

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3034, 16 pp., 4 figures February 25, 1992

Phylogeny of Plecotine Bats (Chiroptera: "Vespertilionidae"): Summary of the Evidence and Proposal of a Logically Consistent Taxonomy

DARREL R. FROST¹ AND ROBERT M. TIMM²

ABSTRACT

Using standard phylogenetic techniques, 25 transformation series of morphological characters and 11 of karyological characters are evaluated in an attempt to recover the phylogenetic history of plecotine vespertilionid bats. Plecotini contains four genera in the topology (*Euderma* (*Barbastella* (*Plecotus Corynorhinus*))). The Plecotini of Hill and Harrison (1987), including *Rhogeessa*, *Baeodon*, *Nycticeius*, and *Otonycteris*, is rejected be-

cause this view is based solely on subjective evaluations of bacular overall similarity, and is clearly in disagreement with other lines of evidence from anatomy and karyology. *Idionycteris* is synonymized with *Euderma* because *I. phyllotis* and *E. maculatum* are sister species. *Corynorhinus* is removed from the synonymy of *Plecotus*. The relationships within *Corynorhinus* and *Plecotus* are not resolved.

INTRODUCTION

Plecotine bats are a small group of large-eared bats found in temperate North America and Europe. The ten species of these vespertilionid bats have been placed implicitly or explicitly either in three (Handley, 1959; Ba-

ker et al., 1974; Koopman, 1984a, 1984b), four (Williams et al., 1970; Honacki et al., 1982; Hill and Harrison, 1987), or five (Tate, 1942) genera. Although it differs from the most recent revisions, for purposes of this

¹ Assistant Curator, Department of Herpetology and Ichthyology, American Museum of Natural History.

² Curator, Division of Mammals, Museum of Natural History; Associate Professor, Department of Systematics and Ecology, The University of Kansas, Lawrence, KS 66044.

study we will use the five-genus taxonomy: *Barbastella* (*B. barbastella*, *B. leucomelas*), *Euderma* (*E. maculatum*), *Idionycteris* (*I. phyllotis*), *Plecotus* (*P. austriacus*, *P. auritus*, and *P. teneriffae*), and *Corynorhinus* (*C. mexicanus*, *C. rafinesquii*, and *C. townsendii*).

The term "plecotine" and its formal equivalents have had a history of varied use. Dobson (1875) recognized the Group Plecoti for "Vespertilionidae"³ having large ears and either rudimentary noseleaves or grooves on the dorsal surface of the muzzle, and Miller (1897) used the name Plecotinae for the American bats of the genera *Corynorhinus* and *Euderma*. Subsequently, however, most authors have either abandoned the use of the formal taxonomic name (e.g., Miller, 1907; Simpson, 1945; Handley, 1959; Sokolov, 1973) or have used it for a tribe, Plecotini, of varying generic content within the "Vespertilioninae" (e.g., Tate, 1942; Baker et al., 1974; Koopman, 1984a, 1984b; Hill and Harrison, 1987). Williams et al. (1970) recognized a Group Plecoti composed of the plecotines in the sense that we use the term. With variation in the number of genera recognized and with the exception of the recent arrangement of Hill and Harrison (1987) (see discussion below) this is generally how the term is currently used.

Handley (1959) provided a wealth of descriptive information on the group and posited a phylogeny of (*Barbastella* (*Euderma* (*Idionycteris* (*Corynorhinus* *Plecotus*))). Williams et al. (1970) suggested, on the basis of karyology, the phylogeny (*Barbastella* ((*Euderma* *Idionycteris*) (*Plecotus* *Corynorhinus*))). The evidence provided by Williams et al. (1970), supporting a special relationship of *Plecotus* and *Corynorhinus*, was solely overall similarity of morphology and karyotype, although the evidence relating *Euderma* and *Idionycteris* was synapomorphic. This view that *Idionycteris* is generically distinct from *Plecotus* (sensu lato as including *Plecotus* and *Corynorhinus*) was disputed by Baker et al. (1974), who argued that the *Idionycteris* karyotype might not be dissimilar enough from the *Plecotus* karyotype to war-

rant generic distinction, particularly without morphological features to support this assertion. Koopman (in Honacki et al., 1982: 177) also disputed the position of Williams et al. (1970) that *Idionycteris* should be considered generically distinct from *Plecotus*, although this view was based on evidence provided by Handley (1959).

Stock (1983) provided a karyologically based three-taxon cladogram of ((*Euderma* *Idionycteris*) *Corynorhinus townsendii*). More recently, Leniec et al. (1987) summarized the karyology of plecotines and supported the monophyly of the group, including *Barbastella*. They also made the novel suggestion that the short-eared bats of the genus *Barbastella* are derived from the large-eared plecotines, in the arrangement ((*Euderma* *Idionycteris*) (*Barbastella* *Plecotus* *Corynorhinus*)).

The objective of this study is to attempt to resolve the alternative phylogenetic hypotheses for plecotines that have been advanced and to suggest a taxonomy of these bats that is logically consistent with recovered phylogeny if previous taxonomies are found to be wanting.

ACKNOWLEDGMENTS

We thank Charles J. Cole, Nancy Simmons, Lynne Frost, Arnold G. Kluge, Karl F. Koopman, and Charles W. Myers for constructive criticism of the manuscript. Karl Koopman was particularly helpful in discussions of bat morphology and relationships, although this should not be construed necessarily as agreement with our conclusions. Arnold Kluge provided especially interesting criticisms regarding methodology and underlying philosophy. We also thank Michael D. Carleton and Linda K. Gordon (National Museum of Natural History [USNM]), Bruce D. Patterson (Field Museum of Natural History [FMNH]), and Karl F. Koopman (AMNH) for access to and loan of specimens under their care. This study was funded in part by a grant to Timm from the University of Kansas General Research Fund.

EVIDENCE OF MONOPHYLY OF THE PLECOTINES AND CHOICE OF OUTGROUPS

Tate (1942) regarded plecotines, *Euderma*,

³ We place quotations around taxonomic names that denote "taxa" that are not demonstrably monophyletic (Wiley, 1979).

