The Systematic Status of *Dermanura concolor* (Peters, 1865) (Chiroptera: Phyllostomidae), with Description of a New Genus

ROBERT D. OWEN[1,2]

ABSTRACT

Dermanura concolor (Peters) was described in 1865 as a member of the large stenodermatine genus *Artibeus*. Andersen (1908) considered it to be allied with the larger species of that genus, but later authors (Cabrera, 1958; Husson, 1978; Handley, 1987) found it to be more closely related to the smaller forms. Owen (1987) concurred that *concolor* was more closely allied with the smaller species, to which he assigned the generic name *Dermanura*; nonetheless, he suggested inclusion of *concolor* within *Dermanura* only "until additional evidence is available."

In the present study, Owen's (1987) discrete-state character set was reanalyzed using Camin-Sokal parsimony for the dental characters. This analysis, using several outgroups, showed *concolor* to be more closely related to the "short-faced" stenodermatine species than to *Dermanura*. *Concolor* is not a natural member of the genus *Dermanura*. Because no generic name is available for this species, a new one is proposed in honor of Dr. Karl F. Koopman.

RESUMEN

Dermanura concolor (Peters) fue descrito en 1865 como miembro del enorme género *Artibeus*. Andersen en 1908 lo consideró aliado con las especies de mayor tamaño de este género. Posteriormente otros autores (Cabrera, 1958; Husson, 1978; Handley, 1987) encontraron una relación más estrecha con las especies más pequeñas. Owen (1987) confirmó que *concolor* es más afín con las especies de menor talla, a las cuales asignó el nombre genérico de *Dermanura*; sugiriendo la inclusión de *concolor* en el género *Dermanura* mientras "evidencia adicional es encontrada."

En el presente estudio, el grupo de caracteres discretos descritos por Owen (1987) fue reanalizado utilizando la parsimonia de Camin-Sokal para características dentarias. Este analisis, utilizando varios grupos ajenos al taxón reveló que *concolor* esta más estrechamente relacionado con las especies "cara-cortas" de los stenodermatines que a *Dermanura*. *Concolor* no es un miembro natural del género *Dermanura*. En ausencia de un nombre genérico para esta especie se propone uno en honor del Dr. Karl F. Koopman.

INTRODUCTION

In 1865, Peters described as *Artibeus concolor* a medium-sized, fruit-eating bat with three molar teeth both above and below, based on a specimen from Paramaribo, Suriname. Later, Andersen (1908), in the only published revisionary study of bats of the genus *Artibeus*, arranged *concolor* as allied to the larger species *A. planirostris* and *A. hirsutus*, and by inference ultimately to *A. jamaicensis* (including *lituratus* and several other larger species as now recognized), principally on the basis of 3/3 molars. Aside from having three molars in each jaw (the third considerably reduced in size but nonetheless a well-de-

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[1] Assistant Professor, Department of Biology, University of Missouri–Kansas City, Kansas City, MO 64110.

[2] Present address: Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409.

veloped tooth), Andersen noted that *A. concolor* was considerably smaller than other species or their supposed relatives that fell in that same category (he described it as "intermediate" in size between the smaller and larger taxa of *Artibeus* exclusive of *Enchisthenes hartii*), had a "peculiarly shortened" rostrum, and differed in other details of morphology from both large and small representatives of the genus. Andersen treated all *Artibeus*-like bats (again other than *Enchisthenes*) as members of single genus, even though the name *Dermanura* Gervais, 1855, was available for the smaller members of the assemblage.

For more than three-quarters of a century following Andersen's monographic treatment, *A. concolor* was more or less universally recognized as a distinct specific entity (see, for example, Cabrera [1958] and Husson [1978]), relatively rare in museum collections, but allied with the smaller *Artibeus* rather than the larger species of that group. Recently, Handley (1987) and Owen (1987) both have addressed the relationships of *concolor* in context with all other small *Artibeus*-like bats. The former author, following description of a new species, provided a synopsis of the "groups" of small taxa of the genus *Artibeus*, of which he recognized six; one of these contained only *concolor*.

Owen (1987), on the other hand, in a phylogenetic analysis of stenodermatine bats, concluded that the smaller species of *Artibeus* (sensu lato) actually represented a distinct genus, for which he employed the name *Dermanura*. Both *concolor* and *hartii* were included within *Dermanura*, although it was noted that the relationships of these two species to other members of the genus were "yet unclear." With this as a background, I here further consider the relationship of *concolor* to its reputed relatives. Although these analyses also are relevant to the status of *hartii*, that question is being addressed separately in a study by Joaquín Arroyo-Cabrales.

