This presentation consists of xx slides
How should we interpret structural similarity among species?

Tubular nostrils

Paranytctimene raptor
Murina leucogaster
Naked-backed bats

*Dobsonia moluccensis*  
*Pteronotus davyi*
Flower-visiting bats

*Megaloglossus*

*Choeronycteris*
Flat-headed bats

Neoplatymops mattogrossensis
Platymops setiger
Sauromys petrophilus
Tylonycteris robustula
Classification should reflect evolutionary history. One step is to describe the organisms, in our case bats. Arrange them in a hierarchy (species, genus, family, etc.) and then determine whether or not the hierarchy reflects evolutionary history. This is much easier (or more difficult) if there is a fossil record.

The challenge … how to recognize parallel and convergent evolution.

The resolution … answer the question, did the common ancestor have the trait(s)?
People have wondered and speculated about the situation in bats.

Simmons & Geisler (1998) presented Dobson’s (1875) view.

Fig. 5. Dobson’s (1875) view of bat relationships (redrawn from Dobson, 1875: unnumbered foldout facing p. 350). The original caption for this figure read “Diagram illustrating the affinities of the families and genera of Chiroptera, and probable lines of descent from ancestral forms (Palaeochiroptera). The families are indicated by circles, the subfamilies by semicircles, and the relative position of both indicates their affinity. In the same manner, the affinity of the generic groups to each other, and to groups of other families, is indicated (as far as possible) by the relative position of the names of these groups in each circle . . . The position of the circle representing the Pteropidae is not intended (as in other cases) to indicate their descent from the Phyllostomidae, but to show their position with regard to the whole suborder Microchiroptera.” We have retained Dobson’s (1875) spellings of group names, many of which are no longer in common usage.
Jepsen (1966) described *Icaronycteris index*, an Eocene bat fossil from Wyoming (Green River Formation).

Jepsen (1970) followed this up with some reflections about the evolution of bats --- suggested that they evolved in caves.
TABLE 2
Higher-level Classification of Recent Bats Proposed by Simmons (1998)

Order Chiroptera
Suborder Megachiroptera
  Family Pteropodidae
Suborder Microchiroptera
  Infracorder incertae sedis
    Superfamily Emballonuroidea
      Family Emballonuridae
  Infracorder Yinchoiroptera
    Superfamily Rhinopomatoidea
      Family Craseonycteridae
    Family Rhinopomatidae
  Superfamily Rhinolophoidea
    Family Nycteridae
    Family Megadermatidae
    Family Rhinolophidae
      Subfamily Rhinolophinae
      Subfamily Hipposiderinae
  Infracorder Yangochiroptera
    Superfamily incertae sedis
      Family Mystacinidae
  Superfamily Noctilionoidea
    Family Noctilionidae
    Family Mormoopidae
    Family Phyllostomidae
  Superfamily Molossoidea
    Family Antrozoidae
    Family Molossidae
      Subfamily Tomopeatinae
      Subfamily Molossinae
  Superfamily Vespertilioidea
    Family Vespertilionidae
      Subfamily Vespertilioninae
      Subfamily Miniopterinae
      Subfamily Myotinae
      Subfamily Murininae
      Subfamily Kerivoulineae
  Superfamily Nataloidea
    Family Myzopodidae
    Family Thyropteridae
    Family Furipteridae
    Family Natalidae

From Simmons and Geisler
1998

From Jones & Teeling
2006
One of the first comprehensive looks at the phylogeny of bats is provided by Simmons and Geisler (1998). This important paper also took into account a variety of fossil bats, including some from the Eocene.

Simmons and Geisler (1998) present several phylogenies and the ones arising from their analyses are supported by appropriate statistic.

But before we delve into phylogeny, we must address the question “are bats monophyletic?” Today the prevailing view is “yes”, but that is not a unanimous view and not the one that was under discussion in the 1980s and 1990s.

Simmons & Geisler 1998
Smith and Madkour (1980) used a variety of penial characters to support the view that bats (Chiroptera) were diphyletic.

