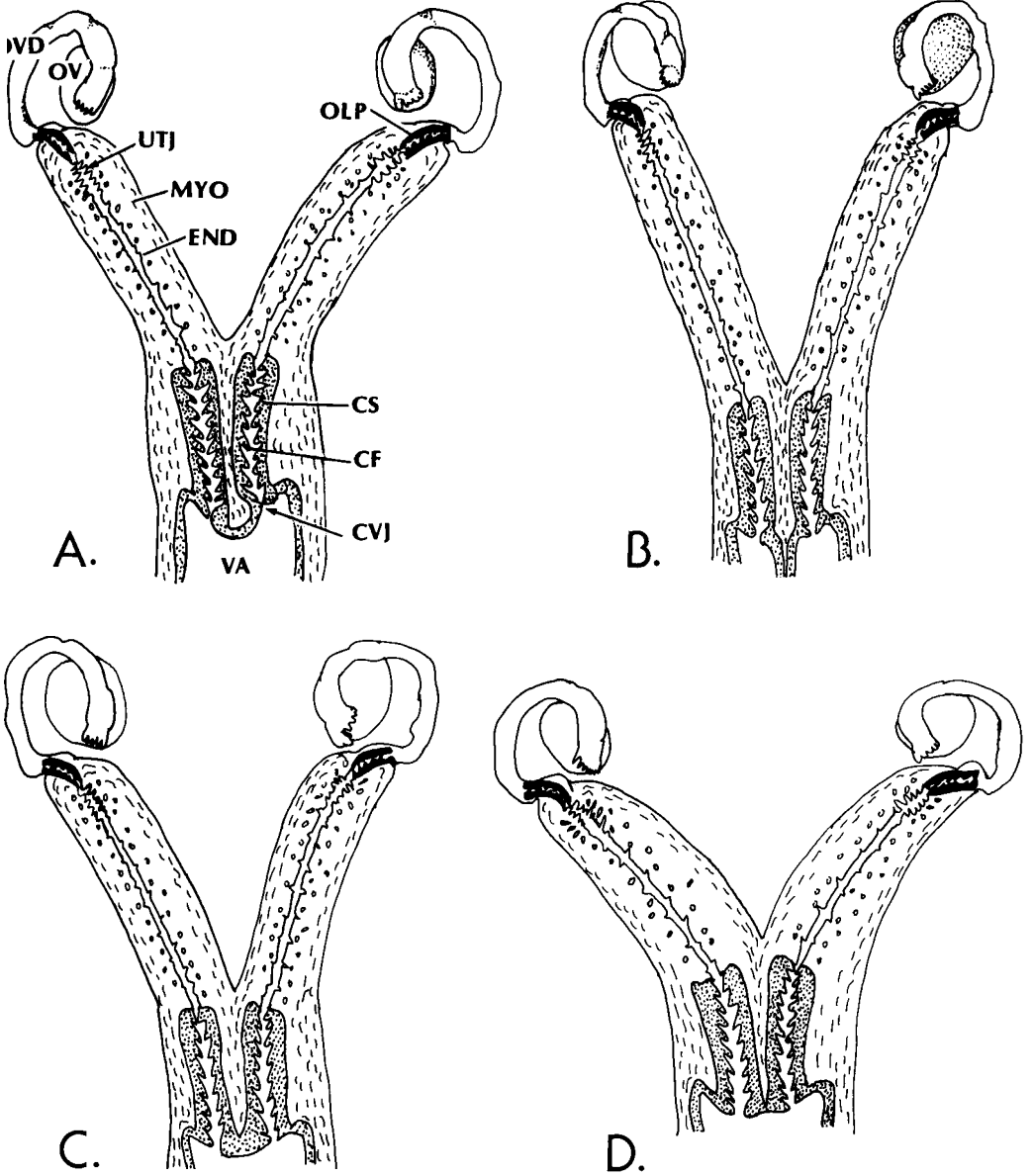


Fig. 4. Semidiagrammatic frontal sections of female reproductive tracts in the pteropodids *Dobsonia moluccensis* (A), *Pteropus neohibernicus* (B), *P. temminckii*

(C), and *P. hypomelanus* (D). Abbreviations as in Figure 2.