Plecotus, *Corynorhinus*, and *Idionycteris*, to be a subgroup, Plecotini, of his "Myotini" (sensu lato). The taxa in the "Myotini" (sensu lato), exclusive of the plecotines, he referred to as "Myotini" (sensu stricto), a residual assemblage containing "*Myotis*" and *Lasionycteris*. Tate's "Myotini" (sensu lato) is characterized by having reduced P2-3/2-3—not a particularly helpful character inasmuch as these teeth are absent in some other groups of vespertilionids (e.g., *Antrozous*) and might actually be synapomorphic of a larger group. Tate considered *Barbastella* to be part of the pipistrelloid radiation, and therefore phylogenetically distant from the plecotines. However, Handley (1959) posited that the traits suggested by Tate that would place *Barbastella* in the pipistrelloid group are plesiomorphies also shared with "*Myotis*," with the exception of the reduction of the P1 in *Barbastella* and "*Pipistrellus*." In our examination of specimens, reduction of the P1 seems to be highly variable within species and is likely either plesiomorphic or too variable to be useful. Handley (1959), following Miller (1907), considered *Barbastella* to be the nearest relative of the plecotine group. This view rested largely on the overall similarity of the dentition and skull, but Handley noted at least one synapomorphy of this group, zygoma not bowed out posteriorly. Additionally, *Barbastella* shares with the other plecotines the ability to roll its ears into a rams-horn shape, as evidenced by the arrangement of cartilaginous supports in the ear (K. Koopman, personal commun.). Another character that may be synapomorphic for the plecotines, although it occurs in many other vespertilionid bats, is the interauricular septum (low in *Corynorhinus*) that is absent in "*Myotis*" and other myotines.

Bickham (1979) considered the plecotines to be within the "*Myotis*" group of genera (vespertilionids excluding *Miniopterus* and the "*Eptesicus*" group of genera) that share a particular karyotype. Although Bickham (1979) regarded the "*Myotis*" karyotype as primitive within the family, Stock (1983) and Leniec et al. (1987) have argued that this karyotype is, in fact, derived from the "*Eptesicus*" karyotype by centric fusion, thereby positing a synapomorphy for the "*Myotis*" group of genera, including the plecotines.

Within the "*Myotis*" generic group, Bickham (1979) suggested that the plecotine (+ *Barbastella*, fide Leniec et al., 1987) karyotype was derived by centric fusion (of chromosomes 15 and 11) from the "*Myotis*" karyotype.

Stock (1983) did not examine *Barbastella* or *Plecotus*, but did concur with Bickham (1979) that the plecotines are closely related to "*Myotis*," differing by a single chromosomal fusion. Leniec et al. (1987) summarized the karyological literature of plecotines and showed that *Barbastella* had a karyotype identical to several members of the plecotine group, further supporting its position as the nearest relative of the group. According to their scheme, however, *Barbastella* was part of a monophyletic group that also included *Plecotus* and *Corynorhinus*, but excluded *Euderma* and *Idionycteris*.

Hill and Harrison (1987) have suggested, on the basis of general trends in bacular morphology, that more proximate relatives to the traditional plecotine group are *Rhogeessa*, *Baeodon* (usually considered part of *Rhogeessa*), *Nycticeius*, and *Otonycteris*, with the myotine group next closest. Our concerns about this arrangement are:

(1) The bacular types of Hill and Harrison are sufficiently subjective that, beyond a general sense of "plecotine-ness," we could not decide from their illustrations and text what characteristics would define a plecotine baculum, although the traditionally viewed plecotine group (including *Barbastella*) does form a morphologically compact cluster. At least some taxa (e.g., *Eptesicus nasutus* and *Bauerus dubiaquercus*), which are excluded from the plecotines by Hill and Harrison, appear to us from their illustrations to have bacula very similar to those of plecotines. Without a more rigorous definition, this general morphology is unlikely to be particularly informative at this level of universality.

(2) Without any discussion of transformational polarity, their taxonomic suggestions rest on overall similarity. The plecotine-type baculum (even if it could be defined adequately) could easily be plesiomorphic within the vespertilionids, in which case the similarities seen by Hill and Harrison would be phylogenetically uninformative.

(3) If the plecotines (sensu Hill and Har-

ri-son) form a monophyletic group (that is, if *Rhogeessa*, *Baeodon*, *Nycticeius*, and *Otonycteris* are plecotines) then the karyological evidence of Bickham (1979) as well as much of the osteological and dentitional evidence presented by Tate (1942) would be phylogenetically incoherent. That Hill and Harrison discounted dentitional evidence as "adaptive" (p. 260) is insufficient; convergence in dentition can only be documented on the basis of other evidence, not merely by asserting that convergence is plausible, just because convergence has been documented elsewhere. Additionally, the congruence of the evidence of Bickham (1979) and Tate (1942) should not be so easily dismissed.

If one takes the trees of Bickham (1979) and Tate (1942) to be undirected diagrams of relationship, considerable consensus exists between them. That is, in both studies *Rhogeessa*, *Baeodon* (not reported by Bickham, but usually considered very close to *Rhogeessa*), *Nycticeius*, and *Otonycteris* (also not reported by Bickham, but also usually considered to be related to *Nycticeius*) are paritrically distant from the traditionally viewed plecotines, and the plecotines are paritrically close to *Lasiurus*, *Lasionycteris*, and "*Myotis*," which has no unambiguous apomorphies with respect to the plecotines. We have therefore set aside Hill and Harrison's (1987) view as based on a morphological system (bacula) whose "window of applicability" would seem to be at a considerably lower level of universality than the level at which it was applied. We have therefore used "*Myotis*" (composed in our analysis of "*M.*" *liebii*, "*M.*" *lucifugus*, "*M.*" *myotis*, "*M.*" *sodalis*, and "*M.*" *thysanodes*) as a functional outgroup on which to root our plecotine tree.