In other words Megachiroptera have a different origin than Microchiroptera.

Fig. 5.—Cladograms that depict phylogenetic relationships among lipotyphlan insectivores and the archontan taxa: Scandentia, Dermoptera, Primates, Megachiroptera, and Microchiroptera. Black bars indicate synapomorphous (shared-derived) features. A, cladogram based on four penial synapomorphies: 1, free and pendulous penis; 2, accessory cavernous tissue absent; 3, distally expanded, vascular corpus spongiosum; 4, baculum absent. B, cladogram based on penial synapomorphic features and: 5, enlarged neocortex; 6, laminar, lateral geniculate nucleus (presumed to be present in Dermoptera); 7, distal radius and lunar carpel broadened; 8, derived, non-insectivorous dentition. C, same as B with the addition of: 9, patagium for gliding or modified as wing. D, cladogram that depicts currently accepted phylogenetic relationships among these taxa, with superimposed distribution of apomorphic characters (1-9). Parentheses around numbers indicate a derived condition that occurs only in a few members (not widespread) of a particular taxa (e.g. character 4, loss of baculum, occurs in some Primates (Homo) and some Microchiroptera (Phyllostomidae, among others). See text for discussion.

Smith and Madkour 1980
Synapomorphies = black bars, shared derived characters

Smith and Madkour 1980
Synapomorphies = black bars, shared derived characters

Smith and Madkour 1980
Enter J. D. (Jack) Pettigrew.

He used electrophysiological and neuroanatomical methods to discover that the pattern of connections between the retina and midbrain differed between the Megachiroptera and the Microchiroptera. The Megachiroptera had an advanced retinotectal pathway previously known only from Primates.

The ancestral condition (synpleiomorphous) of retinotectal connections occurs in the Microchiroptera and in all other vertebrates.
In 1991 most of an issue of Systematic Zoology was dedicated to the question of monophyly in bats.
Pettigrew (1991) laid out four scenarios for the evolution of bats (= flight in mammals).

**Pettigrew 1991**

**Figure 1.** Four of the scenarios that have been proposed to account for the origins of bats. The "flying primate" scenario accounts for a wide range of observations in living and fossil bats, but has the unparsi-monious feature that wings evolve twice, once very early (W1) in the microbat lineage (MIC) and again later (W2) in a branch of the primate lineage leading to the megabats (MEG). The "blind cave bat" scenario has megabats and microbats monophyletic, with the microbats arising from the megabat lineage by the loss of the archontan skeletal and primate brain and genital features; although compatible with some data sets, this scenario is unparsimonious and is incompatible with the relative age of the two bat groups in the fossil record. The "deaf fruit bat" scenario also has bats monophyletic, with megabats losing the ability to echolocate with laryngeal sonar; although compatible with the relative ages of the two bat groups in the fossil record, this scenario lacks parsimony, because the primate features have to evolve independently a number of times. The "fallen angel" scenario is shown for poetic and logical completeness only, because it can be ruled out from the extensive fossil record of the primate lineage; wings evolve first and are later lost in the primate line (flightless bats). MIC, microbats; MEG, megabats; DER, dermopterans; PRI, primates; W, wings; S, laryngeal sonar; P, primate-like features in brain and genitalia; A, archontan skeletal features. Dotted lines indicate loss of the feature.
Pettigrew 1991

**Figure 4.** One of the 60 most parsimonious trees generated from a data matrix of 52 mammalian taxa (including 15 bats) and 287 phylogenetically informative amino acid substitutions. Note that many placements of taxa within the tree are arguable (e.g., kangaroo, rabbit, lemur) but that megabats are recognized as a monophyletic group (Cynopterus, Pteropus poliocephalus, Pteropus alecto, Rousettus), as are nonlemurine primates (human, rhesus, Colobus, Atelis, tamarin, Tarsius, Nycticebus, Galago), carnivores (dog, Felis, raccoon), and cetaceans (minke whale, dolphin, sperm whale). The 11 microbats are not recognized as a monophyletic group, although 5 vesperilionoids and an emballonurid cluster together (Antrozous, Myotis, Chalinolobus, Tadarida, Mormopterus, Taphozous). Three other groups of microbats are paraphyletic, associating either with the megabats (Rhinopoma), with primates (Macrotus, Dremus), or with the whole primate–bat assemblage (Macroderma, Megaderma). These latter three groups of microbats share the smallest number of common substitutions with other microbats and their position within the different trees tends to vary more than does the position of the vesperilionoid cluster.
Figure 5. Consensus tree of all the most parsimonious trees generated from hemoglobin data (52 taxa, 329 amino acid substitutions).
Baker et al. (1991) presented it slightly differently.