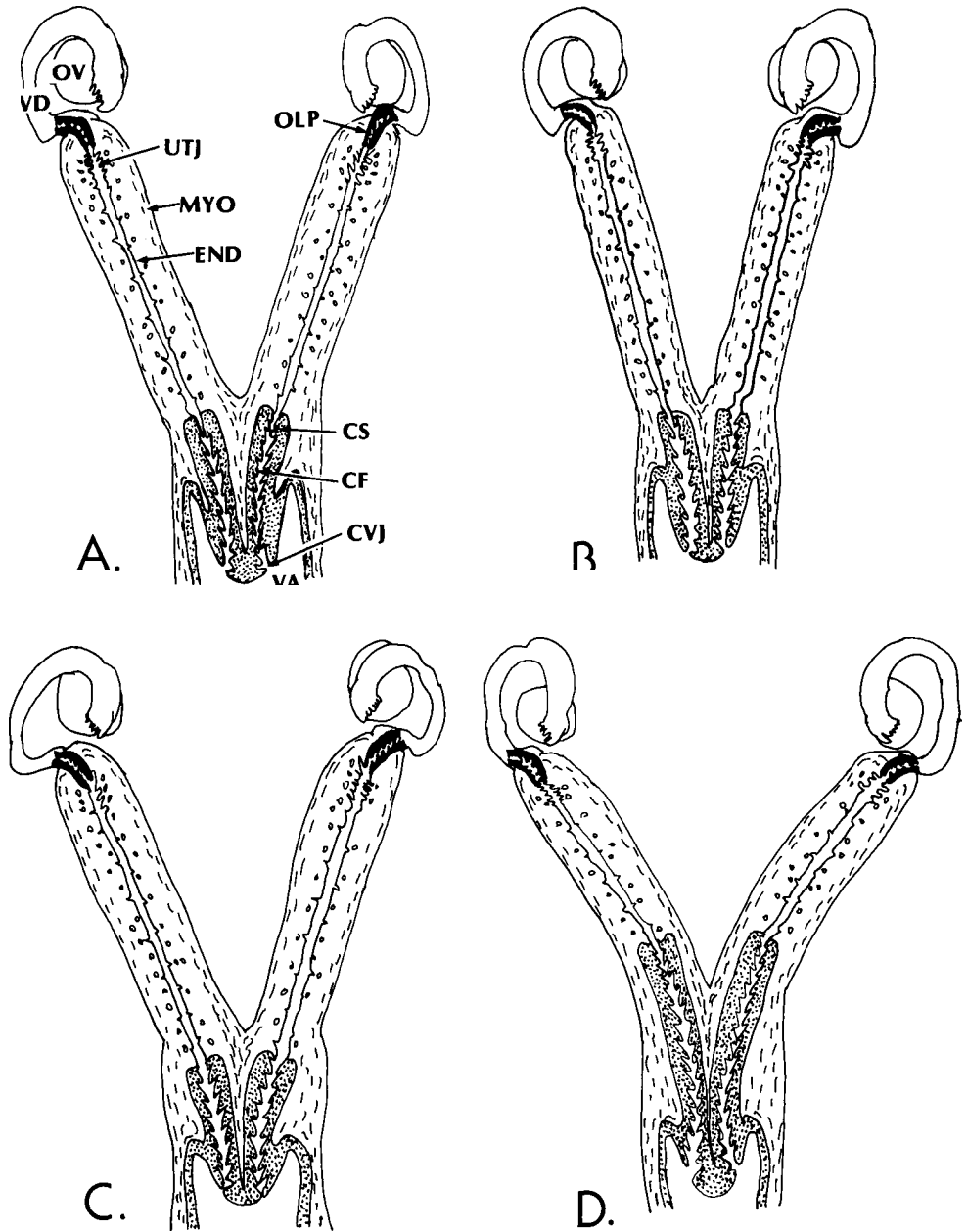


Fig. 5. Semidiagrammatic frontal sections of female reproductive tracts in the cynopterines *Cynopterus brachyotis* (A), *Megaerops niphanæ* (B), *Balionycteris*

maculata (C), and *Nyctimene albiventer* (D). Abbreviations as in Figure 2.

projecting portio vaginalis. These features generally resemble those found in *P. hypomelanus* and *P. temmincki*.

Epomophorines

Three genera, *Epomops*, *Hypsignathus*, and *Micropterus*, of Andersen's ('12) Epomophorine-section were examined. The uteri of all three genera are qualitatively equivalent; *Hypsignathus monstrosus* is illustrated in Figure 3. In these taxa the uterus is V-shaped, with long horns and a slightly rounded common uterine body that measures only one-fourth of the total length of the uterus.

Cynopterines

The uteri of four genera of Andersen's ('12) Cynopterine-section were examined. *Balionycteris maculata* has a Y-shaped uterus, with long horns and a short, round, common body, which constitutes from one-fourth to one-third of its total length (Fig. 5). A small portion of gestational, endometrial-lined uterine lumen is included in this common body. The cervical canals are narrow, laterally flattened, and supported by a histologically well-defined cervical stroma (Fig. 6). A prominent portio vaginalis projects into the vagina as a conical mound distinguishing *Balionycteris* (and other cynopterines) from all other pteropodids examined. The portio is so large that nearly one-half of the extent the cervical canals are contained within this structure. The cervicovaginal junction is variable, and is not always found at the external os. Vaginal epithelium within the cervical canals of one specimen is illustrated in Figure 6.

The uteri of *Cynopterus horsfieldi* and *C. sphinx* are qualitatively equivalent (Fig. 5). The uterus of *C. sphinx* is Y-shaped, with long uterine horns and a short common uterine body that represents about one-fourth of the total length of the uterus; cervical canals open independently into the lateral fornices of the vagina by way of an enormous portio vaginalis that fills most of the cranial end of the vagina. The cervicovaginal junction in *Cynopterus* is extremely complex. Cervical mucosa is ectopic, covering the vaginal surfaces of the portio and lining the fornices.

