DATE DUE	DATE DUE	DATE DUE
OCT 24 2012 10251		

A SYSTEMATIC AND BIOGEOGRAPHIC STUDY OF THE BAT GENUS *RHINOLOPHUS* (CHIROPTERA: RHINOLOPHIDAE)

By

Yining Luo

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1995

ABSTRACT

A SYSTEMATIC AND BIOGEOGRAPHIC STUDY OF THE BAT GENUS *RHINOLOPHUS* (CHIROPTERA: RHINOLOPHIDAE)

By

Yining Luo

The phylogenetic relationships among the Old World horseshoe bats, genus *Rhinolophus*, are studied using morphometric and cladistic analyses. Twenty-seven skull features and 15 skin features were measured from 1120 skull and 668 skin specimens, representing 60 rhinolophid species. Principal components of both correlation matrix and covariance matrix of the data were analyzed using multivariate procedures. The pattern of species along principal components does not indicate the traditional views on the species groups, but displays a separation of species of Africa and west Eurasia from those of southeast Asia. Within species of southeast Asia, similarities exist among the members of the traditional *arcuatus*, *philippinensis*, and *pusillus* groups.

the information contents and transformation series of 26 morphological characters of *Rhinolophus* were examined for cladistic analyses by Wagner parsimony using PAUP 3.1.1. The most parsimonious cladograms strongly suggest four monophyletic groups: the traditional *philippinensis* group, the traditional *philippinensis* group plus *arcuatus* group, all rhinolophids of southeast Asia, and three African members of the traditional *fumigatus* group. A monophyletic group consisting of southeast Asian members of the traditional

pusillus group is weakly suggested. Based on these monophyletic groups, a subgeneric taxonomy of *Rhinolophus* is proposed.

A cladistic biogeographic study of *Rhinolophus* in southeast Asia suggests a progressive subdivision of the areas with distance from the continental Asia. The Australian realm, as defined by Huxley's line and Webber's line of faunal balance, represents a monophyletic area group, whereas the Oriental realm represents a paraphyletic area group. Both the phylogeny and the historical distribution of *Rhinolophus* indicate an African origin of the genus.

ACKNOWLEDGMENTS

I thank the following persons and institutions for providing the specimens used in this study: K. Koopman and American Museum of Natural History, D. A. Schlitter and Carnegie Museum of Natural History, B. Patterson and Field Museum of Natural History, M. Rutzmoser and Museum of Comparative Zoology, L. Gorden and National Museum of Natural History. I thank J. Smith and J. Jankins for their help in laboratory work. Particular thanks go to my major advisor, D. O. Straney. Without his enormous help, this work would not be completed as is. I would like to thank the members of my Committee, R. Snider, J. A. Holman, D. Hall, and G. Bush for their help and encouragement.

CONTENTS

LIST OF TABLES

Sumatra; Bone = Borneo; Java = Java; SulT = Sulawesi and Timor; Mulk = the Maluku Islands; Phil = the Philippine Islands; NewG = New Guinea; Aust = Australia

Table 5.2. Data matrix for rhinolophid distributions in the 11 areas of southeast Asia. Characters 1-24 are based on the distributional data of individual species (listed in Table 5.1). Characters 25-36, listed below, are based on components of relationships from the majority consensus cladograms of all four cladistic analyses. All components that are common to at least two analyses and are not in conflict with other cladograms were selected.

LIST OF FIGURES

Figure 3.2. The display of traditional *ferrumequinum* species group in PC2 and PC3, from the correlation matrix of the pooled skin and skull data. There is extensive overlap between species of this group and other groups. Species group abbreviations: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.3. The display of the traditional *pusillus* species group and *arcuatus* species group in PC2 and PC3 from the correlation matrix of the pooled skin and skull data. There is extensive overlap between species of the *pusillus* group and other groups, but only one species of the *fumigatus* group is inside the *arcuatus* group. Species group abbreviations: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.4. The display of traditional *fumigatus* (= *macrotis*) group and *philippinensis* (= *luctus*) group in PC2 and PC3 from the correlation matrix of the pooled skin and skull data. Extensive overlap exists between species of the *fumigatus* group and other groups. Species group abbreviations: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.5. Figure displays species on the PC2 and PC3 from the correlation matrix of pooled skin and skull data. There is a non-overlapping separation of species clusters associated with their geographic origins: one species cluster from Africa and west Eurasia, and the other from southeast Asia. Species are symbolized in their distribution 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

Figure 3.6. Figure displays species on the PC2 and PC3 from the covariance matrix of pooled skin and skull data. Species of Africa and west Eurasian form a distinct cluster. Species are symbolized in their distribution 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

Figure 3.7. Figure displays species on the PC2 and PC3 from the correlation matrix of pooled skin and skull data. The traditional species groups are more distinct when only those from southeast Asia region is considered. Species are symbolized in their taxonomoc group: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.8. Figure displays species on PC2 and PC3 from the correlation matrix of skull data. Species of Africa and west Eurasia are separated from the species of southeast Asia. . Species are symbolized in their taxonomoc group: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.9. Figure displays species on PC2 and PC3 from the covariance matrix of skull data. Species of Africa and west Eurasia are separated from the species of southeast Asia.

Two arrows indicate two misplaced species. Species are symbolized in their distribution: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

Figure 3.10. Figure displays species on the PC2 and PC3 from the correlation matrix of skull data. Among the southeast Asian species, only members of the traditional *arcuatus* group are close to each other. . Species are symbolized in their taxonomoc groups: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.11. Figure displays the first and second canonical variables (CAN1 and CAN2) for the southeast Asian species. Traditional species groups are used as *a priori* class. Species are symbolized in their group identity: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.12. Figure displays the first and second canonical variables (CAN1 and CAN2) for the southeast Asian species, Andersen's *macrotis* group being merged with *philippinensis* group. Traditional species groups are identified as *a priori* class. Species are symbolized in their group identity: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.13. Figure displays the first, second and fifth canonical variables (CAN1, CAN2 and CAN5) for all species of *Rhinolophus*. Traditional species groups are used as *a priori* classes for southeast Asian species only, and all African and west Eurasian species are assigned to a new class labeled 'W'. Southeast Asian species are symbolized in their group identity: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.14. Figure displays of the third and fourth canonical variables (CAN3 and CAN4) for all species of *Rhinolophus*. Traditional species groups are used as *a priori* class. Species are symbolized in their group identity: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 3.15. Figure displays the first, third and fourth canonical variables (CAN1, CAN3 and CAN4) for all rhinolophids. The *ferrumequinum* group and *fumigatus* group are separated on CAN1 axis. Traditional species groups are used as *a priori* classes. Species are symbolized in their group identity: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Figure 4.1: The shape of the connecting process of the noseleaf (character 1) in lateral view, pointed by arrow. (a) state *a*, height moderate and round (*R. affinis*); (b) state *b*, higher and shaper (*R. macrotis*); (c) state *c*, very low (*R. luctus*); (d) state *d*, horn-shaped (*R. pusillus*); (e) state *e*, anterior base reaches the tip of the sella (*R. pearsoni*).

Figure 4.2. The shape of the sella (character 2), pointed by arrow '↑'. (a) state *a*, narrow (*R. alcyone*); (b) state *b*, broader (*R. funigatus*); (c) state *c*, with lappet, pointed by arrow '↑' (*R. maclaudi*). (From Rosevear, 1965).

Figure 4.3. Illistrations of the horseshoe (character 3). (a) state *a*, narrower (*R. clivosus*); (b) state *b*, broader (*R. fumigatus*). (From Rosevear, 1965).

Figure 4.4. Illustrations of the supplementary noseleaf (character 4). (a) state *a*, not present (*R. luctus*); (b) state *b*, less developed (*R. pusillus*); (c) state *c*, both sides meet at the mid-line (*R. simulator*). The dotted line indicates the horseshoe which usually covers most part of the supplementary noseleaf.

Figure 4.5. Number of the lower lip grooves (character 5), pointed by arrow. (a). state *a*, one groove; (b). state *b*, three grooves.

Figure 4.6. Illustrations of the front ear projection (character 6). (a) state *a*, not present; (b) state *b*, present.

Figure 4.7. The shape of the lancet (character 7). (a) state *a*, hastate; (b) state *b*, nearly triangle. Long hair, shown in B, are frequently present in the lancet. (from Rosevear, 1965).

Figure 4.8. The insertion of the plagiopatatgium (character 10). (a) state *a*, at the ankle (*R. megaphillus*); (b) state *b*, above the ankle (*R. rufus*); (c). state *c*, near the tarsal-metatarsal joint (*R. luctus*). (After Rosevear, 1965).

Figure 4.9. The status of P^2 (character 11), pointed by arrow. (a) state *a*, in the toothrow (*R. ions*) ; (b) state *b*, out of toothrow (*R. ferrumequinum);* (c) state *c*, absent (*R. fumigates*).

Figure 4.10. The shape of P_2 (character 12), pointed by arrow. (a) state *a*, the length and breadth bout equal (*R. mehelyi*); (b) state *b*, length greater than breadth (*R. clivosus*); (c) state *c*, length less than breadth (*R. ions*).

Figure 4.11. The status of P_3 (character 13), pointed by arrow. (a) state *a*, in the toothrow (*R. macrotis*); (b) state *b*, out of toothrow (*R. malayanus*); (c) state *c*, absent (*R. fumigates*).

Figure 4.12. The shapes of the stylarshelf in M^3 (character 15). (a) state *a* (*R. affinis*); (b) state *b*, the posterior v-shaped ridges (pointed by arrow) greatly reduced (*R. fumigatus*).

Figure 4.13. Picture (*R. affinis*) illustrates character 13, the position of the posterior margin of the palate pointed by an arrow. Label 0 through 3 correspond to the states *a* through *d* in the text.

Figure 4.14. The position of the anterior margin of the palate (character 17), pointed by arrow, of *R. affinis*. Label 0 through 2 correspond to the states *a* through *c* in the text.

Figure 4.15. The position of the front margin of anterior nasal swelling (character 18), pointed by arrow, of *R. affinis*. Label 0 through 2 correspond to the states *a* though *c* in the text.

Figure 4.16. Pictures illustrate character 19, the length of median frontal nasal swellings. (a) state *a*, small (*R. affinis*); (b) state *b*, larger (*R. luctus*).

Figure 4.17. The depth of the orbital constriction (charcter 20), pionted by arror. (a). state *a*, shallow (*R. lepidus*); (b). state *b*, deep (*R. creaghi*).

Figure 4.18. The shapes of the infraorbital canal and bar (character 21), pointed by arrows. (a) state *a*, size moderate (*R. affinis*); (b) state *b*, infraorbital bar elongated (*R. clivosus*); (c) state *c*, canal lengthened and bar broader (*R. luctus*).

Figure 4.19: The strict consensus cladogram for the 24 most parsimonious cladograms resulting from the weighted analysis, character 1 ordered. . The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

Figure 4.20: The majority consensus cladogram for the 1200 most parsimonious cladograms resulting from the weighted analysis, character 1 ordered. The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia. The numbers indicate the percentage of cladograms in which this particular branching structure is present.

Figure 4.21: The strict consensus cladogram for the 1300 most parsimonious cladograms resulting from the weighted analysis, character 1 unordered. . The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

Figure 4.22: The majority consensus cladogram for the 1200 most parsimonious cladograms resulting from the weighted analysis, character 1 unordered. The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia. The numbers indicate the percentage of cladograms in which this particular braching stucture is present.

Figure 4.23: The strict consensus cladogram for the 1300 most parsimonious cladograms resulting from the unweighted analysis, character 1 unordered. . The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

INTRODUCTION

Bats of the genus *Rhinolophus*, the horseshoe bats, constitute the only living genus of the family Rhinolophidae (Mammalia: Chiroptera). This genus contains about 60 species distributed throughout the Old World tropical and warm temperate areas, including Africa, the southern Eurasian continent, the islands of southeast Asia, New Guinea and northern Australia (Corbet and Hill, 1981 and 1992; Honacki et al, 1982; Koopman, 1992)(Figure 1.1). While some species, such as *R. ferrumequinum* and *R. clivosus* have transcontinental distribution, many species, especially those in southeast Asia, are known only from very limited areas.

The Rhinolophidae is one of the oldest living bat families. *R. priscus* is the earliest representative of the family, known from the Upper Eocene in France where it co-occurs with bats of the families Hipposideridae, Vespertilionidae and Emballonuridae (Savage and Russell, 1983). Fewer than 20 species of fossil *Rhinolophus* have been described and their distribution in time and space is spotty. The oldest rhinolophid fossil from Australia dates from the Middle Miocene while the oldest fossil from Asia, the likely source of Australian species, is known only from the Pliocene (Koopman and Jones, 1970; Hall, 1989). Due to their habitats of roosting in caves and hollow trees and foraging away from more common deposit sites such as streams and lakes, bats are much less likely to be preserved as fossils than most other mammals (Dawson and Krishtalda, 1984). Bats are the only mammalian order in which fewer fossil species than living species are described. Our understanding of rhinolophid fossil history is consequently very incomplete.

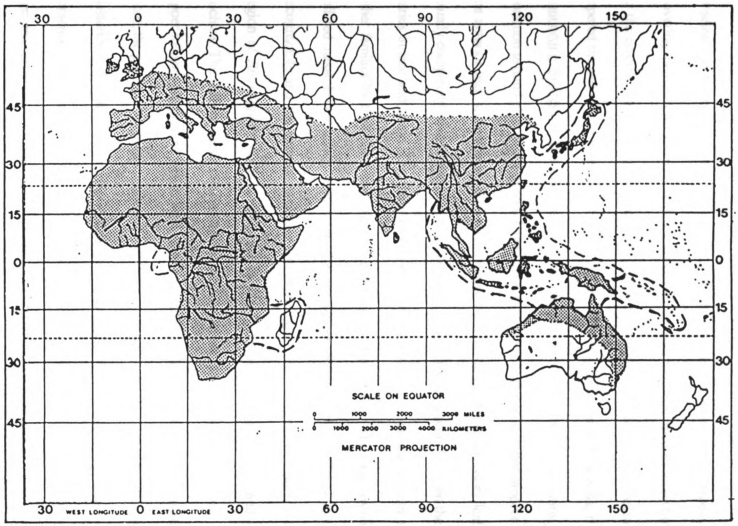


Figure 1.1: The world distribution of the bat family Rhinolophidae (shaded area). (From Koopman, 1984.)

It is generally agreed that the genus *Rhinolophus* is a monophyletic group. Members of the genus share a unique external feature, the horseshoe-shaped noseleaf (Figure 1.2). The noseleaf has three main parts. The anterior leaf, or horseshoe, is a horseshoe-shaped noseleaf covering the upper lip and surrounding the nostrils; the sella is a thick median projection dorsal to the nostrils; and the lancet, or posterior leaf, is the dorsal-most part of the noseleaf with a tapered tip and two or three paired lateral ridges. Between the lancet and the sella, there is a connecting process in the mid-sagittal plane. Individual species display variations on this common ground plan. Some species have lateral extensions of the sella, called lappets. Behind the anterior leaf, some species have an additional piece of noseleaf, the accessory leaf, that is usually completely covered by the anterior noseleaf. The internarial septum between the nostrils varies in size and shape. The skulls of *Rhinolophus* are readily distinguishable from skulls of other families by their nasal swellings and basal region (Figure 1.3). The nasal swellings are inflated nasal bones giving support to the noseleaves. Four or six swellings are usually recognizable and the anterior swellings are often higher than the posterior ones. The basal region of *Rhinolophus* skulls is distinctive in the presence of a pair of large and exposed cochlea. The auditory bulla attaches to the anterior-lateral side of the cochlea. Two pairs of upper incisors are present, but as both nasal and maxillary bones are deeply invaginated in the front, the premaxillary bones connect the maxillary only with a narrow bend of cartilage at their posterior end. Other features that define the genus include the absence of the tragus and the presence of large antitragus on the ears, absence of the postorbital process, and absence of the first phalanx in the second finger.

Students of bat phylogeny agree that hipposiderids, the Old World leaf-nosed bats, are the closest living relatives of rhinolophids (Van Valen, 1979; Koopman, 1984). The

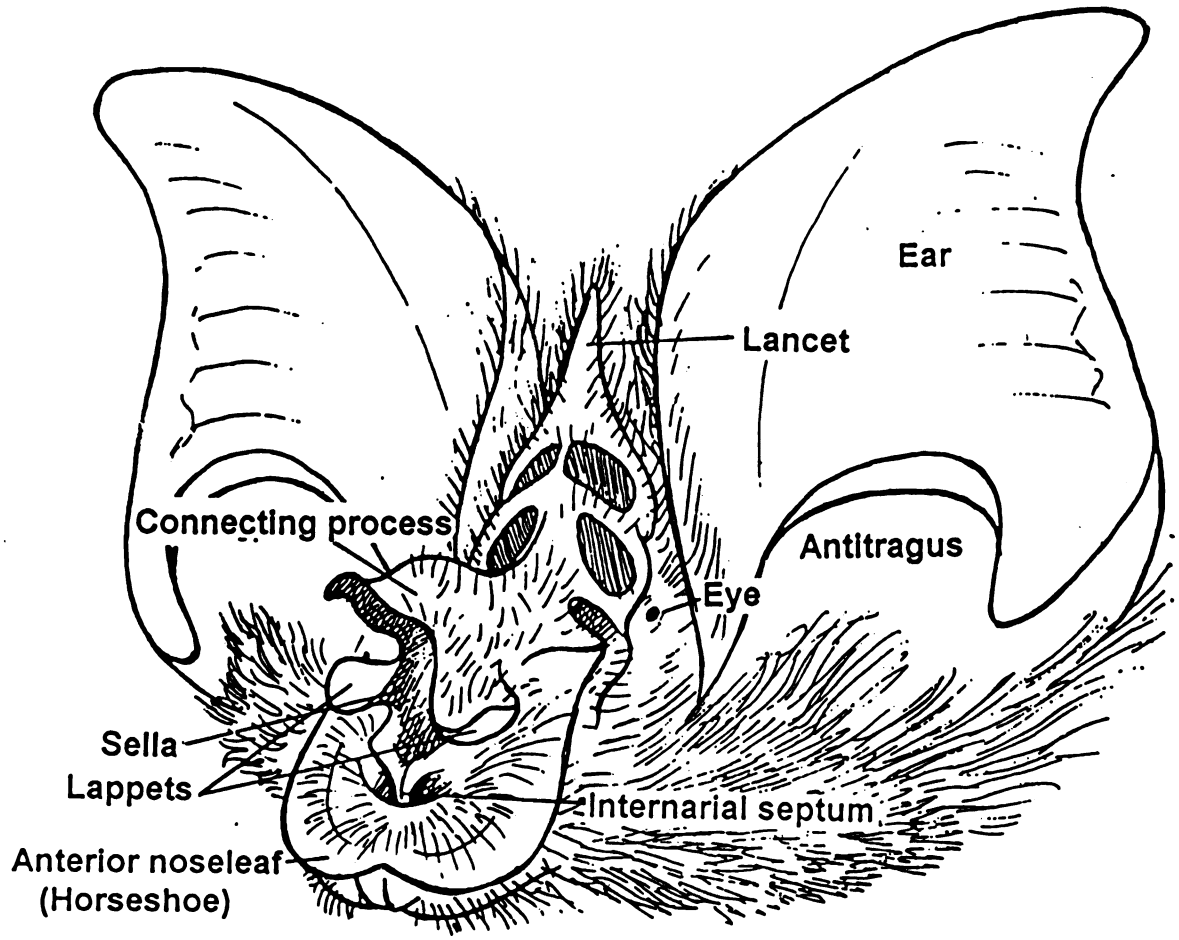


Figure 1.2: The features of the rhinolophid head, with emphasis on the noseleaves. (After Lekagul and McNeely, 1977).

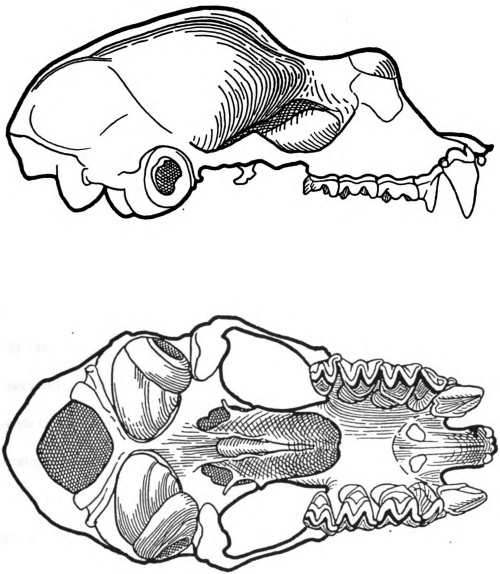


Figure 1.3: The morphology of the rhinolophid skull (From Rosevear, 1965).

family Hipposideridae contains about 60 species of nine genera; all have complex leaflike outgrowths of skin on their muzzle. The noseleaves of the hipposiderids include an anterior leaf, sometimes one or more accessory leaflets, and an erect transverse leaf. Although the noseleaves of the two families are very different in shape, some researchers have homologized the anterior leaf and erect transverse leaf of hipposiderids to the horseshoe and the lancet of rhinolophids. Hipposiderids lack a sella. The hipposiderids differ from the rhinolophids also in having two, instead of three, phalanges in each toes, in lacking P_3 and in details of the structures of the shoulder and girdles.

There are disagreements about the taxonomic relationship of hipposiderids and rhinolophids. Some authors believe that Hipposideridae should be classified as a subfamily of Rhinolophidae (Corbel, 1978; Ellerman and Morrison-Scott, 1966; Koopman, 1970, 1984 and 1992); other workers maintain that the two are distinct families (Miller, 1907, Walker, 1964; Corbet and Hill, 1981 and 1992; Hayman and Hill, 1971). The debate is purely taxonomic and depends on each author's family concept. Nomenclatorical controversy should not obscure a general agreement that hipposiderids are the sister group of rhinolophids.

Since Rhinolophidae is a monotypic family, I will refer to rhinolophids as a genus when I discuss intrageneric phylogeny and as a family when I compare them with bats of other families.

Previous studies on the systematics of rhinolophids

Among the earliest systematic studies of the genus, Andersen's work (1905a, 1905b, 1905c, 1905d, 1905e, 1918) was the most important and has been the foundation for all

subsequent work. Based primarily on the shapes of nose-leaves, premolar dentition, nasal-swellings, palate bridge of the cranium and the size of cochlea, he assigned the species to six species groups: *simplex* group (renamed to *ferrumequinum* group by later researchers; indicated as '= *ferrumequinum* ' below), *lepidus* (= *pusillus*) group, *arcuatus* group, *macrotis* (= *fumigatus*) group, *hipposideros* group and *luctus* (= *philippinensis*) group (Figure 1.4). With the exception of the *arcuatus* group, which is found only in southeast Asia, Andersen's species groups contain species distributed in Asia, Europe and Africa. Andersen identified the similarities between several African and Asian species. He suggested that this resemblance evidenced a close relationship and, in some cases, parallel evolution between the corresponding species (Andersen, 1905a). Figure 1.5 displays Andersen's view of relationships among species of his *ferrumequinum* group. For this group, as in the others, he concluded that southeast Asian species almost always had more primitive features than species from Africa. He concluded that all the Ethiopian species of the genus are of Oriental origin.

In his studies, Andersen identified the following features in *Rhinolophus* as primitive conditions: connecting process low; mental grooves three; front nasal swellings low; sagittal crest low; palatal bridge not shortened; P^2 and P_3 in the tooth row; basisphenoid not narrowed; temporal fossa narrow; metacarpals about equal in length; ratio of 2nd to 1st phalanges of the third and the fourth fingers small. Unfortunately, Andersen did not indicate explicitly the relationships among his species groups (Andersen 1905a, 1905b, 1905d).

Tate and Archbold (1939) revised the rhinolophid species of the Indo-Australian region (Figure. 1.6). Although they used most of Andersen's characters for their group and subgroup identification and their phylogenetic analysis, Tate and Archbold had reservations about the

simplex (*ferrumequinum*) group
- *simplex*
- *megaphyllus*
- *keyensis*
- *borneensis*
- *celebensis*
- *malayanus*
- *virgo*
- *nereis*
- *stheno*
- *simulator*
- *denti*
- *rouxi*
- *thomasi*
- *capensis*
- *affinis*
- *clivosus*
- *darlingi*
- *ferrumequinum*
- *deckenii*

lepidus (*pusillus*) group
- *lepidus*
- *acuminatus*
- *pusillus*
- *cornutus*
- *gracilis*
- *subbadius*
- *monoceros*
- *blasii*
- *landeri*
- *euryale*
- *mehelyi*

midas (*hipposideros*) group
- *hipposideros*

philippinensis (*luctus*) group
- *philippinensis*
- *mitratus*
- *maclaudi*
- *sedulus*
- *trifoliatus*
- *luctus*

macrotis (*fumigatus*) group
- *macrotis*
- *hirsutus*
- *fumigatus*
- *eloquens*
- *hildebrandti*
- *pearsoni*

arcuatus group
- *arcuatus*
- *subrufus*
- *inops*
- *creaghi*
- *coelophyllus*
- *euryotis*

Incertae sedis
- *alcyone*

Figure 1.4. the list of species groups proposed by Andersen (1905b, 1918). The group names that are renamed by later researchers are indicated in the parenthesis.

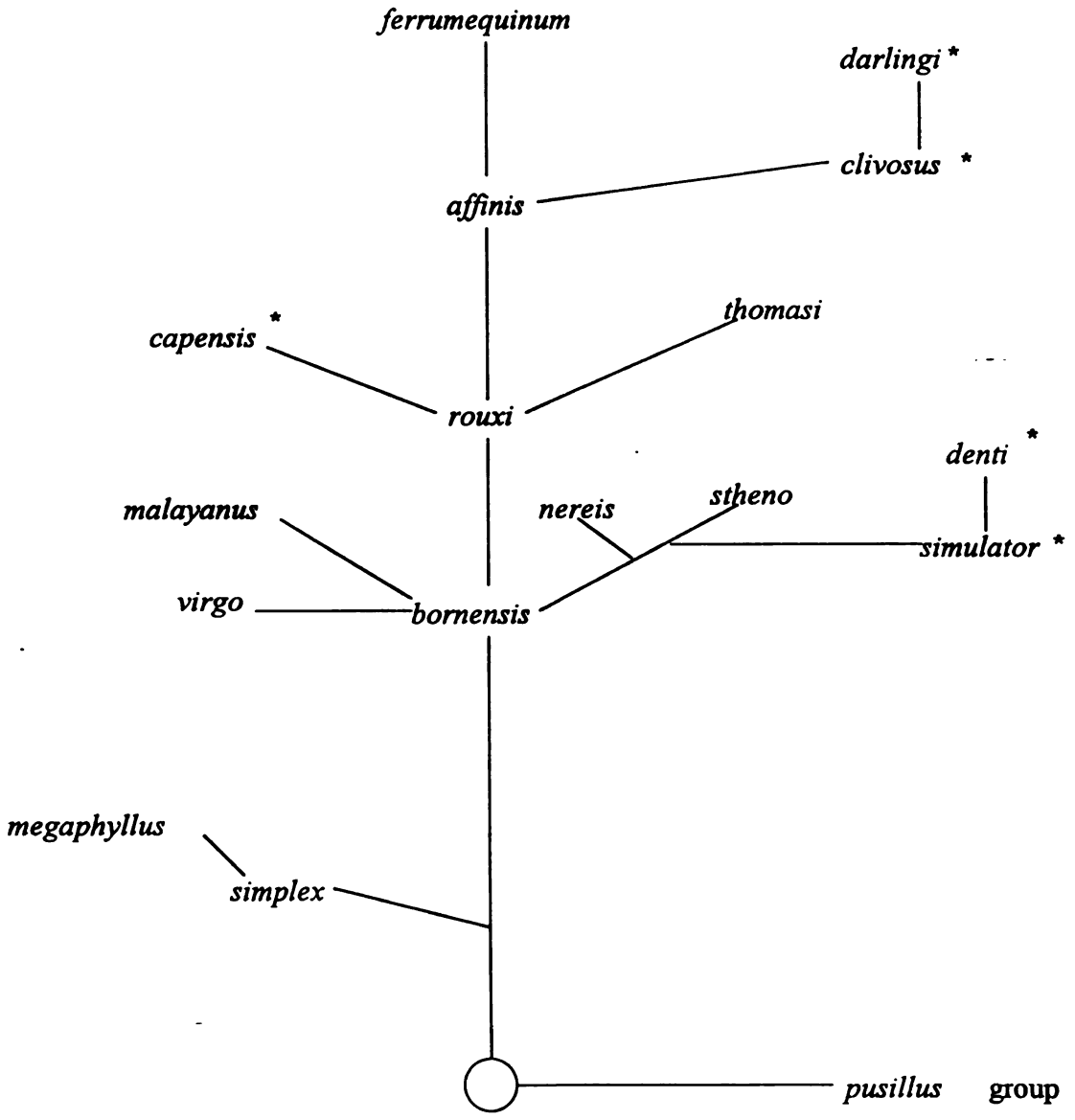


Figure 1.5. The relationships among the species of the *ferrumequinum* group proposed by Andersen. Species of Africa are indicated by '*'. (From Andersen 1905a, p120.)

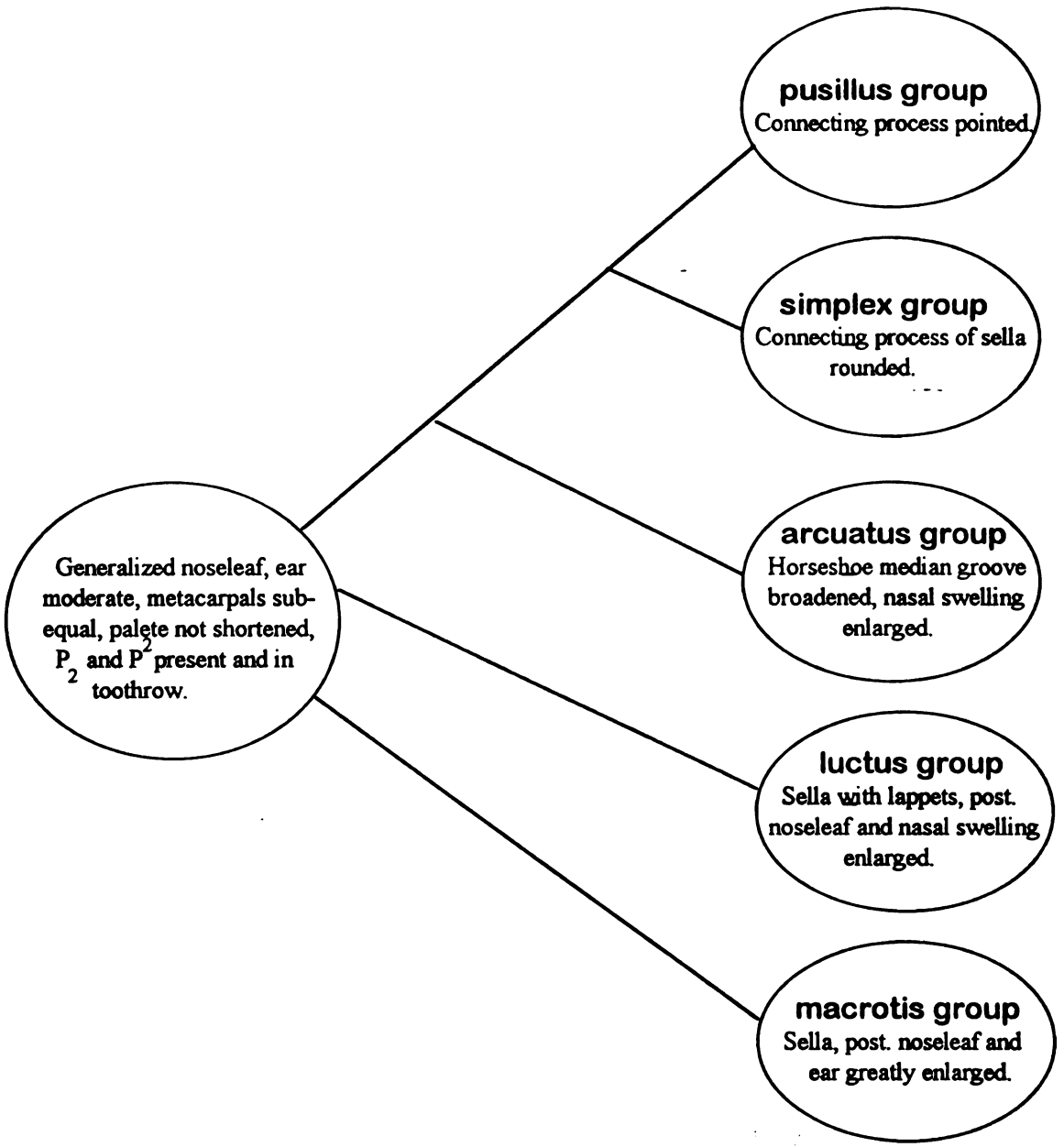


Figure 1.6. The phylogenetic hypothesis proposed by Tate and Archibold (1939). The *simplex* group and *luctus* group are presently referred to as the *ferrumequinum* group and *philippinensis* group respectively.

grounds for Andersen's *philippinensis* group and *macrotis* group. In addition, Tate and Archbold consider that the *arcuatus* group was closely related to the *ferrumequinum* and *pusillus* groups, because the *arcuatus* group seemed to be an early branch from the unspecialized forms of that complex. Among the characteristics Andersen utilized, Tate and Archbold considered that noseleaf structures, particularly the connecting process, were more reliable characters. They used this character as the primary basis of their subgeneric classification. Later, Tate (1943) merged the *macrotis* group with the *philippinensis* group.

In their two review publications of the mammal collections from Paleoarctic and Indian region and from south Africa in the British Museum of Natural History, Ellerman and Morrison-Scott (1953, 1966) merged the *arcuatus* and *philippinensis* groups, recognizing a total of four species groups in the genus. They did not explain the reason for this merger, only claiming that this revision was in agreement with Tate's conclusions. This is inaccurate; Tate and Archbold (1939) clearly indicated that the *philippinensis* group, which branched early in generic evolution, was demonstrated by the coexistence of some primitive features, such as very long palatal bridge, and some highly specialized features, such as the large noseleaf and lappets, in this group.

Working primarily on African bat faunas, Koopman revised Andersen's species groups of *Rhinolophus* in that region (1965, 1975, 1989). Although he retained all the traditional species groups, Koopman's studies contained detailed descriptions and discussions of the morphology and distribution of *Rhinolophus* in the region In his review on the biogeography of Rhinolophidae, Koopman (1970) concluded that either Africa or southern Asia could be its region of origin.

Table 1.1. The diagnostic features for the species groups of Rhinolophus used by Corbet and Hill. (From Corbet and Hill, 1992). Symbols '+', '-' and '+/-' indicate 'present', 'absent', and 'may be present' of the particular character state in the groups respectively.

Sp. grs / Traits	philippinensis gr.	arcuatus gr.	fumigatus gr.	pusillus gr.	ferrum-equinum gr.	hipposideros gr.
Ears very large	+	+	+	-	+/-	-
Antitragal lobe very large	+	+	+	-	-	-
Connecting process triangular	-	-	-	+	-	-
Sella	Large	Large	Moderate	Small	Small	Small
Internarial region expanded	+/-	-	-	-	-	-
Palate long, 1/3 or more length of maxillary toothrow	+	+	-	-	-	-
Cochleae very large	-	-	-	-	-	+
Basioccipital very narrow	-	-	-	-	-	+

Corbet and Hill (1992) revised the rhinolophids of the Indo-Malayan region. Interestingly, except for adding some recently described species and moving *R. macrotis* from Anderson's *macrotis* group to the *philippinensis* group, Corbel and Hill endorsed all the species groups initially proposed by Andersen (1905b). This is not surprising, since the characters used for identifying species groups by Corbel and Hill were virtually the same as used by Andersen (Table 1.1). Due to the morphological homogeneity of this genus and the relatively obvious nature of the traditional characters, it would be surprising if any new result would be considerably different without use of new characters or application of new methods.

The phenetic analysis by Bogdanowicz and Owen (1992) and Bogdanowicz (1992) are based on quantitative characters. Multivariate morphometrics and quantitative character analyses have been applied in the systematics and ecology of other bat families since the early 1970's (e.g. Findley, 1972; Freeman, 1981). In both papers, principal components were calculated from quantitative (continuous) measurements of the skull and wings. Since the first principal component is generally regarded as variation due to size differences between species, which is not very informative about phylogenetic relationship, it was removed from further analysis. Clusters were computed from the remaining principal components which are considered to represent the variation in shape.

Although there is much in common between the results by Bogdanowicz and Owen (1992) and by Bogdanowicz (1992), the latter is by far more interesting. In this second paper, Bogdanowicz noticed two major groups associated with two major geographical regions: one group associated with the Paleoarctic and Ethiopian regions and the other associated with the Australian and Oriental regions, although in his subgeneric classification of the genus into 11 species groups the major geographic groups are not presented (Figure 1.7 and 1.8).

Table 4.2. Summary of taxonomic conclusions based on the monophyletic groups in Figure 4.28. No paraphyletic groups is recognized in this taxonomy. Monophyletic groups of species are recognized at three different levels (supergroup, group, and subgroup). Those species that can not be placed into a monophyletic group are included as 'status uncertain' at the appropriate level.

