

## A moveable face: deconstructing the Microchiroptera and a new classification of extant bats

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Recent comparative-method and molecular studies have called into question both the classic subordinal division of bats into Megachiroptera versus Microchiroptera and the infraordinal separation of microchiropterans as Yinochiroptera and Yangochiroptera: megabats are not necessarily large, nor are microbats uniformly small; some yinochiropterans may be specially related to megachiropterans whilst others are more nearly affiliated with yangochiropterans; and quite apart from the conflict with DNA comparisons, the microbat dichotomy (based on moveable versus fused premaxillae) is neither completely cladistic nor parsimonious. We conclude that current appellations — including the neologism Yinpterochiroptera — no longer embody the authors' intended groups or have been so frequently redefined as to be positively misleading. We therefore adopt the new subordinal names Vespertilioniformes (for the group including Emballonuridae, Nycteridae, and the 'yangochiropterans') and Pteropodiformes (for the taxon comprised of Craseonycteridae, Hipposideridae, Megadermatidae, Rhinolophidae, Rhinopomatidae, and Pteropodidae). These epithets are ultimately based on the oldest valid generic names for included taxa (respectively *Vespertilio* Linnaeus, 1758 and *Pteropus* Brisson, 1762), and are thus impervious to pre-emption or misinterpretation.

*Key words:* Chiroptera, systematics, classification, premaxilla, Megachiroptera, Microchiroptera

### INTRODUCTION

Understanding of bat systematics and evolution has undergone a radical transformation in the last decade as a result of a series of studies employing molecular techniques to investigate higher-level bat relationships (Hutcheon *et al.*, 1998; Teeling *et al.*, 2000, 2002, 2003, 2005; Springer *et al.*, 2001; Hooper *et al.*, 2003; Hutcheon and Kirsch, 2004; Eick *et al.*, 2005). While some conclusions of these papers have garnered more attention than others (e.g., 'microbat paraphyly'), it should be apparent that the overall implications of the

molecular studies go well beyond the replacement of one or two bat families and touch also on issues which relate to the evolution of both flight and echolocation (Hutcheon *et al.*, 1998; Teeling *et al.*, 2000). We begin by discussing the traditional bat classification and its rationale, then go on to consider evidence necessitating its renovation, and finally suggest appropriate nomenclature.

### *The Sizes of Bats*

For over a century and a quarter, most bat biologists have accepted Dobson's

(1875) conclusion that bats could be divided into the two natural (subordinal) groups which he designated Megachiroptera and Microchiroptera, a distinction presumably based on body sizes but later shown also to reflect profound differences such as the respective lack or use of echolocation and its anatomical as well as physiological correlates. Molecular studies have suggested that the time-honoured dichotomy between the suborders might not be as firm as once believed (Hutcheon *et al.*, 1998; Teeling *et al.*, 2000, 2002, 2003, 2005; Springer *et al.*, 2001; Hoofer *et al.*, 2003; Hutcheon and Kirsch, 2004; Eick *et al.*, 2005). Bat body sizes have been the topic of renewed interest and several recent papers have considered the ecological implications of such size differences (Barclay and Brigham, 1991; Jones, 1994; Jones and MacLarnon 2001; Barclay and Harder, 2003; Willig *et al.*, 2003). Moreover, Hutcheon and Garland (2004) have demonstrated with statistical rigour that the actual difference in body masses between the Mega- and Microchiroptera is not as great as is often assumed. In fact, there is a great deal of overlap between the body masses of the two suborders of bats. The genera *Pteropus* and *Acerodon* are often taken as exemplars of the Pteropodidae when they actually represent outliers, a fact that has resulted in an overestimation of how big ‘megabats’ really are. Hutcheon and Garland (2004) did demonstrate that pteropodids were more variable than other bats in their body mass: their body masses encompass a greater range than other bats. Using a variety of phylogenetic statistical techniques, Hutcheon and Garland (2004) estimated that all chiropterans evolved from a common ancestor with a body mass of 21–23 g (95% confidence intervals).