The uterus of *Megaerops niphanae* is Y-shaped, with a less acute angle between horns than is found in other cynopterines (Fig. 5). The common body is short, representing only about one-fourth the total length of the uterus. As in other cynopterines, the cervi-

cal canals are narrow and lumina flattened. *Megaerops* shares with *Cynopterus* an enormous portio vaginalis that fills most of the cranial end of the vagina. Cervical ectopism was noted in one specimen, but did not appear to be as extensive as that found in *C. sphinx*.

The uteri of *Nyctimene albiventer* and *N. uizcaccia* are qualitatively equivalent; *N. albiventer* is illustrated (Fig. 5). The uterus of *N. albiventer* is broadly Y-shaped, with long horns and a moderately long, broad common body which measures nearly one-half of the total length of the uterus. Internally the cervical canals are extremely long, extending into the free uterine horns. The caudal half of the canals possess large, complicated cervical folds that make this area an extremely complex pocketed region. Cervical canals open into the vagina by way of a large, projecting portio vaginalis. The form of the portio vaginalis in *Nyctimene* approximates that found in *Cynopterus* and *Megaerops* in relative size and shape. The cervicovaginal junction, although complicated by the extensive cervical folds within the portio vaginalis, is abrupt; typical vaginal epithelium lines the fornices of the cranial end of the vagina.

Subfamily Macroglossinae

The uteri of all six genera (*Eonycteris*, *Macroglossus*, *Megaloglossus*, *Melonycteris*, *Notopteris*, and *Syconycteris*) of the subfamily Macroglossinae were examined. The uterus of *Megaloglossus woe.rm.anni* is distinctly V-shaped, with extremely long horns and a short common body (Fig. 7). The common body measures only about one-fourth of the total length of the uterus and is slightly rounded in shape; cervical canals are short and narrow, opening independently by way of a barely noticeable portio vaginalis. In all specimens examined, the cervicovaginal junction was abrupt, with cervical histological characteristics ending at the external os of each cervical canal. Uterine histomorphology in *Megaloglossus* is like that found in *Rousettus* and representatives of the Epomophorine-section.

The uterus of *Eonycteris* is Y-shaped, with moderately short horns and a long common body which measures nearly one-half the total length of the uterus (Fig. 7). A median groove is found on the ventral external surface of the common body, and is especially