GENUS *RHINOLOPHUS*

affinis subgenus

philippinensis supergroup

philippinensis group

R. luctus
R. trifoliatus
R. sedulus
R. macrotis
R. marshelli
R. rex
R. paradoxolophus
R. philippinensis

group status uncertain

R. arcuatus
R. canuti
R. creaghi
R. coelophyllus
R. euryotis
R. inops
R. rufus
R. subrufus
R. pearsoni
R. yunanensis

pusillus group

R. acuminatus
R. pusillus
R. cornutus
R. imaizumii
R. osgoodi
R. subbadius
R. lepidus
R. monoceros

group status uncertain
(southeast Asian species of the traditional *ferrumequinum* group)

R. affinis
R. nereis
R. simplex
R. stheno
R. selebensis
R. megaphyllus
R. malayanus
R. rouxi
R. borneensis
R. thomasi

subgenus status uncertain
(All African & west Eurasian species)

fumigatus group

R. eloquens
R. fumigatus
R. hildebrandti

group status uncertain

R. alcyone
R. denti
R. euryale
R. mehelyi
R. landeri
R. blassi
R. adami
R. clivosus
R. ferrumequinum
R. darlingi
R. capensis
R. swinnyi
R. simulator
R. hipposideros

subgenus status uncertain

R. maclaudi

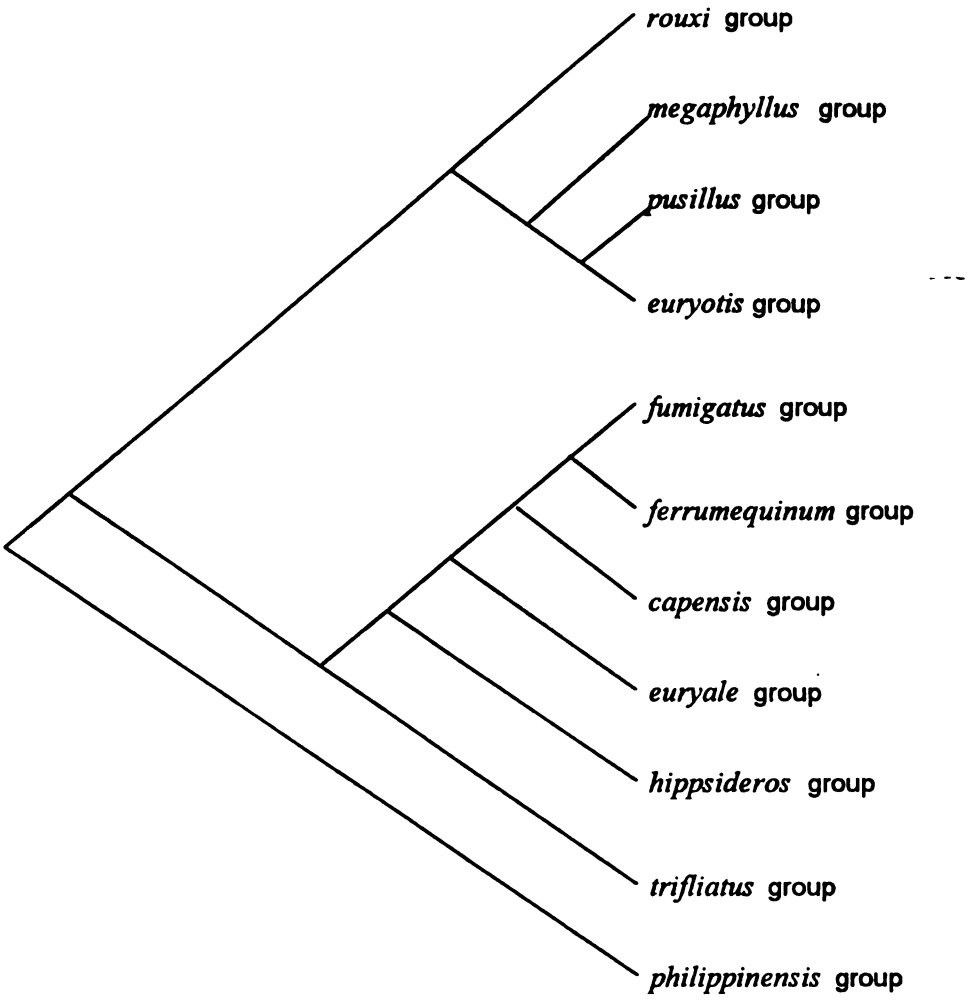


Figure 1.8. The relationships among the 11 species groups proposed by Bogdanowicz (1992). (After Bogdanowicz, 1992.)

Phenetic similarities may be indicative of the true phylogeny when characters are carefully selected and the assumptions associated to the clustering methods are met. I find three reasons to doubt that Bogdanowicz's studies are likely to reflect the phylogeny of the genus. First, his measurement set disregarded some potentially informative qualitative traits, such as noseleaf and dental morphology. The omission of such notable characters due to difficulties of measuring them may produce an incomplete picture of the overall morphological similarity and difference among species. Second, because all variables are transformed to principal components before being converted into similarity or dissimilarity indices in the study, it is very difficult to determine the specific morphological features that define or diagnose each cluster. This in turn makes any analysis of character transformation and the pattern of evolution impossible. Finally, the clustering algorithm Bogdanowicz used assumes that drift, rather than selection, is the cause of evolutionary change (Bogdanowicz and Owen, 1992). It is not evident that this assumption is an appropriate one for *Rhinolophus*. The clusters resulting from the distance analysis probably does not indicate the ancestor-descendent relationship, because the joining points of the phenogram only show the relative degrees of similarity between morphological groups. Bogdanowicz used a single species of hipposiderid (*Aselliscus trisuspisatus*) as an outgroup in his studies; the hipposiderids are a diverse family, and it is not clear this one species is an adequate outgroup.

Genetic studies in the relationships of *Rhinolophus* species are limited. Chromosomal and electrophoretic studies have been carried out on 21 species of *Rhinolophus* (Dulic and Mutere, 1974; Zima, 1982; Ando et al, 1983; Harada et al, 1982; Harada et al, 1985; Qumsiyeh et al, 1988). Although these studies provide useful information about the evolution of the genus, which I will use later in this study, they cover too few species and lack resolving

power to reconstruct the phylogeny of the genus on their own (Qumsiyeh et al, 1988). Clearly, more molecular and cytogenetic study of the genus is needed.

Study of the historical biogeography of *Rhinolophus* has advanced even less than the study of phylogeny since Andersen's early work (Andersen, 1905a and 1905b). Although regional biogeography of the genus has been discussed in a number of area faunal investigations (Hayman and Hill, 1971; Koopman, 1966, 1975 and 1989; Lekagul and Mcneely, 1977; Goodwin, 1979; DeBlase, 1980; Smithers, 1983; Heaney et al, 1987), biogeographic review over the entire distribution of genus had not been undertaken until Bogdanowicz and Owen (1992). Their biogeographic study focused only on the question of where *Rhinolophus* originated, and they supported Andersen's hypothesis that the Oriental region was the center of origin. No vacariance biogeographic study has been conducted on overall or regional distribution of the genus.

In the present study, the search for the phylogeny of *Rhinolophus* is taken in two steps. First, I have performed a morphometric analysis with carefully selected new measurements on skulls as well as the traditional ones in the skull and skin. Emphasis is placed on the nasal region and the basal region of the skull where considerable shape variation occurs. Principal component analysis and canonical discriminant analysis were conducted to find the pattern of clusters and discover the characters which are most responsible for the clusters. Second, traditional qualitative characters and new characters tested in the principal component analysis were selected and analyzed for their phylogenetic information content. After constructing transformation hypotheses for these characters, I performed cladistic analysis using Wagner parsimony to find the phylogenetic relationship among the species of the genus. A hypothesis

of Rhinolophid phylogeny is proposed, and the subgeneric classification of the genus is revised accordingly.

Based on phylogenetic analysis, I review the historical biogeography of the genus. Emphasis is placed on southeast Asian species where great biogeographic interest exists. Following early studies of this region, the southeast Asia region was divided into 11 areas and a cladogram of area relationships was computed using Rhinolophid distribution data. Finally, I suggest that Africa, rather than southeast Asia, might have been the center of origin of the genus.

MATERIALS AND METHODS

Morphological analysis

I recorded data from skins and skulls of specimens in the following museum collections: Field Museum of Natural History (FMNH), National Museum of Natural History (NMNH), American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CMNH), and Museum of Comparative Zoology (MCZ). The specimens used are listed in Appendix 1.

I measured skin dimensions of 608 specimens representing 60 species. Fifteen measurements were taken using digital calipers, except that ear, tail and foot lengths were copied from the specimen label recorded by the collector when they were present. Table 2.1 lists of the skin measurements and their abbreviations used in the morphometric analysis. Only the right side, if available, of the body was measured to the accuracy of one tenth of a millimeter.

The skulls of 1,112 specimens representing 60 species were examined. I photographed each skull in three views: dorsal and ventral cranial views, and lateral cranial views of the cranium and mandible together. The specimens were placed on the top of a small piece of clay attached to a heavy metal base, and the horizontal level of the specimen was judged visually from camera and side view. For the dorsal and ventral cranial views of the cranium, the camera lens was centered at the middle of the specimen which was adjusted to be bilaterally symmetrical in the view finder. For the lateral views of the cranium, the specimen was adjusted so that the tips of canines, last molars and auditory bulla of both sides of the cranium overlap under the camera view.

Table 2.1: The descriptions and abbreviations of the skin measurements.

1. FA	Length of forearm
2. TL	Tail length
3. FT	Length of foot
4. LT	Length of tibia
5. 2Met	Length of second metacarpal
6. 3Met	Length of third metacarpal
7. 3M1P	Length of first phalanx of third metacarpal
8. 3M2P	lentth of second phalanx of third metacarpal
9. 4Met	Length of fourth metacarpal
10. 4M1P	Length of first phalanx of fourth metacarpal
11. 4M2P	Length of second phalanx of fourth metacarpal
12. 5Met	Length of fifth metcarpal
13. 5M1P	Length of first phalanx of fifth metacarpal
14. 5M2P	Length of second phalanx of fifth metacarpal
15. EAR	Length of ear

For the lateral view of the mandible, each specimen was adjusted so that the lower canines and coronoid processes of both sides overlap. Pictures were enlarged to 3 by 5 inches and printed. Only the pictures of ventral and lateral views were actually used for measurements, since some of the landmarks I planned to use on the dorsal view were too obscure on the prints. Fortunately, most of these landmarks were available from the other two views.

Forty landmarks on the ventral view of the cranium and lateral views of the cranium and the mandible were selected. The landmarks were recorded as coordinates using a Summagraphics digitizer. Twenty-seven measurements, either between pairs of landmarks or from a landmark to a line defined by two other landmarks, were calculated using a BASIC program. These measurements include traditional ones, such as dental length and zygomatic arch width, as well as those that are very difficult to measure directly with calipers and had not been analyzed before for *Rhinolophus*, such as size and relative positions of cochlea and auditory bulla, or distance from a point to a line such as the anterior-posterior distance from palatal bridge posterior margin to M^3. The landmarks selected and the measurements used in this study are illustrated in Figure 2.1 and 2.2. Descriptions and abbreviations for the measurements are listed in Table 2.2.

I decomposed some traditionally used, overall distance variables into several regional distance variables to provide a more uniform coverage to the local structures (Strauss and Bookstein, 1982). I replaced the basal length of the cranium with a series of measurements including upper toothrow length, temporal fossa length, basal length from fossa to cochlea, cochlea length and post-cochlea length. Some traditional

Table 2.2: Descriptions and abbreviations of the skull measurements. Numbers correspondent to the labels in illustrations in Figures 2.1 and 2.2.

Ventral view of cranium:

1. P2	Vertical length of P^2
2. PAL	Length of palate bridge
3. M3	Distance between labial-most points of two M^3
4. WM3	Width of M^3
5. LPT	Length between two ptyrogoid processes
6. TEF	Length of temporal fossa
7. LSHF	Length of sphenoid fossa
8. WZA	Width between two lateral most points of zygomatic arches
9. WAB	Width of auditory bullar
10. LAB	Length of auditory bullar
11. BL	Basal length between sphenoid fossa and front tip of the cochlea
12. BB	Basal Breadth between cochlea
13. WCO	Width of cochlea
14. PMP	Distance from posterior margin of palate bridge to line defined by caudal end of both M^3
15. VLC	Vertical length of cochlea
16. VLAB	Vertical length of auditory bullar
17. PB	Posterior brain case length from mastoid process to end of cranium

Lateral views of cranium and mandible:

18. DH	Height of mandibular ramus at lower canine
19. DL	Dental length
20. LINF	Length of infraorbital foramen
21. LOR	Length of orbit from top of infraorbital framen to most restricted point of orbit region
22. HOR	Height of orbit from base of M^3 to groove of orbit
23. P4M3	Length of upper cheek tooth row
24. LBR	Length from end of M^3 to condyle fossa
25. HNS	Height of nasal swelling
26. HCR	Height of cranium
27. HOCC	Height of occipital region

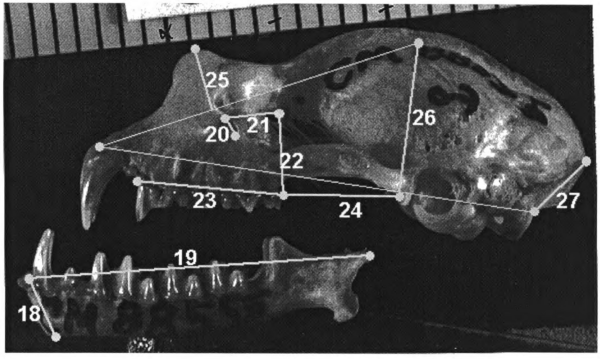


Figure 2.1: Lateral views of cranium and lower jaw with the landmarks and the measurements illustrated. Labels for measurements correspond to the measurements and abbreviations listed in Table 2.1.

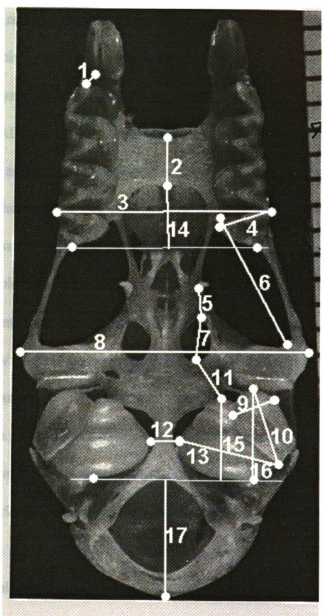


Figure 2.2: Ventral view of cranium with the landmarks and the easurements illustrated. Labels for measurements correspond to the descriptions and abbreviations listed in Table 2.2.

measurements, such as mandibular toothrow length, are omitted due to redundancy. The three measurements between a point to a line, including the distance from posterior margin of palate to posterior end of M^3, post-cochlea cranial length, height of nasal swelling, and nine measurements in the basal and auditory region covering detailed structures of this region were not measured by Bogdanowicz and Owen (1992) nor have they been analyzed before in any group of bats.

The SAS statistical package (Luginbuhl and Schlotzhauer, 1987) was used in the morphometric analysis. For each species, specimen measurement means were calculated to represent that species. A principal-components analysis was used to (1) find the patterns of clusters based on morphological similarities; (2) find the variables that are most responsible for the formation of the clusters. Univariate analyses were conducted on measurements that showed high correlation coefficients with the informative principal components. Variables most responsible for differentiating clusters were selected for later cladistic analysis. The principal components were computed from both correlation and covariance matrices, since variables with high variance are more strongly associated to the first several components when a covariance matrix is analyzed (Luginbuhl and Schlotzhauer, 1987). To better detect importance of significant characters, skin and skull data sets were analyzed separately as well as jointly. The SYSTAT software package (Wilkinson et al, 1992) was used to plot the principal components.

A canonical discriminant analysis was performed to test the validity of traditional species groups as well as those clusters revealed in the principal component analysis.

Characters for cladistic analysis

I selected 26 characters for phylogenetic analysis. They include both traditionally used characters, characters newly identified from alcoholic specimens, and those converted from the quantitative characters after morphometric analysis.

I used four hipposiderid genera (*Asellia, Aselliscus, Cloeotis* and *Hipposideros*) as outgroups for character analysis. In some cases, hipposiderids do not serve well as an outgroup due to their specialization of specific characters. For example, all hipposiderids have lost P_3, which is a derived feature within bats (Van Valen 1979). For some other characters, evidence from other bat families is informative. For example, the number of caudal vertebrae is greater in hipposiderids than in Rhinolophids, and is even greater in the earliest known bats. The conditions in the earliest bats helps confirm the direction of character evolution. In these cases, more remotely related bat families were used as an additional outgroup.

Identifying characters for cladistic analysis is a critical process. Because the subsequent cladistic analysis of characters is, by itself, only a summary of information contained within the data set (Neff, 1986; Bryant, 1989), characters selection largely determines quality and reliability of cladistic results. Character identification requires three steps:

1.) recognizing a morphological series of features between species that can be hypothesized to be homologous;

2.) determining hypotheses of the polarity and transformations among the states of a morphological series, utilizing the tools of outgroup analysis, paleontological analysis developmental biology, etc.;

3.) establishing the distribution of character states and character state transformation among the taxa under study.

Throughout the process of character selection, I attempted to determine as unambiguously as possible the order and polarity of each character. Recognition of homologous states and structural transformation series in *Rhinolophus* is relatively simple. The structures in different species of the genus usually have identical topology and similar position. However, parsing the morphological series into distinct states and proposing the transformation series demands more effort, since considerable intraspecific variation exists in most characters.

Whenever possible, I determined the polarity and transformation matrix of the states for each character. For some characters, two hypotheses in polarity were made and both were used in the phylogenetic analysis. I used the outgroup distribution criterion and ingroup commonality criterion (Watrous and Wheeler, 1981; Maddison et al, 1984) to recognize primitive character states. The complex noseleaf of *Rhinolophus* is unique among bats with which no known homologous structures in any outgroups may be directly compared. I assumed that primitive states for characters on noseleaf are typically the smaller, less developed and less prominent states in a series. This assumption agrees with Hill's descriptions on the primitive *Hipposideros* (Hill, 1963).

I am convinced that all characters should not be weighted equally, Since some characters which are better studied, involve more evolutionary innovations, or are more likely to be synapomorphic than others (Hecht and Edwards, 1977; Neff, 1986). Hecht and Edwards' five weighting types were modified into four categories to fit the situation in *Rhinolophus*. Each character was assigned to one of the four weighting groups. The

characters of weighting group one contain character states where transformation involved simplification or reduction. This group was given the lowest weight. Weighting group two contains features that were not reductional but which had relatively high levels of intraspecific variation or where the boundaries between the states were, to some extent, arguable. This group was given the next lowest weight. Weighting group three contains characters that are relatively unique and innovative in nature, but where distinctions between character states can not be recognized are clearly as the last group, and the boundaries are still more or less arbitrarily determined. This group was given higher weight than the previous two groups. Weighting group four comprises characters that are evolutionary innovations where distinct states can be clearly recognized; these characters are likely to be genealogically most informative and were given the highest weight.

PAUP3.1.1 (Swofford, 1993) was used to compute the most parsimonious trees for the genus, using the heuristic searching algorithm. It was assumed that the three types of transformations (innovative, reversal, and parallel changes) are of equal probability. When a character weighting scheme is applied, weighting group one receives a weight of one unit, weighting group two receives a weight of two units, and so on. Wagner parsimony was applied. The specimens examined for character analysis and cladistic analysis are listed in Appendix 1.

RESULTS

MORPHOMETRIC ANALYSIS

I analyzed separately data from skin measurements, skull measurements and pooled data of skins and skulls for a better identification of individual measurements. The first five principal components (PC1-PC5) were computed from each data set. In a preliminary examination I observed no pattern beyond the PC5, therefore, I chose the first five principal components for detailed analysis. My discussion will focus on the first three PCs, because PC4 and PC5 account for relatively little variation. Two dimensional displays for various combinations of principal components were made to examine patterns of morphological similarity among the species. I examined the correlation between the eigenvectors and the original variables to determine the contribution of each original measurement to the species distribution patterns. Finally, I conducted a canonical discriminant analysis to verify the suggested species groups.

A. The pooled skull and skin data set

The first principal component (PC1) of the covariance matrix accounts for 85.5% of the total variation of the original variables, whereas in the correlation matrix it accounts for 77.2% of the total variation (Appendix 2.1 and 2.2). PC1 has positive correlation coefficients with all the original variables. In such situations, PC1 is commonly interpreted as a size component (Humphries et al, 1981). PC1 is relatively more apparent as a size variable in the correlation matrix where almost all variables have similar (between 0.1 to 0.2) correlation coefficients with PC1. PC1 is less obvious a size component in the covariance matrix, since some of the frequently used size indicators (e.g. DL, LBR in the skull, and FA, 2MET, 3MET,

Table 3.1: The abbreviations and the traditional group identities of each species used in the display of their principal components. f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group. The species groups were originally defined by Anderson (1905b, 1918), and were modified by Tate and Archibold (1939), Koopman (1975), and Corbet and Hill (1992).

Abbr.	Group	species name	Abbr.	Group	species name
ac	p	*acuminatus*			
ad	f	*adami*	md	l	*maclaudi*
af	f	*affinis*	mr	l	*macrotis*
al	p	*alcyon*	ms	l	*marshellli*
ar	a	*arcuatus*	my	f	*malayanus*
bs	p	*blassi*	mg	f	*megaphyllus*
bt	p	*blythi*	mh	p	*mehelyi*
bo	f	*bornensis*	mn	p	*monoceros*
ca	a	*canuti*	ne	f	*nereis*
cp	f	*capensis*	os	p	*osgoodi*
cv	f	*clivosus*	pa	l	*paradoxorous*
ce	a	*coelophyllus*	pe	m	*pearsoni*
co	p	*cornutus*	ph	l	*philippinensis*
cr	a	*creaghi*	pu	p	*pusillus*
da	f	*darlingi*	re	l	*rex*
dk	f	*dekenii*	ro	f	*robinsoni*
dt	p	*denti*	ru	f	*rouxi*
eq	m	*eloquens*	rf	a	*rufus*
el	p	*euryale*	se	l	*sedulus*
et	a	*euryotis*	sh	a	*shameli*
fe	f	*ferrumequinum*	sm	f	*simulator*
fu	m	*fumigatus*	sp	f	*simplex*
hl	m	*hildebrandti*	st	f	*stheno*
hr	l	*hirsutus*	sb	p	*subbadius*
hp	h	*hipposideros*	sr	a	*subrufus*
im	p	*imaizumii*	sw	f	*swinnyi*
in	a	*inops*	th	f	*thomasi*
ke	f	*keyensis*	tf	l	*trifoliatus*
ld	p	*landeri*	vi	f	*virgo*
lp	p	*lepidus*	yu	m	*yunanensis*
lt	l	*luctus*			

4MET, and 5MET in the wing) have relatively low correlation with PC1.

The other four PCs have both positive and negative correlation coefficients with the original variables, indicating that these PCs represent contrasts between sets of measurements. Generally such contrasts are interpreted as reflecting variation in shape (Humphries et al, 1981). In the covariance matrix, the four remaining PCs accounts for 7.7%, 2.3%, 1.7% and 1.1% of the total variance, respectively. In the correlation matrix, these same PCs accounts for 7.0%, 4.4%, 2.2% and 1.7% of the total variance. The variation not accounted for by the first five PCs is much greater for the correlation matrix (7.3%) than for the covariance matrix (1.6%), though the total variance represented in PC2 through PC5 is also greater in the correlation matrix (15.3%) than in the covariance matrix (12.8%) (Appendix 2.1 and 2.2).

Different original variables have high loadings on PC2 and PC3 in the two analyses. For the covariance matrix, the variables having high positive loadings on PC2 are LPF (.23), TEF (.21), HOC (.17) and 4MET (.10); those with high negative loadings are PAL (-.82), VLIB (-.23). PC2 of the correlation matrix has high positive loadings for P4M3 (.49), DH (.26) and 4MET (.20), and has high negative loadings for PAL (-.38), VLIB (-.23) and BB (-.22). PC3 of the covariance matrix has great positive loadings for VLIB (.63) and LFC (.18), and high negative loadings for WAB (-.59) and BB (-.39). For the correlation matrix, those variables having high positive loadings are 2MET (.46) and 3M1P (.30), and those having high negative loadings are PB (-.30), LFC (-.28) and LIF (-.25).

The highly loaded original variables are from both the skin and skull, and are relatively concentrated on the palate and basal regions of the skull. These variables include the length of palate (PAL), length of upper cheek toothrow (P4M3), the length of cochlea (VLIB), length of temporal fossa (TEF), basal breadth between the cochleae (BB), width of the auditory bulla

(WAB), the length from pterygoid fossa to cochlea, and length from mastoid process to the posterior end of the skull. However, they are not restricted to a few particular structures.

No obvious pattern of species clustering can be found in the two-dimension plot of the PC1 by PC2 for the covariance matrix. In the PC1 by PC2 plot of the correlation matrix, there is an imperfect separation of species according to their geographic distribution: species from Africa and west Eurasia make an exclusive convex group and occupy the lower half of the display (Figure 3.1). The separation is almost exclusively along the PC2 axis. No pattern of species distribution is evident along the PC1 axis, suggesting that size is not a major differentiating factor in the subgeneric taxa of *Rhinolophus*. Because the length of the palate bridge has greater absolute correlation coefficient with PC2 (-.82) than any other measurements, three southeast Asian species of Andersen's *philippinensis* group (*R. luctus, R. rex*, and *R. macrotis*) which have the longest palate bridges, are located in the negative side of PC2 axis with the African and west Eurasian species. Three African and west Eurasian species *R. simulator, R. landeri* and *R. alcyone* and one southeast Asian species *R. osgoodi* are also misplaced.

In the displays of species on the display of PC2 by PC3 for the correlation matrix, none of Andersen's species groups can be clearly observed as distinct clusters, except that the species of Andersen's *arcuatus* group are situated close to each other with only two species of Andersen's *ferrumequinum* group distributed inside the *arcuatus* cluster. In Figures 3.2 to 3.4, the distribution of the species of each traditional group is indicated by a convex hull. However, the geographic pattern of taxa in these displays is more apparent than the species-groups patterns. For the correlation matrix, a line can be drawn which separates the genus into two

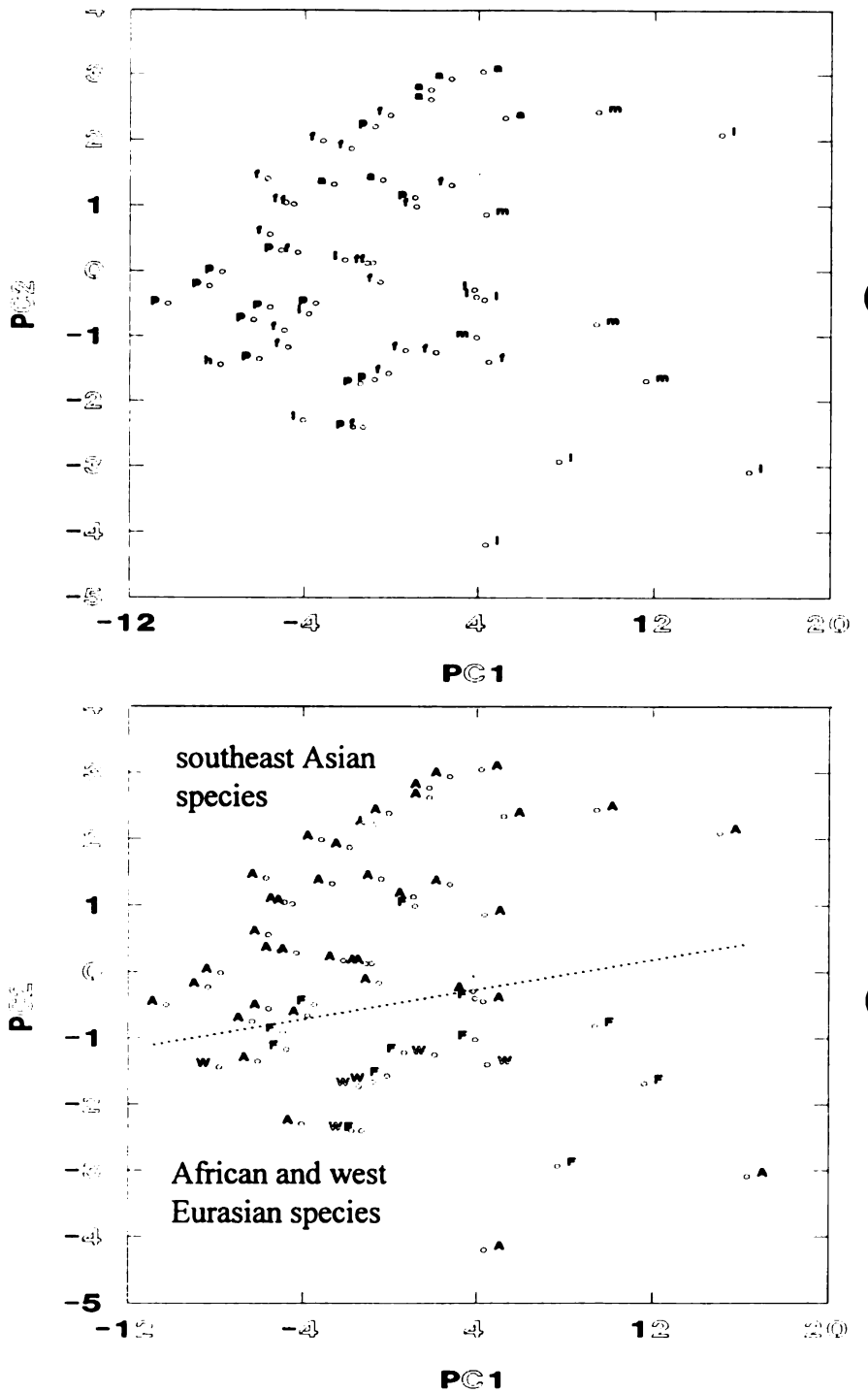


Figure 3.1. Displays of species on PC1 and PC2 of the correlation matrix from the pooled skin and skull data. (a). The separation between the traditional species groups is not clear. Species are symbolized in species group identity: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group. (b) There is a approximate separation of species associated to the geographic origins (dotted line). Species are symbolized in their distribution: 'A' = southeast Asia, 'F' = Africa, and 'W' = west Eurasia.

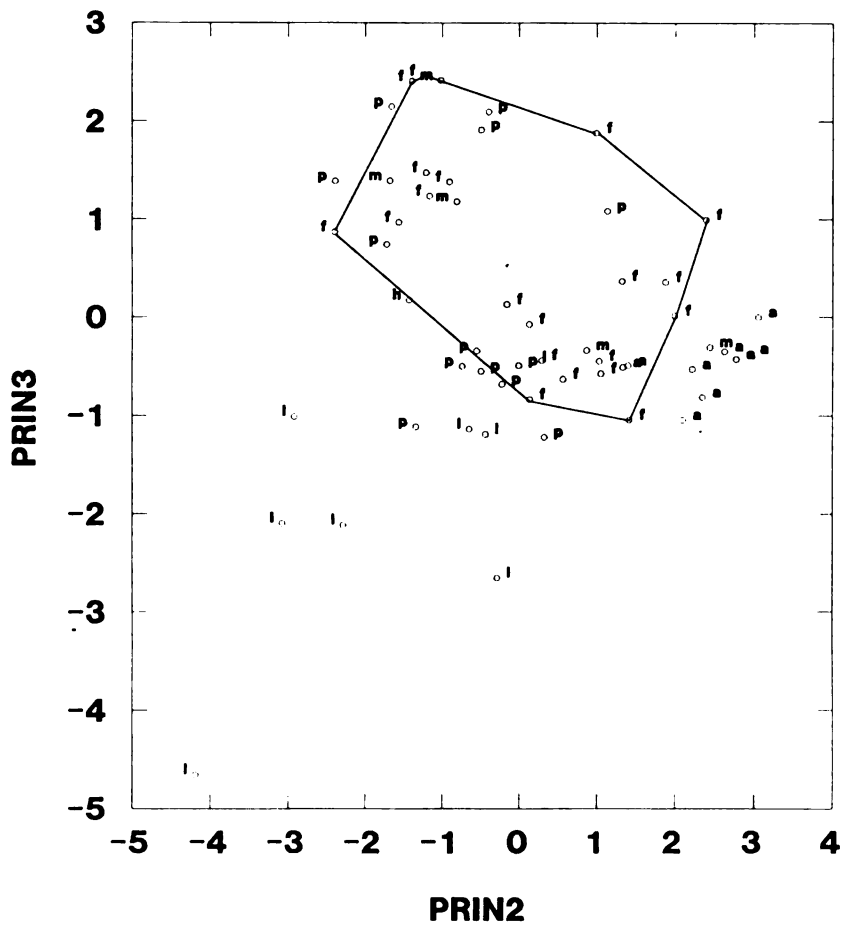


Figure 3.2. The display of traditional *ferrumequinum* species group in PC2 and PC3, from the correlation matrix of the pooled skin and skull data. There is extensive overlap between species of this group and other groups. Species group abbreviations: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

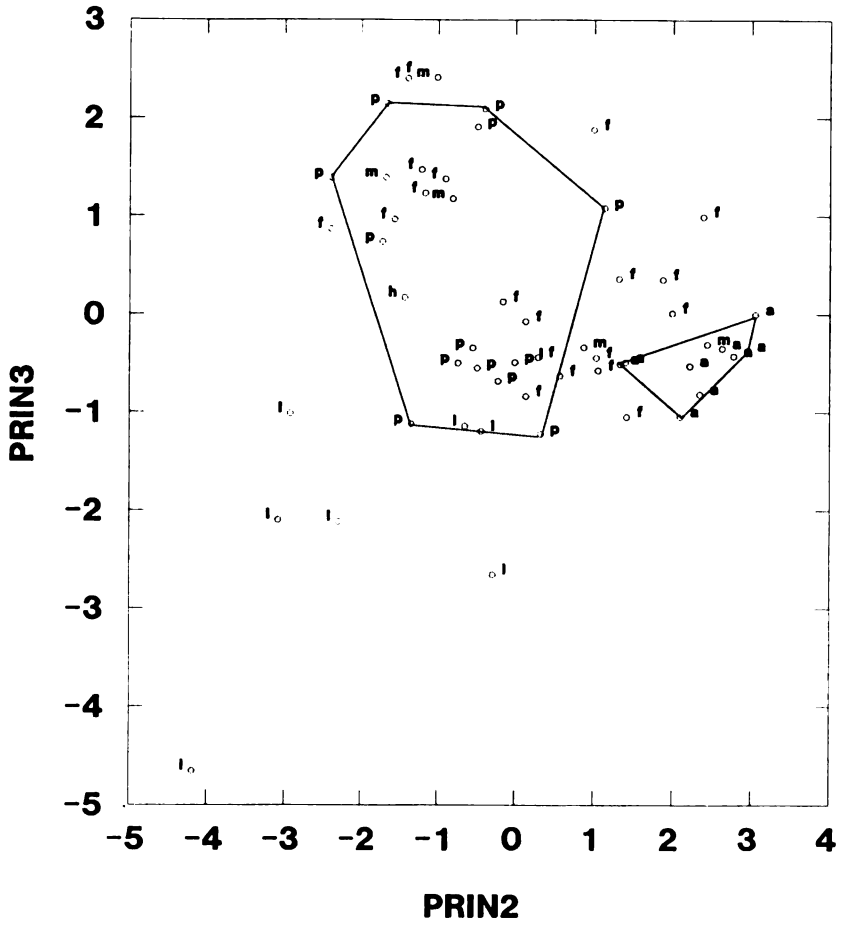


Figure 3.3. The display of the traditional *pusillus* species group and *arcuatus* species group in PC2 and PC3 from the correlation matrix of the pooled skin and skull data. There is extensive overlap between species of the *pusillus* group and other groups, but only one species of the *fumigatus* group is inside the *arcuatus* group. Species group abbreviations: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

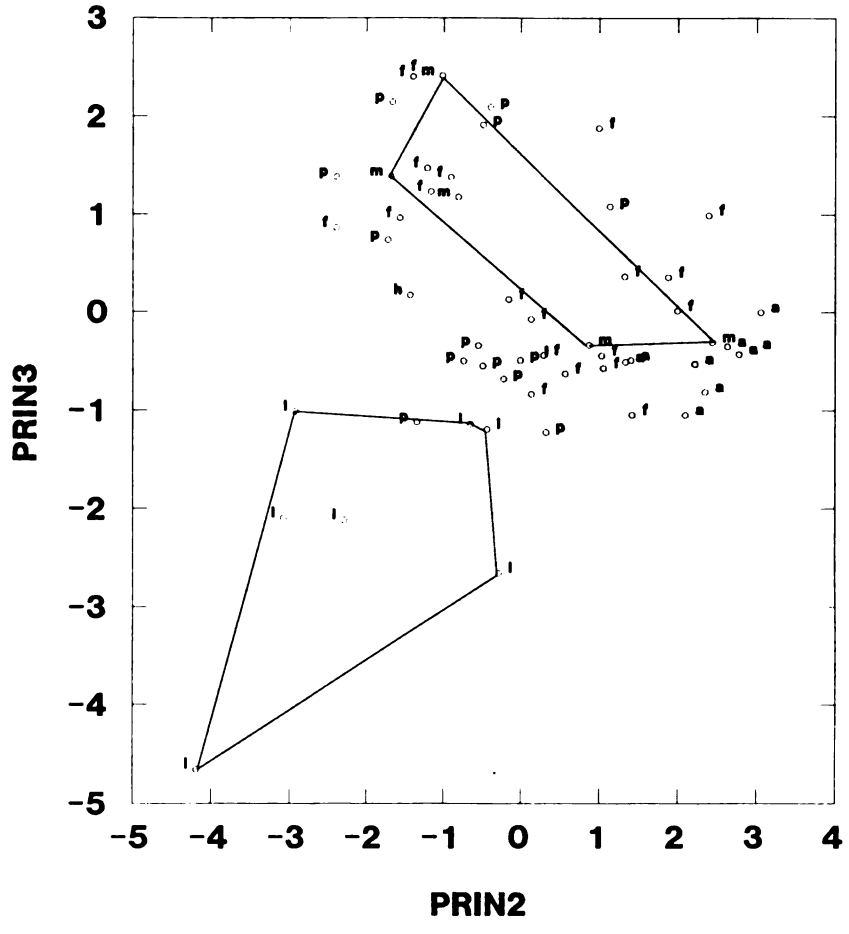


Figure 3.4. The display of traditional *fumigatus* (= *macrotis*) group and *philippinensis* (= *luctus*) group in PC2 and PC3 from the correlation matrix of the pooled skin and skull data. Extensive overlap exists between species of the *fumigatus* group and other groups. Species group abbreviations: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

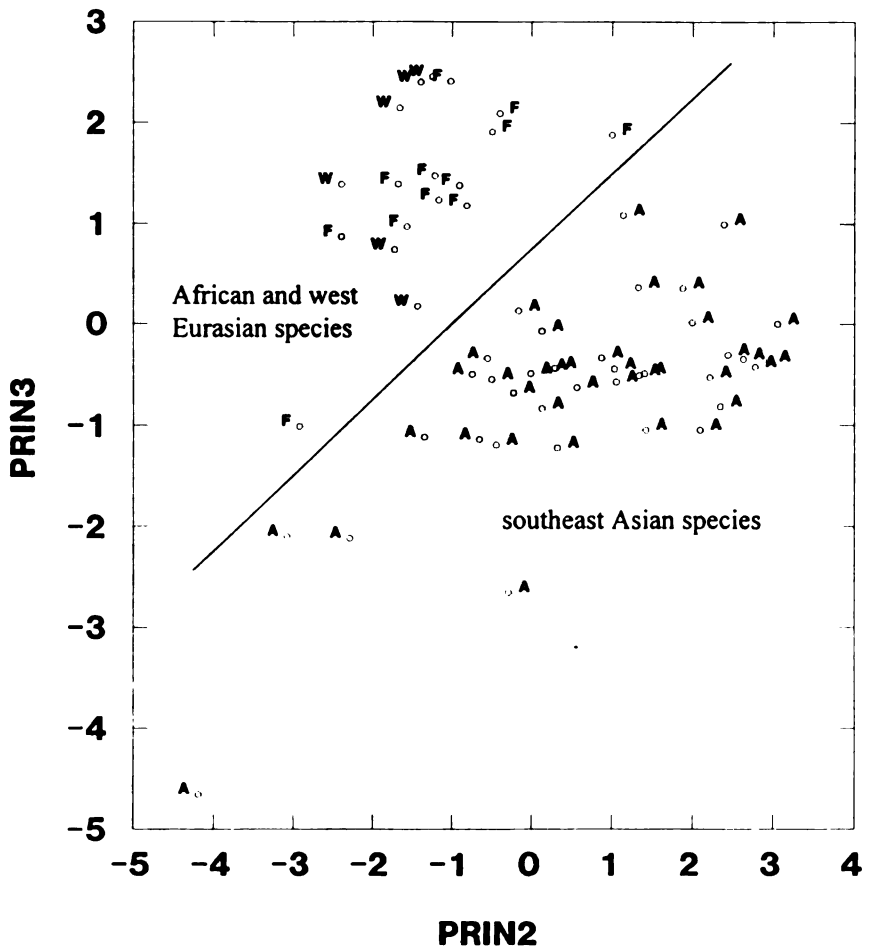


Figure 3.5. Figure displays species on the PC2 and PC3 from the correlation matrix of pooled skin and skull data. There is a non-overlapping separation of species clusters associated with their geographic origins: one species cluster from Africa and west Eurasia, and the other from southeast Asia. Species are symbolized in their distribution 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

groups according to their geographical origin without misplacement or overlap (Figure 3.5). Both PC2 and PC3 contribute to this separation. The PC2 axis shows that the African and west Eurasian species have relatively long palatal bridges and short upper cheek toothrows, and the PC3 axis indicates that these species have relatively long second metacarpals and long first phalanges of the third finger, and short posterior basal areas in the skull. In the display of PC2 and PC3 from the covariance matrix, the genus also appears to form two groups. African and west Eurasian species (with the exception of *R. maclaudi*) form a cluster in the negative sides of both axes, and the southeast Asian species are distributed in the positive side of both axes (Figure 3.6). PC3 in this analysis is the main distinguishing component along which the southeast Asian species show longer cochlea and shorter auditory bullae than African and west Eurasian species. None of the displays containing PC4 or PC5 show any additional patterns of clustering.