MATERIALS AND METHODS

Using information from the literature (e.g., Tate, 1942; Handley, 1959), augmented and verified by our own observations, we recognized 25 transformation series of morphological characters for each species. Additionally, 12 transformation series of karyology were derived from the literature (Bickham, 1979; Leniec et al., 1987; Stock, 1983). Outgroup comparison has been selected as the most general means of polarizing character

transformation series (Watrous and Wheeler, 1981; Farris, 1982; Kluge, 1985; Brooks and Wiley, 1985). These independently polarized transformation series were analyzed by using the branch-and-bound algorithm (Hendy and Penny, 1982) included in the PAUP (Swoford, 1989) and Hennig86 (Farris, 1988) programs under both (1) the assumption of additivity (i.e., multicharacter morphoclines allowed) and (2) not under the assumption of additivity (i.e., multicharacter morphoclines not allowed). This allowed some evaluation of the distortion caused by the assumption of character additivity, rather than simple character matching. Tree fit was evaluated with the consistency index (ci) of Kluge and Farris (1969). In this measure, a value of "1" means that all data are logically consistent with all other data on the tree; decreasing values reflect an increase in homoplasy. Only those features that were placed unambiguously, regardless of the character optimization methodology employed (i.e., accelerated transformation or delayed transformation) or of assumptions about character additivity, were considered to be evidence of relationship.

We have not restricted ourselves to a particular "kind" of data (e.g., morphological vs. karyological) because it is incumbent on us to explain all the evidence at hand (Miyamoto, 1985; Kluge, 1989). Nor have we employed differential character weighting. This practice has been argued against convincingly by Patterson (1982) and Novacek (1986). In short, we think that differential character weighting removes much of the objectivity from discussions of character incongruence.

One multicharacter transformation series was used (Number 16 below) that could not be polarized by appeal to the functional outgroup and was treated as nonadditive even in the additive analysis.

Specimens examined are listed in Appendix 1.

TRANSFORMATION SERIES

The source of the transformation series, if originally gleaned from the literature, is cited. Under the assumption of character additivity, "0" is the plesiomorphic condition, and "1" (and higher integers) represent succes-

sively derived conditions. In the nonadditive analysis, or Transformation Series 16 in the additive analysis, the distance between alternative characters is considered to be 1, regardless of the integer assignments of the characters.

Although some other features (e.g., calcar development [Handley, 1959], attachment point of interfemoral membrane [Handley, 1959], expansion of acromion process and notching of manubrium (= presternum) [Hall, 1934]) have been suggested to reflect phylogenetic information, they have not been included in our list of transformation series because of intraspecific variation or our inability to verify early observations. Synapomorphies of the ingroup (discussed above) and autapomorphies of terminal taxa (e.g., the pink ears and dorsal white spots of *Euderma maculatum*) are excluded from the analysis for clarity of discussion. Transformation series listed below are reflected in the data matrix of Appendix 2. Original sources for each character description are provided.

1. Rostrum (Handley, 1959): (0) flattened, with median concavity; (1) flattened, with slight concavity; (2) arched, without median concavity.

2. Braincase (Handley, 1959): (0) relatively shallow; dorsal surface of skull relatively flat; (1) relatively deep—doming of skull prevents the skull from lying flat while on its dorsal surface.

3. Preorbital-supraorbital region (Handley, 1959): (0) smoothly rounded or faintly ridged; (1) sharply ridged.

4. Temporal ridges (Handley, 1959): (0) confluent medially interorbitally (or nearly so); (1) not confluent medially, with distinct muscle scars. *Idionycteris* and *Euderma* have the temporal ridges completely separated. This condition is approached in *Plecotus*, in which the temporal ridges meet at a point interorbitally but separate posterior to this point. In *Corynorhinus* the temporal ridges meet interorbitally and do not separate posterior to this point. Although we could have cast this transformation into three characters, outgroup comparison difficulties in distinguishing the *Plecotus* and *Corynorhinus* conditions required us to recognize only the *Euderma-Idionycteris* condition as apomorphic.

5. Zygoma, fragility (Handley, 1959): (0) relatively thin and fragile; (1) relatively thick and strong.

6. Zygoma, postorbital expansion (Handley, 1959): (0) postorbital expansion in middle or slightly anterior to middle of zygomatic arch, or not expanded; (1) postorbital expansion in posterior third of arch.

7. Auditory bullae, shape (Handley, 1959): (0) roughly circular in outline, slightly enlarged; (1) enlarged, slightly elongate; (2) enlarged and elliptical.

8. First upper incisors (I1 and I2) (Handley, 1959): (0) I2 and I1 subequal; (1) I1 much taller than I2 (I2 reduced).

9. Upper fourth premolar (P4) (Handley, 1959): (0) much wider than long, posterolingual part of tooth not reduced; (1) approximately equal in length and width, posterolingual part of tooth reduced.

10. Metacone of upper third molar (M3) (Handley, 1959): (0) present; (1) absent.

11. Anterointernal cusp of lower canine (c1) (Handley, 1959): (0) relatively large, ca. 0.66–0.5 size of primary cusp in height; (1) small and greatly exceeded by primary cusp. This feature reflects the absolute size of the secondary cusp.

12. Lower third premolar (p3) (Handley, 1959): (0) cross-sectional outline not distorted; (1) cross-sectional outline distorted. Because *Barbastella* and *Euderma* lack a p3, they are coded as unknown for this feature.

13. Lower third premolar (p3) (Handley, 1959): (0) present; (1) absent.

14. Lower fourth premolar (p4) (Handley, 1959): (0) double-rooted; (1) single-rooted. Handley (1959: 11) reported *Corynorhinus townsendii* as having only one root on the p4. However, all *Corynorhinus* we observed (including *townsendii*) had two roots, although these were very small and in some cases sometimes appeared to be single.

15. Posterior extension of anterior naris (Handley, 1959): (0) vomers not exposed; (1) posterior extension of anterior naris so far back as to expose vomers.

16. Median postpalatal process (Handley, 1959): (0) weak single spine; (1) prominent single spine; (2) bifid prominence; (3) absent. Because of outgroup ambiguity, this must be treated as a nonadditive (= unordered) set of

characters, even though condition 0 (weak single spine) clearly is the ancestral condition.

17. Basial (= basicranial) pits (Handley, 1959): (0) absent; (1) present.

18. Manubrium (= presternum of Hall, 1934; Handley, 1959): (0) as wide or wider than long; (1) distinctly longer than wide.

19. Second phalanx of third digit (Handley, 1959): (0) less than or equal in length to first phalanx; (1) much longer than first phalanx.

20. Nostril (Handley, 1959): (0) unspecialized; (1) great posterior elongation with a conspicuous shallow basin posteriad and separated by a septum.