While no one doubts that pteropodids are a natural group (whatever the foundation for recognising them as such may be), on the basis of molecular data (see below)

their subordinal separation from (all) microbats is clearly untenable.

### *The Moveable Face*

Several superfamilial assemblages of microbats have long been recognised (Dobson, 1875; Smith, 1976; Van Valen, 1979), but the infraordinal groupings familiar to most mammalogists — Yinochiroptera and Yangochiroptera — derive from Koopman’s (1984) classification. Koopman (1984) asserted that alternate states of the premaxilla constituted ‘the most fundamental distinction between bat groups.’ In fact, in forming the microbat subgroups he largely followed the example of Miller (1907). Miller (1907) did not employ any superfamilial or infraordinal names, but in his key to the families the arrangement is nearly identical to Koopman’s (1984).

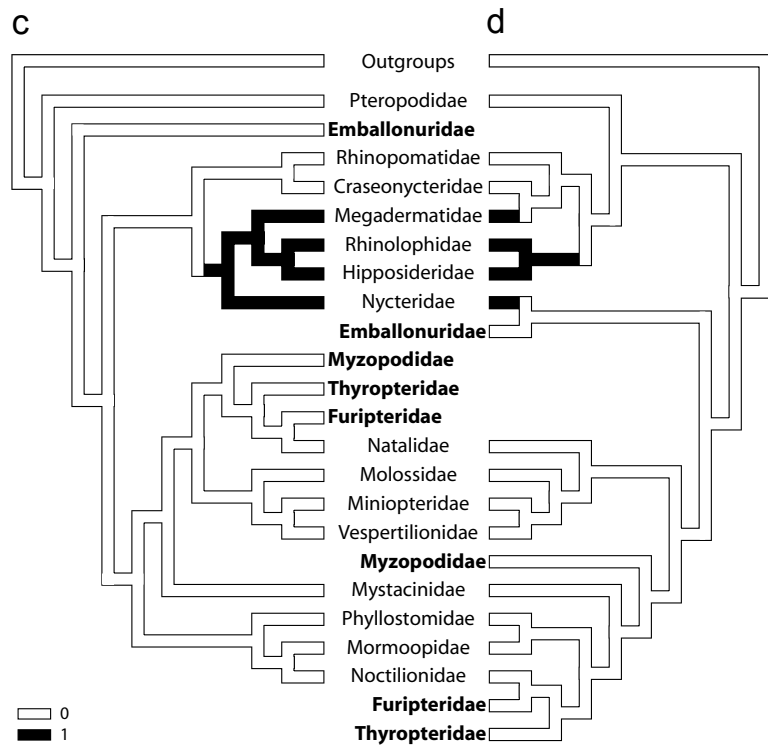
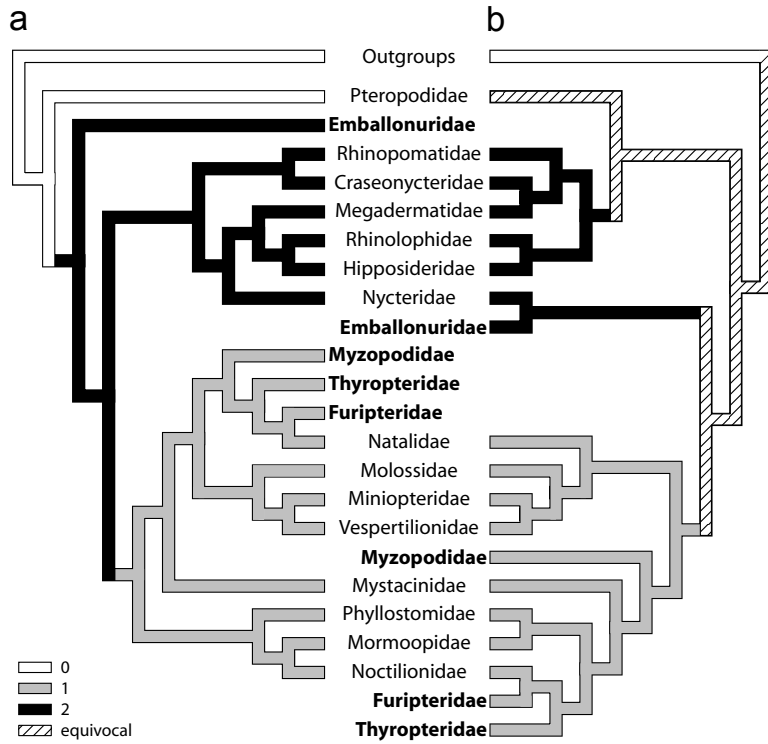
As discussed by Wible and Novacek (1988), a common feature of bats is the reduction (in some cases extreme) of the premaxilla. The fate of the reduced premaxilla in Microchiroptera being either a relatively loose connection to the maxilla via ligaments (as opposed to a more typical skull suture enforced by fibrous cartilage) or complete fusion to the maxilla, Koopman designated two (infraordinal) groups of microbats based on this differentiator: mobile (connection via ligaments) versus immobile (connection via fusion) premaxillae. In Simmons and Geisler’s (1998) discussion of uniting characters of the Chiroptera they comment upon the paucity of synapomorphies for the microchiropteran crown group, but indicate that they consider premaxillary conditions to provide such diagnostics. They recognised three states of their character 9 and optimised these as unordered on their overall phylogeny (Fig. 1a herein). Interestingly, Simmons and Geisler (1998) conclude — with reservations — that the mobile condition is synapomorphic for the