Baker et al. 1991

**Figure 1.** Two competing hypotheses concerning the phylogenetic relationships of microchiropteran bats, megachiropteran bats, primates, dermopterans (gliding lemurs), and scandentians (tree shrews). (a) "Classical" hypothesis, supported by Wible and Novacek (1988) and others. (b) Alternative hypothesis, supported by Pettigrew et al. (1989) and others.
Figure 4. Phylogenetic tree based on DNA sequences inferred from β-globin amino acid sequence data. Modified from Pettigrew et al. (1989: their Fig. 16b).

Baker et al. 1991
Figure 2. The most parsimonious tree generated from a data matrix of 24 neural characters scored in the 14 mammalian taxa shown (PAUP, ordered, branch and bound; 43 steps, CI = 0.907). Note that these neural characters have given a tree in which different primate taxa have accepted relations to each other except for Tarsius, which is the sister group of other primates. The nearest sister group of the primates is the megabats, Pteropus and Rousettus, whose nearest sister taxon, in turn, is the gliding "lemur," Cynocephalus. The two microbats, Macroderma and Mormopterus, are found near the base of the tree, far from the megabats. Despite superficial similarities between the visual systems of the tree shrew, Tupaiia, and the gliding squirrel, Petearista, note that these two taxa are separated by the neural characters used in this analysis.
Baker et al. 1991 ...

a phenetic view

Figure 2. Phylogenetic tree based on phenetic similarity of β-globin amino acid sequence data. Modified from Pettigrew et al. (1989: their Fig. 16a).
Baker et al. 1991, a cladistic view

Figure 3. Phylogenetic tree based on cladistic resemblance of β-globin amino acid sequence data. Modified from Pettigrew et al. (1989; their Fig. 16c).

Baker et al. 1991
Table 1. Unique features of the postcranial musculoskeletal system shared by Microchiroptera and Megachiroptera. Presence of these derived features in bats (but not in any other placental mammals) suggests that Chiroptera is monophyletic.

1. Occipitopricalis muscle along leading edge of propatagium.
2. Reduced supraspinous fossa and enlarged infraspinous fossa on scapula.
3. Strongly arched acromion process on scapula.
4. Distal end of humerus without supratrochlear depression and supinator ridge.
5. Markedly reduced olecranon process on ulna.
6. Digits 2-5 of forelimb greatly elongated.
7. Manus rotated 90°.
8. Proximal metacarpals deeply grooved, strongly imbricated.
9. Claws restricted to digit I or I and II on forelimb.
10. Extreme lateral flaring of pubes.
11. Dorsal ischia meet above vertebral axis.
12. Dorsolateral tilting of sites of origin for gluteal muscles.
13. Iliosacral fusion involving last lumbar vertebra.
14. Hindlimbs rotated 90° outward so knee is directed laterally.
15. Head of femur tilted and nearly aligned with long axis of the shaft.
16. Calcanealastragalar facet on calcaneum concave or trough-shaped (not convex).
17. Loss of medial and lateral guiding ridges on trochlea of astragalus.
18. Presence of calcar and depressor osseus styliformes muscle.

Baker et al. 1991
TABLE 2. Derived features of the skull, cranial vascular system, fetal membranes, and nervous system shared by Microchiroptera and Megachiroptera (from Wible and Novacek, 1988: their Table 3). These features are absent in Primates, Dermoptera, and Scandentia, and were interpreted as synapomorphies of Chiroptera by Wible and Novacek (1988).