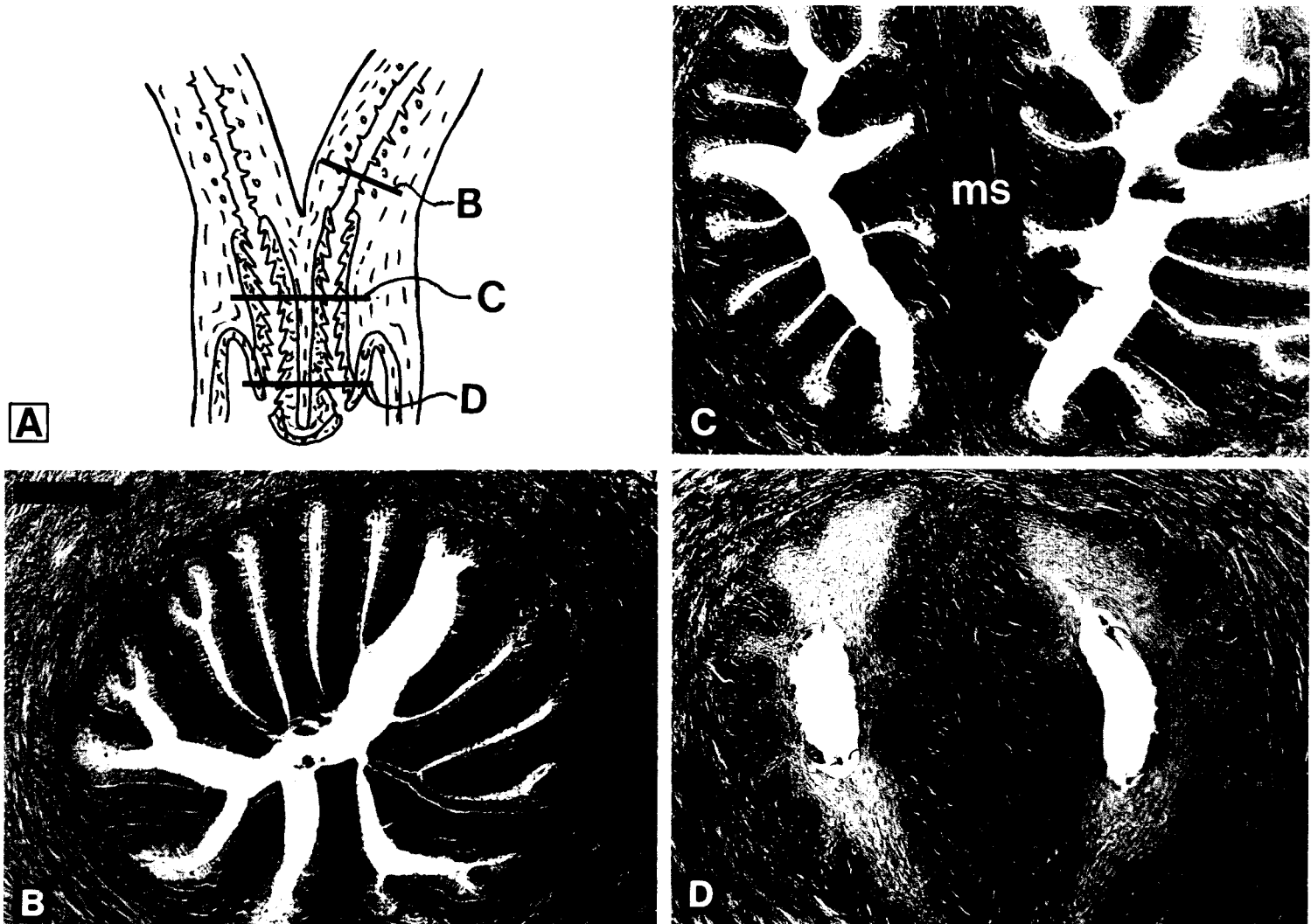


Figure 6

prominent near the junction of the free uterine horns. This feature appears to represent an enlargement of the cervical canals and not a superficial fusion of the cornua, and distinguishes *Eonycteris* and other macroglossines (except *Megaloglossus*) from all other pteropodids. The cervical canals are moderately long and possess numerous long cervical folds, which open independently into the vagina by way of a low, but distinct, portio vaginalis.

The uteri of *Syconycteris australis* and two species of *Macroglossus*, *M. minimus* and *M. sobrinus*, are qualitatively equivalent; *M. minimus* is illustrated (Fig. 7). The uterus of *M. minimus* is Y-shaped, with moderately short horns and a long common body. *Macroglossus* shares with *Eonycteris* an externally visible groove on the ventral surface of the common body, but the common body is further modified by being much enlarged and round or pear-shaped. Internally, the cervical canals are relatively long and possess numerous greatly elongated cervical folds, which make this region appear to possess large pockets that are lined with cervical mucosa. Cervical canals open independently at the edges of a low, rounded portio vaginalis. In all specimens examined, the cervicovaginal junction is abrupt.

The uteri of *Melonycteris melanops* and *Notopteris macdonaldi* are barrel-shaped, with moderately short horns and a large, expanded common body which measures nearly one-half of the total length of the uterus (Fig. 7). *Melonycteris* and *Notopteris* share with *Eonycteris*, *Macroglossus*, and *Syconycteris* a median groove on the ventral surface of the common uterine body. The greatly expanded common body in *Melonycteris* and *Notopteris* appears to be a continuation of that specialization observed in *Macroglossus* and *Syconycteris*. Internally, the cervical canals are greatly expanded, and large cervical folds form a complicated network of pocketed spaces within the body. No portio vaginalis could be distinguished; cervical canals open into the vagina by way of independent openings that are widely separated.

Phylogenetic analyses

The female reproductive tract of the pteropodids examined is relatively conservative. Table 2 lists the distribution of character states among the pteropodid taxa examined. Four characters show derived character states. Character 1, degree of fusion of external uterine anatomy, may be characterized in three character states (0, 1, 1'). Character state 0 is characterized by extremely long uterine horns and a short common body (one-fourth or less of the total length of the uterus) and represents the primitive condition for the family, having been found in several eutherian outgroups (Dermoptera, Rodentia, primitive Primates, and Insectivora). Microchiropteran outgroups have variously derived external morphologies, but among these, *Taphozous* (family Emballonuridae) nearly approaches this state. Derived character state 1 represents fusion of uterine horns resulting in a prominent common uterine body (one-third of the total length of the uterus). Character state 1' represents uterine fusion to its highest degree in pteropodids, resulting in moderately short uterine horns and a large common body (one-half of the total length of the uterus).

Character 2 describes modification of the common uterine body and includes three states (0, 2, 2'). Character state 0, found in outgroups and many pteropodids, is the simple fusion of the uterine cornua resulting in a smooth, tubular, common uterine body. Character state 2 is the presence of a median groove on the ventral surface of the common body. This groove reflects modification of how external fusion has occurred; the cervical canals have enlarged in diameter and are evident externally. Character state 2' is the lateral expansion and enlargement of the cervical canals to form a massive, pear- to barrel-shaped common body.

Character 3 describes modification of the portio vaginalis and includes three states (0, 3, 3'). Character state 0, found in many eutherians and in most microchiropteran outgroups is a low, rounded portio vaginalis. Character state 3 is enlargement of this structure resulting in a portio that is prominent, conical, and projects centrally into the vagina. One-third to one-half of the length of the cervical canals are contained within the portio. Character state 3' is the continued modification of this feature (more than one-half of the length of the cervical canals are contained within the portio), resulting

Fig. 6. Histology of the caudal end of the uterus in *Balionycteris maculata* (A, B, C, D). Cervical canals are laterally flattened (C, D) and surrounded by a muscular layer (MS), that is continuous with the myometrium. Cervical lamina propria (CLP) supports cervical folds. Bar = 0.1 mm for all photographs.