The *ferrumequinum* and *pusillus* species groups have species in both geographical clusters of Figures 3.5. The extent of these two species groups are evident in the plot of PC2 versus PC3. However, when only the southeast Asian members of each species group are examined, relative closeness between species of the same group becomes apparent in four traditional species groups as shown in Figure 3.7. This structure is not apparent among the African and west Eurasian species. The members of the traditional species groups in southeast Asia are noticeably more differentiated from each other than are their relatives in Africa and west Eurasia. The species in the latter two areas are more homogeneous in skull and wing shape variables summarized by PC2 and PC3 then are the southeast Asian species.

B. The skull data set alone

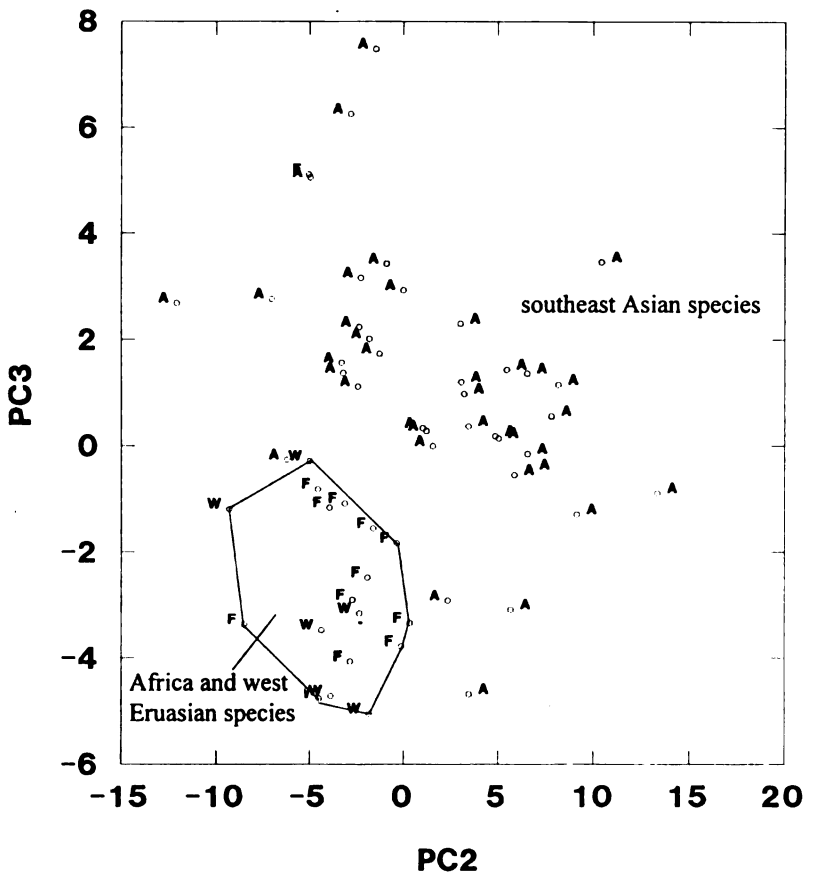


Figure 3.6. Figure displays species on the PC2 and PC3 from the covariance matrix of pooled skin and skull data. Species of Africa and west Eurasian form a distinct cluster. Species are symbolized in their distribution 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

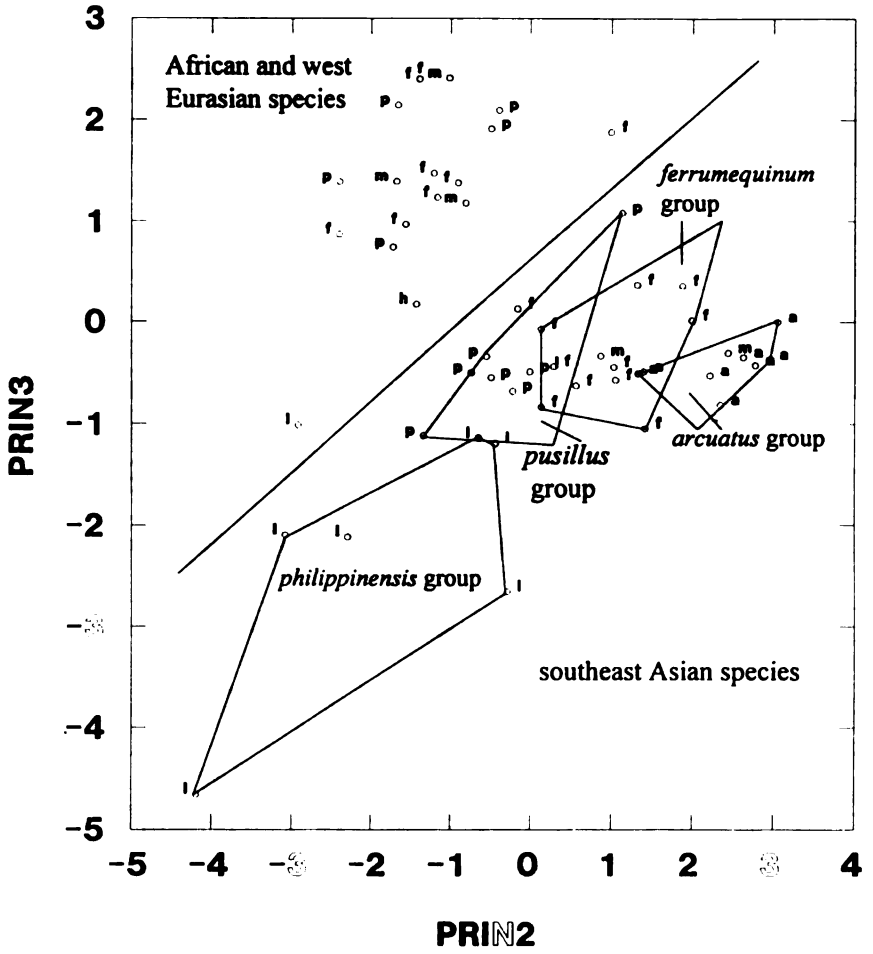


Figure 3.7. Figure displays species on the PC2 and PC3 from the correlation matrix of pooled skin and skull data. The traditional species groups are more distinct when only those from southeast Asia region is considered. Species are symbolized in their taxonomoc group: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

PC1 for the correlation matrix accounts for less total variation (71.6%) than PC1 of the covariance matrix (.90). In the covariance matrix, the correlation coefficients of the original variables with PC1 vary from 0.0 (P2) to .62 (DL), but commonly used size measurements (e.g. DL, WZA and LBR) are highly correlated with PC1. In the correlation matrix, the same correlation coefficients are nearly uniformly positive (Appendix 2). As was the case for the combined data set, PC1 for the skull data set is a size factor.

The measurements PAL, BB, LAB and PB have high correlation with PC2 and PC3 as in the combined data set. But the skull data set shows that PMP, WZA and LIF are major shape variables as well.

The displays of PC2 by PC3 for both correlation matrix and covariance matrix show a good separation between the African and west Eurasian species on the one hand and southeast Asian species on the other, although *R. hipposideros* and *R. adami* are misplaced in the covariance matrix and *R. hipposideros* and *R. simulator* are misplaced in the correlation matrix (Figure 3.8 and 3.9). For both matrices, separation occurs primarily along the PC3 axis, which indicates that African and west Eurasian species have relatively broader zygomatic arches, shorter distance between the posterior margin and posterior end of M^3, shorter mandible lengths, longer lengths from pterygoid fossa to cochlea, and smaller P^2.

C. The wing data set

PC1 of both covariance matrix and correlation matrix account for about the same percent of total variation (86.1% and 85.5%). The high loadings of commonly used size measurements such as FA (.43), 3MET (.28), 4MET (.32) and MET (.34) on PC1 for the covariance matrix, and uniform positive loadings on the same component in the correlation matrix suggest that PC1 is a size component (Appendix 2).

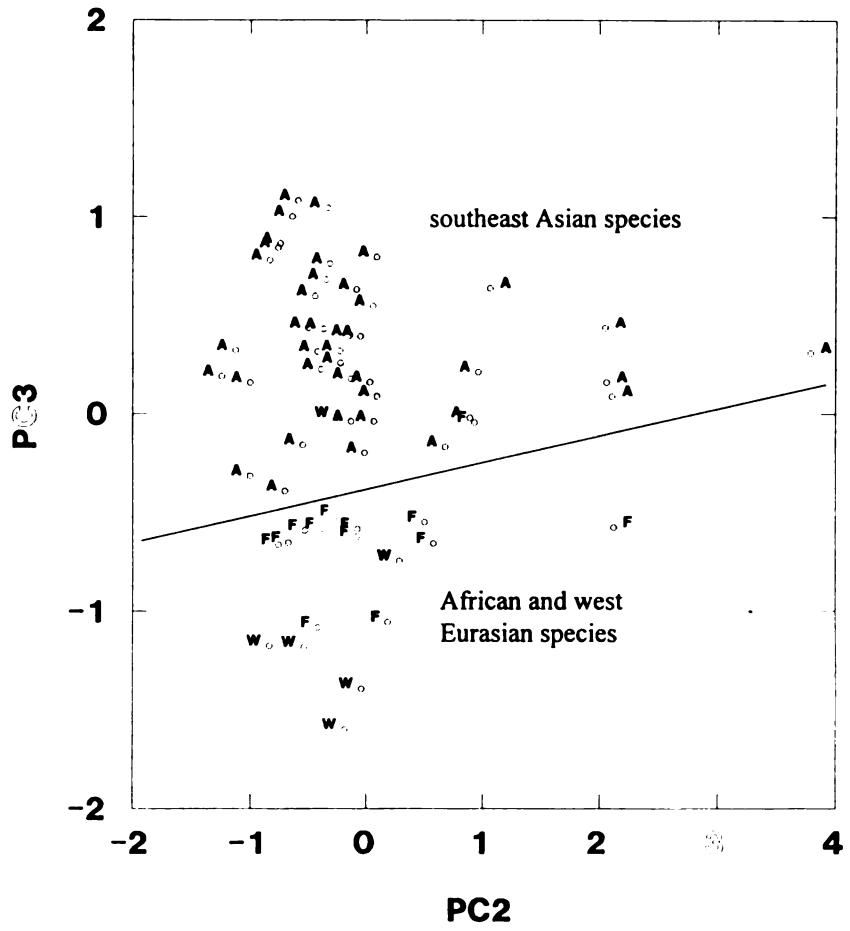


Figure 3.8. Figure displays species on PC2 and PC3 from the correlation matrix of skull data. Species of Africa and west Eurasia are separated from the species of southeast Asia. . Species are symbolized in their taxonomoc group: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

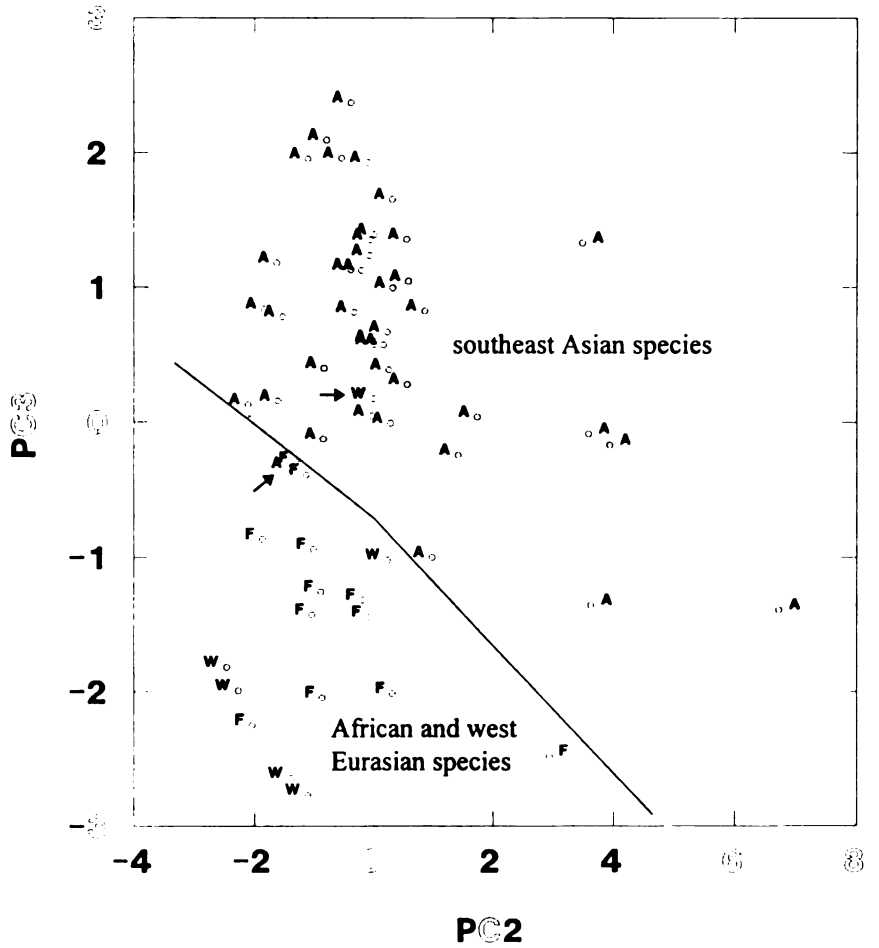


Figure 3.9. Figure displays species on PC2 and PC3 from the covariance matrix of skull data. Species of Africa and west Eurasia are separated from the species of southeast Asia. Two arrows indicate two misplaced species. Species are symbolized in their distribution: 'A' = southeast Asia, 'F' = Africa, and 'W' = west Eurasia.

The display of species in PC2 by PC3 for the covariance matrix shows a geographic pattern where African and west Eurasian species are separated from southeast Asian species, with only three species misplaced. This pattern of separation is move evident in the similar display of PC2 by PC3 for the correlation matrix where only one species is misplaced. The species plot of PC2 by PC3 for the correlation matrix also shows some pattern of traditional species groups among southeast Asian species: the species of the *arcuatus* group and most species of the *pusillus* group are close to each other, but both groups are overlapped with the *ferrumequinum* group which is more scattered (Figure 3.10).

PC2 and PC3 of the skin data reveal several important morphological features which are not disclosed in the pooled data set. The high correlation of these original variables with PC2 and PC3 shows that the African and west Eurasian species have longer tails, longer second phalanges of the fourth finger but shorter first phalanges of the fourth finger, longer second phalanges of the third finger but shorter third metacarpals, and smaller ears (Appendix 2).

D. Remarks on the Principal Component Analyses

Among the traditional species groups, only the *arcuatus* group is distinct in these analyses. The species of the *philippinensis* group span a broader range but do not have extensive overlap with other groups. All other four species groups are not completely distinguishable in any of the three analyses. However, there is a pattern of species separation associated with the two major geographic regions: the Africa and west Eurasian region and the southeast Asian region. When only the southeast Asian species are considered, two additional traditional species groups, the *pusillus* group and the *ferrumequinum* group become distinguishable. The *arcuatus* group is distinct because it contains only southeast Asian species.

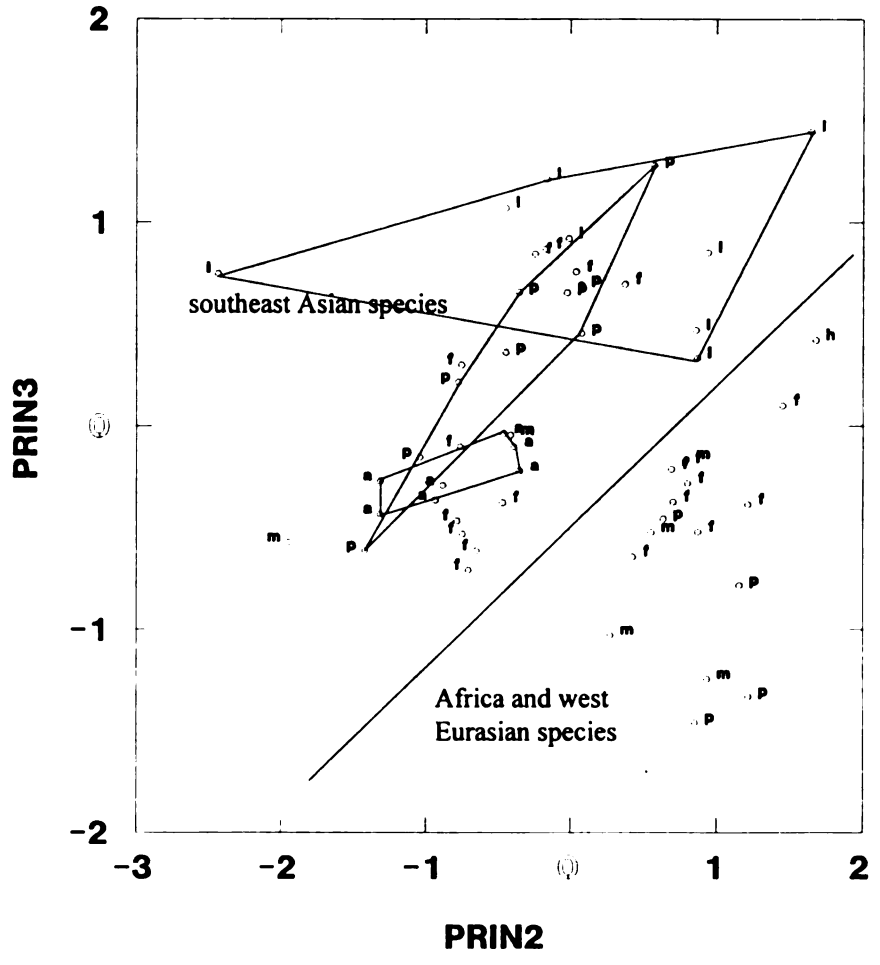


Figure 3.10. Figure displays species on the PC2 and PC3 from the correlation matrix of skull data. Among the southeast Asian species, only members of the traditional *arcuatus* group are close to each other. . Species are symbolized in their taxonomoc groups: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

Considering that all of the species groups recognized have some overlap with other groups and gaps between these groups are small or nonexistent, these analyses indicate that the traditional species groups are only weakly differentiated.

In all data sets and analyses of both correlation and covariance matrices, PC1 can be interpreted as a size component. It is only on the PC3 and PC2 axes that some patterns of clusters are seen. No patterns of distribution are found on PC4 and subsequent PCs. In all principal components on these axes species distributions are rather continuous.

Considering that the morphometric data do not contain characters from the noseleaf which is the most important basis for establishing traditional species groups, the relative distinctiveness of these groups within the southeast Asia region is significant. It is also significant that the same pattern is manifested independently in the skull measurements and in external measurements as well as overall morphology.

Based on the principal component analysis, there is not enough evidence to decide whether the traditional *hipposideros* species group, which contains *R. hipposideros* only, should be considered as a distinct group. Although observations shows that *R. hipposideros* has proportionally larger cochlea, the major shape components do not demonstrate that the difference between *R. hipposideros* and other species with this feature constitutes an important part of overall generic morphological variation of the genus.

The traditional *ferrumequinum* group is recognizable in the correlation matrix of pooled skin and skull data set, but in the displays of other analyses, it has more extensive overlap with the *arcuatus* and *pusillus* species. Both Andersen (1905a) and Tate (1939) observed that the *ferrumequinum* group has less specialized features than other groups (e.g.,

modest-sized ear, cochlea and nasal swellings). Without characters from the noseleaf, skull and skin measurements do not provide enough evidence to unite the species of this group.

Andersen's *macrotis* group originally contained four African species and three southeast Asian species. This group was merged with the *philippinensis* group by Tate (1939) and reinstated by Corbet and Hill (1992). Corbet and Hill renamed it the *fumigatus* group since *R. macrotis* had been moved to the *philippinensis* group. Species of this traditional group are scattered on the PC2 and PC3 in all analyses and, therefore, this group is not confirmed.

Based on the correlation coefficiencies of original variables with PC2 and PC3 of the three analyses, the measurements contributing most to observed clusters are: length of palate bridge (PAL), position of posterior margin of the palate bridge (PMP), length of upper cheek tooth row (P4M3) and width between zygomatic arches (ZAW) in skull measurements; and the tail length (TL), ear size (EAR), length of second phalanx of the third finger (3M2P), length of first and second phalanges of the fourth finger (4M1P, 4M2P) in the skin measurements.

The genus *Rhinolophus* is well known for its homogeneity in morphology. The results of this study confirms this. There is little structure to the phenetic similarity *Rhinolophus* species. Consequently, morphometric data used in this study seem insufficient for reconstructing the phylogeny of this genus. More phylogenetically informative qualitative characters are necessary for this purpose.

E. The Canonical Discriminant Analyses:

A canonical discriminant analysis was used to test the validity of the traditional species groups and the species clusters revealed in the principal component analysis of the pooled skin and skull data set. Three separate tests were conducted. In the first, the traditional species

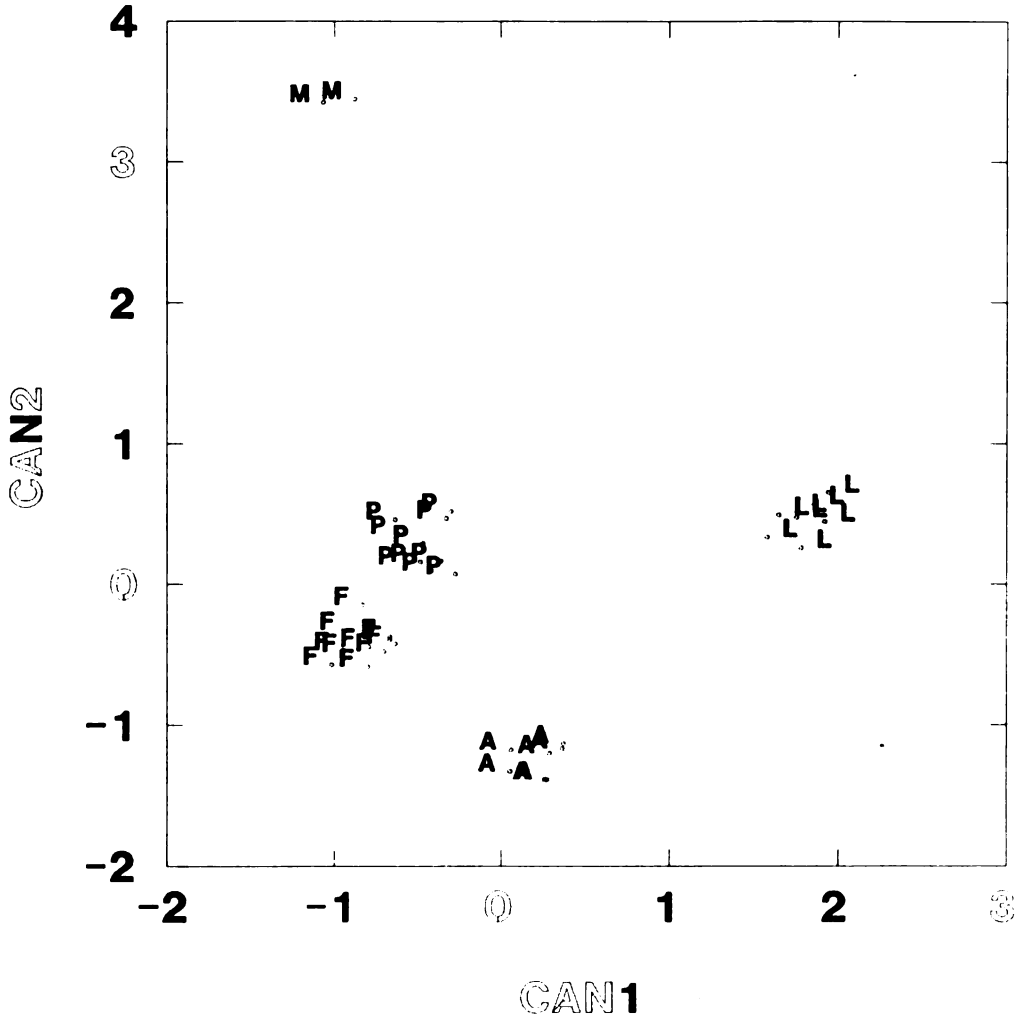


Figure 3.11. Figure displays the first and second canonical variables (CAN1 and CAN2) for the southeast Asian species. Traditional species groups are used as *a priori* class. Species are symbolized in their group identities: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

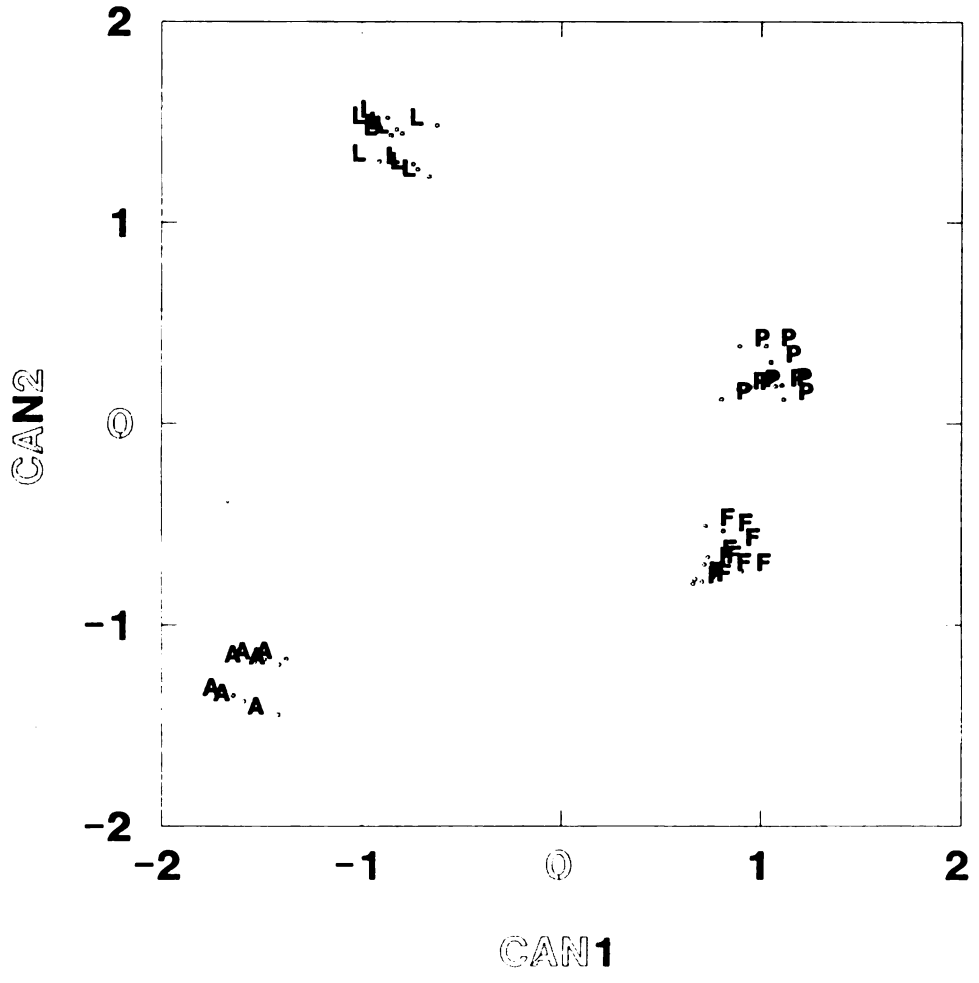


Figure 3.12. Figure displays the first and second canonical variables (CAN1 and CAN2) for the southeast Asian species, Andersen's *macrotis* group being merged with *philippinensis* group. Traditional species groups are identified as *a priori* class. Species are symbolized in their group identities: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

groups were identified as *a priori* classes and the canonical discriminant analysis was done within the southeast Asian species. The display of the first two canonical variables shows five very distinctive species groups and the separation between the five species groups is perfect (Figure 3.11). I then merged the *macrotis* with the *philippinensis* group as Tate (1939) suggested. The distinctiveness of the four species groups are equally apparent in this analysis (Figure 3.12). The test strongly confirmed the existence of these groups.

In the second analysis, I assigned all the species of Africa and west Eurasia to a new *a priori* class, and the species of the southeast Asia remained in their traditional species groups. Figure 3.13 and 14 shows five distinct clusters on the CAN1 by CAN2 plot, and the *ferrumequinum* group and *pusillus* group are well separated in CAN5 (Figure 3.13). The display not only shows an unequivocal separations between groups, but it also shows a larger gap between the species group of African and west Eurasian species and species groups of southeast Asian than among species groups of the southeast Asian region.

In the final test, the traditional species groups were use as *a priori* classes for the entire genus and five canonical variables are computed. Figure 3.14 and 3.15 show six non-overlapping species groups, though the species of individual species group are not as concentrated as the species groups including the southeast Asian species only. It seems that the traditional species groups may be confirmed by this analysis.

Canonical discriminant analysis of the pooled skin and skull data set is able to distinguish species grouped in all of the analyses. While this analysis did confirm that southeast Asian species groups can be distinguished with these data, this form of analysis also readily distinguished between groups whose distinctness was not apparent in the principal component analysis.

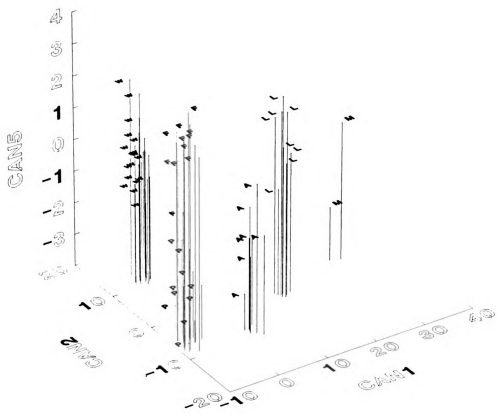


Figure 3.13. Figure displays the first, second and fifth canonical variables (CAN1, CAN2 and CAN5) for all species of *Rhinolophus*. Traditional species groups are used as *a priori* classes for southeast Asian species only, and all African and west Eurasian species are assigned to a new class labeled 'W'. Southeast Asian species are symbolized in their group identity: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

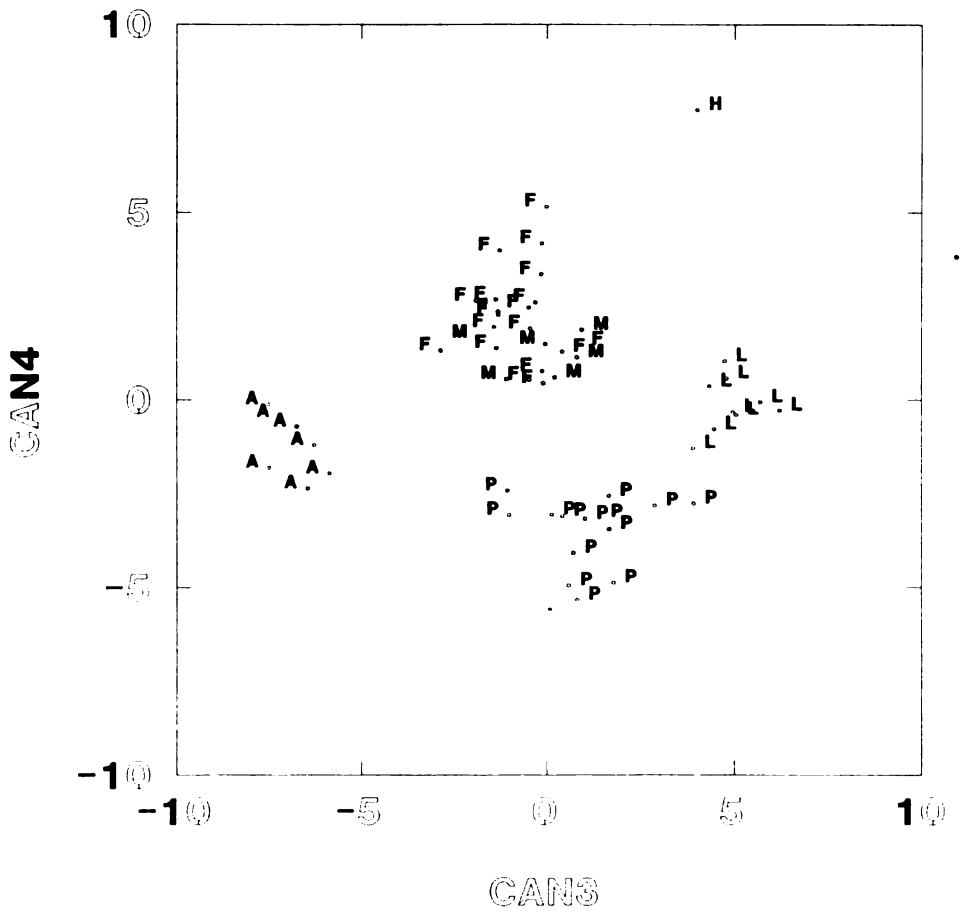


Figure 3.14. Figure displays of the third and fourth canonical variables (CAN3 and CAN4) for all species of *Rhinolophus*. Traditional species groups are used as *a priori* class. Species are symbolized in their group identity: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

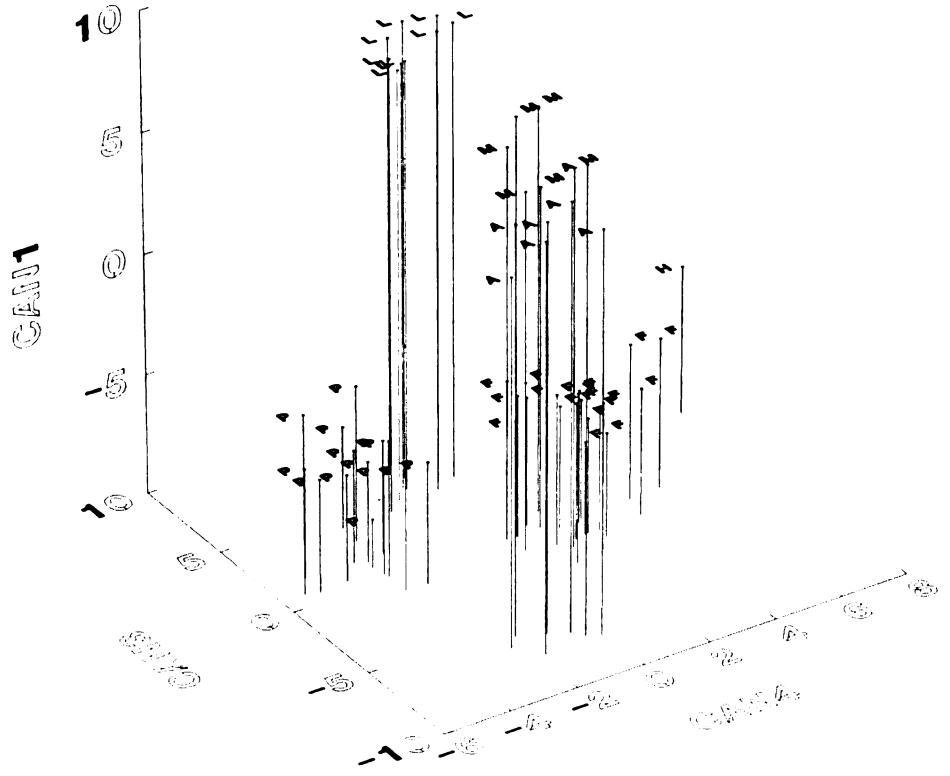


Figure 3.15. Figure displays the first, third and fourth canonical variables (CAN1, CAN3 and CAN4) for all rhinolophids. The *ferrumequinum* group and *fumigatus* group are separated on CAN1 axis. Traditional species groups are used as *a priori* classes. Species are symbolized in their group identity: f: *ferrumequinum* group; p: *pusillus* group; a: *arcuatus* group; h: *hipposideros* group; l: *philippinensis* (= *luctus*) group; m: *fumigatus* (= *macrotis*) group.