21. Muzzle glands (Handley, 1959): (0) absent; (1) present, not greatly enlarged; (2) greatly enlarged.

22. Ears (Dobson, 1875; Handley, 1959): (0) small; (1) extremely enlarged.

23. Tragus (Handley, 1959): (0) narrow, blade-like; no prominent constriction near the base; (1) intermediate; (2) paddle-like, with a prominent constriction near the base.

24. Accessory anterior basal lobe of auricle (Handley, 1959): (0) absent; (1) present (weak in *Plecotus*: a projecting lappet in *Idionycteris*).

25. Transverse ribs on auricle (Handley, 1959): (0) uninterrupted by vertical rib near posterior border; (1) interrupted by vertical rib near posterior border.

26. Chromosome arms 21 and 7 (Bickham, 1979; Leniec et al., 1987): (0) unfused; (1) fused.

27. Chromosome arms 13 and 10 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

28. Chromosome arms 21 and 9 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

29. Chromosome arms 19 and 8 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

30. Chromosome arms 22 and 12 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

31. Chromosome arms 18 and 14 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

32. Chromosome arms 23 and 20 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

33. Chromosome arms 19 and 14 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

34. Chromosome arms 22 and 8 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

35. Chromosome arms 13 and 9 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

36. Chromosome arms 12 and 10 (Stock, 1983; Leniec et al., 1987): (0) unfused; (1) fused.

RESULTS

Statistics presented below, unless bracketed, refer to the analysis in which additivity of multicharacter transformations was assumed. Bracketed statistics refer to the data analysis in which all character matches were regarded as nonadditive (= unordered). Analysis of the data matrix (Appendix 2), with or without the assumption of transformational additivity, produced one most parsimonious tree (fig. 1, Appendices 3 and 4), which has a length of 53 [50] ($ci = 0.792$ [0.840]), and shows *Barbastella* within the plecotines, as the sister taxon of *Plecotus* + *Corynorhinus*, a result in accord with those of Leniec et al. (1987). Because the karyological data were taken directly from the literature and were not our observations we also analyzed a matrix containing only morphological data (Transformation Series 1–25) that we could verify. Under the assumption of additivity this matrix produced three trees (length = 41, $ci = 0.756$), all of which (fig. 2; trees 1–3) show considerably different topologies from that based on the entire data set. Without the assumption of additivity these same three trees were discovered (length = 39; $ci = 0.795$), with the addition of one more of the same length (fig. 2; tree 4). However, if the complete data set (Transformation Series 1–36) is forced onto trees 1–3 (fig. 2), the resulting statistics are length = 57 [55], $ci = 0.737$ [0.764]. In other words, the topologies based solely on morphology require, when assuming additivity, four more steps in the entire data set, and five more steps when additivity is not assumed, than does the most parsimonious topology based on the entire data set. Tree 4 (fig. 2), discovered by the

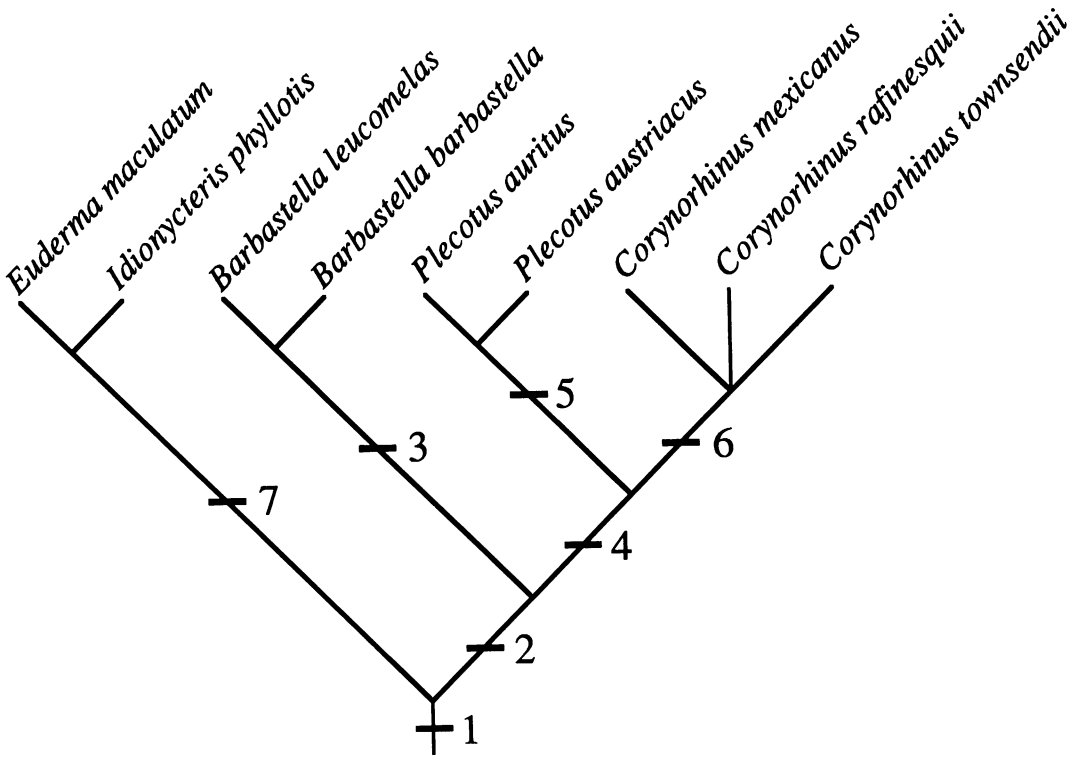


Fig. 1. Most parsimonious tree for all data. Numbered stems are documented in Appendices 3 and 4.

morphology-only data set, when additivity is not assumed, is identical to the topology discovered by the entire data set (fig. 1), both with additivity and without (length = 53 [50]; ci = 0.792 [0.840]). In other words, without additivity assumed, the morphological transformations do not reject the tree that is most parsimonious for all of the data, regardless of the assumptions made about additivity of character matches.