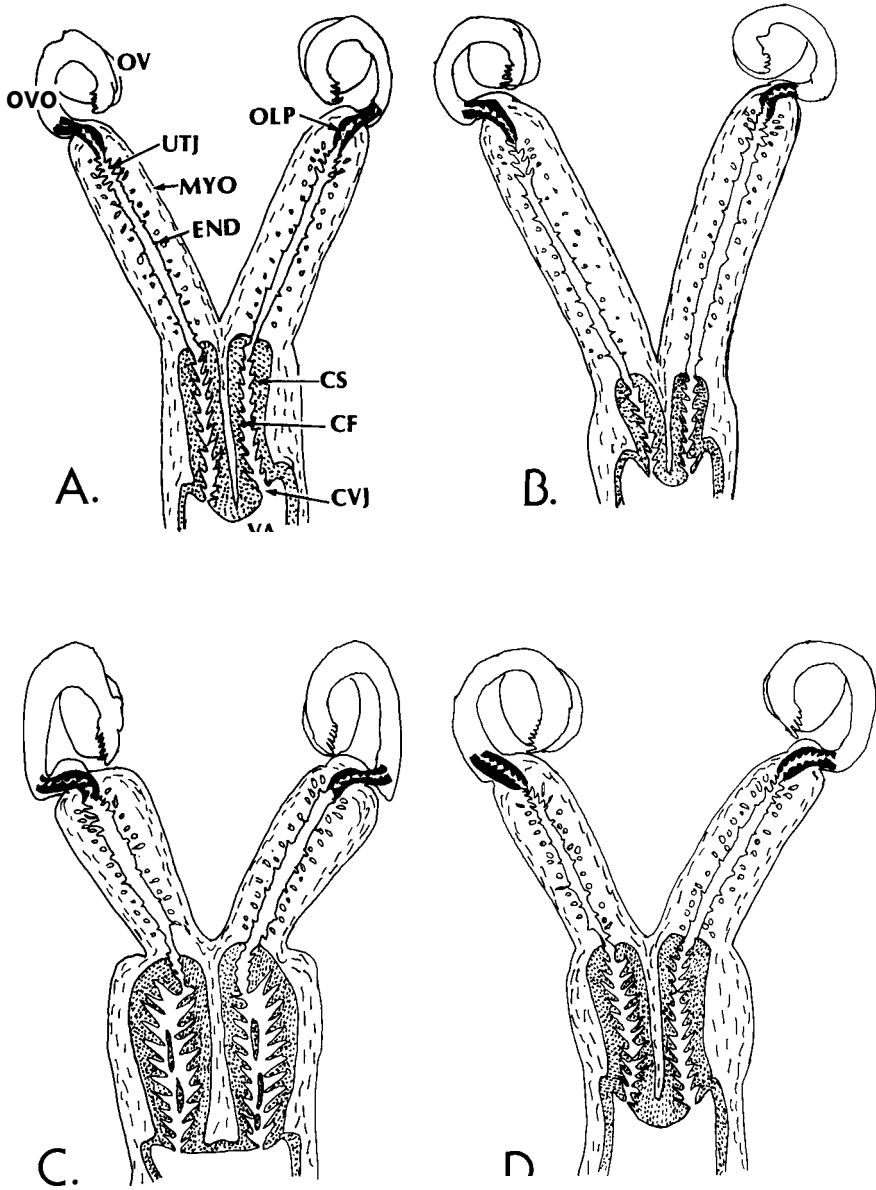


Fig. 7. Semidiagrammatic frontal sections of female reproductive tracts in the macroglossines *Eonycteris spelaea* (A), *Megaloglossus woermanni* (B), *Melonycteris*

melanops (C), and *MacroGLOSSUS minimus* (D). Abbreviations as in Figure 2.

in a massive portio vaginalis that fills most of the cranial end of the vagina.

Character 4 describes the length and extent of the cervix and includes two states (0, 4). Character state 0, found in outgroups and most pteropodids, represents the maintenance of a cervix within the common uterine body. Character state 4 is presence of ex-

tremely long cervical canals that extend into the externally free uterine horns.

DISCUSSION

Phylogenetic implications

Comparisons with outgroups shows that pteropodid bats have retained a relatively primitive duplex uterine morphology. How-

TABLE 2. Distribution of character states for female reproductive data.¹

Taxa	Characters			
	1	2	3	4
Outgroups	0	0	0	0
<i>Rousettus</i>	0	0	0	0
<i>Epomops</i>	0	0	0	0
<i>Hypsignathus</i>	0	0	0	0
<i>Micropteropus</i>	0	0	0	0
<i>Megaloglossus</i>	0	0	0	0
<i>Balionycteris</i>	0	0	3	0
<i>Cynopterus</i>	0	0	3'	0
<i>Megaerops</i>	0	0	3'	0
<i>Pteropus</i>	1	0	0	0
<i>Dobsonia</i>	1	0	0	0
<i>Nyctimene</i>	1	0	3'	4
<i>Eonycteris</i>	1	2	0	0
<i>Macroglossus</i>	1	2'	0	0
<i>Syconycteris</i>	1	2'	0	0
<i>Melonycteris</i>	1	2'	0	0
<i>Notopterus</i>	1	2'	0	0

¹See text for explanation of character coding.

ever, the external and internal morphology of the uterus varies widely among pteropodid bats. This suggests that uterine morphology has undergone more evolution within bat families than in other eutherian orders (Hood and Smith, '82; '83).