I conclude that, while canonical discriminant analysis does confirm the results from principal components, the ability of this technique to differentiate among groups not distinguishable in the principal component analysis makes this result suspect. In canonical discriminant analysis, the number of observations should be at least five times as large as the number of the variables to receive an unbiased and consistent result (Kalayeh and Landgrebe, 1983). When the observation/variable ratio is small, arbitrary separations between *a priori* groups can be made (Ness, 1979; Dubes and Jain, 1991). In my data the observation/variable ratio is less than two. My results suggest this form of analysis is overly powerful at discriminating groups in my data, and is unlikely to be trustworthy for exploring the taxonomic structure in *Rhinolophus*.

CHARACTER ANALYSIS

The transformation series of states for each character were determined by methods described which follow. In general, I first considered the states that have been commonly recognized in systematic studies of this genus, and used outgroup analysis to determine polarity. When the outgroup criteria did not provide sufficient evidence, in-group commonality criteria (Eldredge, 1979) was applied to determine polarity. In some cases, boundaries are not clear between character states previous identified. This usually occurred for regional *Rhinolophus* fauna but not the entire genus. I combined those states that were ambiguous so that the remaining states were reasonably distinct. In cases where there was disagreement in evolutionary direction changes between states, I either took a position when there was enough evidence to do so, or left the states as unordered. I placed each character in one of the four weighting groups described in the Material and Methods section, with group one receiving the lowest weight and group four the highest

1. Shape of the Connecting Process of Sella (ConPr). I recognized 5 states for this character (Figure 4.1): *a*, moderate height and rounded, anterior base not reaching the summit of the sella (e.g. *R. ferrumequinum* and *R. clivosus*); *b*, higher and sharper, anterior base not reaching summit of the sella, as represented by *R. macrotis*; *c.* very low, the anterior base distant from the summit of the sella (e.g. *R. luctus* and *R. trifoliatus*); *d.* dorsal edge with a sharp angle or horn-shaped, the anterior edge forming a notch where it connects to the sella (e.g. *R. acuminatus* and *R. cornutus*); and *e*. dorsal edge low and round, anterior base reaching the tip of the sella (e.g. *R. pearsoni* and *R. arcuatus*). State *e* was described by

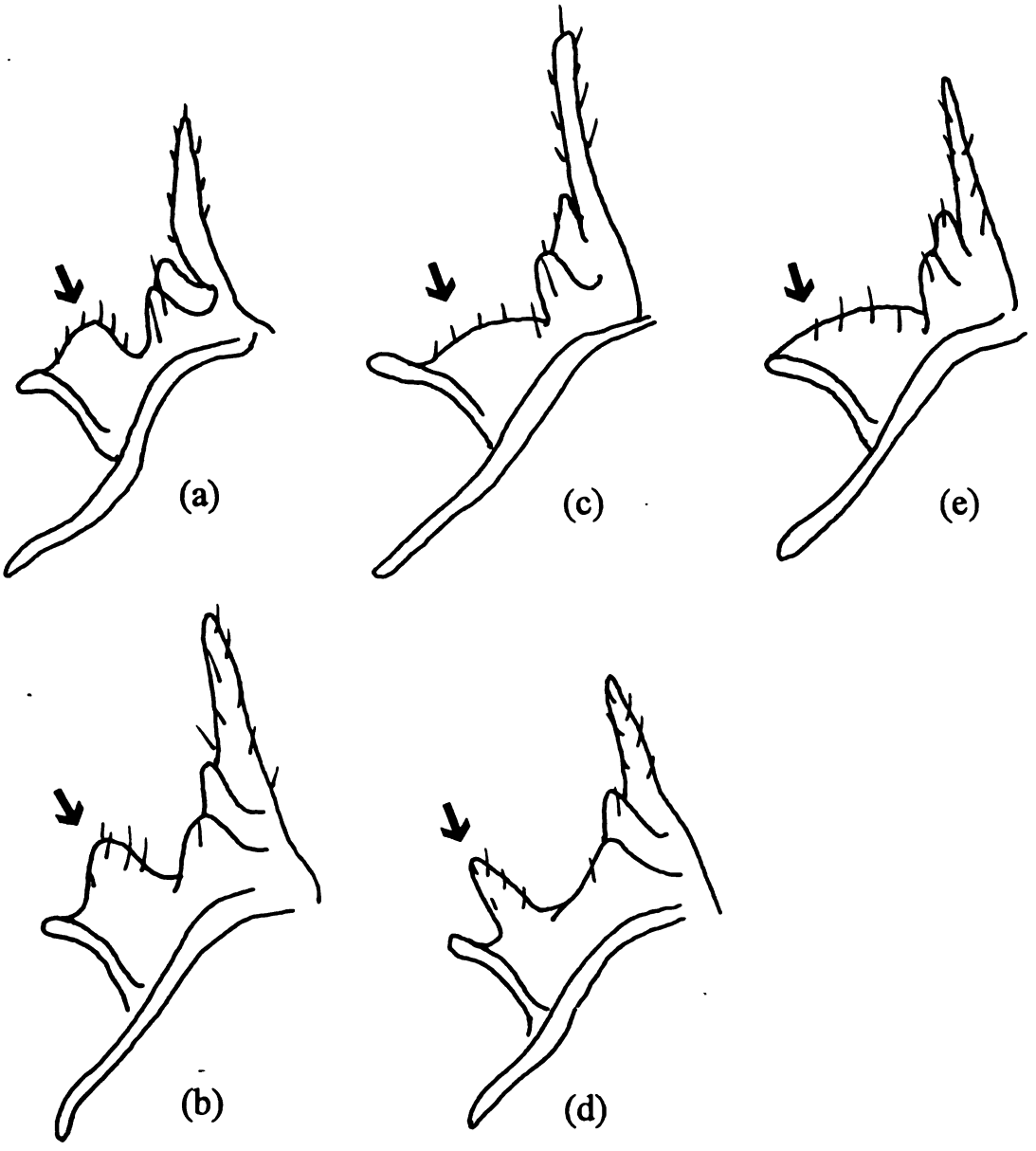


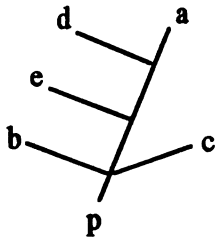
Figure 4.1: The shape of the connecting process of the noseleaf (character 1) in lateral view, pointed by arrow. (a) state *a*, height moderate and round (*R. affinis*); (b) state *b*, higher and shaper (*R. macrotis*); (c) state *c*, very low (*R. luctus*); (d) state *d*, horn-shaped (*R. pusillus*); (e) state *e*, anterior base reaches the tip of the sella (*R. pearsoni*).

Andersen (1905d) for the *arcuatus* groups as "strongly arcuate, almost semicircular in outline and starting from the very summit of the sella". However, few subsequent researchers have utilized this as a character state.

The connecting process shape of the sella is one of the characters used for group identification in this genus. It is the primary distinguishing feature for the *pusillus* group (Corbet and Hill, 1992). Both Anderson (1905a) and Tate (1939) indicated that the connecting process of ancestral rhinolophids was most likely generalized, being low and not pointed. But since the horseshoe of all living species are beyond this hypothetical primitive stage, identifying this primitive state does little to resolve transformations among the observed character states. Andersen and Tate's presumed primitive condition does not include the relationship between the anterior base of the connecting process and the sella. In state *e* the tip of the sella is continuous with the connecting process. In states *a* - *d*, the connecting process is distinctly separate from the tip of the sella. State *e* may be the result of an anterior and dorsal extension of the connecting process, in which case it is likely derived; or it may be the result of a relatively short sella, in which case it could be primitive. In both cases, this distinction between state *e* and other states may indicate a departure of state *e* from all other states.

The states of this character were treated in two ways; both assume that none of the observed states from *a* to *e* are primitive. The first treatment assumed that transformations among the states were indeterminable and treated the states as unordered. This avoided incorrect ordering at the expense of abandoning some useful information. The second approach adopted Tate's view (1939) of transformations indicated in his phylogenetic hypothesis of the genus, assuming an additional primitive state p, with an order illustrated in the following diagram:

Tate's view (1939) of transformations indicated in his phylogenetic hypothesis of the genus, assuming an additional primitive state p, with an order illustrated in the following diagram:



Tate's view of the transformation series for character 1, indicated in his phylogenetic hypothesis of the genus (Tate and Archibold, 1939).

Because this portion of the noseleaf is innovative in nature and is unique to rhinolophids, this character was placed in weighting group four.

2. Sella Shape (Sella). The shape of the sella exhibits three states (Figure 4.2): *a*, narrow, without a lateral process (lappet) (e.g. *R. pusillus* and *R. rouxi*); *b.* broad without a lappet (e.g. *R. macrotis* and *R. inops*); *c.* broad with a lappet (e.g. *R. luctus* and *R. maclaudi*).

This character has also been used previously for species group identification. While the existence of a lappet is readily distinguishable, some sella shape differences between species are difficult to characterize or assign to a transformation series. I have chosen to ignore subtle sella shape differences and focus on obvious differences. Because the sella is a structure unique to rhinolophids, this character was placed in weighting group four. I assumed the sella arose in a simple, narrow form which broadened and gained a lappet later in evolution. This hypothesized sequences from simple to complex yields a transformation series for the three states of *a->b->c*, with state *a* representing the primitive condition.

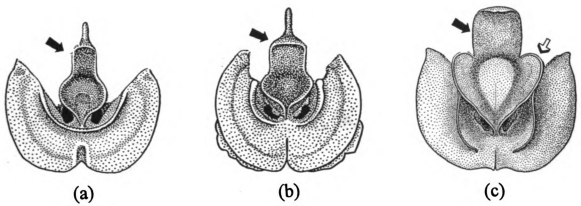


Figure 4.2. The shape of the sella (character 2), pointed by arrow '➡'. (a) state *a*, narrow (*R. alcyone*); (b) state *b*, broader (*R. funigatus*); (c) state *c*, with lappet, pointed by arrow '⇨' (*R. maclaudi*). (From Rosevear, 1965).

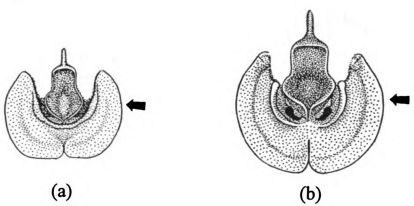


Figure 4.3. Illistrations of the horseshoe (character 3). (a) state *a*, narrower (*R. clivosus*); (b) state *b*, broader (*R. fumigatus*). (From Rosevear, 1965).

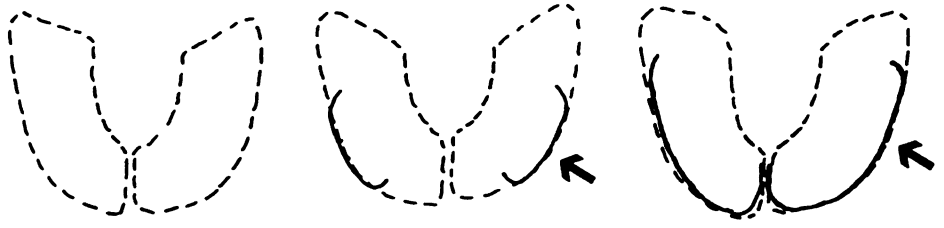


Figure 4.4. Illustrations of the supplementary noseleaf (character 4). (a) state *a*, not present (*R. luctus*); (b) state *b*, less developed (*R. pusillus*); (c) state *c*, both sides meet at the mid-line (*R. simulator*). The dotted line indicates the horseshoe which usually covers most part of the supplementary noseleaf.

Figure 4.5. Number of the lower lip grooves (character 5), pointed by arrow. (a). state *a*, one groove; (b). state *b*, three grooves.

Figure 4.6. Illustrations of the front ear projection (character 6). (a) state *a*, not present; (b) state *b*, present.

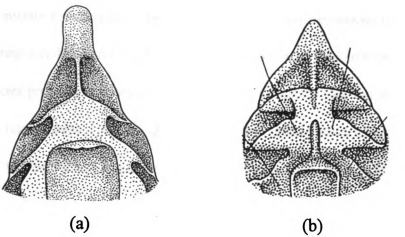


Figure 4.7. The shape of the lancet (character 7). (a) state *a*, hastate; (b) state *b*, nearly triangle. Long hair, shown in B, are frequently present in the lancet. (from Rosevear, 1965).

3. Shape of Anterior Nose-leaf or Horseshoe (ANL). I recognized three states for this character (Figure 4.3): *a*, narrow (e. g *R. euryale* and *R. simulate*); *b*. expanded in one direction, either laterally (e.g. *R. affinis*) or ventrally (e.g. *R. fumigatus*); *c*. significantly expanded in both lateral and ventral directions (e.g. *R. luctus*).

State *b* possibly represents a mixture of stages in the noseleaf development; it may not be uniquely intermediate between states *a* and *c*. I could not unambiguously subdivide state *b* or advance a reliable argument for the sequence between character states. States of this character were treated as unordered. Given the possible heterogeneous nature of states b, and variation within and between species in more subtle details of horseshoe shape, I placed this character in weighting group two.

Horseshoe size has been used in previous taxonomic studies of this genus. Recent studies demonstrate a correlation between horseshoe size and frequencies of ultrasonic pulses bats emit during echolocation (Bogdanowicz, 1992). Some of the variation in horseshoe size between species probably is based in differences in echolocation function and may not reflect phylogenetic relationships. Until we can distinguish how echolocation behavior has evolved in this genus, it will be difficult to interpret horseshoe size as phylogenetic information. I did not attempted to analyze horseshoe size here.

4. Supplementary Leaflet Beneath the Horseshoe (SupLeaf) (Figure 4.4). The supplementary noseleaf, located beneath the horseshoe, displays three states: *a*, not present or not easily identifiable (e.g. *R. trifoliatus* and *R. denti*); *b*, distinct but with a wide median gap between the two pieces (e.g. *R. macrotis* and *R. malayanus*); *c*. pieces of both sides meet or almost meet at midventral line (e.g. *R. cornutus* and *R. stheno*). This character has been used in previous studies for distinguishing species of particular geographic regions but not species

groups. Within each state, differences exist in breadth of the supplementary noseleaf, although previous workers appear to have ignored this variation. It is likely that additional states could be recognized, but at present I am not confident of the criteria that would be used. Hill (1963) argues that the outgroup genus *Hipposideros*, with lateral leaflets that are positionally identical to the *Rhinolophus* supplementary noseleaf, lacked lateral leaflets in its primitive condition. It therefore seems reasonable to identify state *a* as primitive. Although state *c* seems more advanced, there is no evidence that state *b* is a necessary intermediate stage. No order can be determined, except that state *a* is primitive. I placed this character in weighting group three for the reason that it is part of the noseleaf, an innovative complex structure.

5. Number of Mental Grooves or Lower Lip Grooves (LLG). There are two states (Figure 4.5): *a*, one median groove (e.g. *R. hildebrandti* and *R. fumigatus*); *b*, three grooves (e.g. *R. arcuatus* and *R. inops*). Previous studies of this genus have considered this to be a good character because it is unique and invariant within species. For these reasons, I assigned it to weighting group four.

Although this character was described and discussed by Andersen (1905a) and used in regional keys, it was never used to diagnose species groups. Probably because the distribution states of this character is not in conformity with other characters previous taxonomists treated as fundamental (e.g. the noseleaf). Contrary to Andersen's (1905a, p.107) view, outgroup examination indicates that only *Rhinolophus* displays three lower lip grooves. It is most reasonable to consider *a* as a primitive state within this genus.

6. Front Ear Projection (EarPr) (Figure 4.6). There are two character states: *a*, not present (e.g. *R. maclaudi* and *R. landeri*); and *b*, present (e.g. *R. malayanus* and *R.* clear *subbadius*). Although generally very small, this projection is identifiable when present. It is not

whether this projection, located at the basal, rostral-proximal side of the pinna in *Rhinolophus*, is homologous to the tragus of other bat families. No such projection has been found in closely related bat families (e.g. Hipposideridae and Nycteridae), and I hypothesize that this feature is an innovation and unique to rhinolophids. Considering that some variation exists in some species (e.g. 20% absent and 80% present in *R. lepidus*), this character is assigned to weighting group three. The primitive state is *a*.

7. Shape of the Lancet (Lancet) (Figure 4.7). The shape of the lancet encompasses two broad categories: *a*, hastate, abruptly narrowed in its distal half (e.g. *R. lepidus* and *R. clivosus*); and *b*, not hastate, triangular in shape, distal end blunt (e.g. *R. thomasi* and *R. philippinensis*). Despite its frequent usage in regional keys, this character more or less forms a continuum among the entire genus. Intraspecific variation is also present. This character is therefore assigned to weighting group two. I can not establish unambiguously the primitive state of this character. A new state *p* is introduced as a hypothetical primitive state and its relationship with *a* and *b* is unordered.

8. Number of Ear Ridges (EarRg). The ears of *Rhinolophus* posses ridges parallel to ear width. I have partitioned variation in this character into two states: *a*, 10 or more ridges (e.g. *R. blassi* and *R. clivosus*); *b*, 9 or fewer (*R. lepidus* and *R. euryotis*). This character has not been used in earlier work. The character state in each species was determined by examining as many specimens as possible, usually 10 or more. The most frequent number of ear ridges among the specimens examined was used to assign each species to a character state. Division of states is arbitrary and there is some intraspecific variations. In addition, outgroup

testing does not provide evidence for determining the ancestor state, since both states are present in Hipposideridae, the assumed sister group of *Rhinolophus*. For these reasons, the character is assigned to weighting group one and treated as unordered.

9. Number of Free Tail Vertebrae (Tail). Tail length has been a frequently used character in regional studies of *Rhinolophus* species. The variation in tail length is made more discrete by counting the number of vertebrae in the tail which are free from the sacrum. The number of caudal vertebrae has not been used in previous systematic studies of the genus. Perhaps there is intraspecific variations in counts and ambiguity due to vertebrae that are reduced in size or partly attached to the sacrum. To recognize variation present in caudal vertebrae counts, I have recognized only two states: *a*, five or six caudal vertebrae (e.g. *R. ferrumequinum* and *R. euryale*); *b*, fewer than five caudal vertebrae (*R. inops* and *R. subbadius*). The state for each species was determined as the most common count found in examining as many specimens as possible (usually 10 or more). Vertebrae that were greatly reduced in size, or partly connected to the sacrum were counted as 0.5 vertebrae.

Outgroup analysis supported the hypothesis that five to six caudal vertebrae is the primitive condition in *Rhinolophus*. The eight species in four genera examined as outgroups possessed five or six caudal vertebrae. The earliest-known fossil bat (*Icaronycteris index*, Jepsen, 1970) had seven tail vertebrae. I hypothesized that state *a* is primitive (contrary to Andersen's views [1905a, p. 107]), and that evolution within the genus has resulted in a numbers, and likely pattern of reduction of vertebral numbers over time, I considered this reduction of caudal vertebrae number. Because there is intraspecific variation in vertebral character to be in weighting class two.

10. Insertion of Plagiopatagium (TailMem). The wing membrane inserts at three different points along the leg in species of *Rhinolophus:* (Figure 4.8): *a*, at the ankle (e.g. *R. megaphillus, R. bornensis* and most other species); *b*, along the lower leg, 5 mm or more above ankle (e.g. *R. creaghi* and *R. rufus*); and *c*, at or close to the tarsal-metatarsal joint (*R. luctus and R. maclaudi*). Character states of this may be related to body size or feeding habits (Straney, 1984) and in *Rhinolophus* may display homoplasy. Consequently, I placed this character in weighting group two. All three states appear in other bat families; with state *a* by far the most common in outgroups. Parsimoniously, I assume state *a* is primitive and the other two state are independently derived: *c*<- *a* -> *b*.

11. Anterior Upper Premolar (P^2)(Figure 4.9). P^2 in bats displays a common set of character states: *a*, in the toothrow; *b*, small and displaced out of the toothrow; and *c*, absent. It is generally agreed (Slaughter, 1970) and confirmed by outgroup tests, that state *a* is primitive and *c* is most derived. Intraspecific variation is common. Even within the same individual, it sometimes happens that the two P^2 are in different states. The character state for each species was decided by majority rule after examining many specimens, the technique used by Andersen and other researchers. Because I hypothesize P^2 has become reduced and lost over time, and intraspecific variability is present. My criterion placed this character in weighting group one.

12. Shape of the Anterior Lower Premolar (P_2)(Figure 4.10). Variation in the shape of P_2 falls into three categories: *a*, length (rostral-caudal distance) about equal to width (labial-lingual distance) (e.g. *R. macrotis and R. luctus*); *b*, length conspicuously greater (20% or more) than width (*R. arcuatus* and *R. inops*); and *c*, width conspicuously greater than length

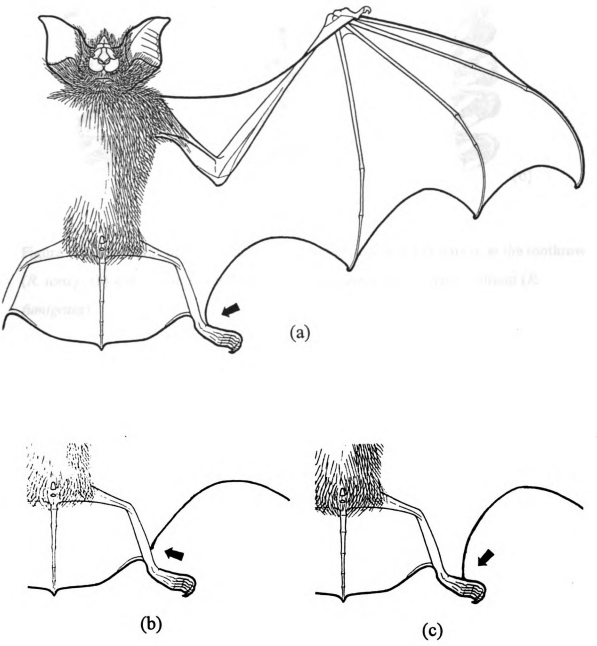


Figure 4.8. The insertion of the plagiopatatgium (character 10). (a) state *a*, at the ankle (*R. megaphillus*); (b) state *b*, above the ankle (*R. rufus*); (c). state *c*, near the tarsal-metatarsal joint (*R. luctus*). (After Rosevear, 1965).

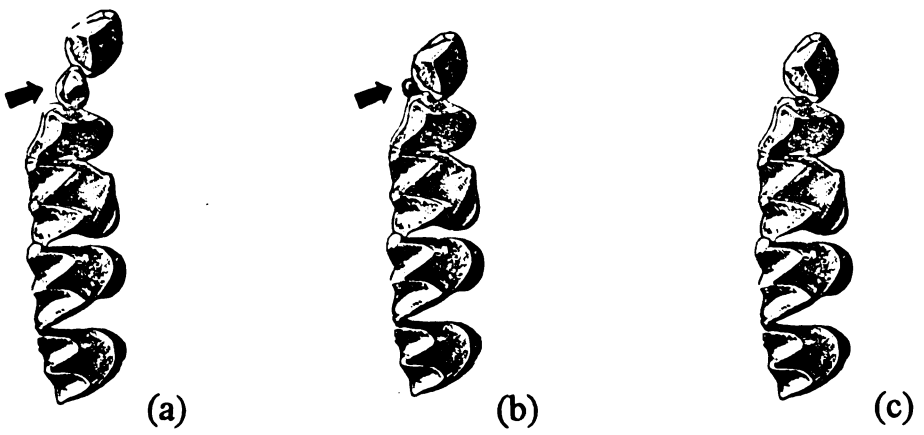


Figure 4.9. The status of P^2 (character 11), pointed by arrow. (a) state *a*, in the toothrow (*R. ions*) ; (b) state *b*, out of toothrow (*R. ferrumequinum*); (c) state *c*, absent (*R. fumigates*).

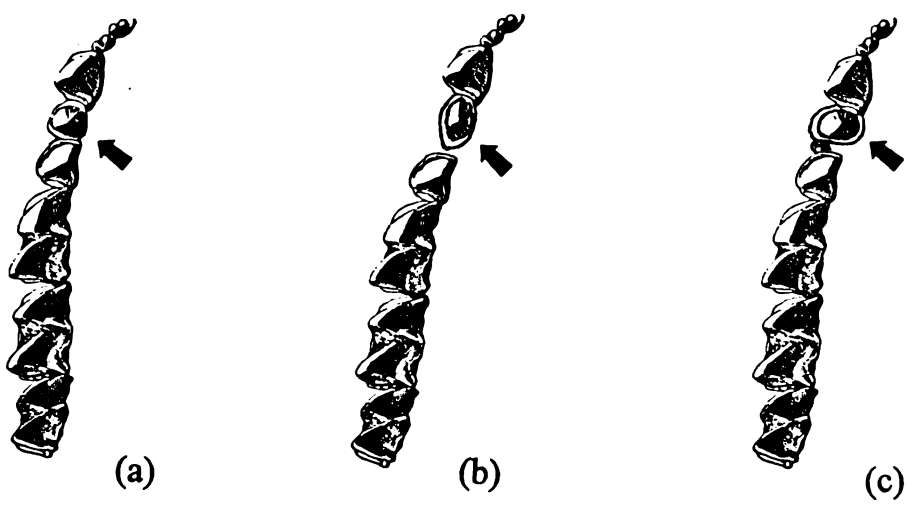


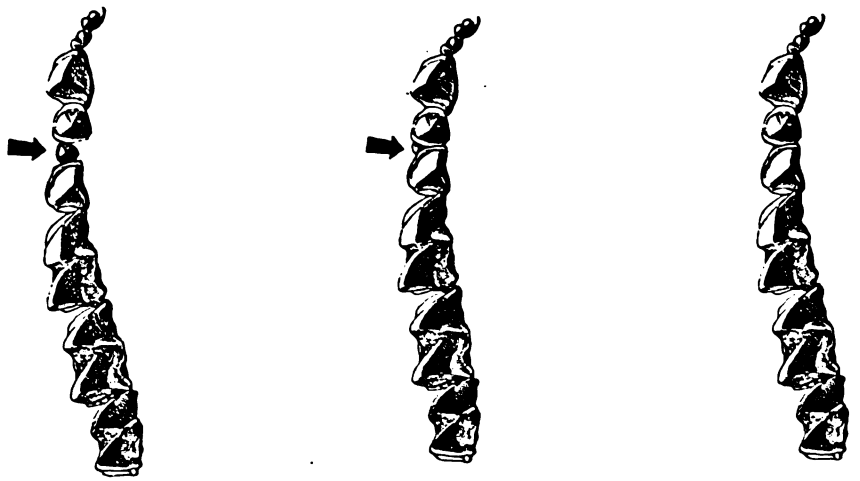
Figure 4.10. The shape of P_2 (character 12), pointed by arrow. (a) state *a*, the length and breadth bout equal (*R. mehelyi*); (b) state *b*, length greater than breadth (*R. clivosus*); (c) state *c*, length less than breadth (*R. ions*).

(*R. euryale* and *R. fumigatus*). The shape of P_2 has sometimes been referred to in species descriptions, but has not been used in previous systematic analyses of *Rhinolophus*. In fact, there is much less intraspecific variation in this feature than in the frequently-used position of P^2 (see above). Considering the conservative nature of rhinolophid dental morphology, distinct shape modifications in P_2 justifiably places this character in weighting group four. Although there seems to be some relationship between the shape of P_2 and compressedness of the cheek toothrow (which is considered a derived feature by Andersen [1905a]), gaps sometimes are found at one or both ends of shortened P_2. Thus, a compressed cheektooth row and short P_2 are not necessarily functionally related. All four genera and eight species of hipposiderids examined as outgroup displays a square shape of P_2. I hypothesize that state *a* is primitive and states *b* and *c* are independently derived: *b* <- *a* -> *c*.

13. Middle Lower Premolar (P_3) (Figure 4.11). This tooth displays three states: *a*, in the toothrow; *b*, small and displaced out of the toothrow; *c*, absent. The discussion for character 11 applies to this one. The states are ordered as *a* -> *b* -> *c*, with state *a* primitive. I placed this character in weighting group one.

14. Cingula of Lower Molars (M_{1-3}). The cingula of the lower molars displays two levels of development: *a*, weakly developed, as in most species; and *b*, strongly developed (e.g. *R. fumigatus* and *R. yunanensis*). Because molar morphology is homogeneous in *Rhinolophus*, the distinction made by this feature is significant. State *a* is by far most frequent in both ingroup and outgroup species; it is reasonable to hypothesize state *a* as primitive. The boundary between the two states is sometimes ambiguous and I have placed this character in weighting group two.

15. Stylarshelf Shelf of M^3: The size of the stylar shelf (the posterior V-shaped triangle



(a) (b) (c)

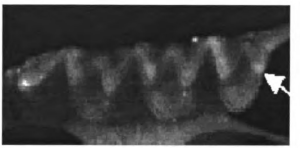
Figure 4.11. The status of P_3 (character 13), pointed by arrow. (a) state *a*, in the toothrow (*R. macrotis*); (b) state *b*, out of toothrow (*R. malayanus*); (c) state *c*, absent (*R. fumigates*).

of the W-shaped outer shelf) in the last upper molar (M^3) varies among species of *Rhinolophus*, it is described by two states (Figure 4.12): *a*, moderately reduced, as in most species; *b*, greatly reduced, with the anterior ridge of the posterior V less than 2/3 the length of the posterior ridge of the anterior V (*R. capensis* and *R. yunanensis*). It is generally agreed (Slaughter, 1970) that the reduction of styleshelf is a derived feature within bats and I hypothesize that state *a* is primitive. Because this character represents a reduction of M^3 and it is a common trend in other families of bats, this character was assigned to weighting group one.

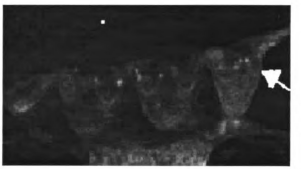
16. Posterior Edge of Palate: The length of the palate is a character widely used in previous taxonomic studies of *Rhinolophus*. The palate varies in length largely due to the depth of the median emargination of its edge. Two species can have the same average palate length, but differ in location of posterior and anterior emargination edges. I recognized two characters that capture the details of palatal morphology in *Rhinolophus*: position, relative to the toothrow, of the posterior edge of the palate (this character), and position of the anterior edge of the palatal emargination (character 17).

The posterior edge of palate displays four character states (Figure 4.13): the posterior edge lies *a*, next to the metastyle of M^2; *b*, between metastyle and metacone of M^2; *c*, between metacone and mesostyle of M^2; and *d*, anterior to mesostyle of M^2. Outgroup analysis indicated that longer, shallowly emarginated palates (state *a*) are primitive within *Rhinolophus*. Consequently, I hypothesized that state *a* is primitive and that the four states were connected in a linear transformational sequence: *a* -> *b* -> *c* -> *d*.

Some intraspecific variation is present for both this character and character 17. I assigned states to species after examining as many specimens as possible (usually 10 or more)



(a)



(b)

Figure 4.12. The shapes of the stylarshelf in M^3 (character 15). (a) state *a* (*R. affinis*); (b) state *b*, the posterior v-shaped ridges (pointed by arrow) greatly reduced (*R. fumigatus*).

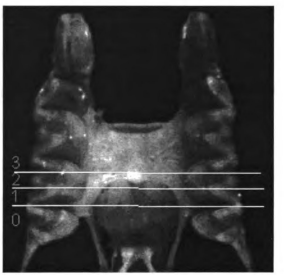


Figure 4.13. Picture (*R. affinis*) illustrates character 13, the position of the posterior margin of the palate pointed by an arrow. Label 0 through 3 correspond to the states *a* through *d* in the text.

and using the state most common within a species. Because of this variation, and the arbitrary nature of the landmarks chosen to recognize character states, I placed this character in weighting group two.

17. Anterior Margin of Palate (AMP) (Figure 4.14). This character has been used in a key to African *Rhinolophus* by Koopman (1975) in which he recognized two states. For species of the entire genus I recognized three states for this character: anterior margin of palate emargination located *a*, anterior to the protocone of P^4; *b*, between protocone of P^4 and mesostyle of M^1; and *c*, at or posterior to the mesostyle of M^1. As discussed in character 16, this character is assigned to weighting group two and state *a* is assumed to be primitive, with transformation series *a->b->c*.

18. Front Margin of Anterior Nasal Swelling (FMNS) (Figure 4.15). The anterior margin of the anterior nasal swelling lies at three different positions relative to the toothrow in *Rhinolophus*: *a*, at or anterior to the parastyle of M^1; *b*, between parastyle and mesostyle of M^1; and *c*, at or posterior to mesostyle of M^1. This character has not been utilized in previous systematic research within the genus. It becomes obvious once photographs of lateral views of the skills are examined. There appears to be some correlation between position of the front margin of this nasal swelling and that of the palate bridge. I do not believe this possible correlation is important for two reasons: first, I know of no functional explanation for such a correlation; second, while it is reasonable to assume that a shallower palatal emargination is a primitive state, it is not at all evident that the relative anterior position of this nasal swelling is primitive. Because no clear homologous structure is present in other closely related bat families, I applied the in-group commonality rule (Watrous and Wheeler, 1981) and

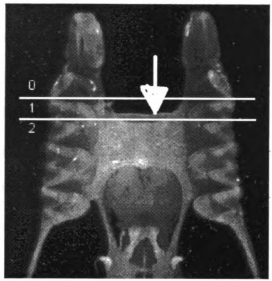


Figure 4.14. The position of the anterior margin of the palate (character 17), pointed by arrow, of *R. affinis*. Label 0 through 2 correspond to the states *a* through *c* in the text.

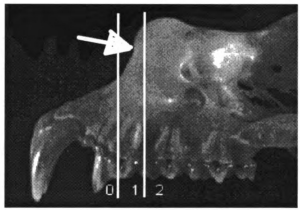


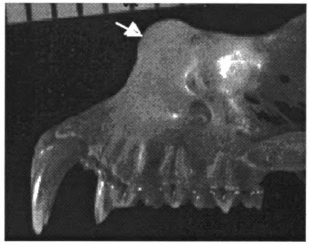
Figure 4.15. The position of the front margin of anterior nasal swelling (character 18), pointed by arrow, of *R. affinis*. Label 0 through 2 correspond to the states *a* though *c* in the text.

hypothesized that state *a* is the primitive state: *a* -> *b* -> *c*. The arbitrary boundary between states placed this character in weighting group two.

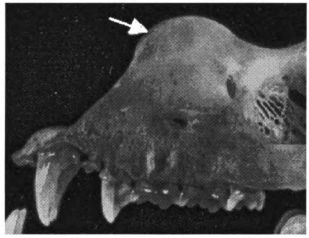
19. Length of Median Frontal Nasal Swellings (LNS) (Figure 4.16). The length of the median frontal nasal swelling varies between species of *Rhinolophus*. A convenient way to characterize this variation is with the following two character states: *a*, small or less than the combined length of M^1 and M^2 located beneath it in lateral view, as is the case of most species; and *b*, large with length greater than the combined length of M^1 and M^2 (e.g. *R. luctus* and *R. sedulus*). Except for a few species with intermediate size (e.g. *R. clivosus*), most species fit relatively easily into these two size categories. The landmarks defining states of this character are arbitrarily chosen for convenience. This character appears to be positively correlated with noseleaf size, although functional reasons for this are unclear. For these reasons, I assigned this character to weighting group two. State *a* is assumed to be primitive for two reasons: first, it is the state found in most species; second, the nasal swelling is a feature unique to *Rhinolophus* and it is parsimonious to assume it arose as a small feature.

20. Depth of Orbital Constriction (OrbC) (Figure 4.17). Variation in the orbital constriction displays two states: *a*, shallow as in most species; and *b*, very deep, the depth greater than half of the front nasal swelling height (e.g. *R. blassi* and *R. creaghi*). State *a* is assumed to be primitive on the basis of its frequency of occurrence both within and outside of the genus. The arbitrary state boundary placed this character in weighting group two.

21. Infraorbital Canal and Bar (InfOrb) (Figure 4.18). The shape of infraorbital canal and bar vary together and fall into three categories: *a*, canal nearly round and infraorbital bar short and narrow (e.g. *R. rouxi* and *R. bornensis*); *b*, canal heightened, bar elongated and thin (e.g. *R. clivosus* and *R. eloquens*); and *c*, canal round but moved anteriorly with the bar

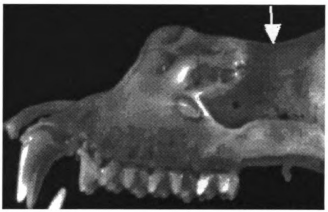


(a)

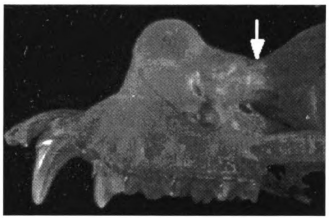


(b)

Figure 4.16. Pictures illustrate character 19, the length of median frontal nasal swellings. (a) state *a*, small (*R. affinis*); (b) state *b*, larger (*R. luctus*).