MATERIALS AND METHODS

Phylogenetic analyses included all species determined to be in the same primary clade as *concolor* (Owen, 1987). These are the species of the genus *Dermanura* (including *Enchisthenes*) and the stenodermatine "short-faced" bats: genera *Pygoderma, Centurio, Phyllops, Ardops, Ariteus, Ametrida, Sphaeronycteris,* and *Stenoderma.* The one recognized species not included in the analysis is the recently described *Dermanura gnoma* (Handley, 1987; as *Artibeus gnomus*). For specimens examined, see Owen (1987: appendix I).

A series of 22 discrete-state characters was utilized for the analyses. These are listed and described in Owen (1987: table 1 and appendix II; the condition of both M3 and m3 was miscoded in the table, even though properly coded in the analyses). A detailed description of the additive binary coding and character rooting procedure was given by Owen (1987). The values for the 46 binary characters are listed in table 1 of this paper, and the characters are defined in the Appendix.

As outgroups for *Dermanura* and the short-faced bats, one member from each of two of the other three primary stenodermatine clades (Owen, 1987: fig. 17) was used. *Sturnira ludovici* was chosen to represent the *Sturnira* clade, and *Artibeus jamaicensis* was chosen to represent the primary clade of *Artibeus, Uroderma, Ectophylla, Platyrrhinus, Vampyrodes, Chiroderma,* and *Vampyressa.* (I follow Gardner and Ferrell [1990] in the use of *Platyrrhinus* rather than *Vampyrops.*) Another outgroup taxon (*Carollia brevicauda*) was chosen to represent the carolliine bats, a sister group of the stenodermatines (Hood and Smith, 1982). (I use "stenodermatines" to mean those genera that composed the recognized subfamily Stenodermatinae prior to Baker et al.'s [1989] revision of Phyllostomidae. Following Baker et al., the stenodermatines, along with the carolliines, compose the tribe Stenodermatini.) In each case, the species selected as an outgroup was thought to represent a relatively primitive morphotype within its clade. In order to determine the response to different outgroup taxa being used to root the trees, analyses were done using each of the outgroup species separately.

Many dental characteristics (e.g., loss of teeth) are known to evolve in parallel or convergent fashion among phyllostomids ("rampant parallelism"—Sluys, 1989). Consequently, these characters were subjected to Camin-Sokal parsimony in the analyses. This means that a forward step (e.g., reduction or

TABLE 1
Character State Values for Each of the 22 Taxa Examined in This Study
(1 = presence of the character state as defined in the Appendix)

Ametrida centurio	000110001010011010011011001101111000001000000 0
Ardops nicholsii	0101000010110110000111010111011110010100000000
Ariteus flavescens	0001100010110110000111000011011111000100001100
Centurio senex	1001110011100110111111110001101111100010000101 1
Dermanura anderseni	0010001100100110000110110011110011000010001011
D. azteca	0100001100110110000110010011011011000000001011
D. cinerea	0000001100100110000110010111010011000000001011
D. concolor	0001000000100111000110011011011110001000000000
D. glauca	0010001100100110000110100010011011000000001110
D. hartii	0001101100110110000110110110011000000010000000
D. phaeotis	0110001100100110000110010111011011100000001011
D. tolteca	0110001100100110000110110111011011101000001011
D. watsoni	0110001100100110000110010010011011001000001110
Phyllops falcatus	0101100010110110000111010111011110101100000000
P. haitiensis	0101110010110110111111110111111110101100000000
P. vetus	0101100010110110000111010110011010000100000000
Pygoderma bilabiatum	0101100010000110000110010111011111010001001011
Sphaeronycteris toxophyllum	0101110010100110110111110011011110000011100010
Stenoderma rufum	0010000010100110100111000111011010001111110000
OUTGROUPS	
Artibeus jamaicensis	0001001100100110000110010011011111001000001110
Sturnira ludovici	0001100000111100000001010011100000001000110000 00
Carollia brevicauda	0000000000000000000000000000000000000000000000

loss of M3) is considered more likely to occur multiple times independently than to be reversed (the tooth to be "regained") in a lineage. Nondental characters (external and cranial) were subjected to strict parsimony in which reversals and convergences are considered to be equally likely.