Phylogenetic relationships of pteropodid bats based on features of the female reproductive tract are presented in Figure 8. Five genera, *Rousettus* (Rousettine-section), *Epomops*, *Hypsignathus*, *Micropteropus* (Epomophorine-section), and the macroglossine *Megaloglossus*, have retained primitive female reproductive features. The remaining taxa are members of two clades. One group, which includes the cynopterines *Balionycteris*, *Cynopterus*, and *Megaerops*, is recognized by a modification of the portio vaginalis (3). Within the group, a further derived character state (3') unites the genera *Cynopterus* and *Megaerops*.

A second monophyletic group, including *Pteropus*, *Dobsonia*, *Nyctimene*, and the macroglossines (excluding *Megaloglossus*) is supported by six derived character states. Within this assemblage are several nested subgroups. *Nyctimene* is associated with *Eonycteris*, *Macroglossus*, *Syconycteris*, *Melonycteris*, and *Notopterus* by a derived character state (!), but also shares an apparently convergent character state (3') with *Cynopterus* and *Megaerops*. The macroglossines (excluding *Megaloglossus*) represent a monophyletic group based on a modification

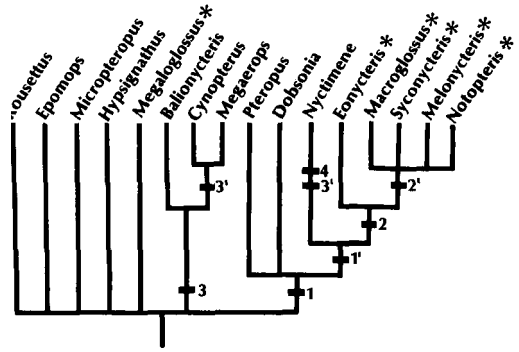


Fig. 8. Cladogram of female reproductive histomorphology. Taxa marked with asterisks had been previously included within the subfamily Macrogloninae. Characters and character states are described in the text.

of the common uterine body (2). *Macroglossus*, *Syconycteris*, *Melonycteris*, and *Notopterus* are distinguished from *Eonycteris* by a further derived condition (2'). The synapomorphy scheme presented here is not fully resolved, but only two homoplasious events were noted (if the character state tree for character 3 is 0 -> 3 -> 3').

The results of the phylogenetic analysis of female reproductive morphology conflict with traditional views of the higher classification of pteropodid bats in several ways (Figs. 1, 8). First, the monophyly of the nectar-feeding subfamily Macrogloninae is rejected. *Megaloglossus* is not a member of the clade that includes other macroglonines, but has retained primitive reproductive features and is associated with non-nectar-feeding taxa. If this hypothesis is correct, then nectarivory has evolved at least twice within the family Pteropodidae. Second, the phylogenetic placement of macroglonine bats (excluding *Megaloglossus*) within the context of the family is predicted as a set of nested relationships with the frugivorous genera *Pteropus*, *Dobsonia*, and *Nyctimene*. These sister-group relationships provide a phylogenetic framework for future studies. Third, Andersen's ('12) Epomophorine- and Cynopterine-sections are not contradicted by the results of the present study. Epomophorines have retained primitive female reproductive features, whereas cynopterines are supported as a monophyletic group on the basis of shared derived features.

The phylogenetic implications of this study are highly concordant with those obtained

by recent immunoelectrophoretic and chromosomal studies (Haiduk et al., '80, '81, '83; Haiduk, '83). Thus a general hypothesis of phylogenetic relationship for pteropodid bats based on biochemical, chromosomal, and anatomical data predicts that 1) nectarivory must have evolved at least twice within the family, 2) macroglossines (excluding *Megaloglossus*) have nested sister-group relationships with *Pteropus*, *Dobsonia*, and *Nyctimene*, and 3) epomorphorines and cynopterines are monophyletic groups.

Functional explanations of reproductive tract evolution

What features of reproduction could explain the variation in uterine morphology observed among pteropodid bats? Wimsatt ('75, '79) and Mossman ('77) have discussed aspects of reproductive biology that apparently are correlated with uterine morphology in mammals. The most important and consistent correlation is that of litter size. Mammals with short, bicornuate and simplex uteri carry only one or a few young, whereas longer, duplex uteri characterize taxa with large litters. Bats represent a major exception to this "rule." The vast majority of bat species, including pteropodids, produce litters of one (many vespertilionids have twins), whereas uterine morphology varies from simplex to duplex (Luckett, '80; Hood and Smith, '82). Adaptation towards a smaller litter size does not explain the evolution of uterine morphology in bats.