(a)



(b)

Figure 4.17. The depth of the orbital constriction (charcter 20), pionted by arror. (**a**). state *a*, shallow (*R. lepidus*); (b). state *b*, deep (*R. creaghi*).

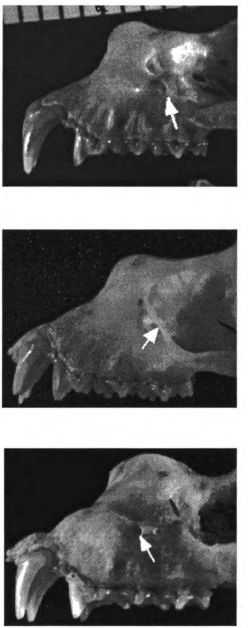


Figure 4.18. The shapes of the infraorbital canal and bar (character 21), pointed by arrows. (a) state *a*, size moderate (*R. affinis*); (b) state *b*, infraorbital bar elongated (*R. clivosus*); (c) state *c*, canal lengthened and bar broader (*R. luctus*).

greatly broadened (e.g. *R. luctus* and *R. trifoliatus*). It is not entirely clear which is the primitive state. Because it is most common in both ingroup and outgroup, state *a* is most likely to be the primitive state with an order of *b* <- *a* -> *c*. Except for a few species (e.g. *R. inops* and *R. euryotis*), most can be assigned a state without difficulty. This character was placed in weighting group three.

22. Shape of Internairal Region (IntNa). Two states were identified: *a*, not expanded, (e.g. *R. pusillus* and *R. affinis*); and *b*, expanded (e.g. *R. trifoliatus* and *R. arcuatus*). This character is used traditionally to separate the otherwise similar *arcuatus* group from the *fumigatus* group of species. I recognize such separation of two character states despite the somewhat arbitrary boundary between states. For the same reasons I discussed in characters 1 through 4 on noseleaves (noseleaf structures are highly informative, and small feature size is primitive), I hypothesized, that state *a* is primitive, and assigned this character to weighting group three.

Continuous characters

Characters 23 to 26 are external measurements of specimens, adjusted by body size. These continuous characters are coded into discrete states using gap-coding (Michevich and Johnson, 1976). The means and standard deviations of each variable (a ratio in this case) for each species were calculated. The pooled standard deviation (*Sd*) for each variable was also computed. For each variable, species means were sorted and gaps greater than (*Sd* * *C*) were identified between successive species. Species on the two sides of these gaps belong to two distinct character states. *C* was chosen to set the overlap between species on different sides of the gap to a predetermined level. When $C = 0.25$, the percent of overlap between two species

separated by a gap is 45%; when $C = 0.5$, the overlap is 40.1%; when $C = 1$, the overlap is 30.9% and when $C = 2$, the overlap is 15.9% (Archie, 1985).

This method, the discrete-state coding methods in general, is associated with a weak assumption that gaps stand for significant evolutionary steps that occur less often than evolutionary changes between gaps. (Felsenstein, 1988). There is no *a priori* reason to believe this assumption models correctly the pattern of rhinolophid evolution. The gap-coding method also has the disadvantage that gaps tend to become less numerous when the number of species involved becomes larger. The present study contains a large enough number of species to suspect that gaps used here are conservative estimates of the true, 'evolutionary' gaps. Since I chose C between 0.1 and 0.25, which was necessary to recognize 4 or 5 distinct states for each character, overlap between species separated by a gap may be more than 50%. I utilized gap coding to transform continuous variables, viewed by previous workers as important indicators of species differences, into discrete states that can be compared and analyzed with previously described characters. I am more concerned with the comparability gap coding transform makes possible than with special assumptions about the way continuous character evolve in *Rhinolophus*. Due to the significant overlap evolution in between species separated by gaps, I placed character 23 - 26 in weighting group two.

23. Relative Ear Size (Ear/Fa). Ear size was adjusted using forearm length as an estimator of the body size. With $C = 0.15$, four states were identified among *Rhinolophus* species, state *a* representing the smallest ratio. This character was used because relatively larger ears (and antitragus) have been used by previous taxonomists to distinguish the *philippinensis* and *arcuatus* groups. While it is generally accepted (and confirmed by outgroup comparison) that relatively larger ears is a derived feature in rhinolophids, it is doubtful whether the smallest

ratio is the primitive state within the genus. I hypothesized that (by far) the most common state, state *b*, is primitive, yielding a polarity of *a* <- *b* -> *c* -> *d*.

24. Relative Phalangeal Length of Digit 3 (1/2F3). The relative lengths of the third digit first and second phalanges have been widely used in previous studies of *Rhinolophus*. With C = 0.11, four states were identified with state *a* representing the smallest ratio. Both ingroup and outgroup examinations demonstrated that *b* is the most common state. I hypothesize that state *b* is primitive, and the polarity is *a* <- *b* -> *c* -> *d*. Both a reduction in second phalanx length and an elongation of the third resulted in an increase of this ratio.

25. Relative Phalangeal length of Digit 4 (1/2F4). The relative lengths of the fourth digit first and second phalanges has been used in regional keys for *Rhinolophus*, and is a diagnostic character for several species (e.g. *R. mehelyi* and *R. euryale*). Variation in the relative phalangeal length of the fourth digit is greater than that of the third digit due to a more remarkable reduction in the first phalanx. With C = 0.25, five states were recognized with state *a* representing the smallest ratio. Because state *b* was the most common state both in this genus and in outgroup, I hypothesized that state *b* is primitive and the order was assumed *a* <- *b* -> *c* -> *d* -> *e*.

26. Relative Length of the Third and Forth Metacarpal (M3/M4). The ratio of the third and the forth metacarpal has been used in regional species diagnosis of *Rhinolophus* and in recognizing relationships within species groups. With C = 0.1, four states were recognized, state *a* representing the smallest ratio. It is generally agreed that state *d* (two metacarpals being about equal in length) is the primitive state, and that the decrease of this ratio is due primarily to a shortening of the third metacarpal (Andersen, 1905a). The present data also showed that

state *d* is the most common in the genus. For these reasons, I hypothesized a polarity of *a* <- *b* <- *c* <- *d* for this character.

Table 4.1 summarizes the distribution of the character states described above. The cladistic analysis is based on this character analysis.

Table 4.1. The character transformation series matrix used in the cladistic analysis. Numeric numbers 1, 2, ... are correspondent to the states *a, b,* ... in the section of character analysis respectively. Missing data are represented by '?'.

Spp. \ character#	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
R. acuminatus	4	1	2	2	2	0	1	1	1	2	0	2	1	0	0	1	2	1	0	0	12	0	2	2	2	4
R. adami	2	2	4	?	1	0	2	?	?	2	1	?	2	0	?	0	2	0	0	0	0	0	2	2	5	2
R. affinis	1	1	3	3	2	1	1	1	1	1	1	2	1	0	0	3	1	1	0	0	1	0	2	2	2	4
R. alcyon	4	1	4	3	1	1	1	1	1	2	0	0	1	0	0	0	2	1	0	0	1	0	2	3	5	2
R. arcuatus	5	2	3	3	2	1	1	1	1	2	0	2	1	1	0	3	1	0	0	1	0	1	2	2	2	4
R. blassi	4	1	3	1	1	0	1	0	1	2	0	0	1	0	0	0	2	1	0	0	0	0	2	2	4	3
R. bornensis	1	1	3	2	2	1	2	1	1	2	0	2	1	0	0	2	1	1	0	0	0	0	2	2	2	3
R. canuti	5	2	4	3	2	1	2	1	1	1	1	0	2	1	1	3	1	0	0	1	0	1	2	2	2	4
R. capensis	1	1	1	1	1	0	1	0	0	2	0	1	1	0	1	0	2	2	0	0	1	0	2	2	4	3
R. celebensis	1	1	1	3	2	1	1	1	1	1	0	2	1	0	0	2	1	1	0	0	0	0	2	2	2	4
R. clivosus	1	1	1	3	1	0	1	0	0	2	1	1	2	0	0	1	2	2	0	0	1	0	2	2	3	2
R. coelophyllus	5	2	3	2	2	1	2	1	1	1	0	2	1	1	0	2	1	1	0	1	0	1	2	2	2	4
R. cornutus	4	1	1	3	2	1	2	1	1	1	0	2	0	0	0	2	1	1	0	0	0	0	2	2	2	4
R. creaghi	5	2	4	3	2	1	1	0	1	1	0	1	1	1	0	3	1	0	0	1	0	1	2	2	2	4
R. darlingi	1	1	1	3	1	0	1	0	1	2	1	1	1	0	0	1	2	1	0	0	0	0	2	2	4	2
R. denti	4	1	3	1	2	0	1	0	0	2	0	0	1	0	0	1	2	2	0	0	1	0	2	2	4	2
R. eloqens	1	2	4	2	1	0	2	1	0	2	2	1	2	0	1	1	2	1	1	0	1	0	2	4	4	3
R. euryale	4	1	1	1	2	0	1	0	0	1	0	0	1	0	0	0	2	2	0	0	0	0	2	4	5	3
R. eruyotis	5	2	4	2	1	1	2	1	1	1	0	2	1	1	0	3	1	0	0	1	1	1	1	2	2	4
R. ferrumequinum	1	1	1	3	1	1	1	0	0	2	1	1	0	0	0	1	1	1	0	0	1	0	2	2	3	2
R. hildebrandti	1	2	3	2	1	0	1	0	0	2	1	1	1	2	0	1	2	1	1	0	1	0	2	3	4	3
R. hipposideros	1	1	1	3	1	0	2	0	0	2	0	0	1	0	0	1	2	0	0	0	0	0	2	2	4	2
R. inops	5	2	4	3	2	1	2	1	1	1	0	2	1	1	0	3	1	0	0	1	1	1	2	2	2	4
R. landeri	4	1	1	1	1	0	1	0	0	2	0	0	1	0	0	1	2	1	0	0	1	0	2	2	5	2
R. lepisus	4	1	1	3	2	1	1	1	1	2	0	0	1	0	0	2	1	1	0	0	0	0	2	2	2	4
R. luctus	3	3	4	1	1	1	1	1	1	3	0	0	1	0	0	2	0	0	1	1	2	1	3	2	2	1
R. imaizumii	4	1	1	3	2	1	0	0	1	2	0	2	1	0	0	2	1	1	0	0	0	0	2	2	2	4
R. maclaudi	3	3	4	2	1	0	2	1	0	3	0	0	0	1	0	0	1	1	1	1	2	1	4	2	3	3
R. macrotis	2	2	4	2	2	1	2	1	1	2	0	0	0	0	0	0	0	1	1	0	2	1	3	2	2	4
R. malayanus	1	1	2	2	2	1	1	1	1	2	0	1	1	0	0	3	1	0	0	1	1	0	2	2	2	4
R. marshalli	3	3	4	?	2	?	2	0	?	3	0	0	0	0	0	0	0	0	1	0	2	1	3	2	2	4
R. megaphyllus	1	1	1	3	2	1	2	1	1	2	0	0	1	0	0	2	1	1	0	1	1	0	2	2	2	4
R. mehelyi	4	1	1	1	2	0	1	0	0	2	1	0	1	0	1	0	2	2	0	1	1	0	2	5	5	4
R. monoceros	4	1	1	3	2	1	1	1	1	2	0	0	1	0	0	2	1	1	0	0	0	0	2	2	2	4
R. nereis	1	1	2	3	2	1	2	1	1	1	0	2	1	0	0	3	1	0	0	0	0	0	2	2	2	2

Figure 4.1. (Continued.)

Spp. \ character#	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
R. osgoodi	4	1	1	3	2	1	2	0	0	1	0	2	0	0	0	0	1	1	0	0	0	0	2	2	2	4
R.paradoxolophus	3	2	4	?	2	?	2	0	?	?	0	2	1	0	0	0	0	0	1	0	2	1	2	2	2	4
R. pearsoni	5	2	4	2	1	1	2	1	1	2	0	2	0	1	0	2	0	1	0	0	1	0	2	2	2	2
R. philippinensis	3	2	4	2	2	1	2	0	1	2	0	2	0	0	0	1	0	0	1	1	0	1	3	2	2	4
R. pusillus	4	1	1	2	2	0	1	1	0	2	0	2	0	0	0	2	1	1	0	0	0	0	2	2	2	4
R. rex	3	3	4	1	2	1	2	0	1	3	0	2	0	0	0	0	0	0	1	1	2	1	2	2	2	4
R. rouxi	1	1	3	2	2	1	1	1	1	2	0	1	1	0	1	2	2	1	0	0	0	0	2	2	2	4
R. rufus	5	2	4	1	2	1	1	1	1	1	0	2	1	1	2	3	1	1	1	1	2	1	2	2	1	4
R. shameli	5	2	4	3	2	1	2	1	1	1	0	2	1	1	0	2	1	0	0	1	0	1	2	2	2	4
R. sedulus	3	3	3	1	1	1	1	1	1	2	0	2	1	0	0	3	1	0	1	1	1	1	2	2	2	1
R. simplex	1	1	1	3	2	1	1	1	1	3	0	2	1	0	0	3	1	0	0	0	2	0	2	2	2	4
R. simulator	1	1	3	3	2	1	2	0	0	2	0	0	1	0	0	0	1	1	0	0	1	0	2	2	4	2
R. stheno	1	1	1	3	2	1	1	1	1	1	0	2	1	1	0	3	2	2	0	1	0	0	2	2	2	4
R. subbadius	4	1	1	3	2	1	1	1	1	1	0	2	0	0	0	3	1	1	0	0	0	0	2	2	2	3
R. subrufus	5	2	4	2	2	1	2	1	1	2	0	2	1	1	0	3	1	0	1	1	0	1	2	1	1	4
R. swinny	1	1	3	3	2	1	1	0	1	2	1	0	1	0	1	1	3	1	0	0	1	0	2	2	5	2
R. thomasi	1	1	1	2	2	1	2	1	1	2	0	2	1	0	0	2	2	1	0	0	0	0	1	2	2	4
R. trifliatus	3	3	4	1	1	1	1	1	1	3	0	0	1	1	0	1	0	0	1	1	2	1	2	2	2	1
R. vergo	1	1	1	3	2	1	2	1	0	2	0	2	1	0	0	3	1	0	0	0	0	0	2	2	2	3
R. yunanensis	5	2	4	1	1	1	2	1	1	2	0	2	1	0	1	2	1	1	1	1	1	0	2	2	2	3
outgroup	0	1	1	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	4

CLADISTIC ANALYSIS

I performed a cladistic analysis of the characters described above for 56 species of *Rhinolophus*. This analysis was based on characters that were, for the most part, ordered into transformation series that could be weighted for their likely content of phylogenetic information. Several characters, though, were assigned transformation series that were uncertain. Character 1, in particular, was assigned a transformation series based more on traditional arguments than on compelling evidence. I believed the this was one of the most informative characters. Since the manner of relating its character states was likely to influence the structure of a phylogenetic hypothesis based on them, I performed the cladistic analysis in two ways: treating character 1 as unordered; and as ordered into the transformation series described in the previous section. Additionally, the use of character weights in phylogenetic analysis is controversial (Sneath and Socal, 1973; Sharkey, 1989). To judge the effect of weighting characters on the resulting cladograms, I performed the analysis both with and without character weighting. In all, four sets of analyses were performed: (a) characters weighted and character 1 ordered into a transformation series; (b) characters weighted and character 1 unordered; (c) characters unweighted and character 1 ordered; and (d) characters unweighted and character 1 unordered. A monophyletic group present in all analyses represents a phylogenetic hypothesis better supported by the data than those present only in some, but not all, analyses (Straney, 1981). The outgroup used is a hypothetical organism with the primitive state for all characters except for characters whose polarities are unclear, where an additional hypothetical primitive state is assigned to it.

For each set of analyses, I used the PAUP 3.1.1 program, as described in the Materials and Methods section above. This program calculates the shortest cladogram for a set of input data, cladogram length being measured by the total number of evolutionary steps required by a particular hypothesis of phylogenetic relationships[1]. Because of the relatively large number of species examined in this study (56 species), the practical limitations of the programs required use of the heuristic search procedure to search for the shortest cladogram or cladograms for that data set[2]. Some of my analyses resulted in thousands of cladograms of equivalent shortest length. Available computer memory limited the number of cladograms that could be stored to about 1300. Consequently, only the first 1300 shortest cladograms identified by the program could be saved and analyzed. This limitation introduces a possible source of inaccuracy, as the heuristic search procedure is sensitive to the order of samples in the input data matrix (Geske, 1992). To minimize the effect of this limitation I repeated the computer analysis for the same data set and each time rearranged the species positions in the data matrix. The number of steps in the shortest cladograms derived from differently rearranged data matrices was invariable. I further computed strict consensus cladograms (Swofford and Begle, 1993) for each set of 1,300 shortest cladograms. The discrepancies between these strict consensus cladograms were very small and insignificant. To show variation among the shortest cladograms I also computed the consensus cladogram under majority rule for each set. Particular relationship was preserved if it was common to fifty percent or more of the shortest cladograms.

---

[1]When the characters are weighted, however, the transformations occurring in different characters are themselves weighted. For example, if one transformation occurred in a character having a weight of two, then that change accounts for 2 units of length.

[2]The algorithm for exhaustive search of shortest tree is computationally intractable. Such searching algorithms are not practical for large data sets regardless of the computer system and the program (Garey and Johnson. 1991).

The use of heuristic search and consensus cladograms has become a standard approach to cladistic analysis of large data sets (Swofford and Begle, 1993; Maddison and Maddison, 1992). Three additional considerations justify the use of heuristic search and consensus methods in the present study. First, a data set with more than 20 taxa (more than 20 species in the present case) can not be analyzed using exhaustive search procedure (Swofford and Begle, 1993). The computational feasibility of heuristic search procedure with more than 20 taxa is achieved at the expense of optimal results. There is no guarantee, when the heuristic algorithm is used, that the true, most parsimonious cladogram is included in the set of shortest cladograms. As a result, in many cases the phylogenetic relationship for a relatively large group is computationally an approximation. Second, as the sample set of the shortest cladograms taken from all possible shortest cladograms was quite large (1300). The possibility that this sample set is unrepresentative of the total set should be relatively small. Indeed, the 1300 shortest cladograms produced by repeated analyses of the (same) reordered data matrix show very little, and often no, discrepancy in the topology of the consensus cladograms they entail. Finally, because strict consensus, extracts only the relationships common to all shortest cladograms produced by a given analysis, it provides a very conservative estimate of relationships.

Analysis of Weighted Characters, Character 1 Ordered

The strict consensus and majority consensus cladograms for this analysis are presented in Figure 4.19 and 4.20, respectively. The species names are followed by symbols for their geographic distribution in parenthesis (A = 'southeast Asia', F = 'Africa', E = 'western Eurasia and Africa'). The species' identity in the traditional species groups is the same as in Table 3.1.

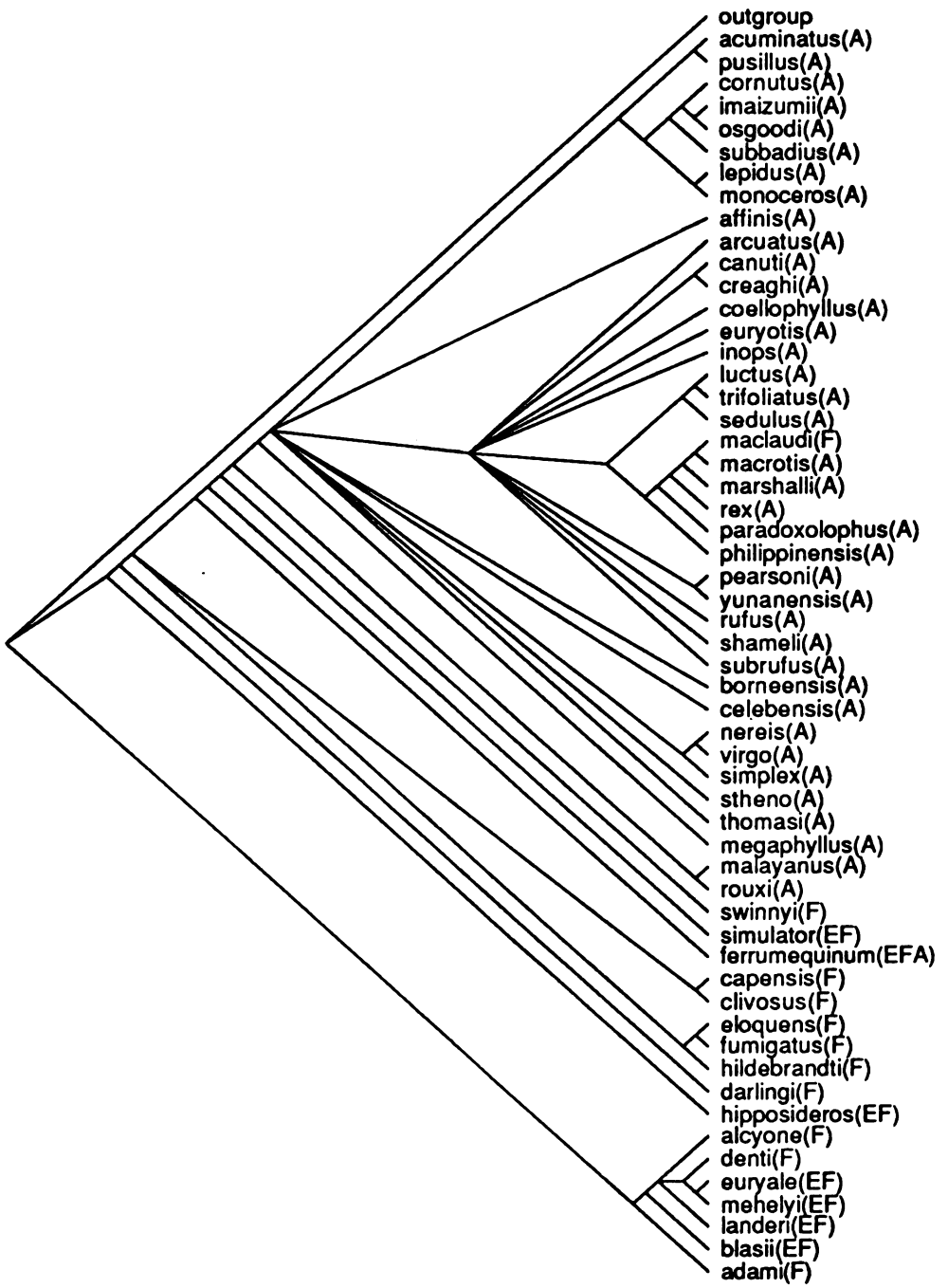


Figure 4.19: The strict consensus cladogram for the 24 most parsimonious cladograms resulting from the weighted analysis, character 1 ordered. . The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

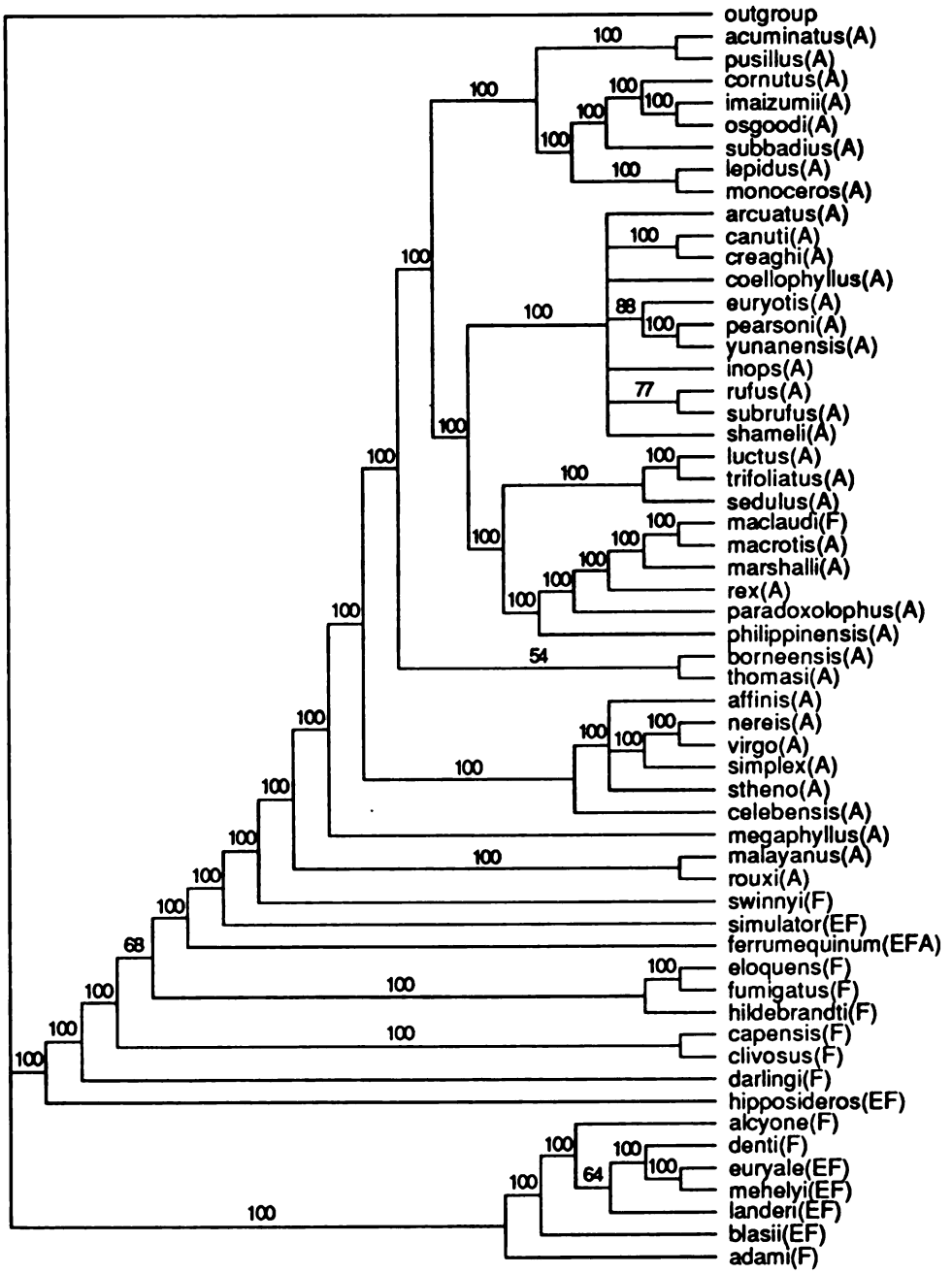


Figure 4.20: The majority consensus cladogram for the 1200 most parsimonious cladograms resulting from the weighted analysis, character 1 ordered. The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia. The numbers indicate the percentage of cladograms in which this particular branching structure is present.

One of the most obvious patterns present in this cladogram is the species branching from Africa and western Eurasia near the root of the cladogram. While all species distributed in southeast Asia plus one African species (*R. maclaudi*) constitute a monophyletic group (synapomorphies in characters 8, 16, 24, 25), as a sister group of the African species *R. swinnyi*. Among African and western Eurasian rhinolophids, seven species, *R. alcyone, R. denti, R. euryale, R. mehelyi, R. landeri, R. blassi,* and *R. adami* form a group that is separated basally from the remaining species. Except for *R. adami* which has been placed in the *ferrumequinum* group, all these species are members of the traditional *pusillus* group. This group of seven species is defined by synapomorphies in characters 1, 3 and 24. Another group of three species, *R. eloquens, R. fumigatus* and *R. hildebrandti*, recognized by Andersen (1905b) as African members of the *fumigatus* group, also form a monophyletic group defined by synapomorphies in characters 2, 4, 19, 24 and 26. The remaining African and western Eurasian species are resolved into a series of dichotomous relationships.

Two major monophyletic groups are apparent within the southeast Asian clade in this reconstruction. The first includes *R. acuminatus, R. pusillus, R. cornutus, R. imaizumii, R. osgoodi, R. subbadius, R. lepidus*, and *R. monoceros*, all southeast Asian members of the traditional *pusillus* group. The only synapomorphies for these species is state *d* in character 1, which has been the primary feature defining the traditional *pusillus* group. The second major monophyletic group of southeast Asian species includes *R. luctus, R. trifoliatus, R. sedulus, R. maclaudi, R. macrotis, R. marshalli, R. rex, R. paradoxolophus*, and *R. philippinensis*, all species of the traditional *philippinensis* group. In this clade, *R. macrotis* differs from all other species in its higher and relatively more acute connecting process (character 1). Three species, *R. macrotis, R. paradoxolophus*, and *R. philippinensis* are more primitive by absence of sella

lappets (character 2). The synapomorphies invariably present in all species of this clade are enlarged nasal swellings (state *c* in characters 19) and expended sella (state *c* in character 2). It is very interesting that this clade also includes *R. maclaudi*, the only African species found in this monophyletic group of an otherwise exclusively southeast Asian species group. *R. maclaudi* clearly presents character states in characters 1, 2, 19 which are synapomorphies for this clade. Apparently, these remarkable similarities between *R. maclaudi* and the southeast Asian species of the traditional *philippinensis* group placed this African species with the southeast Asian species, even though *R. maclaudi* does not possess derived states in character 5 and 9 which are synapomorphies for all southeast Asian rhinolophids.

Eleven other species join the *philippinensis* group to form a larger monophyletic unit. Phylogenetic relationships among these species were not resolved in the consensus cladogram. Nine of these species, constituting the traditional *arcuatus* species group, are *R. arcuatus, R. canuti, R. creaghi, R. coelophyllus, R. euryotis, R. inops, R. rufus, R. shameli,* and *R. subrufus*. The other two species , *R. pearsoni* and *R. yunanensis*, are Asian members of the traditional *fumigatus* group. The phylogenetic reconstruction implied by Figure 4.19 indicates that the hypothetical ancestor of this larger monophyletic group had synapomorphies in characters 2, 3, 20, and 22.

The remaining southeast Asian species, which together constitute the southeast Asian members of the traditional *ferrumequinum* group, are situated at the base of the southeast Asian clade. Relationships among these 11 species are not resolved in the consensus cladogram. Under this reconstruction, even the southeast Asian members of the *ferrumequinum* group are paraphyletic. Without additional shared derived characters, the shared shape of the connecting process alone (the state used traditionally to define this species

group) did not provide sufficient evidence to unite these species. Their shared shape in connecting process is not a true synapomorphy. The synapomorphies defining the clade of all southeast Asian species are characters 5, 8, 9, and 16.

In general, then, the strict consensus of this data set yields a phylogenetic hypothesis that recognizes six major monophyletic groups: (a) southeast Asian species of the traditional *pusillus* group; (b) African and western Eurasian species of the *pusillus* group; (c) species of the traditional *philippinensis* group; (d) species of the traditional *philippinensis* and *arcuatus* groups; (e) all species from southeast Asia plus *R. maclaudi* from Africa; and (f) African species of the traditional *fumigatus* group. The majority consensus cladogram (Figure 4.20) indicates that two additional monophyletic groups are supported by a majority of, but not all, shortest cladograms in the analysis. The majority consensus recognizes the traditional *arcuatus* group as a monophyletic group, and groups several species of the traditional *ferrumequinum* group together as a monophyletic group. The presence of these two monophyletic groups in the majority consensus, but not in the strict consensus, suggests that the data provide weaker support for a phylogenetic hypothesis that recognizes these as monophyletic.

The shortest cladograms have a consistency index (the ratio of the length of innovative transformation length to total length of transformation) of 0.228. This means that on average there are nearly 3.5 convergence or reversals after each original character transformation. This low consistency index indicates that a considerable number characters used in this analysis are relatively unstable. Each of the characters 3, 7, 9, 15, 20 and 21, in particular have homoplasy ratio of six or greater. The phylogenetic relationships based on these characters should be carefully examined.

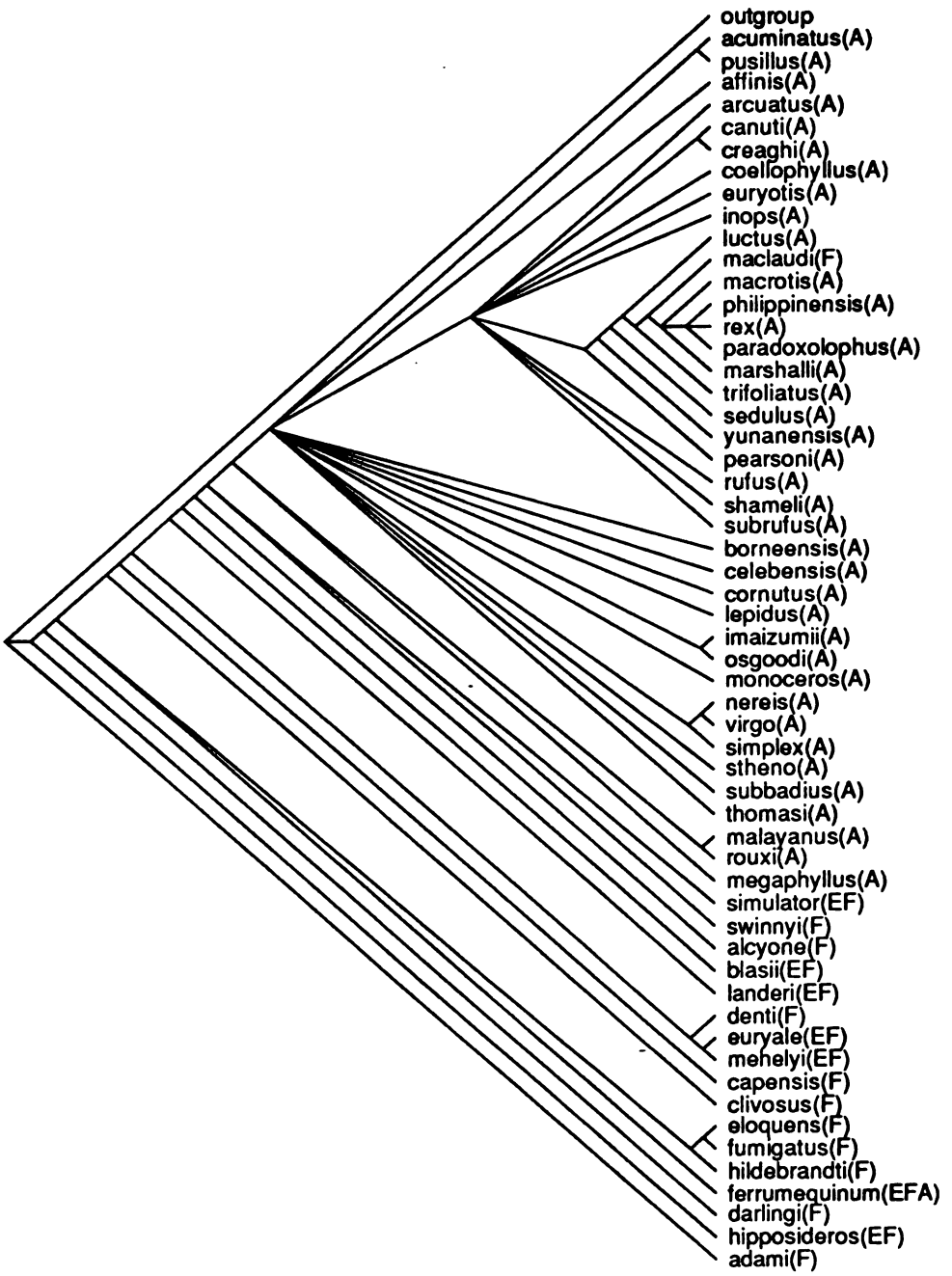


Figure 4.21: The strict consensus cladogram for the 1300 most parsimonious cladograms resulting from the weighted analysis, character 1 unordered. . The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

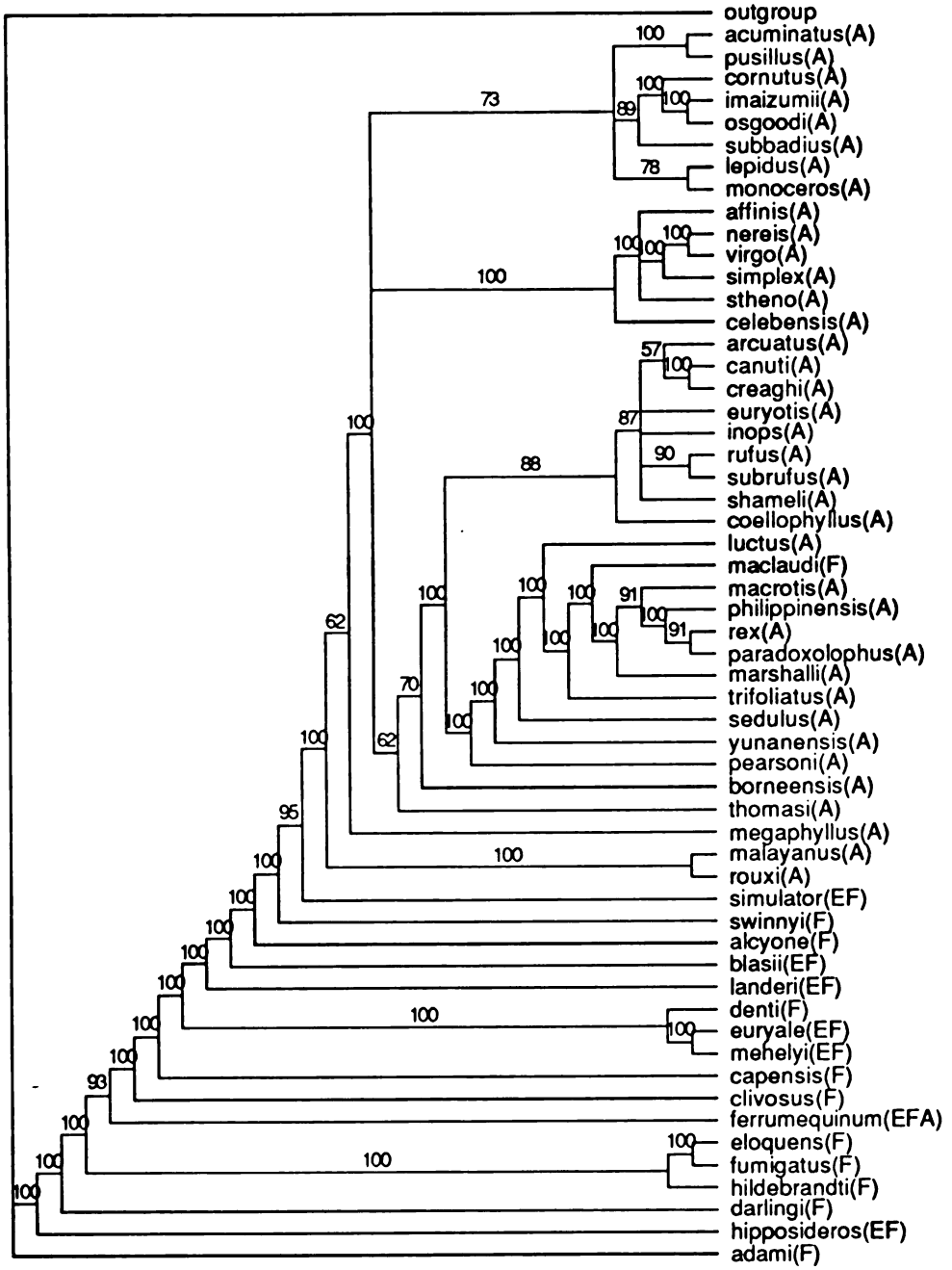


Figure 4.22: The majority consensus cladogram for the 1200 most parsimonious cladograms resulting from the weighted analysis, character 1 unordered. The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia. The numbers indicate the percentage of cladograms in which this particular braching stucture is present.