Because several equally parsimonious trees were found in each analysis, a majority-rule consensus tree (Felsenstein, 1988) was computed for the trees resulting from analysis with each of the three outgroup taxa. Finally, an overall consensus tree was computed from these three consensus trees. Character states then were mapped onto this tree in order to evaluate the characteristics (synapomorphies) that define each clade.

In order to evaluate the supposition that the dental characters have evolved in a method concordant with Camin-Sokal parsimony, another set of analyses was conducted as just described, except that all characters were subjected to Wagner (strict) parsimony. All analyses were done using PHYLIP version 3.1 (Felsenstein, 1988).

ACKNOWLEDGMENTS

Dr. J. Knox Jones, Jr. made a substantial contribution to this paper by independently examining a number of specimens and by providing a large portion of the introductory and descriptive text. In fairness to Knox, it should be noted that he does not agree with the primary conclusions of this paper.

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RESULTS

The overall consensus of the three analyses using Camin-Sokal parsimony on the dental characters (fig. 1) indicates that the short-faced bats compose a monophyletic group, and that the genus *Dermanura* (exclusive of *concolor* and *hartii*) also is monophyletic. The species *concolor* is shown as a sister of the short-faced bats, with *D. hartii* a sister of the *concolor* and short-faced group. Two of the three consensus trees (from the separate Camin-Sokal analyses, using different outgroups) show *concolor* as sister of the short-faced clade, and the third (with *Sturnira* as the outgroup) shows *concolor* as a member of that clade. Two of these three consensus trees show *hartii* to be the next sister taxon, whereas one (again with *Sturnira* as the outgroup) shows *Dermanura* (exclusive of *concolor* and *hartii*) as the next sister group, with *hartii* the sister of all other taxa in the study.

The overall consensus of the all-Wagner analyses is concordant with the Camin-Sokal analyses in showing *concolor* as sister of the short-faced clade (fig. 2). This tree differs from figure 1 in the placement of *hartii* (here placed among the short-faced bats) and in some relationships within the two larger groups. In each of the three consensus trees from the Wagner analyses, *concolor* is the sister taxon of the short-faced group.

DISCUSSION

The two overall consensus trees from the two parsimony algorithms are concordant with respect to a number of clades (figs. 1, 2). Both show *Dermanura* (exclusive of *concolor* and *hartii*) to be monophyletic. Both also show the short-faced bats as monophyletic (except that *hartii* is included in this clade in the Wagner results). It appears that the effect of imposing Camin-Sokal or Wagner parsimony on the dental characters is seen primarily with respect to the placement of *hartii* and some arrangements within *Dermanura*. In either case, the monophyly of *Dermanura* (sensu stricto) and the placement of *concolor* and *hartii* outside of that clade seem to be stable components of the analytic results.

In none of the most-parsimonious trees, using any of the three outgroups, for either type of analysis (Camin-Sokal or Wagner parsimony) was *concolor* shown to be a member of, or the immediate sister of, the other species of *Dermanura*. Based on these analyses of external, cranial, and dental characters, as well as the studies of Koop and Baker (1983) of isozymes and Tandler et al. (1986) of submandibular secretory granules, I conclude that *concolor* is not a natural member of the *Dermanura* group, and should no longer be recognized as congeneric with species therein, nor is it a member of any other genus-level group among the bats considered in this study and by Owen (1987). As no generic name is available for this species, I am pleased to propose the name below.

Koopmania, new genus

TYPE SPECIES: *Koopmania concolor* (Peters, 1865). The genus as currently conceived comprises only the type species, which is monotypic (Jones and Carter, 1976).

ETYMOLOGY: This taxon is named in honor of Dr. Karl F. Koopman, a man and scientist for whom I have the utmost admiration and respect. Karl's contributions to Neotropical bat systematics have been profound, and it is my privilege to count him as a friend and colleague.

GEOGRAPHIC DISTRIBUTION: Northern South America in the Guianas, southern Venezuela, southeastern Colombia, Amazonian Peru, and northern Brazil (Koopman, 1982).