crown-group microbats (that is, was a defining feature of their most recent common ancestor). Within Microchiroptera, the fused yangochiropteran condition is then necessarily derived directly from the mobile. However, given that some pteropodids also possess fused premaxillae, an argument could be mustered that this condition is in fact the initial state for all bats and hence plesiomorphic for Microchiroptera [but see Gunnell and Simmons' (2005) revised coding of character 9, discussed in the next paragraph]. Yet Simmons and Geisler's (2005) conclusion is unassailable given their phylogeny (with Emballonuridae sister to all other microbats), and optimisation on a DNA-based phylogeny (Fig. 1b; see discussion below) is less parsimonious. In fact, many mammalian groups display both suturing and fusion of bones, either in the course of ontogeny or as characters of subsidiary taxa; with respect to rostral elements, fusion is often concomitant with reduction or loss of incisors — and in bats is likely related to excision of mass in adaptation to flight (Simmons and Geisler, 1998). Thus we believe that it might be more appropriate to regard character 9 as in fact comprising two binary features, with suturing leading to complete fusion in one character and to mobility in the other, although this would require additional steps on either the anatomical or molecular phylogeny.

Nevertheless, we must add that recently Gunnell and Simmons (2005) revisited bat phylogeny, using an anatomical matrix, which overlaps and enhances the earlier data set of Simmons and Geisler (1998) with new characters and additional taxa, including more outgroups and fossil bats. Character 9 is now treated as ordered (to facilitate binary coding), but the moveable premaxilla is coded 0, suturing or fusion respectively 1 and 2, and Pteropodidae as monomorphic for state 1. The new analyses return Emballonuridae to a position as sister

to other yinochiropterans rather than to microbats as a whole, so that character 9 maps parsimoniously. But it does so also under the earlier coding, when ordered, the only difference being the state inferred at the base of Microchiroptera. Thus, the moveable and fused premaxillae are mapped as separate derivations from the sutured state under the new coding (rather than the moveable condition deriving from the fused with the earlier transformation series), just as we have here argued would be a sensible interpretation of character 9.