Analysis of Weighted Characters, Character 1 Unordered

This analysis differs from the preceding one by removing the transformation series for character 1 and treating this character as unordered. The strict and majority consensus cladograms from this analysis are presented in Figures 4.21 and 4.22, respectively. The topologies of these consensus cladograms differ from those of the previous analysis in important ways, indicating the important role of character 1 in delineating monophyletic groups within the genus.

The monophyletic group containing the traditional *philippinensis* and *arcuatus* groups Previously analyzed remains in the consensus cladogram for the present study. Within this group, two species (*R. pearsoni* and *R. yunanensis*) are placed with the traditional *philippinensis* group species rather than the *arcuatus* group. More markedly, the traditional *pusillus* group, clearly monophyletic in the previous analysis, is less consistently present in the cladograms produced by the present analysis. This group is not present in the strict consensus cladogram of Figure 4.22, although it is present in the majority consensus (Figure 4.22). This outcome is likely due to the decreased number of steps needed to change between certain states of character 1 from multiple to single step. A change between state *c* (e.g. *R. philippinensis*) and state *d* (e.g. *R. pusillus*) of character 1 in an ordered analysis adds a length of 16 units to the cladogram. An unordered analysis adds only four units to the cladogram, which makes a group primarily defined by character 1 less stable. As shown in the previous analysis, only two synapomorphies for the southeast Asian member of *pusillus* group were characters 1 and 7, in which character 7 is in the second lowest weighting group. The features

of the traditional *pusillus* group are otherwise relatively primitive. A small clade, including three species of *ferrumequinum* group (*R. nereis, R. virgo* and *R. simplex*), is present.

Both consensus cladograms for this analysis indicated a more dichotomous pattern of relationship for African and western Eurasian species than did the previous analysis. This was primarily due to the disintegration of the clade consisting of the African and west Eurasian members of the traditional *pusillus* group. This clade, defined by synapomorphies in characters 1, 3, 9 and 25 and containing 7 species in Figure 4.19, was reduced to a much smaller clade of only 3 species in the present analysis. When the hypothesized transformation series for character 1 was applied (ordered), a transformation from state *a* (represented by *ferrumequinum* group) to state *d* (represented by *pusillus* group) required two steps; when no particular transformation series for character 1 was assumed or unordered, the same transformation is achieved in one step. The species of the traditional *pusillus* group have moved from the base of the cladogram to more derived positions among the African and west Eurasian species in which a reversal of character 1 occurred. Three species of the traditional *fumigatus* group, *R. eloquens, R. fumigatus* and *R. hildebrandti*, form a monophyletic group as they did in the previous analysis. No monophyletic groups that were identified in this analysis were not found in the previous analysis. The characters responsible for this dichotomous branching pattern near the base of the cladogram in the present analysis include characters 1, 4, 7, 11, 12, 16, 18, 21, and 25.

Overall the unordered analysis resulted in less resolved consensus cladograms than the ordered analysis. The strict consensus identifies three major monophyletic groups: a clade for all members of the traditional *philippinensis* group, a clade for all members of the traditional *arcuatus* and *philippinensis* groups, and a clade for all southeast Asian species plus *R.*

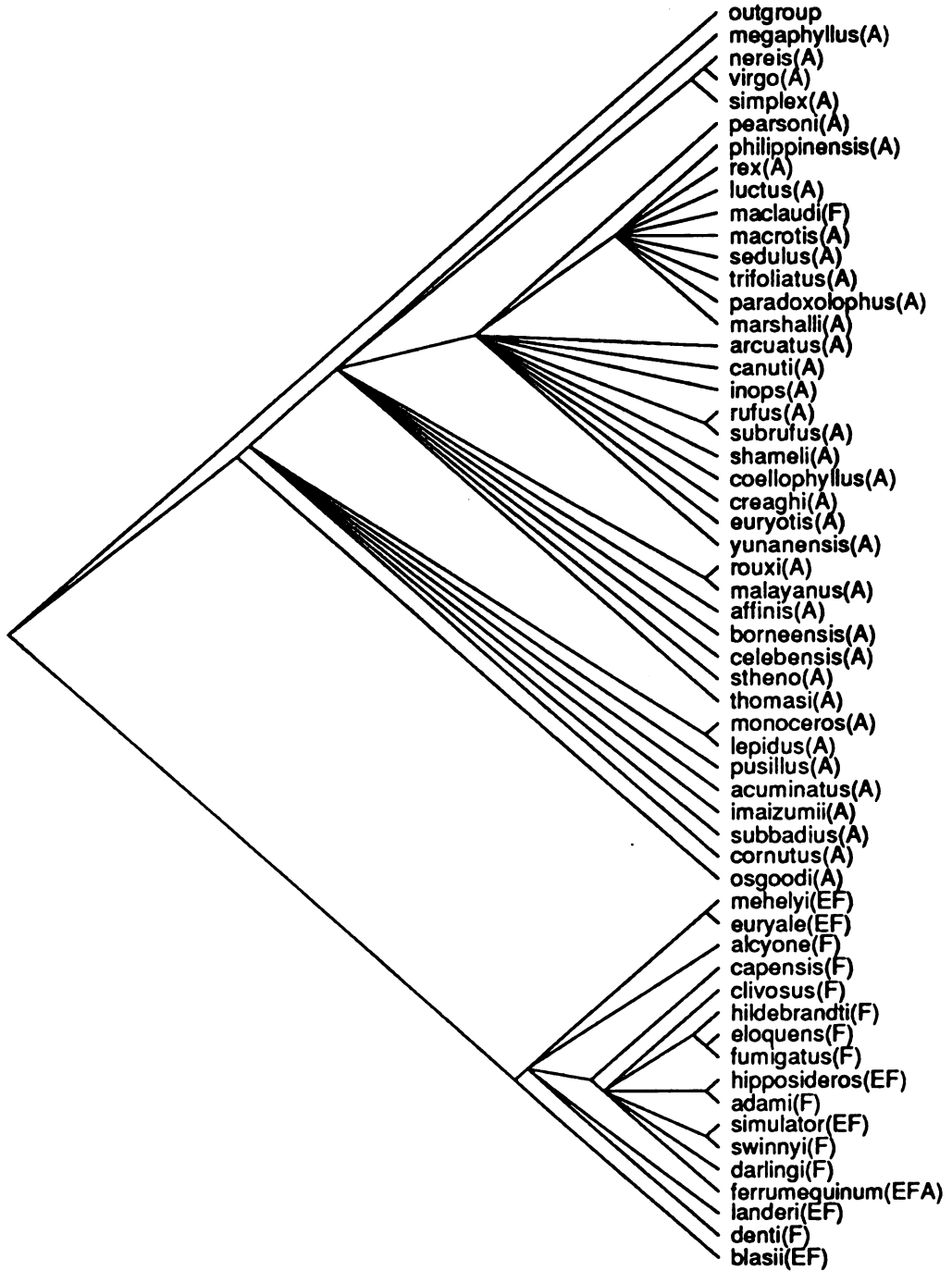


Figure 4.23: The strict consensus cladogram for the 1300 most parsimonious cladograms resulting from the unweighted analysis, character 1 unordered. . The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

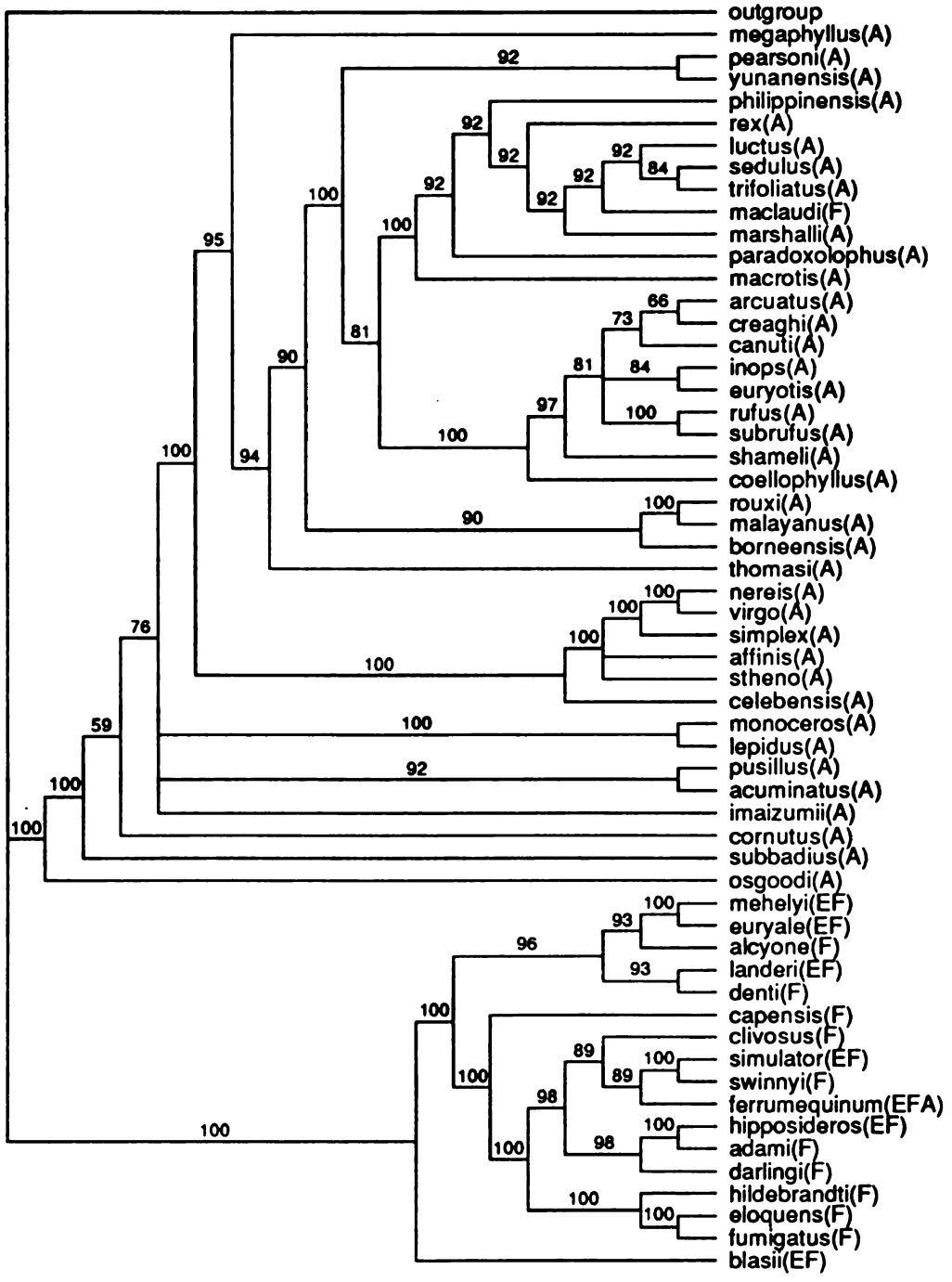


Figure 4.24: The majority consensus cladogram for the 1200 most parsimonious cladograms resulting from the unweighted analysis, character 1 ordered. The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia. The numbers indicate the percentage of cladograms in which this particular braching stucture is present.

maclaudi. The majority consensus cladogram identified two additional monophyletic groups, one for eight species of the traditional southeast Asian member of the *pusillus* group and the other for six species of the traditional southeast Asian member of the *ferrumequinum* group. The synapomorphies for both clades were the same as those in consensus cladograms from weighted and ordered analysis.

The consistency index for the most parsimonious cladograms of this analysis was 0.23, slightly higher than that in the previous analysis.

Analysis of Unweighted Characters, Character 1 Ordered

The strict and majority consensus cladograms from this analysis are presented in Figures 4.23 and 4.24, respectively. When characters were unweighted, the resulting strict consensus cladogram indicated a clear division between southeast Asian species and African and western Eurasian species of the genus; both form distinct, monophyletic groups. The monophyletic African and western Eurasian clade in this analysis, a paraphyletic group in the previous two analyses (above), is defined by synapomorphies in characters 13, 17, 25, and 26, while the monophyletic group of southeast Asian species are related by synapomorphies in character 1, 4, 5, 6, 7, 8. As happened in the weighted analyses, the African species *R. maclaudi* is found in the southeast Asian clade.

In the southeast Asian clade, Figure 4.23 shows the outlines of the traditional *ferrumequinum, arcuatus, pusillus* and *philippinensis* species groups though virtually no pattern of relationship is resolved within each group. The cladogram indicates that the traditional *philippinensis* group is the most derived. The *philippinensis* group and *arcuatus* group together constitute a larger clade defined by the same set of synapomorphies, character

1, 2, and 3, as in the weighted analyses. These two groups are further joined by 10 species of the traditional *ferrumequinum* group, making a more inclusive clade, defined only by synapomorphy in character 1. Finally, members of the traditional *pusillus* group are found at the base of the southeast Asian clade.

The present study recognized a monophyletic group of 10 species within the African and western Eurasian clade, *R. clivosus*, *R. simulator*, *R. swinnyi*, *R. ferrumequinum*, *R. hipposideros*, *R. adami*, *R. darlingi*, *R. hildebrandti*, *R. eloquens*, and *R. fumigatus*, which was not found in previous, weighted analyses. The synapomorphies for this clade were characters 4 and 11. This clade, joined by one more species, *R. capensis*, forms a larger monophyletic group defined by synapomorphies in character 1 and 12, including all the African and west Eurasian species of the traditional *ferrumequinum* and *fumigatus* group. The monophyletic group of *R. eloquens*, *R. fumigatus* and *R. hildebrandti*, found in the previous two analyses, is also present in Figure 4.23. However, the monophyletic group found in the first analysis (Figure 4.19), consisting of all African and west Eurasian species of the traditional *pusillus* group, was not present. These species branch from the base of the clade, with otherwise unresolved relationships.

The majority consensus cladogram displays the relationships within the traditional *philippinensis* and *arcuatus* groups; these two groups are resolved into sister groups. Two more monophyletic groups, one for 7 southeast Asian species of the *ferrumequinum* group and another for 5 African and west Eurasian species of the *pusillus* group are present in the majority consensus cladogram.

The most significant difference of this analysis from the weighted analysis is the presence of a clade for all the African and west Eurasian rhinolophids. Most of the

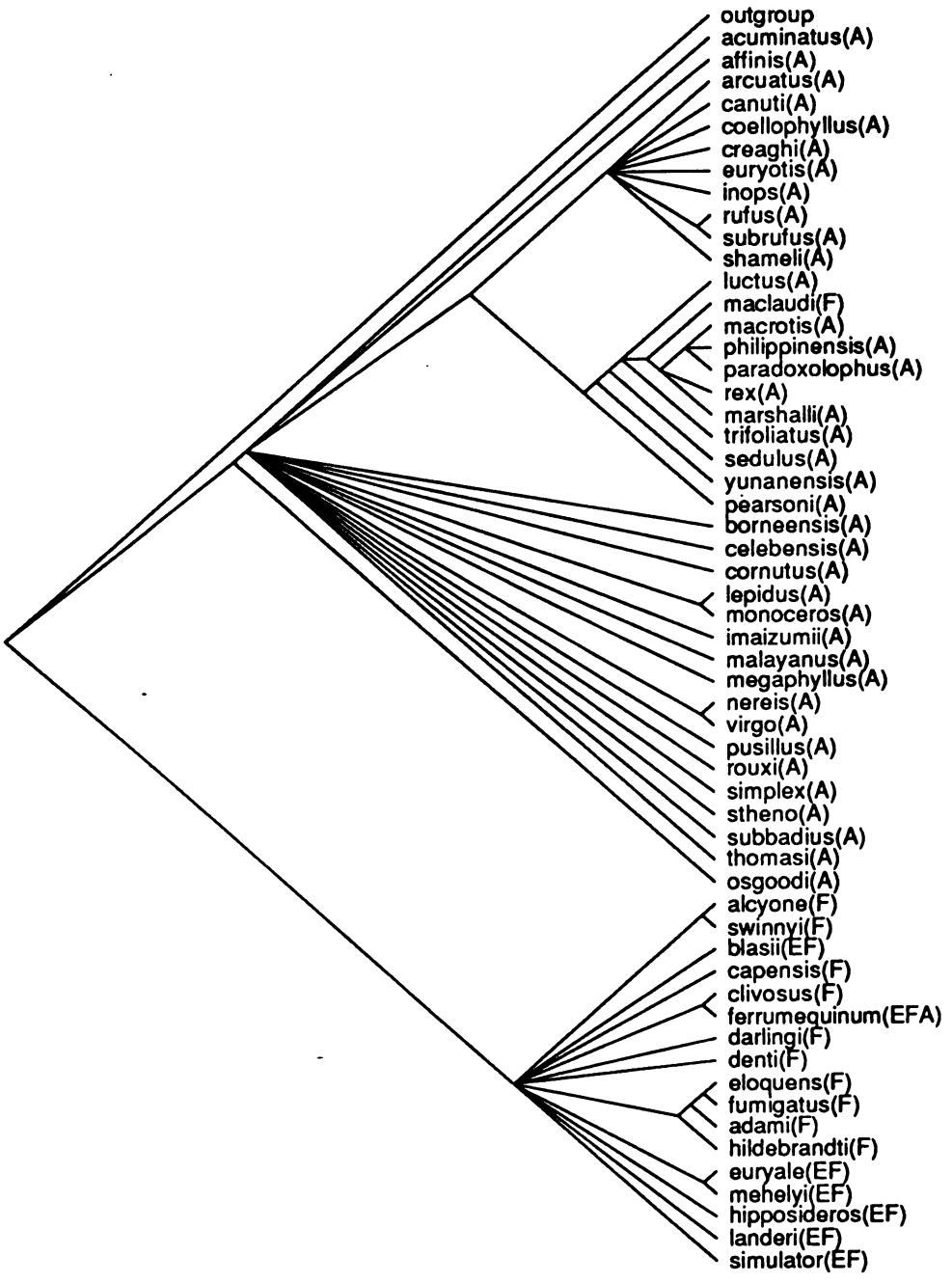


Figure 4.25: The strict consensus cladogram for the 1300 most parsimonious cladograms resulting from the unweighted analysis, character 1 unordered. The geographic location of the species is indicated by letters in parentheses: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia.

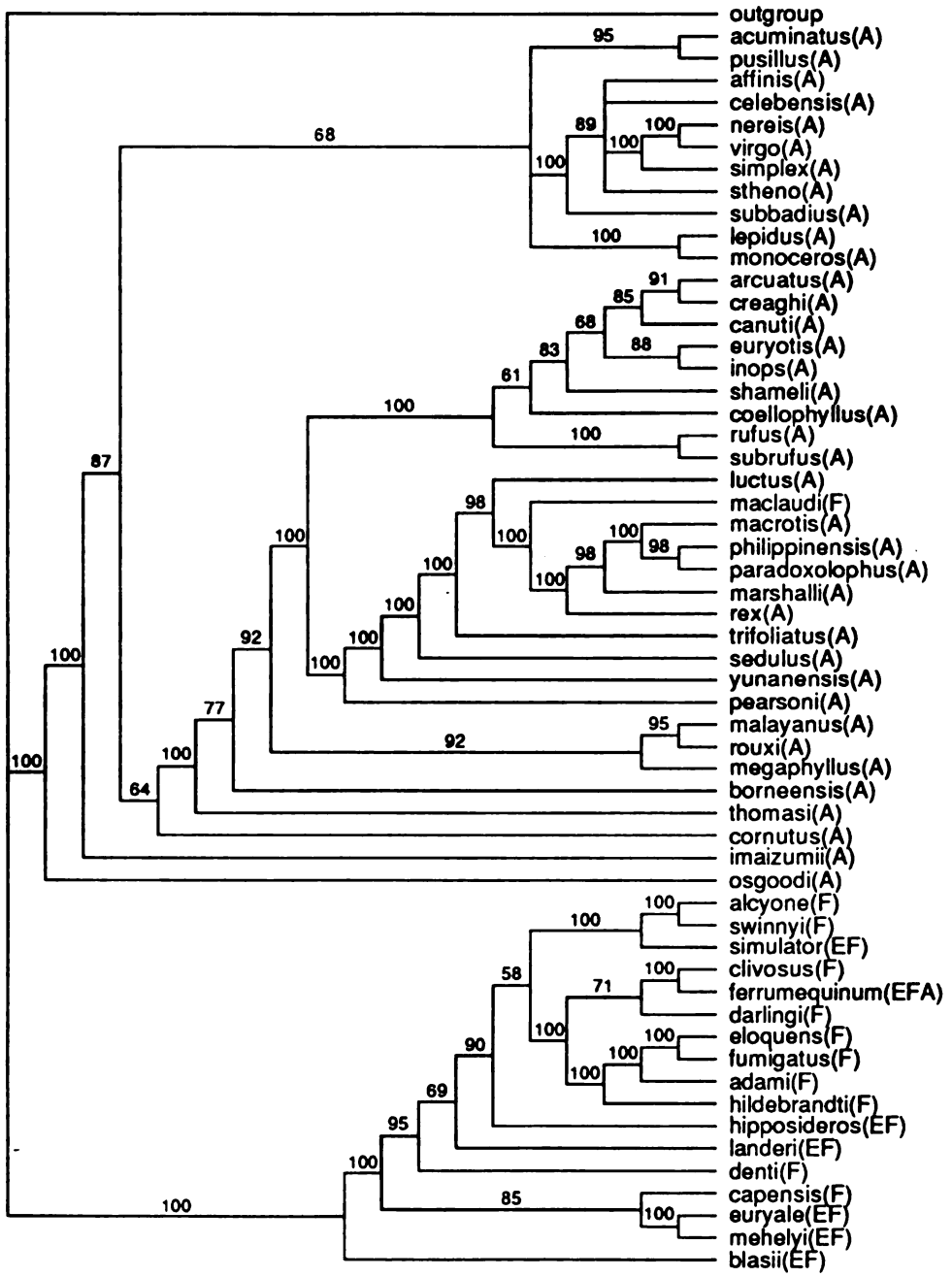


Figure 4.26: The majority consensus cladogram for the 1200 most parsimonious cladograms resulted from the weighted analysis, character 1 ordered. The geographic location of the species is indicated in the letters in the parenthesis: 'A' = southeast Asia, 'F' = Africa, and 'E' = west Eurasia. The numbers indicate the percentage of cladograms at which this particular braching stucture is present.

synapomorphies for this clade, character 13, 17, 25, and 26, had low weight in the previous, weighted analyses. When characters were unweighted, the relatively large number of shared derived characters constitute strong evidence to support this monophyletic group. In contrast, two monophyletic groups in the first analysis (Figure 4.19), consisting of the traditional *pusillus* group species from two different regions, both defined by a single synapomorphy in high weight character 1, disappeared in this analysis.

The consistency index for the shortest cladograms in this analysis is 0.222, slightly lower than those in the two previous analyses. The total number of transformations implied by the phylogenetic hypotheses is higher in the weighted analysis (245) than in the present analysis (238). But by reducing the number of convergent and reversal transformations in high weighting characters, phylogenetic reconstruction of the weighted analyses had higher consistent indices.

Analysis of Unweighted Characters, Character 1 Unordered

Figures 4.25 and 4.26 present strict and majority consensus cladograms, respectively, for analyses of unweighted characters, with character 1 not ordered by a transformation series. As was the case in the previous unweighted analysis, African and western Eurasian species form a clearly monophyletic clade. This clade was defined by synapomorphies in characters 7, 13, 25, and 26. The southeast Asian clade, on the other hand, is defined by synapomorphies in characters 4, 5, 6, 7, and 12. Character 1 did not play a role in the major division of the genus in either unweighted analyses.

In the strict consensus cladogram from this analysis, an additional monophyletic group, not found in the previous unweighted analysis, was apparent. This group contains all the

species of the traditional *arcuatus* group, defined by synapomorphies in characters 10 and 26. Together with another monophyletic group of the traditional *philippinensis* group, they form a larger monophyletic group recognized by the other three analyses. As with the previous unweighted analysis, there was very little pattern of relationships among African and western European species in the strict consensus cladogram of this analysis. The four species, *R. eloquens, R. fumigatus, R. hildebrandti* and *R. adami* form a monophyletic group defined by synapomorphies in characters 4 and 11. The first three species constitute a monophyletic group in the previous three analyses.

The majority consensus cladogram from this analysis was similar to that from the previous unweighted analysis in the relationships displayed for the southeast Asian species. Within southeast Asian species, an additional monophyletic group containing 11 species (defined by the synapomorphies in character 7) was present. Among the 11 species, six species of the traditional *ferrumequinum* group form a smaller clade, which was also present in the majority consensus of all three previous analyses; the other five species were from the traditional *pusillus* group. The relationships among the African and west Eurasian clade resulting from this analysis did not agree well with those from the previous three analyses. *R. simulator*, a species of the traditional *ferrumequinum* group, was found closely related to two species of the *pusillus* group (*R. denti* and *R. landeri*). This clade has a single synapomorphy in character 26.

The consistency index for the most parsimonious cladograms in this study was 0.220, being slightly lower than other three analyses.

The Status of the *fumigatus* Group.

Two of the traditional species groups recognized within *Rhinolophus* have not been discussed in the foregoing descriptions of the cladistic analyses. One, the *hipposideros* species group of Andersen (1905b), is monotypic, containing only the species *R. hipposideros*. This species 'group' was trivially present in all of the analyses, because the cladograms do not reflect the degree of specialization any particular species may reach. The other species group, Corbet and Hill's (1992) *fumigatus* group, formerly the *macrotis* group of Andersen (1918), deserves more discussion.

Andersen (1918) and Corbet and Hill (1992) diagnosed the *fumigatus* group based on sella shape and connecting process (characters 1 and 2), the margins of the palate (characters 16 and 17), and ear size (character 23). Although these characters were included in the cladistic analysis, none of the cladograms indicated a monophyletic group of these 5 species (*R. eloquens, R. fumigatus, R. hildebrandti, R. pearsoni* and *R. yunanensis*). Bogdanowicz (1992) further divided the *fumigatus* group, separating *R. pearsoni* and *R. yunanensis* (Asian species) as the *pearsoni* species group distinct from a restricted *fumigatus* group containing the three African species only. This view was supported by my analysis, since these three African species (*R. eloquens, R. fumigatus, R. hildebrandti*) from a monophyletic group in all of the consensus cladograms. However, the justification for a distinct group containing *R. pearsoni and R. yunanensis* was not as evident. Although these two species are very close in all consensus cladograms, they did not appear to be sister species in all the consensus cladograms. Their relationships with other species are also sensitive to the change of assumptions. In the strict consensus cladogram of the weighted analysis where character 1 is ordered, these two species are within the monophyletic group containing the traditional *arcuatus* and

philippinensis groups, sharing derived characters 2, 3, 20 and 22. In the strict consensus cladograms of the two analyses where character 1 is unordered, they are sister species of the monophyletic group containing traditional the *philippinensis* group only, sharing derived characters 5 and 21 with them. There were some suggestive evidence that *R. pearsoni* and *R. yunanensis* are distinct from the traditional *arcuatus* and *philippinensis* groups. Based on the relationships that are common to all the strict consensus cladograms, these two species are members of the *arcuatus* + *philippinensis* (+ *R. pearsoni* and *R. yunanensis*) clade but not within the *philippinensis* clade. In the absence of evidence that would further clarify their relationships. I treated these two species as unresolved within the former clade.

Comparisons Between the Analyses

The four sets of cladistic analyses differ in character weighting and whether or not character 1 was represented by a particular transformation series. The substantial differences between these assumptions could have produced totally different patterns of relationship in the resulting consensus cladograms. That many of the same monophyletic groups appeared in most, if not all, analyses was therefore surprising. It is necessary to examine the details of the monophyletic groups present in each analysis to reach an appropriate phylogenetic hypothesis for the genus *Rhinolophus*.

Four monophyletic groups were consistently present in the strict consensus cladograms of all four analyses. The first included species of the traditional *philippinensis* group. The second was the first clade plus species of the traditional *arcuatus* group and two Asian species of the traditional *fumigatus* group. The third group contains all the species from southeast Asian plus the African *R. maclaudi*. The final clade contains the three species, *R. eloquens*,

R. fumigatus, and *R. hildebrandti*. Because these groups are present in all cladograms produced in this study, despite very different assumptions involved, I concluded that those four monophyletic groups are very strongly supported by the data set.

One monophyletic group, containing all African and west Eurasian species (except the African species of *R. maclaudi*), supported by a relatively large number of synapomorphies (characters 7, 13, 25, and 26), was present in the strict consensus cladograms from the unweighted analyses but not in those from the weighted analyses. This difference poses a question about the basic phylogenetic division of genus: whether the group of southeast Asian species were derived from the group of African and west Eurasian species, or these two are sister groups. I decided that the southeast Asian group was derived from the African and west Eurasian species for two reasons. First, all of the synapomorphies that define the African and west Eurasian clade are relatively low in information content (discussed in Character Analysis) and were placed in weighting groups one (characters 13, 25, 26) or weighting group two (characters 7). The groups defined by these characters, therefore, were less reliable. Second, a consensus cladogram for the results from both the weighted analyses and unweighted analyses (Figure 4.27) would place all the African and west Eurasian species as well as the monophyletic group of southeast Asian species at the root. Although the relationships among African and west Eurasian rhinolophids remain unresolved, the cladogram clearly suggested that the species of southeast Asia were derived from the ancestors in the Africa and west Eurasia.

Relationships patterns among the African and western Eurasian species differ greatly among the analyses. The relationships among these species were not resolvable with the current data set. At the very least, to determine a reasonable hypothesis of relationship among these species would require deciding whether characters should be weighted, and whether the

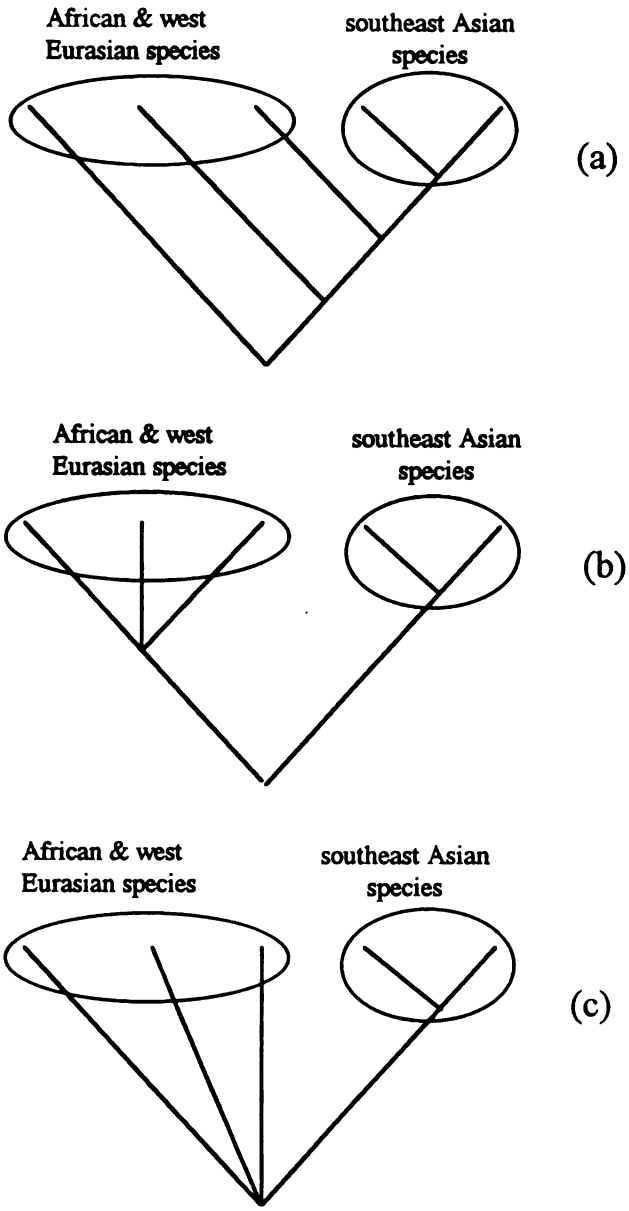


Figure 4.27. Cladograms illustrate the consensus between the results from the weighted and the unweighted analyses. (a) Results from the weighted analyses, African and west Eurasian species branch from the base of the cladograms; (b) Results from the unweighted analyses, African and west Eurasian species constitute a monophyletic group; (c) In the consensus cladogram for (a) and (b), African and west Eurasian species as well as the monophyletic group of southeast Asian species branch from the multichotomous root.

proposed transformation series for character 1 is really appropriate. With the current data set, the relationships among the African and western Eurasian species are very sensitive to how these questions are resolved. I concluded that the present data set does not support an unambiguous hypothesis for the relationships of these species. Two more significant monophyletic groups are unique to the weighted and character 1 ordered analysis. They are the species of the traditional *pusillus* group from southeast Asian and those from Africa and west Eurasia, respectively. Character 1 is virtually the only synapomorphy for both groups.

Inconsistencies due to different assumptions about southeast Asian species are less sever; two monophyletic groups, one for all species of the traditional *philippinensis* group, another for all species of traditional *philippinensis* group plus *arcuatus* group, were present in all consensus cladograms. The monophyletic group for the southeast Asian members of the traditional *pusillus* group was present in the strict consensus cladogram from the weighted and ordered analysis and in the majority consensus cladogram from the weighted and unordered analysis, but is not present in unweighted analyses. Because this inconsistency was about resolution rather than conflict, this monophyletic group should be accepted based on the present data. Another group containing six southeast Asian members of the traditional *ferrumequinum* group (*R. affinis*, *R. nereis*, *R. virgo*, *R. simplex*, *R. stheno*, and *R. celebensis*) was present in the majority consensus cladograms of all analyses but not present in any of the strict consensus cladogram. Because both synapomorphies of this group (characters 7 of weighting group two and character 10 of weighting group one) were of lower information content, I considered that this group was unreliable.

The African species of *R. maclaudi* is in the traditional *philippinensis* group clade in all the consensus cladograms and it was placed in the *philippinensis* group by most previous

researchers (Andersen, 1918; Koopman, 1975). Nevertheless, it has primitive features in character 5 (with one lower lip groove) and character 9 (with more than five caudal vertebrae) which resembles other African and west Eurasian species. A more serious question is how it occurs so distant from all other species of that group. There is no indication of such distributional pattern in other groups of the genus. Considering the marked rate of homoplasy in the morphology of the genus revealed by this study, a convergent evolution of species acquiring features characteristic of the *philippinensis* group can not be entirely ruled out. Without further morphological and distributional evidence about the this group, I find the status of *R. maclaudi* can not be concluded at this time.

Taxonomic Summary

I present the summary cladogram in Figure 4.28 to indicate the monophyletic groups strongly supported by my data set. This cladogram includes all monophyletic groups present in all strict consensus cladograms from the four analyses, plus the clade containing southeast Asian species of the traditional *pusillus* group present in strict consensus cladogram in Figure 4.20 (weighted and character 1 ordered) and majority consensus cladogram in Figure 4.23 (weighted and character 1 unordered). The species at the base of the southeast Asian clade, all belonging to the traditional *ferrumequinum* group, are not resolved into a clade in any consensus cladogram and, are represented as an unresolved group. This cladogram does not resolve the relationships of all of the species of *Rhinolophus*. Instead, it draws attention to those members of the genus whose phylogenetic relationships are supported well enough in this analysis to merit taxonomic recognition at this time.