1. Premaxilla greatly reduced.
2. Jugal greatly reduced.
3. Tegmen tympani tapers to a slender process that projects ventrally into the middle-ear cavity medial to the epitympanic recess.
4. Two entotympanic elements in the floor of the middle-ear cavity: a large caudal element and a small rostral element grooved by (or forming a canal around) the internal carotid artery.
5. Ramus inferior of the stapedial artery passes through the cranial cavity dorsal to the tegmen tympani.
6. Ramus infraorbitalis of the stapedial artery passes through the cranial cavity dorsal to the alisphenoid.
7. Preplacenta broad and horseshoe-shaped, with definitive placenta more localized.
9. Cortical somatosensory representation of forelimb reverse of that in other mammals.

Baker et al. 1991
By 1994, most biologists informed about the situation agreed that Chiroptera were monophyletic. Simmons (1994) summarized the situation. Jack Pettigrew remains unconvinced (I think).

If Chiroptera are monophyletic, then the retinotectal pathway similarities between Primates and Pteropodidae represents a convergence.
Simmons and Geisler (1998) presented the results of a phylogenetic analysis with 195 morphological features and 12 rDNA (restriction sites) features. Considered digital and multistate features.

Consensus tree from 208 discrete features.

Fig. 36. Results of Analysis 2, which included all characters and all taxa (see text for discussion). Parsimony analysis resulted in a single most-parsimonious tree (680 steps; CI = 0.393; RI = 0.587), which is shown here. The numbers below internal branches are bootstrap values; numbers above the branches are decay values. The bootstrap analysis was constrained to consider only trees in which Chiroptera was monophyletic.
Since 1998, further analysis, including a growing genetic data base, support monophyly of living bats but the classification has changed dramatically.

Megachiroptera and Microchiroptera are no longer valid terms, replaced by Yinpterochiroptera and Yangochiroptera.
The situation today. Yinpterochiroptera and Yangochiroptera become suborders.

Jones & Teeling 2006
Make the comparison … new and old

Jones & Teeling 2006
Teeling (2009) outlines four alternatives.
Echolocation an ancestral condition

Echolocation evolved four times in bats

Teeling 2009
Teeling 2009
Recall from Pettigrew 1991

W = wings
S = laryngeal echolocation
P = primate features
A = archontan skeletal features
--- = loss
The situation today. Yinpterochiroptera and Yangochiroptera become suborders.
What next?

*FoxP2* is the “mammalian vocalization gene. Mice without this gene do not produce isolation calls. Li et al. (2007) looked at this gene in a variety of bats. *FoxP2* is extremely diverse in echolocating bats … but not enough information to determine if pteropodids had had and then lost the ability to echolocate.
Li et al. (2008) then looked at the “hearing gene” *Prestin*. *Prestin* is said to be the cochlear amplifier. Encodes transmembrane motor proteins that drive electromotility of outer hair cells. Two different phylogenetic signals in the data.

Analyses of entire coding region suggests echolocating bats are monophyletic.

Phylyogenetic analyses of amino acids found in transmembrane regions alone supported the current phylogeny (Yinpterochiroptera and Yangchiroptera).

Bottom line, no clear answer.
Eick et al. 2005 presented another analysis … same picture pretty much … bit there are some important differences. Note the Laurasiathelae connections. Vertical arrows indicate unique indel events supporting phylogenetic associations.
Echolocation an ancestral condition

Echolocation evolved more than once (perhaps four times) in bats

Teeling 2009
What is the essence of a bat?

WINGS

When did they appear? 60 million years ago (at least)

Why did they appear?

What are convergent characters?

What are parallel characters?

Perhaps the current view brings classification and evolutionary history into closer agreement.
*Onychonycteris finneyi* … could it echolocate?

Simmons et al. 2008.
Literature Cited

Dobson, G.E. 1875. Conspectus of the suborders, families and genera of Chiroptera arranged according to their natural affinities. Annals of the Magazine of Natural History, Series 4, 16:345-357.