DIAGNOSIS: Size medium, intermediate between species assigned to *Artibeus* and those assigned to *Dermanura* by Owen (1987); forearm, 43–52 mm (Handley, 1987); plagiopatagium attaching to metatarsal–phalangeal joint; females averaging larger than males (Eisenberg, 1989); facial stripes indistinct; molars 3/3, with m3 much smaller than in *hartii*; M1 with strongly developed hypocone; lower incisors forming a solid arcade; braincase highly vaulted, highest just anterior to midpoint; rostrum broad and short (shorter than in *Dermanura* species except *D. gnoma* [Handley, 1987]), with rostral shield well developed; rostrum distinctly dished in lateral view; mesopterygoid fossa broadly U-shaped; paraoccipital processes absent or indistinct; postpalatal shelf shorter than in *Dermanura*.

COMMENTS: Assuming figure 1 to be the working hypothesis of phylogenetic relationships among the species considered, I mapped character state changes onto this tree, again treating dental characters as Camin-Sokal parsimonious. The *Dermanura* clade is characterized by six character state changes (see Appendix). Absence of characters 3 and 4

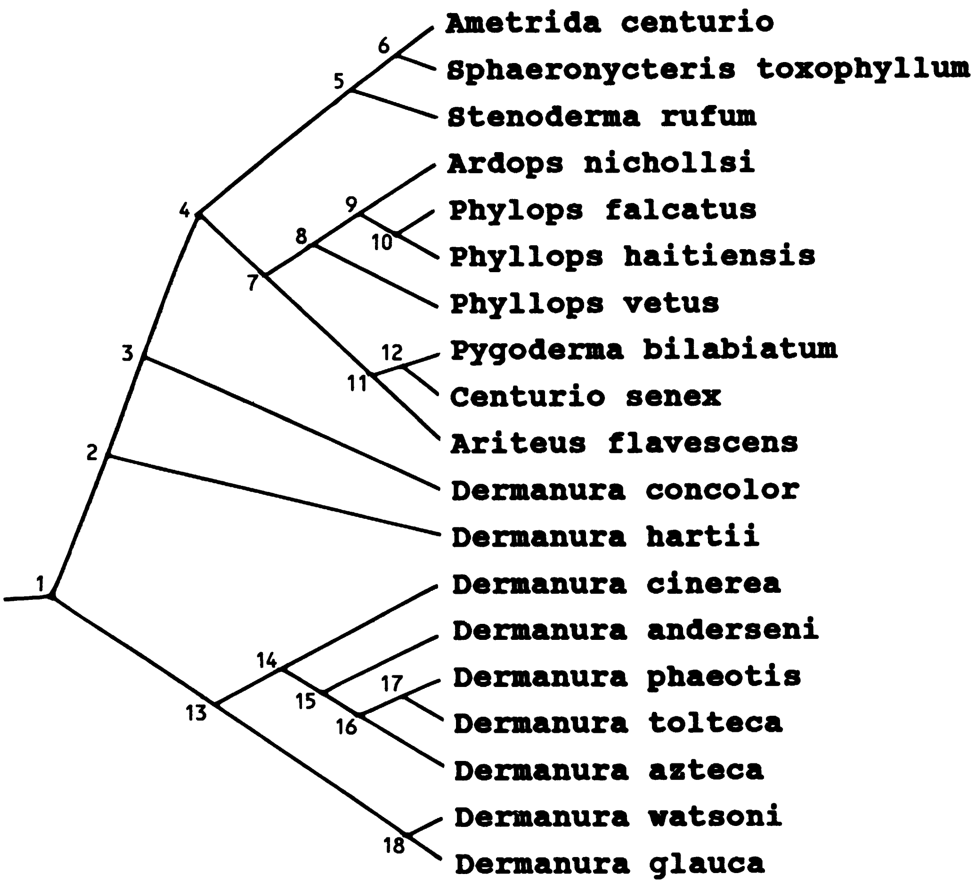

Fig. 1. Proposed phylogeny of species examined in this study. This consensus tree is derived from three analyses using Camin-Sokal parsimony on the dental characters and Wagner parsimony on the other characters. Estimated character state changes (with character state in parentheses for each character) for each node and species are: **1:** 30(1); **2:** 3(0), 4(1), 31(1); **3:** 7(0), 8(0), 28(1), 33(1); **4:** 9(1), 22(1); **5:** 17(1), 39(1); **6:** 5(1), 23(1), 32(1), 38(0); **7:** 5(1), 38(1); **8:** 2(1), 12(1), 26(1); **9:** 