Even as a basis for grouping within Microchiroptera, however, we see at least two problems with emphasis on the moveable premaxilla as a presumed synapomorphy, namely convergence and anatomical complexity, which we consider separately below. Convergence would provide a sufficient explanation for the unparsimonious distribution of mobility. Craniokinesis is fairly common in most vertebrate classes, frequently as a specialisation for feeding (Wible and Novacek, 1988; Smith, 1993), but appears to be unknown in mammals other than bats. The obvious association of such a character with ingestion (e.g., of large objects which would not otherwise fit in the mouth or throat) would seem to cast doubt on its utility as a phylogenetically informative tool, given the clear potential for homoplasy. Bats confront unique challenges in obtaining and processing food and have developed singular abilities (at least for mammals) in meeting these challenges: flight and laryngeal echolocation. Because the forelimb is primarily dedicated to flight, much of the required food manipulation must be carried out orally. And because so many other features of the mammalian skull — dental morphology, cranial shape, and modelling determined by chewing muscles — are correlated with diet (Pedersen, 1998; Dumont, 2004), it would seem likely that aspects of the premaxilla would be as well



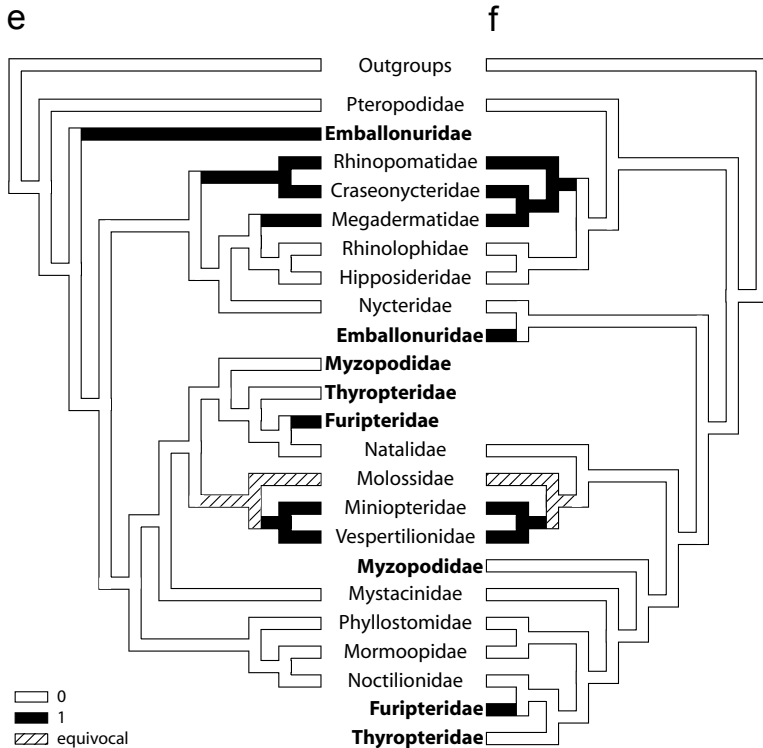


FIG. 1. Optimisation of the states of premaxillary characters 9, 10, and 11 from Simmons and Geisler (1998) on their anatomical phylogeny (left member of each pair); and on the arrangement of Teeling *et al.* (2002), based on DNA sequences (right member of each pair). Note that neither group of authors recognised miniopterines as a full family. Taxon names that could not be aligned between the two trees are duplicated and shown in bold-face. Character 9 is mapped as a three-state unordered feature in Fig. 1a and 1b (a cartilaginous articulation is primitive; sutural fusion corresponds to state 1; mobility is state 2), and requires an extra step on the molecular tree. Some pteropodids display the primitive state and others state 1. Character 10 is two-state, the derived condition being reduction or absence of the nasal branch of the premaxilla; three derivations are required by the DNA phylogeny (Fig. 1d). Character 11 is also two-state, where the palatine branch is reduced or absent, and both trees (Fig. 1e and 1f) require several changes. Condition of character 11 among Molossidae varies

(Smith, 1993, 1997). But what advantages accrue from a moveable premaxilla? A short list might conceivably include increased manipulatory ability, wider gape, and added force in clamping the mouth. In fact, the case for trophic involvement is strengthened by the multiple occurrences of a moveable premaxilla, at least on the DNA tree, as the repeated evolution of a feature is corroborative evidence for an adaptationist hypothesis (Smith, 1993).