For those trees that are supported under the assumption of additivity, the morphological evidence is only marginally incongruent with the karyological data, regardless of the most parsimonious trees produced solely by morphology. When additivity is assumed, the restricted morphological data set cast onto the topology produced by the entire data set has a length of 42 (ci = 0.738), which is only one step longer than the trees (fig. 2, trees 1–3) based solely on the morphological data set (length = 41, ci = 0.756). This means that regardless of the relatively high consistency indices produced by the morphology-only

analyses, it is clear that the morphology-only data set is only marginally more supportive of its peculiar trees (fig. 2, trees 1–3) than that tree that is most parsimonious of all data (fig. 1 and fig. 2, tree 4). This is a good example of why consistency indices should not be taken as measures of tree stability. We hesitate to make any generalizations about character additivity, inasmuch as we think that this particular issue is inextricably joined to the issue of how similar character matches must be for the systematist to hypothesize homology. However, in this particular case, the only serious departure from congruence between the additive and nonadditive analysis is in the placement of characters in Transformation Series 7 (bullae shape and size).

Although we accept the tree most supported by the complete data set, this means that we must accept either that enlarged ears of *Euderma* + *Idionycteris* are not homologous with those in *Corynorhinus* + *Plecotus*, or that *Barbastella* has, as a synapomorphy

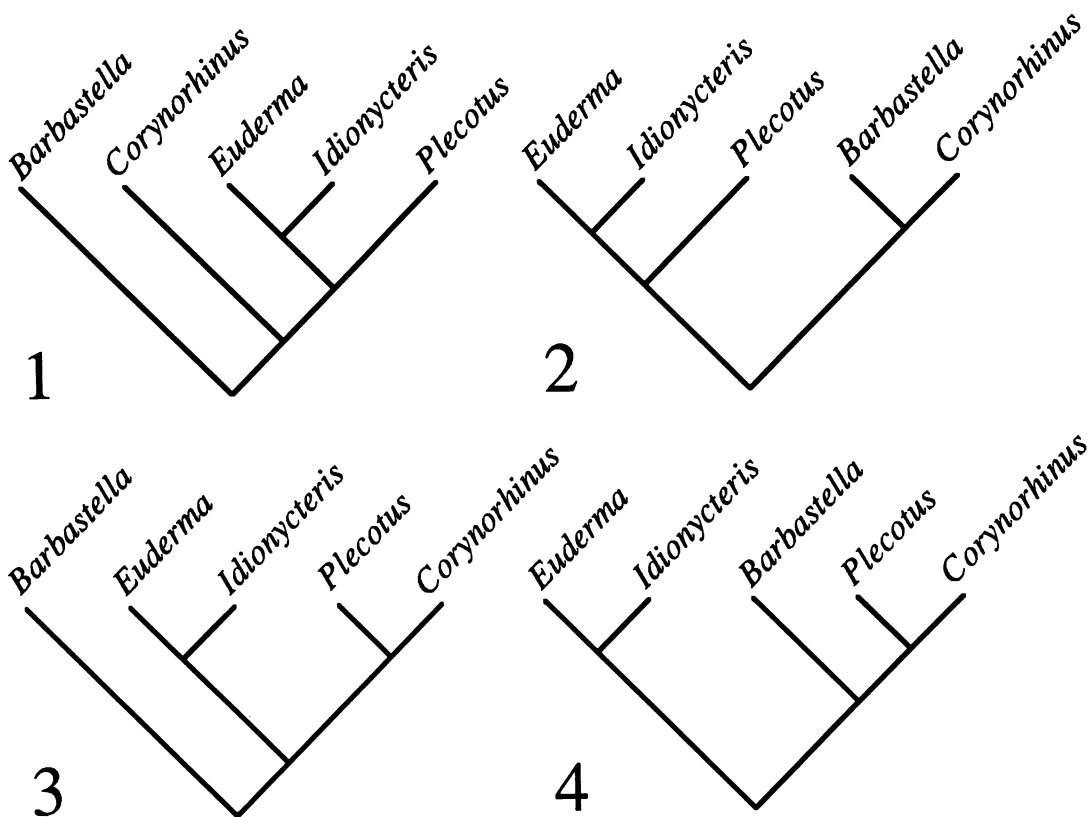


Fig. 2. Alternative trees produced solely by the morphological subset of the data.

of that genus, reduced the size of the ears from "enlarged" to "normal." Although we suspect that *Barbastella* has reduced its ear size, this issue cannot be resolved by this data set.

Data supporting the stems noted in figure 1 are noted in Appendices 3 and 4.

COMPARISON WITH PREVIOUS VIEWS

Only Leniec et al. (1987) have suggested that *Barbastella* is within the traditional plecotines, rather than the sister taxon of traditional plecotines. Because a large proportion of the data here analyzed are theirs, it is not surprising that we came to identical conclusions. However, as discussed above, the morphological data are only marginally at variance with the karyological evidence.

Excluding the placement of *Barbastella*, our arrangement is most similar to that proposed by Williams et al. (1970), but contrasts with

that of Handley (1959). The tree suggested by Handley (1959) (fig. 3) fared particularly poorly (length = 68 [65], ci = 0.62 [0.65]), when the entire data set is cast upon it, requiring an additional 16 convergences under the assumption of additivity and 13 without this assumption. This is not surprising, because Handley (1959) based his view on an evaluation of overall similarity. The tree suggested by Williams et al. (1970) (fig. 4) (identical to our Tree 3 in fig. 3 for the morphology-only data set) fared better (length = 57 [55], ci = 0.74 [0.76]), largely because of the placement of *Idionycteris* as the sister taxon of *Euderma* rather than the sister taxon of *Corynorhinus* + *Plecotus* as posited by Handley.

SELECTION OF A TAXONOMY

A taxonomy should be logically consistent with that which it purports to document (Hull, 1964; Wiley, 1981), which, as most system-

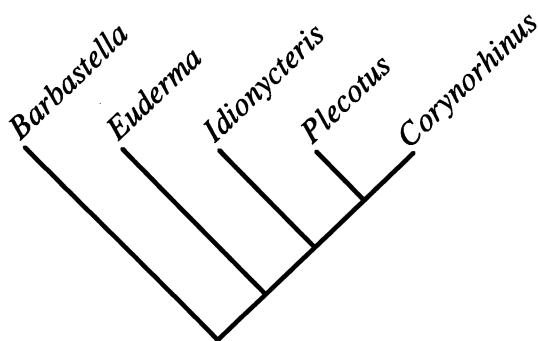


Fig. 3. Phylogeny posited by Handley (1959).