32(1); **10:** 35(1), 37(1); **11:** 32(1), 34(1), 43(1); **12:** 12(0), 45(1), 46(1); **13:** 4(0), 5(0), 33(1), 34(1), 43(1), 45(1); **14:** 28(1), 46(1); **15:** none; **16:** 2(1), 31(1); **17:** 3(1), 26(1), 35(1); **18:** 3(1), 28(0), 31(1), 44(1); *Ametrida centurio:* 22(0), 40(0), 41(0); *Sphaeronycteris toxophyllum:* 2(1), 6(1), 18(1), 40(1), 41(1), 45(1); *Stenoderma rufum:* 3(1), 4(0), 5(0), 24(0), 26(1), 37(1), 38(1), 40(1), 41(1), 42(1); *Ardops nichollsi:* 5(0), 36(1); *Phyllops falcatus:* none; *P. haitiensis:* 6(1), 17(1), 18(1), 19(1), 23(1), 29(1); *P. vetus:* 28(0); *Pygoderma bilabiatum:* 2(1), 11(0), 22(0), 24(1), 26(1), 36(1), 38(0), 40(1); *Centurio senex:* 1(1), 6(1), 10(1), 17(1), 18(1), 19(1), 23(1), 24(0); *Ariteus flavescens:* 12(1), 24(0), 44(1); *Dermanura concolor:* 5(0), 16(1), 25(1), 32(1), 37(1); *D. hartii:* 5(1), 12(1), 23(1), 26(1), 28(0), 39(1); *D. cinerea:* 3(0), 26(1); *D. anderseni:* 3(1), 23(1), 29(1), 39(1); *D. phaeotis:* none; *D. tolteca:* 23(1), 37(1); *D. azteca:* 3(0), 12(1); *D. watsoni:* 2(1), 37(1); *D. glauca:* 23(1), 24(0). Characters are listed and described in Appendix.

indicates a lengthening of the nose leaf (convergent in *Stenoderma, Ardops,* and *Koopmania*). Presence of character 33 reflects a reduction of M3 (convergent for the clade containing *concolor* and the short-faced bats); 34 a loss of M3 (convergent with *Ariteus, Pygoderma,* and *Centurio*); 43 the loss of a premolar; and 45 the reduction of m3 (convergent in *Sphaeronycteris, Pygoderma,* and *Centurio*).

The clade of *Dermanura hartii, Koopmania,* and the short-faced bats is characterized by a long nose leaf (characters 3 and 4; however, these characters map ambiguously in