Simmons and Geisler (1998) discuss the dorsiflexion of the snout in emballonurids,

and speculate on the possibility that movement of the premaxilla might have had some role in the evolution of nasal involvement in echolocation (emballonurids, sister to all other microbats in Simmons and Geisler's phylogeny, are oral emitters and so may be plesiomorphic in this respect). A relationship between mobility and mode of emission is possible, but nasal emission of the echolocation pulse occurs in both rhinolophoid bats (with freely moveable premaxillae) and phyllostomid bats (with fused premaxillae), yet the diets of these two types of

bats are markedly different. All things being equal, diet rather than style of echolocation would therefore seem to be a more likely source of premaxillary variation. Nonetheless, other differentiators of the premaxillary articulation (see below) correlate with the phyletic separation of emballonurids from other putative yinochiropterans.

Thus, rather than regarding the mobile or immobile premaxilla as a neutral phyletic marker, the primary alternative interpretation of this character is that it might be a convergent trophic adaptation in some or all of the families displaying it. Indeed, in the context of the molecular phylogeny, the moveable premaxilla appears not to be the apomorphic condition for a specific clade of bats but to have evolved twice (see Fig. 1b).

The second problem is that of anatomical complexity. While it is possible to speak generally of the premaxilla, in fact there are nasal and palatine branches of this bone which are differentially represented in bats. Some families — and the Megadermatidae would represent an extreme example of this — effectively have no palatine branches and have the nasal ones reduced to tiny slivers. Thus, the nasal branches are the articulating (and only) portions of the premaxillae. In other bat families, the opposite obtains and the palatine branches are represented to the exclusion of the nasal ones. These several conditions are represented by characters 10 and 11 in Simmons and Geisler (1998), but mapping them onto Fig. 1c–f indicates just how tenuous the utility of the ensemble of premaxillary characters is. One might hope for mutual reinforcement from the several derived states, but compared with character 9 (Fig. 1a and 1b), it is clear that mobility does not track entirely with any one particular branch of the premaxilla: only the derived state of character 10 uniquely defines a clade (of non-emballonurid yinochiropterans),

and then only on the anatomical phylogeny (Fig. 1c).

In summary, instead of representing a truly fundamental character for documenting the broad pattern of chiropteran evolution, the premaxilla of bats may simply have been a useful tool for Miller (1907) and Koopman (1984): taxonomic efficiency need not translate into phylogenetic utility. Indeed, Novacek (1993) presented an illustration which suggests that if there is any value to the premaxilla as a character it might lie in the fact that this bone is extremely reduced in all bats relative to other mammals. And so, while the moveable face may be an ecologically important feature, it is probably not a particularly useful one for phylogeneticists.

#### *Implications of Molecular Studies*

Accumulating molecular evidence has called into question both the traditional subordinal and newer infraordinal distinctions (Pettigrew and Kirsch, 1995; Hutcheon *et al.*, 1998; Teeling *et al.*, 2000, 2002, 2003, 2005; Springer *et al.*, 2001; Hofer *et al.*, 2003; Hutcheon and Kirsch, 2004; Eick *et al.*, 2005), further, and as discussed above, the anatomical characters supporting each dichotomy seem less consistent than when they were first proposed. The contents of Koopman's infraorders in particular have now been altered several times — first on anatomical grounds (which go well beyond the premaxilla) by Simmons (1994), who removed the emballonurids from Yinochiroptera to a position as sister-group to all other microchiropterans [although Gunnell and Simmons (2005) have recently returned Emballonuridae to a position as sister to the other Yinochiroptera]; and later by ourselves and other molecular systematists (Hutcheon *et al.*, 1998; Teeling *et al.*, 2000, 2002, 2003, 2005; Springer *et al.*, 2001; Hofer *et al.*, 2003; Hutcheon and Kirsch,