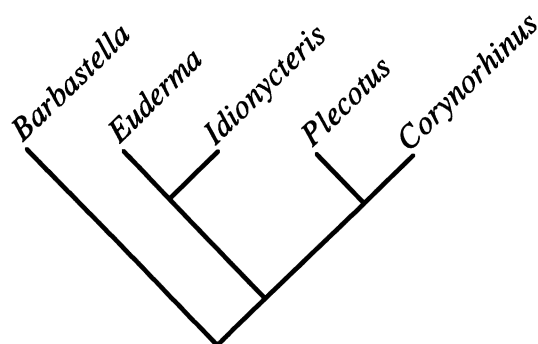


Fig. 4. Phylogeny posited by Williams et al. (1970).

artists now agree, is recovered phylogenetic history. A rather large number of alternative taxonomies exist that are logically consistent with our preferred cladogram (fig. 1) (e.g., one genus for all ingroup species, or different genera for each species in the ingroup). However, we think that a taxonomy should maximize phylogenetic retrievability without undue violence to the traditional taxonomy or to perturbability from future discoveries. For this reason we recommend the following taxonomy:

Tribe Plecotini Dobson, 1875

Euderma H. Allen, 1892

E. maculatum (J. A. Allen, 1891)

E. phyllote (G. M. Allen, 1916)⁴

Barbastella Gray, 1821

B. barbastella (Schreber, 1774)

B. leucomelas (Cretzschmar, 1826)

Plecotus Geoffroy Saint-Hilaire, 1818

P. auritus (Linnaeus, 1758)

P. austriacus (Fischer, 1829)

P. teneriffae Barrett-Hamilton, 1907⁵

Corynorhinus H. Allen, 1865

C. mexicanus G. M. Allen, 1916

C. rafinesquii (Lesson, 1827)

C. townsendii (Cooper, 1837)

Idionycteris is synonymized with *Euderma* because they are sister species with few autapomorphies. We could have retained *Corynorhinus* as a subgenus of *Plecotus*, but this taxonomy is dependent on a cladogram whose arrangement is only slightly more parsimo-

nious than trenchantly different arrangements that would not place *Corynorhinus* and *Plecotus* as sister taxa (e.g., considering *Barbastella* and *Corynorhinus* to be sister taxa requires only one additional step in the overall tree assuming additivity and only two more steps without this assumption).

TAXONOMIC ACCOUNTS

With the exception of the diagnosis for the Plecotini which lists all known unambiguous synapomorphies, the intention of the diagnoses below is to provide a list of morphological characteristics for identifying named taxa. Unambiguous synapomorphies of diagnosed groups are italicized. Unnamed taxa are diagnosed in Appendix 4.

TRIBE PLECOTINI

Plecoti Dobson, 1875: 349. Type genus: *Plecotus* Geoffroy Saint-Hilaire, 1818.

DIAGNOSIS: *Zygomatic arches do not extend far from the skull; fusion of chromosome arms 15 and 11; ears connected by an interauricular septum (low in Corynorhinus).*

DISTRIBUTION: Temperate Eurasia, North Africa, and North America.

Genus *Euderma*

Euderma H. Allen, 1892 [1891]: 467. Type species: *Histiotus maculatus* J. A. Allen, 1891.

Idionycteris Anthony, 1923: 1. Type species: *Idionycteris mexicanus* Anthony, 1923 (= *Corynorhinus phyllotis* G. M. Allen, 1916).

DIAGNOSIS: Rostrum not flattened, with median concavity (flattened with slight concavity in *Plecotus* and arched with median

⁴ The original formation of the species name as an adjective rather than a noun makes for this rather unhappy spelling.

⁵ Provisionally allocated here; specimens not seen.

concavity in *Corynorhinus*); braincase dorsally flattened as in *Plecotus* (domed in *Corynorhinus* and *Barbastella*); zygoma with postorbital expansion in middle or slightly anterior to middle of zygomatic arch (posterior expansion in posterior third of arch in *Corynorhinus*); auditory bullae very enlarged and elliptical (slightly enlarged, circular in *Barbastella*; enlarged and slightly elongate in *Corynorhinus* and *Plecotus*); P4 much wider than long (length and width subequal in *Plecotus*); metacone on M3 present (absent in *Plecotus*); p3 absent in *E. maculatum*, present in *E. phyllote* (also absent in *Barbastella*); p4 single rooted (double-rooted in *Corynorhinus*, *Barbastella*, and *Plecotus*); basal pits absent (present in *Corynorhinus*); ears extremely enlarged (small in *Barbastella*); tragus paddlelike, with a prominent constriction near the base (narrower in *Plecotus*, *Barbastella*, and *Corynorhinus*); muzzle glands not enlarged (weakly enlarged in *Plecotus*; very enlarged in *Corynorhinus* and *Barbastella*); transverse ribs on auricle uninterrupted by vertical rib near posterior border (interrupted in *Corynorhinus*).

CONTENT: *Euderma maculatum* (J. A. Allen, 1891), and *E. phyllote* (G. M. Allen, 1916).

DISTRIBUTION: Western North America from southwestern Canada to San Luis Potosi and Mexico City, Mexico.

Genus *Barbastella*

Barbastella Gray, 1821: 300. Type species: *Vespertilio barbastellus* Schreber, 1774.

Synotis Keyserling and Blasius, 1839: 305. Type species: *Vespertilio barbastellus* Schreber, 1774.

DIAGNOSIS: Rostrum flattened, with median concavity (with slight concavity in *Plecotus* and arched in *Corynorhinus*); braincase dorsally domed as in *Corynorhinus* (flattened in *Euderma* and *Plecotus*); zygomatic arch with expansion near middle (in posterior third in *Corynorhinus*); auditory bullae slightly enlarged, circular in outline (enlarged in *Plecotus*, *Corynorhinus*, and *Euderma*); P4 much wider than long (subequal in *Plecotus*); metacone of M3 present (absent in *Plecotus*); p3 absent (present in *Euderma phyllote*, *Plecotus*, and *Corynorhinus*); p4 double rooted (single rooted in *Euderma*); basal pits absent

(present in *Corynorhinus*); ears of moderate size (extremely enlarged in *Euderma*, *Corynorhinus*, and *Plecotus*); tragus narrow (wider in *Plecotus* and *Euderma*); muzzle glands greatly enlarged; transverse ribs on auricle not interrupted posteriorly by vertical rib on posterior border (interrupted in *Corynorhinus*).