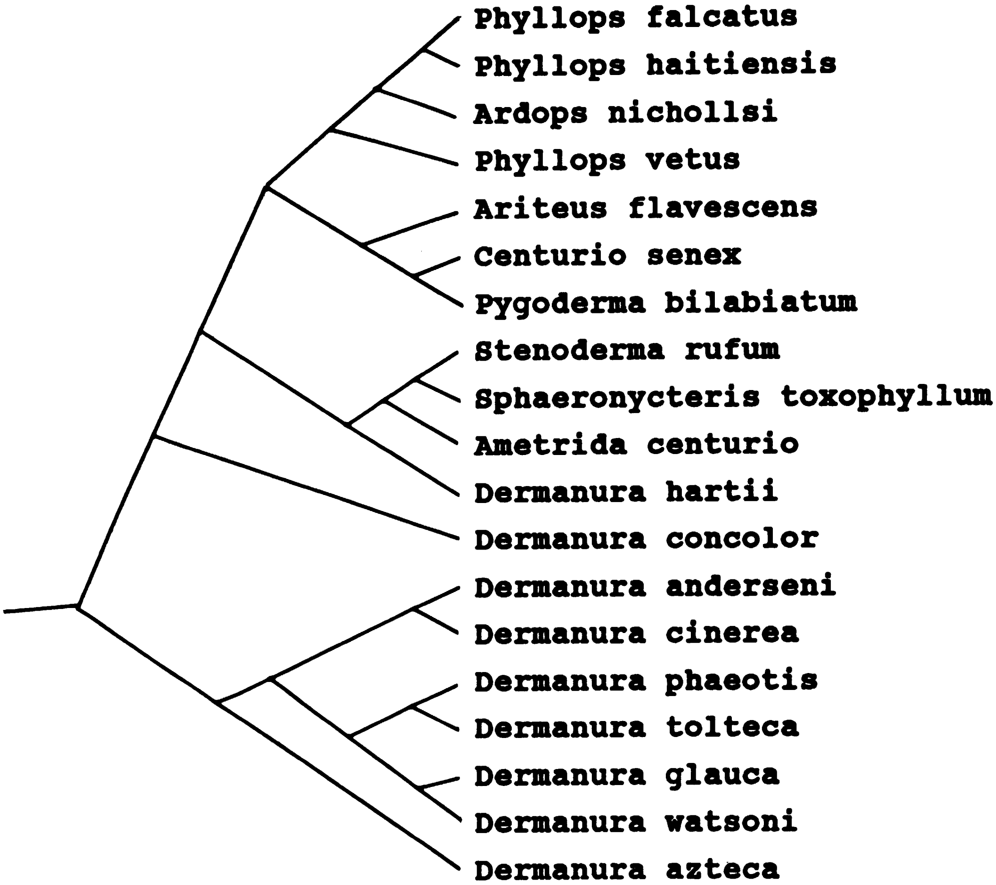

Fig. 2. Consensus tree derived from three analyses using Wagner parsimony on all characters.

several parts of the tree, and likely are not particularly informative) and a moderate development of the M1 hypocone (convergent with a majority of the *Dermanura* species). The clade containing *Koopmania* and the short-faced bats is defined by three-banded dorsal hair (character 7), loss of facial stripes (character 8), moderate basisphenoid pits (character 28, reversed in *Phyllops vetus* and convergent in most *Dermanura*), and reduction of M3 (33, noted earlier as convergent with the *Dermanura* clade).

Koopmania is characterized by loss of character 5 (i.e., increase in nose leaf length), attachment of the plagiopatagium to the metatarsal–phalangeal joint (16), loss of paraoccipital process (25), strong development of M1 hypocone (32), and loss of secondary foramen of the occipital condyle (37). The plagiopatagial and paraoccipital process conditions serve as synapomorphies that distinguish *Koopmania* from all other taxa within this evaluation. The others are convergent with various taxa on the tree (fig. 1).

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APPENDIX

The characters listed below were analyzed in this study. The 46 characters were derived by additive binary coding from the 22 multistate characters listed by Owen (1987: table 1 and appendix II). Two characters (1 and 10) are autapomorphic for *Centurio* and were not informative in these analyses.

1. Anterioproximal lobe on pinnae.
2. Lateral emargination of pinnae extending three-fourths of the ear length (versus one-half).
3. Nose leaf quite long (> 1½ times width).
4. Nose leaf shorter than in 3 (> width).
5. Nose leaf shorter than in 4 (length = width).
6. Nose leaf shorter than in 5 (length < width).
7. Two discrete bands on dorsal hair (versus three).
8. Facial stripes.
9. White shoulder patch.
10. Ribbed pattern on patagium mediad to fourth digit.
11. Uropatagium shorter than one-half the sacrum-to-calcar distance.
12. Uropatagia connected only adjacent to sacrum.
13. Uropatagia not connected.
14. Plagiopatagium attaches distally to tarsus.
15. Plagiopatagium attaches distally to metatarsus.
16. Plagiopatagium attaches distally to metatarsal–phalangeal joint.
17. Incisive foramen medium.
18. Incisive foramen small, anteriorly located.
19. Incisive foramen minute or absent.
20. Nasal septal foramen absent.
21. Hard palate extends no farther posterior to orbital anterior than palatal width.
22. Hard palate does not extend posterior to orbital anterior.
23. Hard palate posterior border squared (versus V-shaped).
24. Two parapterygoid foramina present (versus one).

25. Paraoccipital process absent (versus small).
26. Paraoccipital process enlarged (versus small).
27. Basisphenoid pits deep (versus exceptionally deep).
28. Basisphenoid pits moderately deep.
29. Basisphenoid pits shallow.
30. M1 hypocone a slight protuberance (versus absent).
31. M1 hypocone moderately developed.
32. M1 hypocone strongly developed.
33. M3 reduced (versus fully developed).
34. M3 absent.
35. Hypoglossal foramen absent (versus small).
36. Hypoglossal foramen medium (versus small).
37. Secondary foramen of occipital condyle absent.
38. Postglenoid foramen present.
39. External nares extend caudad so that bony palate clearly visible from dorsal view.
40. Rostrum flat or slightly troughed (versus dorsally convex).
41. Rostrum moderately troughed.
42. Rostrum strongly troughed.
43. Loss of lower premolar (from three to two).
44. Loss of lower incisor (from two to one).
45. m3 reduced (versus fully developed).
46. m3 absent.