2004; Eick *et al.*, 2005), who have combined some rhinolophoids with pteropodids and removed other yinochiropterans to the expanded Yangochiroptera (specifically, Nycteridae and again — but with a position more deeply embedded within Yangochiroptera — Emballonuridae). One melancholy result of these frequent rearrangements is that the sub- and infraordinal divisions of bats appear to have lost any stability (Springer *et al.*, 2001). We suggest that abandonment of the august subordinal names as well as the more recently proposed infraordinal ones is mandated both by cladistic practice and molecular realities, and below we argue for a new arrangement of bats at the highest categorical level, proposing names that should, for all time, be immune to replacement or changes in content of the designated taxa.

### *Choosing Subordinal Names*

The principal aim in designating groups should always be stability, both in resistance to alternative subdivision and changes in nomenclature. Our ambition here is to recognise the natural suborders of bats and to provide them with names neither subject to the vicissitudes of realignments based on incremental taxonomic coverage [for which reason we reject Springer *et al.*'s (2001) premature concatenation of yinochiropterans and pteropodids as the Yinpterochiroptera] nor allusive of supposedly universal characteristics (for which reason we reject the argument that names must have 'meaning'). We can now declare about bat molecular phylogeny what we could not have said even a few years ago: that while the exact interrelationships of some bat families may still be obscure, the primary dichotomy among crown-group taxa is virtually certain, and corresponds to an association of yangochiropterans with Emballonuridae and Nycteridae as opposed to

the Pteropodidae with all remaining yinochiropterans. So long as the formal suborders be founded on taxa which are ineluctably associated with these groupings — sensibly and respectively, a yangochiropteran and a megabat, say — those suborders should prove impervious to any other proposed distribution of taxa.

Important means of achieving the not-unrelated goal of nomenclatural stability are through strict adherence to the principles of typification, priority, and (to a lesser extent) attribution and proper formation of names. Recent iterations of the International Code of Zoological Nomenclature (ICZN) are virtually silent on these principles as they apply to taxa in categories above the family-group levels. Nonetheless, taking some cues from botanical practice we will argue here that extension of rules governing family-level taxa (subtribute to superfamily, inclusive) to bat subordinal classification will rectify the current instability.

The most critical of these principles is typification — published specification of a valid and available name (i.e., based on a taxon properly diagnosed or described, or with contents enumerated) which leaves no doubt about the irreducible inclusiveness of the typified group. For family-level animal taxa, this must be a genus, and in botanical classification the name of a higher-category taxon is said to be automatically typified if based on a genus-name (International Code of Botanical Nomenclature, 2000: Articles 10.7 and 16). The so-called Copenhagen Decisions of 1953 recommended similar typification of higher-category zoological taxa, but that suggestion was rejected in formulating the 1961 and subsequent editions of the ICZN (see discussion in Blackwelder, 1967).

The importance of priority in choosing family-group names is implied in the common (but not mandatory) choice of the apparently oldest valid genus as type;

Recommendation 16B of the International Code of Botanical Nomenclature suggests that priority be followed for typified names of higher-ranking taxa as well. A good reason for preferring the oldest name is not that the designated taxon is necessarily primitive for its larger group, nor even representative, but that the name is less likely to carry a burden of synonymy or obscure and earlier-proposed epithets that when detected may force a name change. However, the current rules (ICZN, 2000: Article 40) do allow for unusual circumstances to supersede priority at the family-group level, mainly on grounds of familiarity or common usage — or lack thereof. Thus the 1961 and subsequent versions of the ICZN mandate that replacement of an older family-group name by a younger is allowed if the younger name had come into common use prior to 1961, irrespective of whether the name of the type genus is valid or available.