CONTENT: *Barbastella barbastella* (Schreber, 1774), and *B. leucomelas* (Cretzschmar, 1826).

DISTRIBUTION: Western Europe, Morocco, and Ethiopia to Caucasus, Pamirs, and western China; Japan.

Genus *Plecotus*

Plecotus Geoffroy Saint-Hilaire, 1818: 212. Type species: *Vespertilio auritus* Linnaeus, 1758.

DIAGNOSIS: Rostrum flattened, with slight concavity (convexly arched in *Corynorhinus*, larger concavity in *Euderma*); braincase dorsally flattened as in *Euderma* (domed in *Corynorhinus* and *Barbastella*); zygomatic arch with expansion near middle (in posterior third in *Corynorhinus*); auditory bullae enlarged, slightly elongate (smaller in *Barbastella*; much larger in *Euderma*); P4 subequal in length and width (much wider than long in *Euderma*, *Barbastella*, and *Corynorhinus*); metacone of M3 absent (present in *Euderma*, *Barbastella*, and *Corynorhinus*); p3 present (absent in *Barbastella* and *Euderma maculatum*); p4 double rooted (single rooted in *Euderma*); basal pits absent (present in *Corynorhinus*); ears very large (smaller in *Barbastella*); tragus moderately broad (very broad in *Euderma*; narrow in *Corynorhinus* and *Barbastella*); muzzle glands visible but not greatly enlarged (large in *Corynorhinus* and *Barbastella*); transverse ribs on auricle not interrupted posteriorly by vertical rib on posterior border (interrupted in *Corynorhinus*).

CONTENT: *Plecotus auritus* (Linnaeus, 1758), *P. austriacus* (Fischer, 1829), and *P. teneriffae* Barrett-Hamilton, 1907.

DISTRIBUTION: Norway, England, Spain, and Senegal to Mongolia, Japan; Canary and Cape Verde Islands.

Genus *Corynorhinus*

Corynorhinus H. Allen, 1865: 173. Type species: *Plecotus macrotis* Le Conte, 1831 (= *Plecotus rafinesquii* Lesson, 1827).

DIAGNOSIS: *Rostrum arched, without median concavity* (flattened with varying degrees of development of median concavity in *Euderma*, *Barbastella*, and *Plecotus*); braincase dorsally domed as in *Barbastella* (flattened in *Euderma* and *Plecotus*; *expansion of zygomatic arch in posterior third* (near middle in *Euderma*, *Barbastella*, and *Plecotus*); auditory bullae enlarged, slightly elongate (larger, more elongate in *Euderma*; less enlarged in *Barbastella*); P4 much wider than long (subequal in *Plecotus*); metacone of M3 present (absent in *Plecotus*); p3 present (absent in *Barbastella* and *Euderma phyllote*); p4 double rooted (single rooted in *Euderma*); *basial pits present* (absent in *Euderma*, *Barbastella*, and *Plecotus*); ears very large (smaller in *Barbastella*); tragus narrow, bladeliike (broader in *Plecotus* and *Euderma*); *muzzle glands greatly enlarged* (smaller in *Euderma*, *Barbastella*, and *Plecotus*); *transverse ribs on auricle interrupted by vertical rib near posterior border* (uninterrupted in *Euderma*, *Plecotus*, and *Barbastella*).

CONTENT: *Corynorhinus mexicanus* G. M. Allen, 1916, *C. rafinesquii* (Lesson, 1827), and *C. townsendii* (Cooper, 1837).

DISTRIBUTION: Southern British Columbia (Canada) and Virginia (USA) south to southeastern Mexico and the Isthmus of Tehuantepec.

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APPENDIX 1

Specimens Examined

Unless noted otherwise, specimens are skin and skull. AMNH = American Museum of Natural History; FMNH = Field Museum of Natural History; KU = Museum of Natural History, University of Kansas; USNM = National Museum of Natural History, Smithsonian Institution.

OUTGROUP TAXA: "*Myotis*" *liebii*: KU 48123 (skull). "*M.*" *lucifugus*: AMNH 245599 (alcoholic); KU 45526–27, 45536, 48123 (skull). "*M.*" *myotis*: AMNH 256285 (alcoholic). "*M.*" *sodalis*: KU 10798 (skull). "*M.*" *thysanodes*: KU 116323, 116325.

INGROUP TAXA: *Barbastella barbastella*: AMNH 233147–49 (alcoholics; x-rays), 245381 (skull); KU 88261; USNM 37568, 121022 (alcoholic; x-ray), 142583, 540789. *B. leucomelas*: AMNH 245382 (skull); FMNH 34768 (alcoholic; x-ray), 82737–38; KU 121516. *Corynorhinus mexicanus*: KU 29892 (skull), 29924–27 (alcoholics), 29929–37 (skeletons), 29938–48 (alcoholics), 108977 (alcoholic), 111616–20 (alcoholics); USNM 81654–55 (alcoholics). *C. rafinesquii*: KU 11183, 11264–67, 71989, 99392; USNM 512000 (alcoholic; x-ray), 512003 (alcoholic, x-ray). *C. townsendii*: AMNH 1499–1501 (alcoholics), 9800–01 (skeletons), 11938–39 (skeletons), 243896 (skull), 74902 (alcoholic); FMNH 73998 (partial skeleton); KU 5210 (skull), 34903–10 (skeletons), 82217 (alcoholic), 98488–527 (alcoholics); USNM 297269 (alcoholic, x-ray), 552875 (alcoholic, x-ray). *Euderma maculatum*: FMNH 106698 (skull); KU 119275 (skin and skull), 139030 (skin, skull, and alcoholic body). *E. phyllote*: AMNH 185341 (skull); FMNH 959214 (partial skeleton); KU 73211, 73594 (skull), 83649–52 (skeletons), 93100 (skull), 98548–49, 107498–500; USNM 314878 (alcoholic; x-ray). *Plecotus auritus*: AMNH 31780 (alcoholic), 70615 (skull), 146504 (skull), 247035 (alcoholic; x-ray); FMNH 91634; KU 11362 (skull), 35428 (skull), 64422 (alcoholic), 88262; USNM 18487 (skull), 219176–78. *P. austriacus*: AMNH 233150 (alcoholic; x-ray); FMNH 102776; KU 88263.