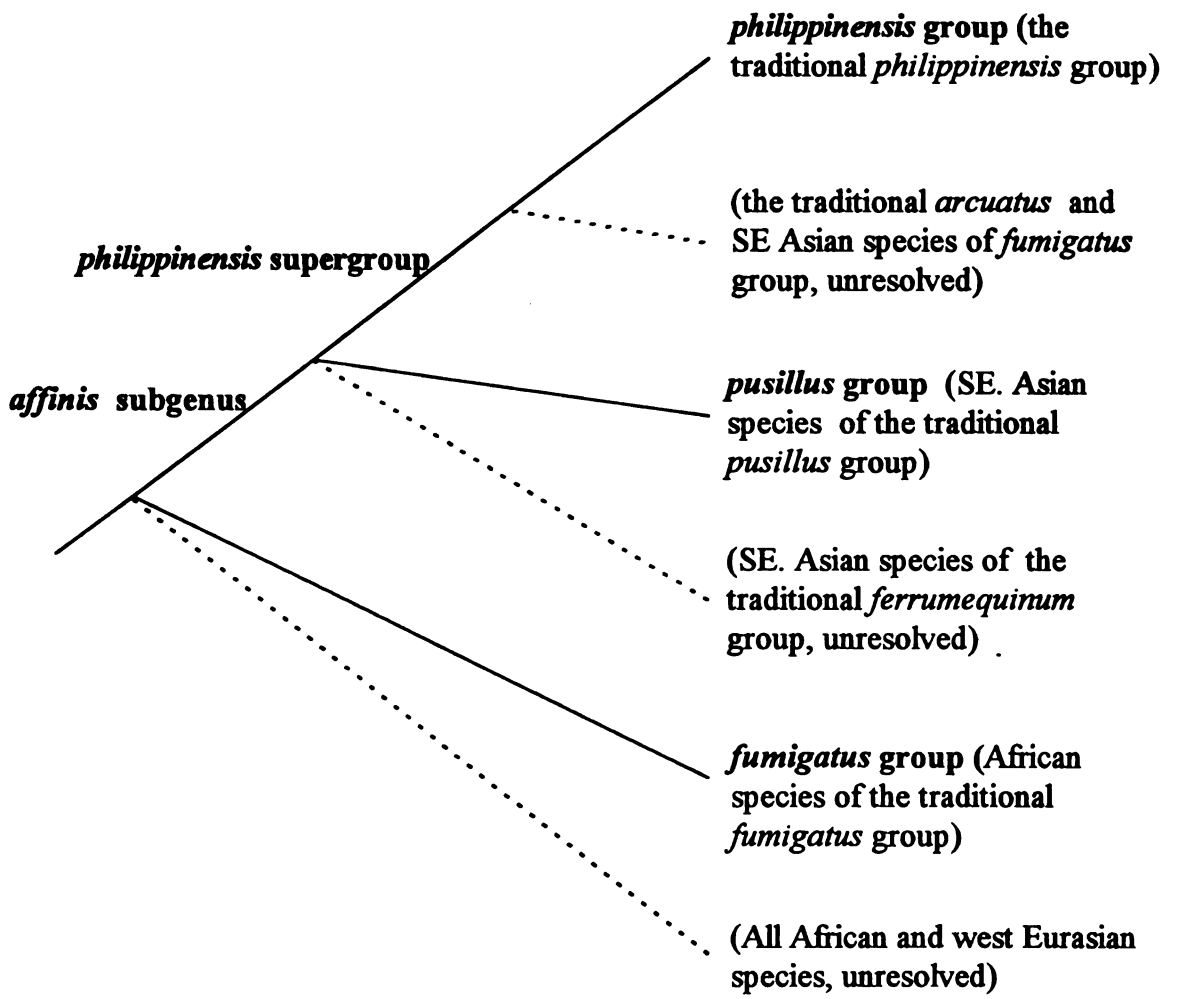


Figure 4.28. The phylogenetic relationships within the genus *Rhinolophus* based on the present study. The monophyletic groups (bold faced) strongly supported by my data set are indicated by solid lines. A dotted line represents a set of species branching from that point; relationships among these species are unresolved.

Table 4.2. Summary of taxonomic conclusions based on the monophyletic groups in Figure 4.28. No paraphyletic groups is recognized in this taxonomy. Monophyletic groups of species are recognized at three different levels (supergroup, group, and subgroup). Those species that can not be placed into a monophyletic group are included as 'status uncertain' at the appropriate level.

GENUS *RHINOLOPHUS*

affinis subgenus

philippinensis supergroup

philippinensis group

R. luctus
R. trifoliatus
R. sedulus
R. macrotis
R. marshelli
R. rex
R. paradoxolophus
R. philippinensis

group status uncertain

R. arcuatus
R. canuti
R. creaghi
R. coelophyllus
R. euryotis
R. inops
R. rufus
R. subrufus
R. pearsoni
R. yunanensis

pusillus group

R. acuminatus
R. pusillus
R. cornutus
R. imaizumii
R. osgoodi
R. subbadius
R. lepidus
R. monoceros

group status uncertain
(southeast Asian species of the traditional *ferrumequinum* group)

R. affinis
R. nereis
R. simplex
R. stheno
R. selebensis
R. megaphyllus
R. malayanus
R. rouxi
R. borneensis
R. thomasi

subgenus status uncertain
(All African & west Eurasian species)

fumigatus group

R. eloquens
R. fumigatus
R. hildebrandti

group status uncertain

R. alcyone
R. denti
R. euryale
R. mehelyi
R. landeri
R. blassi
R. adami
R. clivosus
R. ferrumequinum
R. darlingi
R. capensis
R. swinnyi
R. simulator
R. hipposideros

subgenus status uncertain

R. maclaudi

Table 4.2 summarizes my taxonomic conclusions based on the monophyletic groups of Figure 4.28, and the diagnosis for these monophyletic groups is presented in Table 4.3. Monophyletic groups of species are recognized at the species group, supergroup, and subgenus levels. Only the four monophyletic groups which are strongly indicated in all the analyses, and the *pusillus* group which is indicated in two weighted analyses, are assigned group (subgenus, group, and subgroup) names. The decision to recognize the *pusillus* group does not affect the relationships among the other monophyletic groups. I chose not to recognize paraphyletic groups in this taxonomy. Those species that can not be placed into a monophyletic group are included as 'status uncertain' at appropriate levels. While this approach results in an unusual number of 'status uncertain' designations, it does draw attention to the parts of the taxonomy that require further clarification.

Among the five designated monophyletic groups, the *philippinensis* group contains the same species as the traditional *philippinensis* group (Andersen, 1905b, 1905f; Tate, 1943; Corbet and Hill, 1992), referred to as the *luctus* group Andersen, (1918); Ellerman et al, (1953); Koopman, (1975). Although the species name of *R. luctus* Temminck, 1835 predates the species name of *R. philippinensis* Waterhouse, 1843, the latter name was the first to be used for this species group. By Article 23 (Principle of Priority) of the International Code of Zoological Nomenclature (Ride et al, 1985, referred to as the Code in this section), *philippinensis* is the valid name of the group. The *pusillus* group contains the southeast Asian member of the traditional *pusillus* species group. Since this monophyletic group includes the nominaltypical species, *R. pusillus*, of the traditional species group, by Article 37 (Nominotypical taxa) of the Code, this nominotypical group retains the group name. The monophyletic *fumigatus* group of African species retains the traditional group name for the

Table 4.3. Diagnostic characters for the infrageneric taxa of *Rhinolophus* based on the monophyletic groups illustrated in Figure 4.27. Species with phylogenetic relationships unclear are treated as status uncertain at appropriate levels.

<table>
<tr><td rowspan="2">subgenus</td><td colspan="2">subgenus status uncertain</td><td colspan="4">affinis subgenus</td></tr>
<tr><td colspan="2"></td><td colspan="4">1. Three lower lip grooves;
2. Caudal vertebrae fewer than five;
3. P_2 length greater than width;
4. Palate situated relatively rostral with posterior margin rostral to M^3.</td></tr>
<tr><td rowspan="2">supergroup</td><td colspan="2" rowspan="2"></td><td colspan="2" rowspan="2"></td><td colspan="2">philippinensis supergroup</td></tr>
<tr><td colspan="2">1. Sella and anterior noseleaf broadened;
2. Orbital constriction deep;
3. Internairal region expanded.</td></tr>
<tr><td>group</td><td>group status uncertain</td><td>fumigatus group</td><td>groups status uncertain</td><td>pusillus group</td><td>group status uncertain</td><td>philippinensis group</td></tr>
<tr><td></td><td></td><td>1. Sella and anterior leaf broadened.
2. Nasal swellings enlarged.
3. Ratio of first/second phalanges of forth finger greater than 1.7.</td><td></td><td>1. Connecting process pointed</td><td></td><td>1. Ears and antitragus greatly enlarged;
2. Palatal bridge longer than 1/2 of upper tooth row;
3. Nasal swellings enlarged.</td></tr>
</table>

same reason. Both the *philippinensis* supergroup and *affinis* subgenus of southeast Asian species are new taxa. The *philippinensis* supergroup contains a single designated group; by Article 36 (Principle of Coordination) in the Code, it is appropriate to name the group after its only designated subgroup. I choose *R. affinis* Horsfield, 1823, the earliest designated nominal species of the group, as the name of the subgenus. Table 4.3 presents diagnostic characters for the infrageneric taxa I recognize.

This taxonomy of *Rhinolophus*, though leaving much for future studies, clearly indicates the basic phylogenetic relationships and patterns of character evolution within the genus. This taxonomy differs from the traditional taxonomy of the genus in three significant aspects. First, this taxonomy identifies a monophyletic group (as a subgenus) consisting of all the southeast Asian species, while leaving the taxonomic status of the remaining species as largely unsolved. Because I used a much larger collection of characters than has been used in the previous phylogenetic analysis, I was able to detect considerable homoplasy in a broad range of characters including some widely used in the past (e.g., the shape of connecting process and the shape of the sella). I found that those species groups defined by these characters are polyphyletic (e.g., the traditional *pusillus* group and *fumigatus* group). Second, this taxonomy does not recognize the traditional *ferrumequinum* group as a valid species group. The present phylogenetic study indicates that this traditional species group is paraphyletic, representing a collection of species that arise at different points in the phylogeny. The relationship among species of the traditional *ferrumequinum* remains unresolved. Third, only monophyletic groups are recognized as taxa in this taxonomy, leaving unresolved groups as status uncertain.

My phylogenetic hypothesis of the relationships among the southeast Asian species is similar to that of Andersen (1905a, 1905d, 1905e). However, the present hypothesis differs from that of Tate, since I consider the traditional *arcuatus* group closely related to the traditional *philippinensis* group whereas Tate viewed the former group to be closer to his *pusillus* and *ferrumequinum* groups.

The recognition of the subgenus for all southeast Asian species also distinguishes this taxonomy from the one proposed by Bogdanowicz (1992). Although the separation of species from the two major geographic regions is to a degree indicated in his phenetic analysis, Bogdanowicz did not recognize the southeast Asian rhinolophids as a monophyletic group and did not present them as a distinct taxon in his taxonomy. Furthermore, by recognizing the monophyletic groups at different taxonomic levels, this taxonomy presents a clear view of fundamental intrageneric relationships. In Bogdanowicz's taxonomy the relationships between his 11 species groups unresolved. In the underlying phylogenetic hypotheses, the present study hypothesizes that the *philippinensis* group is a most derived monophyletic group, whereas in their phenograms (Bogdanowicz and Owen, 1992; Bogdanowicz,1992) this group of species is divided into two distantly related groups and one of them is the earliest branch of the genus. Finally, this taxonomy provides a diagnosis for each designated taxon and the hypothesis of character evolution of the genus, both of which are not available for his taxonomy.

DISCUSSIONS

The consistency indices (CI) are rather low (from 0.22 to 0.23) for all the shortest cladograms computed. This means that the ratio of convergent and reversive transformation to the innovative transformations is more than four to one for the characters used in the present study of *Rhinolophus*. The differences in the CIs between the four analyses are very

Table 4.4 : A comparison in the patterns of transformation between the weighted and unweighted analyses, character 1 unordered, for each character. In each analysis, one shortest cladogram, which has a topology identical to the majority consensus of that analysis, is summarized. Shading indicate the characters with lower occurrence of homoplasy ratio.

charac-ters	weight-ing group	minimal number of transformation	number of transformation in first analysis (weighted)	ratio of homoplasy in first analysis	number of transformation in third analysis (unweighted)	ratio of homoplasy in third analysis
1	4	5	10	1	10	1
2	3	2	6	2	7	2.5
3	3	2	17	7.5	14	6
4	3	2	12	5	11	4.5
5	4	1	5	4	7	6
6	3	1	4	3	6	5
7	2	2	15	7.5	12	5
8	2	1	7	6	7	6
9	2	1	9	8	9	8
10	1	2	13	5.5	11	4.5
11	1	2	8	3	7	2.5
12	4	2	9	3.5	10	4
13	1	2	11	4.5	11	4.5
14	2	1	6	5	5	4
15	1	1	7	6	7	6
16	3	3	17	4.7	16	4.3
17	3	2	11	4.6	13	5.5
18	3	2	12	5	13	5.5
19	2	1	5	5	5	4
20	1	1	8	7	6	5
21	3	2	14	6	14	6
22	3	1	2	1	2	1
23	2	3	6	1	6	1
24	1	4	6	0.5	6	0.5
25	1	4	9	1.3	8	1
26	1	3	16	4.3	15	4
Sum		53	245	111.9	238	107.3

small, but the ratio of convergent and reversive to the innovative transformations varies greatly among characters. Table 4.4 shows the minimal number of necessary transformation (without homoplasy), the actual number of transformations based on the phylogenetic hypotheses, and the ratio of homoplasy to minimal transformation present in each of the four analyses. Characters 1 and 2 have relatively low rate of homoplasy in both weighted and unweighted analyses (between 1 and 2.5). This agrees with the assumption that these characters are more informative due to their conservativeness. Four of the characters converted from continuous measurements (characters 22, 23, 24, and 25) also display little homoplasy. They were assigned low weight because the boundaries between the states of these characters are relatively arbitrary. Characters 3, 7, 9, and 20 have very high rate of homoplasy; they contributed less reliable evidence about the phylogeny of the genus.

The fact that some highly weighted characters are less consistent with the shortest trees does not constitute a compelling reason for a character weight change, since a review of character analysis after cladistic analysis does not convince me to change the weighting criteria. However, the low consistency index does reiterate an early recognition that there are many convergent and reversive changes in the rhinolophid morphology.

Despite a high rate of homoplasy, certain patterns of character evolution can be seen from the phylogenetic hypothesis in Figure 4.27. The hypothesized ancestors of *Rhinolophus* most likely had a small sella and anterior noseleaf, a connecting process of state *a*, one lower lip groove, 5 to 6 caudal vertebrae, P_2 width greater than length, and posterior palatal margin not rostral to M^3. The sella and anterior noseleaf become broader and the internairal region expanded in more derived groups (e.g. in the *philippinensis* group of the present taxonomy); both the ear and antitragus are expanded and the nasal swellings are

enlarged in the most derived group (the *philippinensis* subgroup). The connecting process (character 1) was derived independently in the Africa and west Eurasian species and in southeast Asian species, though only the latter developed all five states of this character. State *e* of character 1 did not evolve in African species, and it is unclear whether the state *c* has evolved in African species, since the phylogenetic position of *R. maclaudi* is still questionable. Another trend in character evolution is the reduction of the first/second phalangeal ratio in the third and fourth fingers, which reached the most derived state, state *d*, in some of the African and west Eurasian species (e.g. *R. mehelyi*, and the *fumigatus* group). The evolutionary significance of most of these morphological changes within *Rhinolophus* is still not clear.

Based on their karyotypic studies, Harada et al (1985) classified the genus into three groups based on the number of chromosomes. The first group included *R. creaghi, R. acuminatus, R. cornutus, R. imaizumii, R. malayanus, R. coelophyllus, R. pusillus, R. affinis, R. stheno and R. marshalli*, all with 2n = 62 including 30 acrocentric autosome pairs. The second group comprised *R. euryale, R. blassi, R. mehelyi, R. darlingi, R. denti, R. ferrumequinum* and *R. hildebrandti*, with 2n = 58 including 25 acrocentric pairs and two metacentric pairs. The third group included *R. hipposideros, R. luctus* and *R. yunanensis*, all with some large metacentric autosome pairs and 2n = 32. The last group is most similar to the karyotype of *Hipposideros*. Furthermore, considerable variation in chromosome number was found within the three subspecies of *R. luctus*.

The first two karyotypic groups correspond to the two major geographic groups discussed in this study. My results suggest that the 2N = 62 karyotype may represent a derived karyotype, since it occurs in the *affinis* subgenus. If so, I would expect this karyotype to be

found in other members of the group (or serve as the ancestral karyotype for others that might be found there). The 2N = 58 karyotype may represent a more primitive karyotype since it is present in species that are scattered across the phylogeny. My results do not support the notion that the 2N = 32 karyotype is primitive to the genus. The three *Rhinolophus* with this karyotype are not clearly related in my phylogenetic hypothesis, nor are they located near the base of the cladogram. I predict that the karyotypes of these species will be found to be convergently similar to each other and to *Hipposideros*. While the karyotypic data available is incomplete, it offers tantalizing suggestions about the complexity of generic chromosomal evolution in the genus.

Considering the rate of homoplasy in the morphological characters used in this study, a more conclusive view of the phylogeny and systematics of *Rhinolophus* may require more molecular and cytogenetic technology data.

THE HISTORICAL BIOGEOGRAPHY OF SOUTHEAST ASIAN *RHINOLOPHUS*

INTRODUCTION

I concluded in a previous section that the species of *Rhinolophus* occurring in southeast Asia constitute a monophyletic group. To use Sclater's classic biogeographic terms, this distribution covers most of the Oriental realm, northern part of the Australian realm and a small southeastern portion of the Paleoarctic realm regions (Holloway and Jardine, 1968). This general area inhabited by *Rhinolophus* in southeast Asia has frequently been referred to as the Indo-Australian region (Tate, 1939) and the Indo-Malay region (Koopman, 1989; Corbet and Hill, 1992). Figure 5.1 shows the southeast Asian region.

Southeast Asia has been of great biogeographic interests since Alfred Wallace's (1860) publication which demonstrated the strikingly discontinuous faunas present on adjacent islands in the Malay Archipelago. Wallace recognized these discontinuities by what is now referred to as Wallace's line. A somewhat different line was proposed by Huxley (1868). Biogeographic studies of diverse animal and plant groups have been carried out in this region, resulting in various different proposals for where a line should be drawn to delimit the Oriental biota from the Australian biota (George, 1981). Some of these lines are illustrated in Figure 5.2.

There have been two basic approaches to recognizing the biotic regions in southeast Asia. One approach has been to draw a single line separating the two regions. Among them Weber's line, originally proposed by Pelseneer (1904) and often called the 'line of faunal

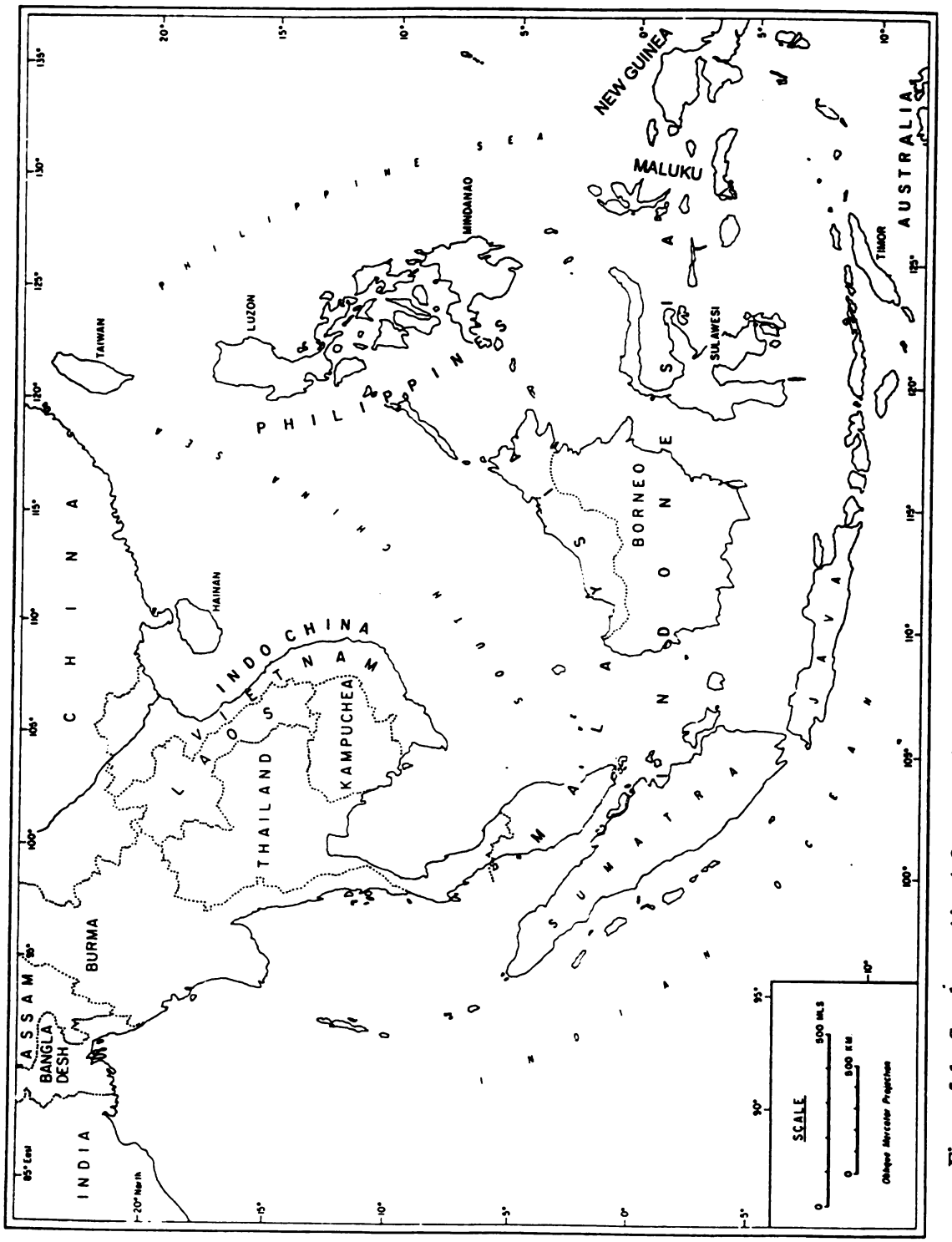


Figure 5.1. Southeast Aisa (after Hutchinson, 1989).

Figure 5.2. Faunal boundaries suggested within the south-east Asia region. Line A, Huxley (1868); Line B, Wallace (1860); Line C, Pelseneer (1904, Weber's line of faunal balance); Line D, Lydekker (1896); Line E, Gressitt (1956); Between line A and line D, Tate's (1946) 'Wallacean region'; Between line C and line E, Gressitt's (1956) 'Papuan region'. (After Holloway and Jardine, 1968).

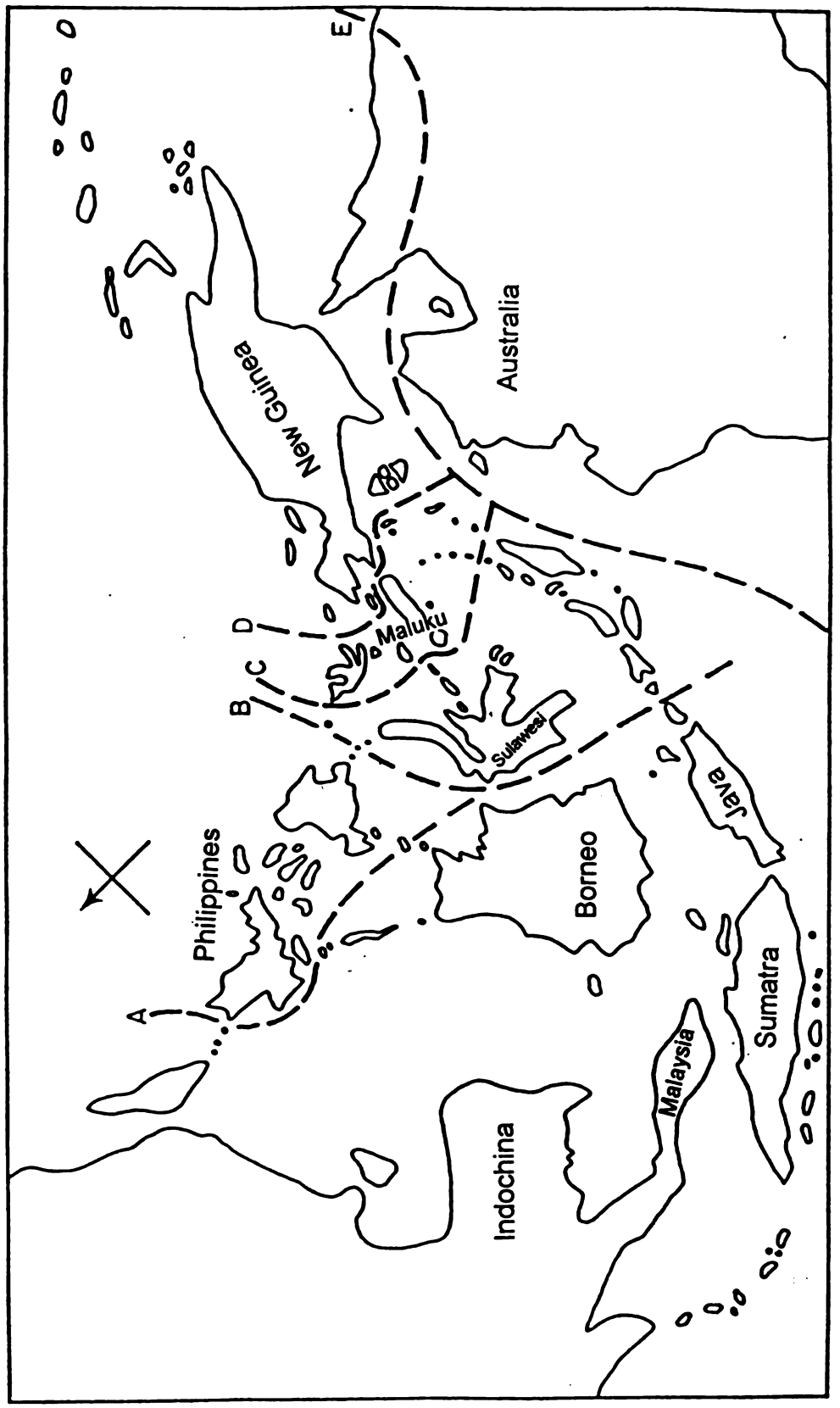

A
B
C
D
E
Philippines
New Guinea
Australia
Maluku
Sulawesi
Borneo
Java
Sumatra
Malaysia
Indochina

Figure 5.2.

balance', has been the most commonly accepted. The other approach, in contrast, has been to recognize a broad transitional zone between the two biotas. Tate (1946), based on the distribution of bats, proposed the 'Wallacean region' which includes Sulawesi, the Philippine Islands and the Maluku Islands. Gressitt (1956) used data on the distribution of the insect order Coleoptera to propose the 'Papuan region' which includes the Maluku Islands, New Guinea and northern Australia.

Biogeographers have identified the geomorphological areas that may represent the boundary between the Oriental and Australian biotas. The southeast Asian continental shelf extends offshore to include islands separated by water gaps less than 200 meter deep. This area, the Sunda Shelf, represents an area where land (or fresh water) organisms may have been distributed during periods of low sea levels. In a similar manner, the Australian continental Shelf (the Sahul Shelf) extends off the shore of that continent to include islands that were likely connected to Australia by land during times of low sea levels. The two continental shelves are separated by deep water areas that may mark the historical limits of the two biotas. Studies of organisms with limited vagility confirm that the boundary between the two continental shelves predicts well the limits of the two biotas (Drandsfield, 1981; Cranbrook, 1981).

Very vagile organisms, however, pose a problem for recognizing biota boundaries. Bats, birds, and butterflies, for example, can easily fly across water barriers that would limit the dispersal of other organisms. Biogeographers have been interested in studying the patterns of vagile organisms such as bats to determine how they deviate from patterns obtained from study of less vagile species. Holloway and Jardine (1968), for example, examined the biogeographic patterns of bats, butterflies, and birds in southeast Asia. They used a phenetic analysis of faunal

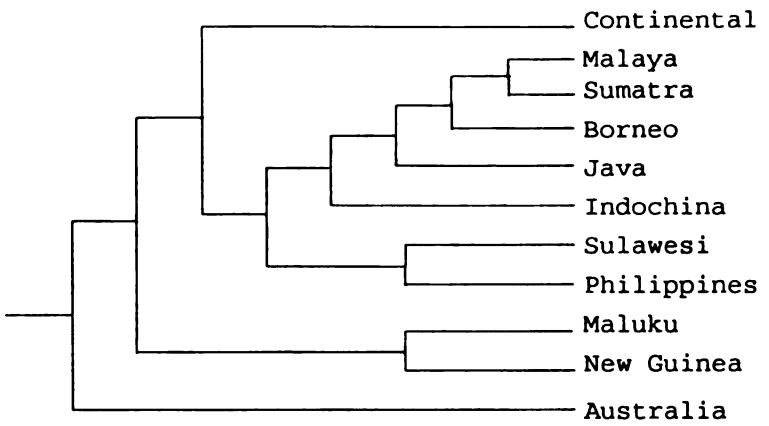


Figure 5.3: The dendrogram calculated from the coefficients of faunal dissimilarities among the areas of southeast Asia for butterflies (After Holloway and Jardine, 1968).

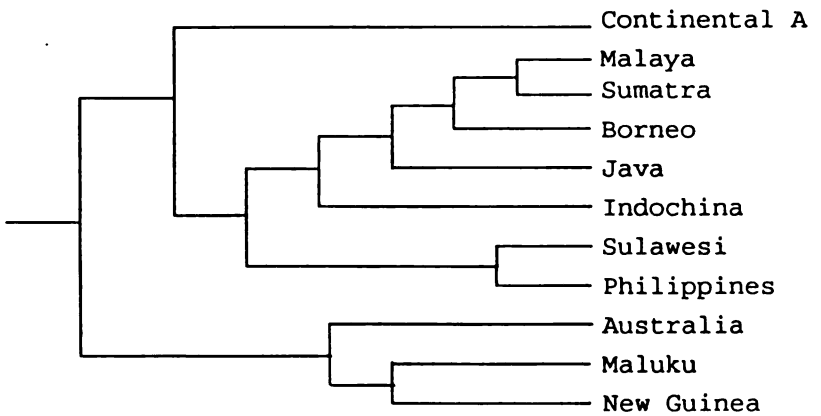
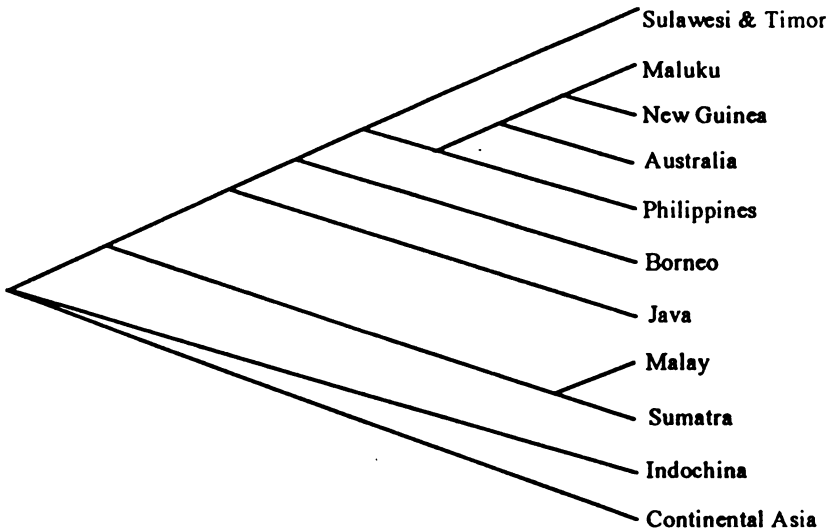
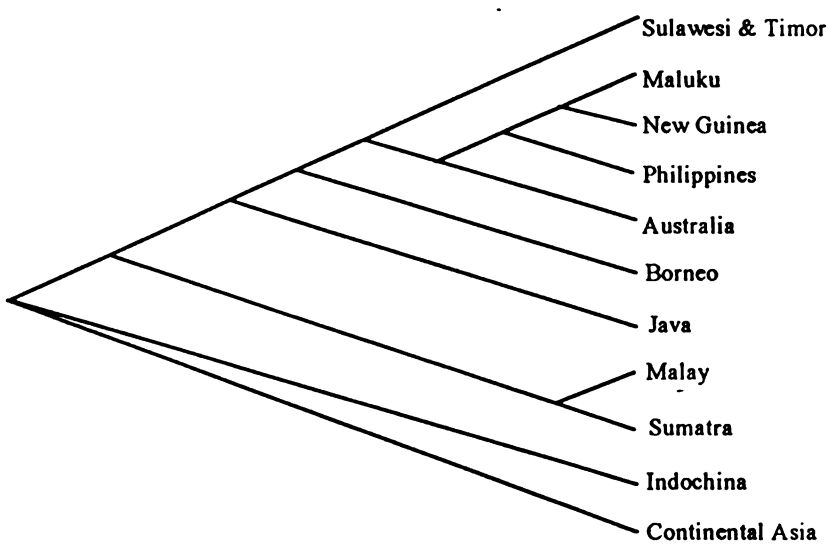


Figure 5.4: The dendrogram calculated from the coefficients of faunal dissimilarities among the areas of southeast Asia for birds (After Holloway and Jardine, 1968).



(a)



(b)

Figure 5.7. The two most parsimonious area cladograms computed from the distributional data of *Rhinolophus* in southeast Asia.

similarity between the continents and major islands of this region to identify geographically coherent areas based on shared species. The dendrograms in Figures 5.3, 5.4 and 5.5 summarize their conclusions on what the distribution of butterflies, birds and bats implies about the historical breakup (vicariance) of southeast Asian habitats. Nelson and Platnick (1980) have further analyzed Holloway and Jardine's results, using vicariance biogeographic methods, to produce area cladograms for southeast Asia. They conclude that the patterns displayed by birds and butterflies are concordant but different from the pattern displayed by bats. The consensus area cladogram for all three groups is uninformative (Figure 5.6).

As interesting as these studies of southeast Asian biogeography might be, they are generally not based on phylogenetic analysis of the organisms that comprise the biota. In resent years, several studies have appeared that use cladistic techniques to examine biogeographic patterns in this region (Wiley, 1988b). Because bats have been viewed as a biogeographically anomalous part of the southeast Asia biota (e.g., Nelson and Platnick, 1981), it is of interest to determine to what extent that view changes if it is based on cladistic methods. Because a monophyletic subgroup of the genus *Rhinolophus* is distributed throughout southeast Asia, and is represented there by numerous species, it is a natural choice to reexamine chiropteran biogeography in this region from a phylogenetic perspective.

METHODS

This cladistic analysis of the biogeography of southeast Asian rhinolophids is based on the results of my generic phylogenetic analysis. In this study, geographic areas are the operational taxonomic units (OTUs) and distributional data of species are the characters. The presence of a species or a monophyletic group in two or more areas constitutes a shared 'derived' character relating the areas. The data matrix, in which the columns are area OTUs

and the rows are distributional characters, is analyzed in the same way as phylogenetic analysis, and the results are cladograms. The most parsimonious area cladogram resulting from this analysis hypothesizes the historical biogeographical relationships among the areas based on the phylogeny of organisms that inhabit them (Nelson and Platnick, 1980; Cracraft, 1988; Wiley, 1988a).

I used the same area identifications as Holloway and Jardine (1968) used in their biogeographic study of bats, except that three small areas they recognized were joined into an single adjacent larger area because the distributional data of *Rhinolophus* in these small areas was too limited. The 11 areas I used and their abbreviations are: (1) continental southeastern Asia including India, southern China, and the adjacent major islands including Taiwan (Cont); (2) Indochina including Burma, Thailand, Cambodia, Vietnam and Laos (Indc); (3) the Malay Peninsula (Maly); (4) Sumatra (Sumt); (5) Borneo (Bone); (6) Java (Java); (7) Sulawesi and Timor (SulT); (8) the Maluku Islands (Mulk); (9) the Philippine Islands (Phil); (10) New Guinea (NewG); (11) Australia (Aust). Some areas include adjacent smaller islands. Thirty-five species of *Rhinolophus* are reported in the southeast Asian region. Table 5.1 is the distributional data of *Rhinolophus* in these 11 areas, based on data in Corbet and Hill (1992) and Honacki et al (1982).

Each species present in two or more areas represents a distributional character. Areas where this species occurs were assigned the 'derived' character state for this character and the areas without this species were assigned the 'primitive' state. A species present in only a single area was not informative about the relationships between the areas; this information was not included in the character set.

Table 5.1. The distribution of *Rhinolophus* species in the 11 areas of the southeast Asia region. The abbreviations for the area names are: Cont = continental southeastern Asia including India, southern China, and the adjacent major islands including Taiwan; IndC = Indochina including Burma, Thailand, Cambodia, Vietnam and Laos; Maly = the Malay Peninsula; Sumt = Sumatra; Bone = Borneo; Java = Java; SulT = Sulawesi and Timor; Mulk = the Maluku Islands; Phil = the Philippine Islands; NewG = New Guinea; Aust = Australia

	Cont	IndC	Maly	Sumt	Bone	Java	SulT	Mulk	Phil	NewG	Aust
R. acuminatus		+	+	+	+	+	+				
R. affinis	+	+	+	+	+	+	+				
R. anderseni									+		
R. arcuatus			+	+			+	+	+		
R. borneensis		+	+		+	+					
R. canuti						+	+				
R. celebensis						+	+	+			
R. coelophyllus		+	+								
R. creaghi					+	+					
R. euryotis							+	+		+	
R. inops									+		
R. lepidus	+	+	+	+							
R. luctus	+	+	+	+	+	+					
R. macrotis	+	+	+	+					+		
R. malayanus		+	+								
R. marshalli		+									
R. megaphillus		+	+				+	+		+	+
R. monoceros	+										
R. nereis			+	+							
R. osgoodi	+										
R. paradoxolophus		+									
R. philippinensis					+		+		+		+
R. pusillus	+	+	+	+	+	+					
R. rouxi	+	+									
R. rufus									+		
R. sedulus			+		+						
R. shameli		+									
R. simplex						+					
R. stheno		+	+	+		+					
R. subbadius	+	+									
R. subrufus									+		
R. thomasi	+	+									
R. trifoliatus	+	+	+	+	+	+					
R. virgo									+		
R. yunanensis	+	+									
Area total species	13	19	14	10	10	11	7	4	8	3	2
Endemic species	2	2	0	0	0	1	0	0	6	0	0

Table 5.2. Data matrix for rhinolophid distributions in the 11 areas of southeast Asia. Characters 1-24 are based on the distributional data of individual species (listed in Table 5.1). Characters 25-36, listed below, are based on components of relationships from the majority consensus cladograms of all four cladistic analyses. All components that are common to at least two analyses and are not in conflict with other cladograms were selected.