Anatomical and physiological asymmetry is a striking feature of many chiropteran species (Wimsatt, '79; Rasweiler, '79, '82; Hood and Smith, '83). Unilateral oviductal and uterine reactions have been described in some phyllostomoids (Rasweiler, '78, '79), emballonurids (Rasweiler, '82), and pteropodids (Marshall, '49, '53). Although the widespread distribution of these features would suggest their independent evolution in several families, they may have value in explaining some aspects of uterine variation within particular groups. Few data are available on pteropodid reproductive biology. However, local unilateral reactions which alternate between sides have been found in species of *Pteropus*, *Eonycteris*, and *Macroglossus* (Marshall, '49, '53; Beck and Lim, '73; Rasweiler, '79; Bhat et al., '80; Hood and Smith, '84). Until we understand the nature of the association of various derived or unique reproductive features with uterine

morphology, it will be difficult to provide strong explanations for the functional significance of variation in uterine morphology among bats.

ACKNOWLEDGMENTS

I thank Drs. R.J. Baker, R.K. Chesser, C. Jones, J.K. Jones, Jr., and M. Willig for critically reviewing earlier drafts of this paper. C. Gans and four anonymous reviewers contributed important critiques that improved the manuscript. For aid in fieldwork I gratefully acknowledge M.W. Haiduk, K. McBee, C.J. Phillips, D. Pumo, L.W. Robbins, D.A. Schlitter, J.D. Smith, K.M. Studhoime, S.L. Williams, and S. Yenbutra. R.L. Honeycutt (MCZ), K.F. Koopman (AMNH), and D.A. Schlitter (CMNH) kindly allowed me to dissect specimens housed in museum collections. Support was provided by the Institute of Museum Research, Carnegie Museum of Natural History, Hofstra University, Loyola University Faculty Research Grant, Sigma Xi, American Society of Mammalogists, an Albert R. and Alma Shadle Fellowship, and an Ernst Mayr Grant (Museum of Comparative Zoology). This paper represents part of a Ph.D. dissertation completed at Texas Tech University.

LITERATURE CITED

- Andersen, K. (1912) Catalogue of the Chiroptera in the Collection of the British Museum. London: British Museum (Nat. Hist).
- Beck, A.J., and B.L. Lim (1973) Reproductive biology of *Eonycteris spelaea* Dobson (Megachiroptera) in West Malaysia. *Acta Trop.* (Basel) 30:251-261.
- Bhat, H.R., M.A. Sreenivasan, and P.G. Jacob (1980) Breeding cycle of *Eonycteris spelaea* (Dobson, 1871) (Chiroptera, Pteropodidae, Macroglorinae) in India. *Mammalia* 44:343-347.
- Dobson, G.E. (1875) Conspectus of the suborders, families, and genera of Chiroptera arranged according to their natural affinities. *Ann. Mag. Nat. Hist. Ser. 4*, 16:345-357.
- Farris, J.S. (1982) Outgroups and parsimony. *Syst. Zool.* 37:328-334.
- Gopalakrishna, A., and P.N. Choudhari (1977) Breeding habits and associated phenomena in some Indian bats. Part 1.—*Rousettus leschenauiti* (Desmaret)—Megachiroptera. *J. Bombay Nat. Hist. Soc.* 74:1-16.
- Hafez, E.S.E., and S. Jaszczak (1972) Comparative anatomy and histology of the cervix uteri in non-human primates. *Primates* 23:297-314.
- Haiduk, M.W. (1983) Evolution in the Family Pteropodidae (Chiroptera: Megachiroptera) as Indicated by Chromosomal and Immunoelectrophoretic Analyses. Ph.D. Thesis, Texas Tech University; Lubbock.
- Haiduk, M.W., L.W. Robbins, R.L. Robbins, and D. A. Schlitter (1980) Karyotypic studies of seven species of African megachiropterans (Mammalia: Pteropodidae). *Ann. Carnegie Mus. Nat. Hist.* 49:181-191.
- Haiduk, M.W., R.J. Baker, L.W. Robbins, and D.A. Schlitter (1981) Chromosomal evolution in Af-