APPENDIX 2

Data Matrix

	1	11111	11112	22222	22223	333333	
	12345	67890	12345	67890	12345	67890	123456
Hypothetical Ancestor	00000	00000	00000	00000	00000	00000	000000
<i>Barbastella leucomelas</i>	01000	00100	0?101	00000	20000	?????	??????
<i>Barbastella barbastella</i>	01000	00100	0?101	00000	20000	10000	001111
<i>Euderma maculatum</i>	00111	02000	0?110	20110	01200	01111	110000
<i>Idionycteris phyllotis</i>	00111	02100	00010	30110	01210	01111	110000
<i>Plecotus auritus</i>	10101	01111	10000	00001	11110	10000	001111
<i>Plecotus austriacus</i>	10101	01111	10000	00001	11110	10000	001111
<i>Corynorhinus mexicanus</i>	21000	11100	11000	11011	21001	?????	??????
<i>Corynorhinus rafinesquii</i>	21000	11100	11000	11011	21001	?????	??????
<i>Corynorhinus townsendi</i>	21000	11100	11000	11011	21001	10000	001111

APPENDIX 3
Changes, by Transformation Series, for the Stems
Noted on Figure 1

Trans. series	ci	Steps	Change	Along stem
1	1.000	1	‡0 → 1	4
		1	‡1 → 2	6
2	0.500	1	‡0 → 1	2
		1	‡1 → 0	5
3	0.500	1	0 → 1	5
		1	0 → 1	7
4	1.000	1	0 → 1	7
5	0.500	1	0 → 1	5
		1	0 → 1	7
6	1.000	1	0 → 1	6
7	0.667	1	†0 → 1	1
		1	†1 → 0	3
		1	1 → 2	7
[7	1.000	1	0 → 1	4]
		1	0 → 2	7]
8	0.500	1	‡0 → 1	1
		1	‡1 → 0	<i>E. maculatum</i>
9	1.000	1	0 → 1	5
10	1.000	1	0 → 1	5
11	1.000	1	0 → 1	4
12	1.000	1	0 → 1	6
13	0.500	1	0 → 1	3
		1	0 → 1	<i>E. maculatum</i>
14	1.000	1	0 → 1	7
15	1.000	1	0 → 1	3
16	1.000	1	0 → 1	6
		1	‡0 → 2	7
		1	‡2 → 3	<i>I. phyllotis</i>
17	1.000	1	0 → 1	6
18	1.000	1	0 → 1	7
19	0.500	1	0 → 1	6
		1	0 → 1	7

APPENDIX 3—(Continued)

Trans. series	ci	Steps	Change	Along stem
20	1.000	1	0 → 1	4
21	0.667	2	0 → 2	2
		1	†2 → 1	5
22	0.500	1	‡0 → 1	1
		1	‡1 → 0	3
23	0.667	1	0 → 1	5
		2	0 → 2	7
24	0.500	1	0 → 1	5
		1	0 → 1	<i>I. phyllotis</i>
25	1.000	1	0 → 1	6
26	1.000	1	0 → 1	2
27	1.000	1	0 → 1	7
28	1.000	1	0 → 1	7
29	1.000	1	0 → 1	7
30	1.000	1	0 → 1	7
31	1.000	1	0 → 1	7
32	1.000	1	0 → 1	7
33	1.000	1	0 → 1	2
34	1.000	1	0 → 1	2
35	1.000	1	0 → 1	2
36	1.000	1	0 → 1	2

† Denotes a change placed on that stem under only one character transformation optimization (e.g., accelerated transformation in this case) under the assumption of character additivity.

‡ Denotes ambiguous placement due to character optimization alternatives under no assumption of character additivity. For transformation series 7, the alternative arrangement in brackets refer to results under no assumption of additivity.

APPENDIX 4

Apomorphy Lists by Stem from Figure 1

Stem	Trans. series	Steps	ci	Change
1	(7	1	0.667	†0 → 1)
	8	1	0.500	‡0 → 1
	22	1	0.500	‡0 → 1
2	2	1	0.500	‡0 → 1
	21	2	0.667	0 → 2
	26	1	1.000	0 → 1
	33	1	1.000	0 → 1
	34	1	1.000	0 → 1
	35	1	1.000	0 → 1
	36	1	1.000	0 → 1
3	7	1	0.667	†1 → 0
	13	1	0.500	0 → 1
	15	1	1.000	0 → 1
	22	1	0.500	‡1 → 0
4	1	1	1.000	‡0 → 1
	[7	1	1.000	0 → 1]
	11	1	1.000	0 → 1
	20	1	1.000	0 → 1
5	2	1	0.500	‡1 → 0
	3	1	0.500	0 → 1
	5	1	0.500	0 → 1
	9	1	1.000	0 → 1
	10	1	1.000	0 → 1
	21	1	0.667	†2 → 1
	23	1	0.667	0 → 1
6	24	1	0.500	0 → 1
	1	1	1.000	‡1 → 2
	6	1	1.000	0 → 1
	12	1	1.000	0 → 1
	16	1	1.000	‡0 → 1
17	1	1.000	0 → 1	

APPENDIX 4—(Continued)

Stem	Trans. series	Steps	ci	Change
7	19	1	0.500	0 → 1
	25	1	1.000	0 → 1
	3	1	0.500	0 → 1
	4	1	1.000	0 → 1
	5	1	0.500	0 → 1
	(7	1	0.667	1 → 2)
	[7	1	1.000	0 → 2]
	14	1	1.000	0 → 1
	16	1	1.000	†0 → 2
	18	1	1.000	0 → 1
	19	1	0.500	0 → 1
	23	2	0.667	0 → 2
	27	1	1.000	0 → 1
	28	1	1.000	0 → 1
	29	1	1.000	0 → 1
30	1	1.000	0 → 1	
31	1	1.000	0 → 1	
32	1	1.000	0 → 1	
<i>E. maculatum</i>	8	1	0.500	‡1 → 0
	13	1	0.500	0 → 1
<i>I. phyllotis</i>	16	1	1.000	‡2 → 3
	24	1	0.500	0 → 1

† Denotes a transformation whose placement is dependent on a particular character optimization (e.g., accelerated transformation) under an assumption of character additivity.

‡ Denotes a transformation whose placement is dependent on a particular character optimization under no assumption of additivity. Transformations in brackets are only in the results of the nonadditive analysis; those in parentheses are only in the additive analysis.

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