As applied to bat infra- and subordinal names, giving weight to familiarity would, of course, encourage continued use of Megachiroptera, Microchiroptera, Yinochiroptera, and Yangochiroptera. Yet, these names suffer the burden of implying contents not supported by newer data — a disadvantage far worse than substitution of new names based on typical genera. By fiat, the oldest generic name of a bat must be Linnaeus' *Vespertilio* of 1758, which was equivalent to the entire order of bats as then known including *Pteropus*, not separately named until 1762. So far as we are aware, no other valid or relevant bat genus was named between 1758 and 1762, so *Vespertilio* Linnaeus, 1758 and *Pteropus* Brisson, 1762 are unquestionably the type genera of their respective families; and the names themselves cannot be displaced. These genera would be sensible and stable choices as types of chiropteran suborders, because whatever the extension of those suborders should be found to be, it is unlikely that

vespertilionids would ever be determined to be more closely related to pteropodids than are (some) other microbats, at least among crown-group chiropterans. And, once more, no other names could claim priority over *Vespertilio* and *Pteropus*.

Felicitously, Gray's (1821) families Vespertilionidae and Pteropidae (the latter possibly based on a misunderstanding of the suffix of *Pteropus* and therefore legally amended as Pteropodidae by subsequent authors) are the oldest proposed family names for taxa including, respectively, *Vespertilio* and *Pteropus*. Attribution (authorship and date) of a zoological family-group name is not the same as that for the type genus, however; rather, it is to the first proposal of such a name, at whatever level within the family group, so that all levels take that authorship and date (ICZN, 2000: Article 36.1) — a rule that many animal taxonomists have ignored. Again, we suggest extending this rule to higher-category taxa, and therefore attribute our proposed suborders to Gray (1821).

But if the ICZN has become somewhat inconsistent regarding the application of priority to family-group names, and remains indifferent to typification above that level, it is now utterly silent on the subject of the formation of higher-category epithets, except for the implied dicta that they should be uninominal and convey an odour of classicism. This reticence is, we believe, retrogressive in view of the renewed enthusiasm for construction of phylogenies at the most inclusive levels engendered by the cladistic and molecular revolutions; a result is the concomitant proliferation of novel, ephemeral, and often barbaric names. Again, upward extension of the lexicographical rules applying at family-group levels seems desirable, but while prefixes for our new subordinal names are obvious, suffixes are not. We suggest endings modelled (appropriately enough for the only flying mammals!) on



ornithological usage, as the commonly used ‘chiroptera’ is both redundant and in combination with either familial root would lack euphony.

### Recommendations

In summary, we endorse extension of the venerable rules of typification, priority, attribution, and name-formation enacted for family-group taxa to the newly-organised suborders of extant bat families — those groups including, on the one hand, Pteropodidae and some rhinolophoids (Craseonycteridae, Hipposideridae, Megadermatidae, Rhinolophidae, and Rhinopomatidae); and, on the other, the remaining ‘yinochiropterans’ (Emballonuridae, Nycteridae) together with all other microbats, the former ‘yangochiropterans’. It is in the interest of forestalling further nomenclatural changes that we propose to base each subordinal name on that of the oldest included, valid genus. Therefore and indisputably, the name of the latter suborder — Vespertilioniformes — would ultimately be based on Linnaeus’ *Vespertilio* of 1758 (type of Vespertilionidae Gray, 1821) and that of the former — Pteropodiformes — on *Pteropus* Brisson, 1762 (type of Pteropodidae Gray, 1821); and each suborder would be typified by the appropriate genus, with its name taking the authorship and date Gray, 1821. No other genus-name could possibly displace either *Vespertilio* or *Pteropus*, and we see no basis or need for infraordinal groupings at this point. We have argued that the new molecular phylogenies require this rethinking of the subordinal classification of bats and that the existing names are untenable due to non-monophyly (Microchiroptera) or because of redefinition to the point of confusion even among experts (e.g., of Yino- and Yangochiroptera). Thus we have proposed entirely new epithets, but ones which observe both the spirit and letter of the rules

of nomenclature. Once again, the overwhelming advantage of our proposal is that, being based on typification and nomenclatural priority, and rejection of the notion of descriptive intent, the proffered groups and their names are virtually impervious to further redistribution of constituent taxa.

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