- rican Megachiroptera: G- and C-band assessment of the magnitude of change in similar standard karyotypes. *Cytogenet. Cell Genet.* 29:221-232.
- Haiduk, M.W., L.W. Robbins, and D.A. Schlitter (1983) Chromosomal banding studies and their systematic implications in African fruit bats (Chiroptera: Pteropodidae). *Ann. Mus. Voor Midden-Africa, Belgium*, 257-259.
- Hood, C.S., and J.D. Smith (1982) Cladistical analysis of female reproductive histomorphology in phyllostomatoid bats. *Syst. Zool.* 32:241-251.
- Hood, C.S., and J.D. Smith (1983) Histomorphology of the female reproductive tract in phyllostomatoid bats. *Occas. Papers Mus. Texas Tech Univ.* 86:1-38.
- Hood, C.S., and J.D. Smith (1984) Histology of a sexually dimorphic integumentary gland in *Macroglossus lagochilus* (Chiroptera: Pteropodidae). *J. Mamm.* 65:1-19.
- Humason, G.L. (1972) *Animal Tissue Techniques*. San Francisco: W.H. Freeman.
- Kanagawa, H., and E.S.E. Hafez (1973) Morphology of cervix uteri of Rodentia, Carnivora, and Artiodactyla. *Acta Anat.* 84:118-128.
- Karim, K.B. (1975) Utero-vaginal junction in the Indian fruit bat, *Rousettus leschenauitii* (Desmaret). *Curr. Sci.* 44:706, 707.
- Karim, K.B., W.A. Wimsatt, A.C. Enders, and A. Gopalakrishna (1979) Electron microscopic observations on the yolk sac of the Indian fruit bat, *Rousettus leschenauitii* (Desmaret) (Pteropidae). *Anat. Rec.* 295:493-509.
- Kluge, A.G., and J.S. Fan-iss (1969) Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 28:1-32.
- Koopman, K.F. (1984) Bats. In S. Anderson and J.K. Jones, Jr. (eds): *Orders and Families of Recent Mammals of the World*. New York: John Wiley and Sons, pp. 145-186.
- Lauder, G.V. (1981) Form and function: Structural analysis in evolutionary morphology. *Paleobiology* 7:430-442.
- Lauder, G.V. (1982) Historical biology and the problem of design. *J. Theor. Biol.* 97:57-67.
- Lauder, G.V. (1983) Functional design and evolution of the pharyngeal jaw apparatus in eutelostean fishes. *Zool. J. Linn. Soc.* 77:1-38.
- Liem, K.F., and D.B. Wake (1985) Morphology: current approaches and concepts. In M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake (eds): *Functional Vertebrate Morphology*. Cambridge: Belknap Press, pp.366-377.
- Lombard, R.E., and D.B. Wake (1986) Tongue evolution in the lungless salamanders, family Plethodontidae. IV. Phylogeny of plethodontid salamanders and the evolution of feeding dynamics. *Syst. Zool.* 35:532-551.
- Luckett, W.P. (1980) The use of fetal membrane data in assessing chiropteran phylogeny. In D.E. Wilson and A.L. Gardner (eds): *Proceedings of the Fifth International Bat Research Conference*. Lubbock: Texas Tech Press, pp. 245-265.
- Maddison, W.P., M.J. Donoghue, and D.R. Maddison (1984) Outgroup analysis and parsimony. *Syst. Zool.* 33:83-103.
- Madkour, G. (1976) External genitalia and mammary glands of Egyptian female bats. *Zool. Anz.* 297:62-66.
- Marshall, A.J. (1949) Pre-gestational changes in the giant fruit bat, (*Pteropus giganteus*), with special reference to an asymmetrical endometrial reaction. *Proc. Linn. Soc. London* 762:26-36.
- Marshall, A.J. (1953) The unilateral endometrial reaction in the giant fruit bat (*Pteropus giganteus* Brunnich). *J. Endocrinol.* 9:42-44.
- Matthews, L.H. (1941) Notes on the genitalia and reproduction of some African bats. *Proc. Zool. Soc. Lond. Ser. B* 222:289-346.
- Mossman, H.W. (1977) Comparative anatomy. In R.M. Wynn (ed): *The Biology of the Uterus*. New York: Plenum Press, 2nd edition, pp. 19-34.
- Mossman, H.W., and K.L. Duke (1973) *Comparative Morphology of the Ovary*. Madison: Univ. Wisconsin Press.
- Rasweiler, J.J., IV (1978) Unilateral oviductal and uterine reactions in the little bulldog bat, *Noctilio aiiventris*. *Biol. Reprod.* 29:467-492.
- Rasweiler, J.J., IV (1979) Early embryonic development and implantation in bats. *J. Reprod. Fertil.* 56:403-416.
- Rasweiler, J.J., IV (1982) The contribution of observations on early pregnancy in the little sac-winged bat, *Pteropteryx kappleri*, to an understanding of the evolution of reproductive mechanisms in monovular bats. *Biol. Reprod.* 27:681-702.
- Robin, H.A. (1881) Recherques anatomiques sur les Mammiferes de l'ordre des cheiropteres. *Ann. Sci. Nat., Ser. 6, Zool.* 22:1-180.
- Schaefer, S.A., and G.V. Lauder (1986) Historical transformation of functional design: evolutionary morphology of feeding mechanisms in loricatoroid catfishes. *Syst. Zool.* 35:489-508.
- Smith, J.D., and C.S. Hood (1984) Genealogy of the New World nectar-feeding bats reexamined: a reply to Griffiths. *Syst. Zool.* 33:435-460.
- Thompson, S.W. (1966) *Selected Histochemical and Histopathological Methods*. Springfield: Charles C. Thomas Publ.
- Wake, D.B., and A. Larson (1987) Multidimensional analysis of an evolving lineage. *Science* 238:42-48.
- Watrous, L.E., and Q.D. Wheeler (1981) The out-group comparison method of character analysis. *Syst. Zool.* 30:1-11.
- Wimsatt, W.A. (1975) Some comparative aspects of implantation. *Biol. Reprod.* 22:1-40.
- Wimsatt, W.A. (1979) Reproductive asymmetry and unilateral pregnancy in Chiroptera. *J. Reprod. Fertil.* 56:345-357.
- Wimsatt, W.A., and A.C. Enders (1980) Structure and morphogenesis of the uterus, placenta, and paraplacental organs of the Neotropical disc-winged bat, *Thyroptera tricolor spix* (Microchiroptera: Thyropteridae). *Am. J. Anat.* 259:209-243.
- Wood Jones, F. (1917) The genitalia of the chiroptera. *J. Anat. Physiol.* 52:36-60.