25: *R. nereis* + *R. virgo*

26: *R. nereis* + *R. virgo* + *R. simplex*

27: *R. nereis* + *R. virgo* + *R. simplex* + *R. affinis*

28: *R. nereis* + *R. virgo* + *R. simplex* + *R. affinis* + *R. celebensis*

29: *R. acuminatus* + *R. pusillus*

30: *R. rouxi* + *R. malayanus*

31: *R. creaghi* + *R. canuti*

32: *R. creaghi* + *R. canuti* + *R. arcuatus*

33: *R. creaghi* + *R. canuti* + *R. arcuatus* + *R. euryotis*

34: *R. creaghi* + *R. canuti* + *R. arcuatus* + *R. euryotis* + *R. shameli*

35: *R. creaghi* + *R. canuti* + *R. arcuatus* + *R. euryotis* + *R. shameli* + *R. yunanensis*

36: *R. macrotis* + *R. philippinensis*

The abbreviations for the area names are: Cont = continental southeastern Asia including India, southern China, and the adjacent major islands including Taiwan; IndC = Indochina including Burma, Thailand, Cambodia, Vietnam and Laos; Maly = the Malay Peninsula; Sumt = Sumatra; Bone = Borneo; Java = Java; SulT = Sulawesi and Timor; Mulk = the Maluku Islands; Phil = the Philippine Islands; NewG = New Guinea; Aust = Australia.

Species	Areas										
	Cont	IndC	Maly	Sumt	Bone	Java	SulT	Mulk	Phil	Newg	Aust
1 R. acuminatus	0	1	1	1	1	1	1	0	0	0	0
2 R. affinis	1	1	1	1	1	1	1	0	0	0	0
3 R. arcuatus	0	0	0	1	1	0	0	1	1	1	0
4 R. borneensis	0	1	1	0	1	1	0	0	0	0	0
5 R. canuti	0	0	0	0	0	1	1	0	0	0	0
6 R. celebensis	0	0	0	0	0	1	1	1	0	0	0
7 R. coelophylllus	0	1	1	0	0	0	0	0	0	0	0
8 R. creaghi	0	0	0	0	1	1	0	0	0	0	0
9 R. euryotis	0	0	0	0	0	0	1	1	0	1	0
10 R. lepidus	1	1	1	1	0	0	0	0	0	0	0
11 R. luctus	1	1	1	1	1	1	0	0	0	0	0
12 R. macrotis	1	1	1	1	0	0	0	0	1	0	0
13 R. malayanus	0	1	1	0	0	0	0	0	0	0	0
14 R. megaphillus	0	1	1	0	0	0	1	1	0	1	1
15 R. nereis	0	0	1	1	0	0	0	0	0	0	0
16 R. philippinensis	0	0	0	0	1	0	1	0	1	0	1
17 R. pusillus	1	1	1	1	1	1	0	0	0	0	0
18 R. rouxi	1	1	0	0	0	0	0	0	0	0	0
19 R. sedulus	0	0	1	0	1	0	0	0	0	0	0
20 R. stheno	0	1	1	1	0	1	0	0	0	0	0
21 R. subbadius	1	1	0	0	0	0	0	0	0	0	0
22 R. thomasi	1	1	0	0	0	0	0	0	0	0	0
23 R. trifoliatus	1	1	1	1	1	1	0	0	0	0	0
24 R. yunanensis	1	1	0	0	0	0	0	0	0	0	0
25	0	0	1	1	0	0	0	0	1	0	0
26	0	0	1	1	0	1	0	0	1	0	0
27	1	1	1	1	1	1	1	0	1	0	0
28	1	1	1	1	1	1	1	1	1	0	0
29	1	1	1	1	1	1	1	0	0	0	0
30	1	1	1	0	0	0	0	0	0	0	0
31	0	0	0	0	1	1	1	0	0	0	0
32	0	0	1	1	1	1	1	1	1	0	0
33	0	0	1	1	1	1	1	1	1	1	0
34	0	1	1	1	1	1	1	1	1	1	0
35	1	1	1	1	1	1	1	1	1	1	0
36	1	1	1	1	1	0	1	0	1	0	1

Each pair of sister species or monophyletic groups, if they together occupy more areas than either of them does alone, also defines a distributional character. Cladistic biogeography assumes that the combined distribution of sister species or groups indicates the distribution of their immediate common ancestors. The areas they occupy were assigned the derived state, and other areas were assigned the primitive state of this character. But if the distribution of one of the sister species or group completely covered that of the other species or group, or the two sister groups together occupied all the areas, then the combined areas of this pair do not constitute an informative character since this distributional information is redundant. Successively more inclusive monophyletic groups were treated in the same way to identify additional characters.

The phylogenetic data of *Rhinolophus* was based on the majority consensus cladograms from all four cladistic analyses (section 'Cladistic Analysis'). I used majority consensus cladograms because they had the necessary resolution in species relationships for area analysis. Only those components which were common to at least two analyses and were not in conflict with other analyses were selected to construct the distributional characters. I consider the relationships selected in this way to be strongly supported by the data because they were invariant to modification in the assumptions of cladistic analysis, although some of the relationships were not present in all the shortest cladograms.

A total of 36 area characters were defined. Among them 24 characters were based on the distributional data of individual species, including all the species that occurred in two or more areas. The other 12 characters were based on the distributional data of monophyletic groups. The characters of the second type were not as numerous as I expected because, as sister species were joined into more inclusive monophyletic groups, the monophyletic groups

soon became large enough to occur in the entire region. Any monophyletic group distributed in all areas would not define a new area character.

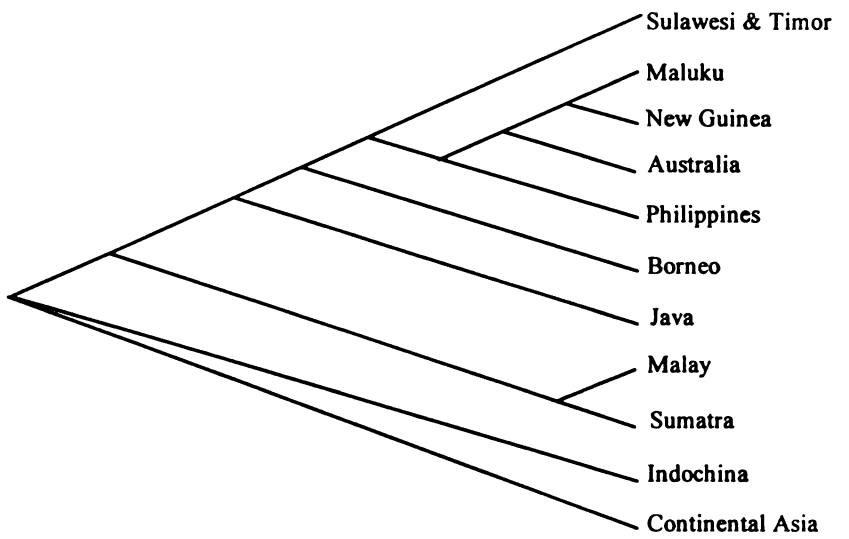
In addition to information about the shared occurrence of species or monophyletic groups, the total number of species and the number endemic species for each area were counted. The resulting distributional data matrix (Table 5.2) was analyzed using PAUP version 3.1.1 (Swofford and Begle, 1993) to identify most parsimonious area cladograms.

Because the phylogenetic analysis in the previous section has clearly indicated that the genus *Rhinolophus* was originated in African and west European region, the earliest rhinolophids of southeast Asian are likely to occur in continental Asia. Accordingly, I rooted the area cladogram at continental Asia in my area analysis. However, in comparing the various proposed lines dividing the Oriental and the Australian biotas, I treated the cladogram as unrooted. This treatment simulated the traditional research in which only regional distributional similarities or dissimilarities between areas were considered.

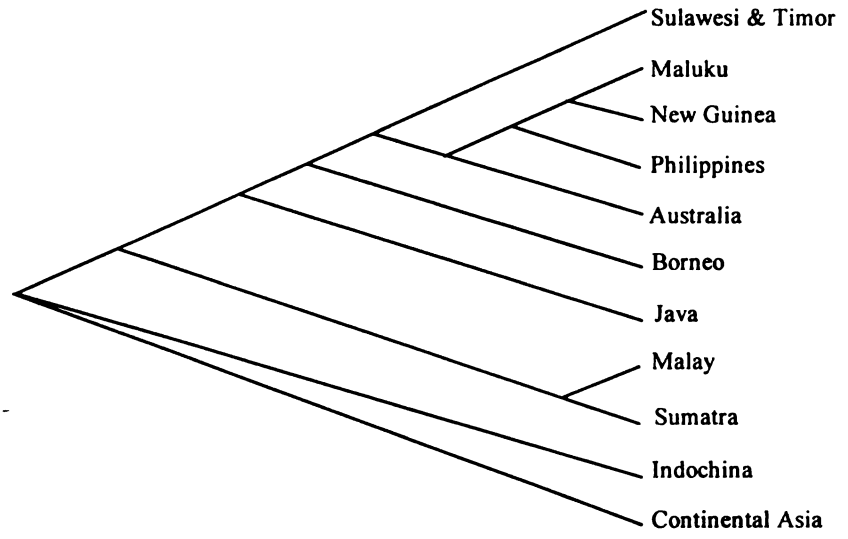
RESULTS

Two most parsimonious area cladograms were identified from cladistic analysis (Figure 5.7). These two cladograms are similar, differing only in the positions of Australia and the Philippines about which area is closer to the Maluku and New Guinea group. The strict consensus cladogram computed from these two cladograms contains a trichotomous node, leaving the relationships among Australia, the Philippines, and the area group of Maluku and New Guinea unresolved (Figure 5.8).

The branching pattern of the consensus area cladogram suggests a progressive subdivision of areas with distance from continental Asia. The partitions of the southeast



(a)



(b)

Figure 5.7. The two most parsimonious area cladograms computed from the distributional data of *Rhinolophus* in southeast Asia.

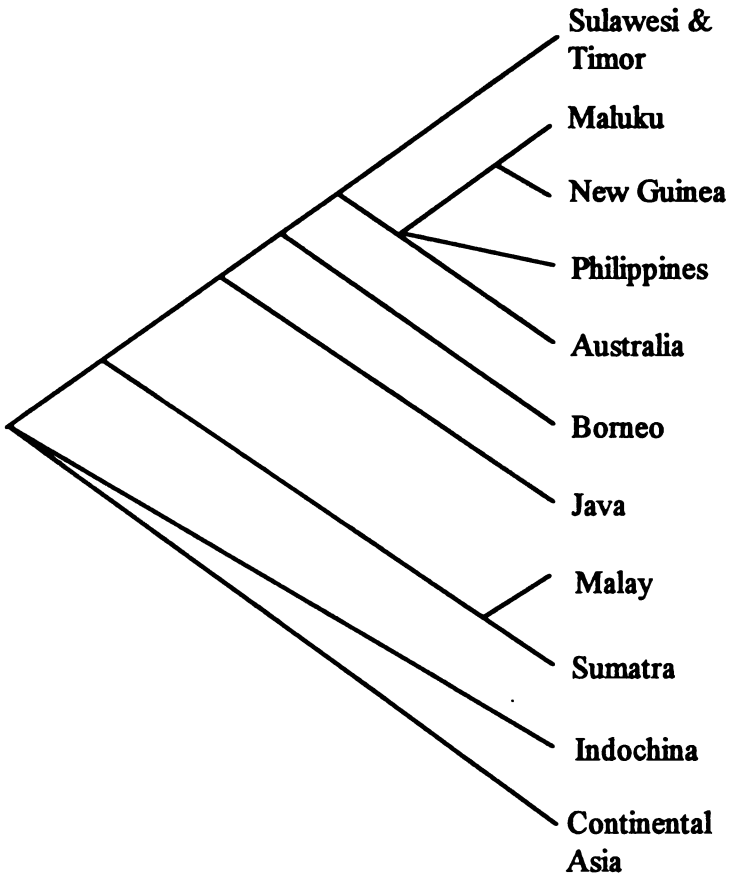


Figure 5.8. The consensus cladogram for the two most parsimonious area cladograms computed from the distributional data of *Rhinolophus* in southeast Asia.

Asian biota occurred first between continental Asia and Indochina, and successively took place southeastwards. Each of the partitions separates one area from all areas located farther from the continental Asia. The areas at the east end of the region, Maluku and New Guinea, where the most recent vicariant events is inferred, have the most derived rhinolophid biotas.

This pattern parallels the species diversity of pattern the genus (Table 5.2). Species diversity is highest in Indochina, declining steadily in the southeast Asian islands with distance from Indochina, being lowest in New Guinea and Australia. The lower level of species diversity in continental Asia can be explained by subtropical temperature conditions there that may be less conducive to these bats than the tropical monsoon forests of Indochina. The reduction of diversity towards more remote southeast Asian islands may be explained by the islands' distances from the continent. Island biogeography has demonstrated, in other organisms, that species diversity is negatively related to the distance of an island from the mainland, and positively related to the size of the island (MacArthur and Wilson, 1967; Lomolino, 1994).

As the partitioning of biota occurred progressively towards one direction, geographically adjacent areas are generally closely related. Both continental Asia and Indochina are situated at the root of the cladogram. Two pairs of adjacent areas, one for the Malay Peninsula and Sumatra, and the other for Maluku Islands and New Guinea, appear to be sister areas. Four eastmost areas, the Philippines, Maluku, New Guinea, and Australia, form a monophyletic area group. These four areas, together with Sulawesi, constitute a larger monophyletic area group of five areas.

The consensus area cladogram from the distributional data of *Rhinolophus* indicates that the Oriental realm, as defined by all proposed lines in Figure 5.2, is a paraphyletic area group. In contrast, the Australian realm, as defined by the Huxley's line (1864) or by the

Weber's line of faunal balance, is a monophyletic area group. In both most parsimonious area cladograms Australia and New Guinea are closer to the Philippine Islands than to Sulawesi. For this reason, a separation of the Australian realm from the Oriental realm by any other proposed line (see Figure 5.2) would result in both realms paraphyletic or polyphyletic.

The area cladogram of the present study does not support the 'Wallacean' zone suggested by Tate (1946) or the 'Papuan zone' suggested by Gressitt (1956). The 'Wallacean' zone represents a polyphyletic area group in the rhinolophid area cladogram; the 'Papuan zone', consisting of Maluku and New Guinea, on the other hand, is a most derived area group. However, since the present study indicates that the Australia realm is a derived monophyletic group, a sister area of the Australian realm may be close to what a 'transitional zone' would suggest. Such 'transitional zone' would have been evolved from the Oriental realm with the Australian realm but lacks the synapomorphies that the Australian realm has. A possible candidate for such a transitional zone is Sulawesi. In the consensus area cladogram, Sulawesi is a sister area to the monophyletic group containing the Philippines, Australia, Maluku, and New Guinea. In a strict cladistic point of view, though, a sister group does not suggest a transitional zone.

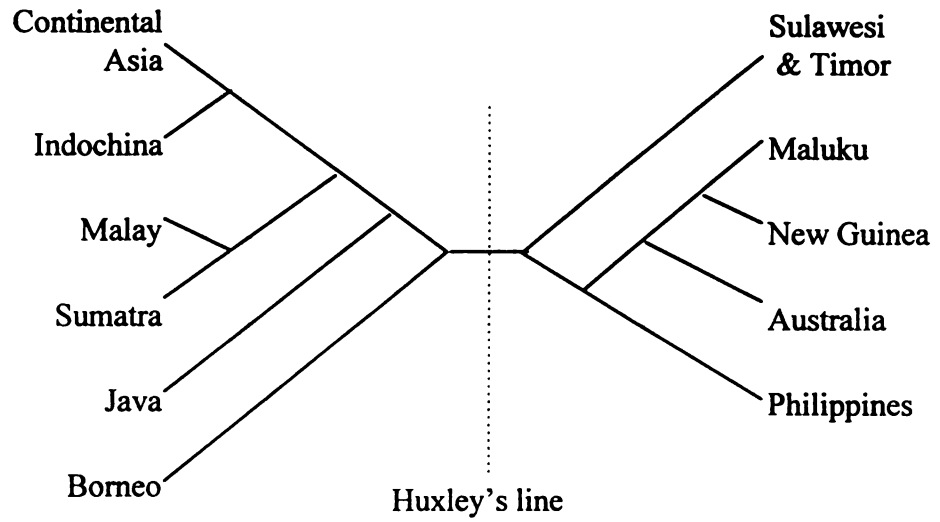
DISCUSSION

I did not attempt a cladistic analysis of biogeography over the entire distribution of *Rhinolophus*. In my phylogenetic hypothesis of the genus, the relationships among the African and western Eurasian species are unresolved. Because the rhinolophids of southeast Asia have been clearly identified as a monophyletic group, a cladistic biogeographic analysis of *Rhinolophus* for that region is not only interesting but achievable.

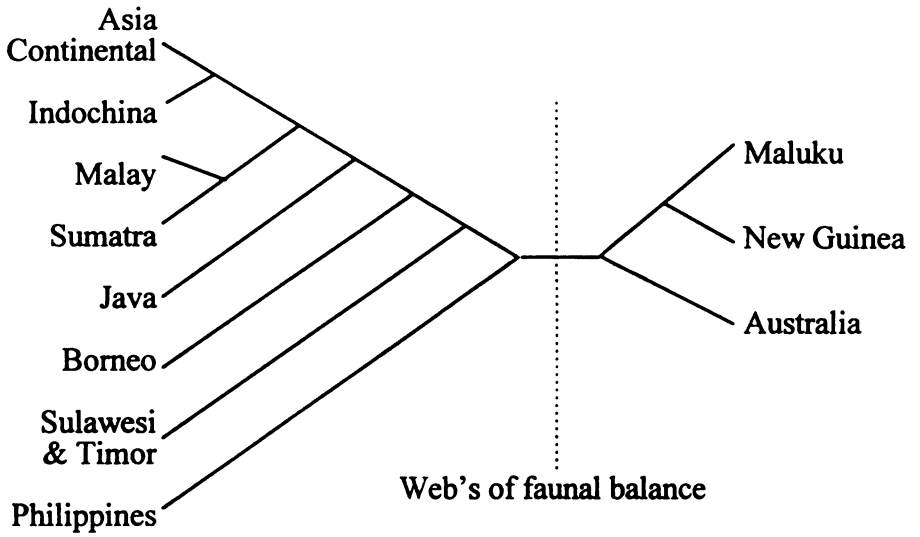
With 24 out of 36 area characters based on data of individual species distribution, the area character data inherit a substantial portion of information present in the traditional similarity matrix used by Holloway and Jardine (1968). The critical data in the present analysis are the 12 phylogenetically based area characters. Relationships between the species that inhabit these areas are likely to preserve certain distributional patterns of the past which are not visible in individual species distributions.

The interpretation of the area cladograms in the present study is greatly affected by the assumption about where the first ancestors of southeast Asian rhinolophids occurred. The panbiogeographic approach assumes that the earliest southeast rhinolophids inhabited the entire region (Craw, 1988). Under this assumption the hypothetical area relationships will be presented in an unrooted area cladogram which is ambiguous to many specific questions regarding area relationships (e.g. one of the most parsimonious cladograms, shown in Figure 5.6a, when unrooted, may support both Huxley's line and the Line of Faunal Balance, as illustrated in Figure 5.9). An alternative approach assumes particular areas as the most likely earliest distribution, suggesting a specific pattern of the regional biota fragmentation. My decision to root the cladograms at continental Asia, assuming that continental Asian is the most likely earliest habitat of southeast Asian rhinolophids, was based on my conclusion that the earliest members of the genus inhabited Africa before they emerged in southeast Asia.

Andersen (1905a) noted that many rhinolophid species in Africa were closely related to species in southeast Asia. Andersen believed that in each of these groups of species the Oriental form displayed more primitive features. He concluded that the Oriental region was the site of generic origin, and multiple dispersal of rhinolophids from southeast Asia to Africa had



(a)



(b)

Figure 5.9. One of the most parsimonious cladograms of southeast Asia based on rhinolophid distributional data (Figure 5.7 a). When unrooted, it supports both Huxley's line and the Line of Faunal Balance.

occurred. Koopman (1970) was more cautious. He concluded that either Africa or southern Asia could be the center of origin for this genus. Bogdanowicz and Owen (1992) and Bogdanowicz (1992), based on their multivariate morphometric study of the genus, questioned the close relationships among corresponding forms between Africa and southeast Asia proposed by Andersen. They maintained that the center of origin of the genus was southeast Asia and used two arguments to support their conclusion. First, Bogdanowicz argued that rhinolophids of southeast Asia region were phenetically most diverse. This is not a compelling argument. In determining the geographic origin of a group, morphological diversity should be defined in phylogenetic terms. Presence of a greater number of living species in southeast Asia, or presence in these species of more derived character states does not necessarily indicate that area was the site of the earliest distribution of the genus. Furthermore, relative morphological diversity for a group of organisms in a particular region can be affected by many geographical and ecological factors. In this particular region, repeated isolation and reconnection of southeast Asia islands associated with the rise and fall of sea levels may have played an important role in the divergent rhinolophid evolution.

Second, Bogdanowicz stated that no *Rhinolophus* species has been found in Madagascar. In contrast, there are five species of *Rhinolophus* in the Japanese Islands. Bogdanowicz argues that the chance of rhinolophids dispersing from a continental region to its offshore islands may be proportional to the length of time they were present on that continent. Therefore, the absence of rhinolophids in Madagascar may indicate that they have been in Africa for less time than in southeast Asia. He neglects the fact that some offshore islands are separated from the continent by a shallow continental shelf. These islands had extensive land

connection with the continent during the periods when the sea level fell. Animals could disperse from the continent to these islands through land connections.

According to Vail and Mitchell (1979), the fall of sea levels to more than 200 meters below present level has occurred three times since the Oligocene. The first was in the late Oligocene about 29 million years ago when sea level was about 250 meters lower than present. The second period was near the end of the Miocene when sea level fell about 200 meters below present level. The third period was in the beginning of the Pleistocene when sea levels fell to about 200 meter below present level. The Korea Strait and Yellow Sea, which separate the Japanese Islands form the Asian continent, are both less than 200 meters deep. So are the seas isolating Taiwan, Sumatra, Borneo and Java. Although Sulawesi, the Philippine Islands and New Guinea are detached from the Asian continental shelf by seas of more than 200 meters, they are linked with the Asian continental shelf by many small islands. Australia and New Guinea are connected by Sahul shelf which is less than 200 meters in depth. In contrast, the Mozambique Channel which isolates Madagascar from the African continent is more than 3,000 meters deep in its stretch of greater than 235 km (Brenan, 1972).

The fossil occurrence of *Rhinolophus* species supports an African origin of the genus. The earliest *Rhinolophus* is known at Robiacian of the Upper Eocene in France. Also appearing first in the same formation were representatives of the bat families Hipposideridae, Emballonuridae and Vespertilionidae (Savage and Russell, 1983). These fossils represent the oldest extant bat families we know of. On the other hand, the earliest rhinolophids found in southeast Asia are Pliocene in age (Savage and Russell, 1983). These fossil discoveries, as well as fossil bats belonging to the family Palaeochropterygidae found in the Lower and Middle Eocene of Europe, suggest an extensive family level divergence of bats during the middle of

the Eocene. Without further evidence, it is more parsimonious to conclude that modern family divergence occurred first in west Eurasia or Africa. To suppose that rhinolophid ancestors of moved to southeast Asia, where the family then arose, and new family members migrated back to west Europe is an unnecessarily complex hypothesis. The fact that the earliest rhinolophids and their close relative, *Hipposideros spp.*, were discovered in the same formation supports the hypothesis that rhinolophids evolved from common ancestors close to that region.

It has been proposed that more advanced vertebrate orders and families originated in areas characterized by large geographic size, heterogeneous topography, warm and relatively steady temperatures, and maximum species diversity (Briggs, 1984; Darlington, 1958). Although most early fossil species of *Rhinolophus* were unearthed from Europe, this region does not meet the conditions suggested above. However, Europe is close to the African continent. All the living species of *Rhinolophus* in Europe are present in Africa. It is possible that the rhinolophid faunas of these two continents have had easy communication since early in rhinolophid evolution. While both Africa and southeast Asia are in the tropical region, Africa is much larger than southeast Asia in land area. The Indian subcontinent had been isolated from both Africa and Eurasian continents since Early Cretaceous times and did not join the Eurasian plate until Early Eocene times (Briggs, 1989). The discovery of several early bat families in west Europe may indicate that the origin of these bat families is somewhere in the general vicinity of the fossil sites. The best candidate for the center of origin is tropical Africa. It is likely that a group of early rhinolophids migrated to eastern Asia and then to southeast Asia after Late Eocene times. These immigrants became the ancestors of all present rhinolophid species of that region.

APPENDIX 1

Appendix 1.

Eigenvalues of the Correlation Matrix for pooled skin and skull data

	Eigenvalue	Difference	Proportion	Cumulative
PC1	31.6678	28.7948	0.772386	0.772386
PC2	2.8730	1.0336	0.070073	0.842459
PC3	1.8394	0.9226	0.044864	0.887323
PC4	0.9169	0.2235	0.022363	0.909686
PC5	0.6934	.	0.016912	0.926598

Eigenvectors for pooled skin and skull data

	PC1	PC2	PC3	PC4	PC5
P2	0.172418	-.083247	-.040117	-.023871	-.124842
PAL	0.109400	-.376085	0.003675	-.255750	0.128854
M3	0.162211	-.079260	-.015707	-.284690	-.083366
WM3	0.168653	0.029704	-.058913	-.219661	-.020514
LPT	0.155555	0.064086	0.021484	-.177906	-.351054
TEF	0.169703	-.028797	-.079167	0.012044	-.152928
LSHF	0.167963	-.019548	-.092259	0.049479	-.185398
WZA	0.162510	-.163413	-.015354	-.194893	0.109304
WAB	0.159313	-.152750	0.189751	-.033099	-.058756
LAB	0.173056	-.084008	-.024395	-.053937	-.092963
BL	0.147886	-.020179	-.277334	-.075955	0.067196
BB	0.149697	-.223336	0.216808	-.079916	-.052380
WCO	0.173658	-.064537	-.023871	-.058046	-.076075
PMP	0.154513	-.179875	-.011526	-.253997	0.084077
VLAB	0.146259	-.232026	-.165428	0.070126	-.081830
PB	0.133495	-.200016	-.303237	0.163660	-.084484
DH	0.155997	0.257842	0.011993	-.126961	0.075170
DL	0.166992	0.165475	0.079035	-.076298	0.071835
LINF	0.153470	-.042989	-.247919	0.339418	-.034871
LOR	0.157654	-.024207	0.173877	-.078762	-.034122
HOR	0.158598	0.091240	-.129096	0.107009	0.039947
P4M3	0.074910	0.487515	-.090402	-.215033	0.152157
LBR	0.157694	0.120396	-.097730	0.170772	0.013017
HNS	0.157232	-.027819	-.194245	0.311190	0.032402
HCR	0.157377	-.031913	0.185730	0.016893	-.223995
HOCC	0.171319	0.136549	-.019199	0.005108	0.028054
FA	0.157678	-.099449	0.166521	-.009323	0.194144
TL	0.164202	0.034843	0.181913	-.034848	0.240700
FT	0.173948	0.086503	0.019445	0.025176	0.047405
LT	0.169151	0.048470	0.102121	0.005459	0.212480
2Met	0.102772	0.097246	0.465489	0.282857	0.053452
3Met	0.130181	-.112146	-.244813	0.036792	0.599065
3M1P	0.121998	-.108303	0.296024	0.338833	0.229818
3M2P	0.169543	0.105244	0.028385	-.061263	0.026027
4Met	0.159412	0.201372	-.022670	0.157464	-.161098
4M1P	0.170793	0.147164	0.005296	-.011604	0.038829
4M2P	0.174779	0.026485	0.027528	0.048558	0.040217
5Met	0.154596	0.182958	-.170745	0.047629	-.036945
5M1P	0.172724	0.068675	-.008331	0.065893	-.108945
5M2P	0.150633	-.151323	0.124112	0.214585	-.156713
EAR	0.156812	0.185484	0.104708	-.086978	-.078796

Eigenvalues of the Covariance Matrix for pooled skin and skull data

	Eigenvalue	Difference	Proportion	Cumulative
PC1	301.554	274.436	0.854695	0.854695
PC2	27.119	18.946	0.076862	0.931557
PC3	8.172	2.130	0.023163	0.954720
PC4	6.042	1.900	0.017126	0.971846
PC5	4.143	.	0.011742	0.983588

Eigenvectors for pooled skin and skull data

	PC1	PC2	PC3	PC4	PC5
P2	0.427171	0.138884	-.006055	-.103191	-.179621
PAL	0.279135	-.820383	-.022807	-.420030	0.031011
M3	0.129803	-.002387	0.006303	0.000956	0.249672
WM3	0.222023	0.151601	0.022316	-.055488	0.524562
LPT	0.030818	0.031388	-.009520	-.014099	0.030517
TEF	0.293281	0.208402	0.090323	-.253996	-.260799
LSHF	0.276359	0.225703	0.131221	-.249152	-.328737
WZA	0.166513	-.075781	-.052433	0.077341	0.275196
WAB	0.276712	-.039657	-.585712	0.388955	-.163227
LAB	0.317651	0.089441	-.015351	-.033877	-.022903
BL	0.093535	0.056973	0.187981	-.225879	0.054846
BB	0.164808	-.103041	-.398292	0.210823	-.110767
WCO	0.341564	0.142149	-.057450	-.044121	0.027353
PMP	0.152527	-.107637	-.001925	0.074744	0.366343
VLC	0.284149	-.234686	0.626665	0.636720	-.127412
VLAB	0.000020	0.006808	0.044724	-.004527	0.011480
PB	0.029617	-.007122	0.082531	0.036843	-.033621
DH	0.015491	0.029456	-.003447	-.013971	0.056562
DL	0.065836	0.090218	-.051316	-.021181	0.156842
LINF	0.029250	0.016785	0.070297	0.024068	-.042669
LOR	0.019358	0.007809	-.032990	0.017429	0.024704
HOR	0.026326	0.027774	0.027835	0.023040	0.024010
P4M3	0.009339	0.075096	0.018613	-.042883	0.155333
LBR	0.014869	0.021814	0.006932	-.000818	0.006819
HNS	0.024373	0.017809	0.038639	0.020813	-.014912
HCR	0.027615	0.009511	-.030425	0.029557	-.012436
HOCC	0.138000	0.175018	0.033671	0.044094	0.275876
FA	0.021468	-.007831	-.023292	0.000334	0.018353
TL	0.032023	0.019015	-.053734	0.033227	0.068681
FT	0.042457	0.042998	-.002678	0.024002	0.062385
2Met	0.007249	0.011792	-.039148	0.018211	0.007149
3Met	0.027470	-.006274	0.044977	-.007597	0.044210
3M1P	0.015478	0.000017	-.035292	0.005859	-.038744
3M2P	0.034888	0.036070	-.012491	0.005158	0.069851
4Met	0.055394	0.100559	0.046933	0.022899	0.071356
4M1P	0.056720	0.074534	-.003652	-.008974	0.110922
4M2P	0.055252	0.035594	-.007278	0.044363	0.061603
5Met	0.029090	0.042546	0.055189	0.000702	0.055357
5M1P	0.047814	0.042473	0.011225	0.019577	0.027394
5M2P	0.024961	-.005790	-.008093	0.041172	-.034141
EAR	0.021570	0.032357	-.021238	0.002602	0.047342

Eigenvalues of the Correlation Matrix for skull data

	Eigenvalue	Difference	Proportion	Cumulative
PC1	19.3322	16.4191	0.716007	0.716007
PC2	2.9131	1.1508	0.107893	0.823899
PC3	1.7623	1.1855	0.065271	0.889170
PC4	0.5768	0.0532	0.021362	0.910532
PC5	0.5235	.	0.019390	0.929923

Eigenvectors for skull data

	PC1	PC2	PC3	PC4	PC5
P2	0.009179	0.415359	0.391855	0.131644	0.468400
PAL	0.148541	0.379935	-.165256	0.076674	0.186574
M3	0.210370	-.135304	0.188235	-.104874	-.040451
WM3	0.219435	-.120614	0.048376	-.068119	-.035555
LPT	0.180877	-.084540	0.365858	0.151442	0.075115
TEF	0.217341	-.126597	-.080247	-.020207	0.016237
LSHF	0.175958	0.276401	-.164580	-.239902	0.103061
WZA	0.222428	-.079249	-.046037	-.026750	-.055110
WAB	0.175435	0.262821	-.117214	0.028417	-.089472
LAB	0.195812	0.259159	-.038921	0.073811	-.049812
BL	0.198548	-.092717	-.191659	0.079955	0.072128
BB	0.145993	-.263847	-.330174	-.255487	0.327620
WCO	0.210154	0.075651	0.038124	-.210022	-.035638
PMP	0.118714	-.215496	0.543588	-.196547	-.119163
VLC	0.205497	0.092993	0.077554	0.100176	-.063990
VLAB	0.191459	0.258466	-.043733	0.249588	-.097418
PB	0.198089	-.105206	-.224834	-.193158	0.264186
DH	0.207777	-.129494	0.058281	0.005960	0.156400
DL	0.224207	-.013410	0.056064	0.015884	0.043478
LINF	0.136774	-.270597	-.172971	0.742782	-.106497
LOR	0.158542	0.233621	-.071250	-.217513	-.659519
HOR	0.215988	-.094500	0.031123	0.003797	-.099984
P4M3	0.223480	-.057426	0.058355	0.006167	-.040874
LBR	0.222934	0.008333	-.073397	0.046122	-.033217
HNS	0.206121	0.091284	0.202106	0.074482	0.039103
HCR	0.222773	0.018588	-.024679	-.005238	0.115746
HOCC	0.207672	-.159877	0.051933	-.046481	0.033146

Eigenvalues of the Covariance Matrix for skull data

	Eigenvalue	Difference	Proportion	Cumulative
PC1	19.0069	18.1599	0.900603	0.900603
PC2	0.8470	0.4302	0.040135	0.940738
PC3	0.4169	0.2133	0.019752	0.960490
PC4	0.2036	0.0575	0.009646	0.970136
PC5	0.1461	.	0.006922	0.977058

Eigenvectors for skull data

	PC1	PC2	PC3	PC4	PC5
P2	0.000066	0.098295	0.194460	-.044111	-.025751
PAL	0.098809	0.543833	0.025836	-.194663	-.257108
M3	0.076232	-.098997	0.072820	0.050225	0.015220
WM3	0.303104	-.251654	-.075799	0.177502	-.021176
LPT	0.049636	-.070836	0.143034	-.027437	0.038633
TEF	0.203941	-.121266	-.268494	-.029665	-.006642
LSHF	0.050712	0.187641	0.004688	-.014028	0.125452
WZA	0.409631	-.120652	-.396100	0.269466	0.070962
WAB	0.072276	0.237217	0.005220	-.009809	0.308227
LAB	0.110873	0.313789	0.093354	0.008567	0.356226
BL	0.079485	-.002290	-.177160	-.047223	-.081392
BB	0.028784	-.052631	-.157202	-.042350	-.010142
WCO	0.113467	0.086922	0.092509	0.083209	0.302898
PMP	0.078624	-.385170	0.553803	0.190585	0.209492
VLC	0.065010	0.051937	0.033462	0.071895	0.102953
VLAB	0.094873	0.269371	0.046182	0.051082	0.064888
PB	0.106582	-.008067	-.269528	-.191774	0.380480
DH	0.106173	-.096452	0.000927	-.149642	0.187939
DL	0.615513	0.021842	0.312321	-.276641	-.394067
LINF	0.038669	-.081645	-.140076	-.095937	-.136892
LOR	0.098389	0.306155	0.039306	0.788146	-.131604
HOR	0.152446	-.080203	-.015337	0.041119	0.004925
P4M3	0.255446	-.082392	0.069473	0.027845	-.056648
LBR	0.232025	0.107344	-.160786	-.038530	-.043887
HNS	0.130262	0.082608	0.306489	-.096184	0.160635
HCR	0.198609	0.094811	-.029875	-.121372	0.335269
HOCC	0.098873	-.111734	-.023634	-.049602	0.127937

Eigenvalues of the Correlation Matrix for skin data

	Eigenvalue	Difference	Proportion	Cumulative
PC1	12.8459	12.0224	0.856395	0.856395
PC2	0.8235	0.3547	0.054899	0.911294
PC3	0.4688	0.1990	0.031253	0.942546
PC4	0.2698	0.0484	0.017989	0.960535
PC5	0.2214	.	0.014761	0.975297

Eigenvectors for skin data

	PC1	PC2	PC3	PC4	PC5
FA	0.275035	-.121487	-.071431	0.099358	-.079332
TL	0.206276	0.604998	0.420025	0.356650	0.204390
FT	0.261894	0.009019	0.041509	-.423584	0.110276
LT	0.261612	-198163	-048781	-453206	.159603
2Met	0.266481	-.268150	-.041156	0.189945	-.116367
3Met	0.262670	-.306383	-.027219	0.226376	-.179791
3M1P	0.268462	0.151158	0.052295	-.197703	0.183863
3M2P	0.257280	0.177362	-.481256	0.097662	-.045640
4Met	0.276293	-.093600	-.070184	0.024855	-.072220
4M1P	0.237179	-.370892	0.500884	0.179606	0.244728
4M2P	0.250366	0.314792	-.449177	0.146815	0.046789
5Met	0.275339	-.134645	-.093647	0.013465	-.008840
5M1P	0.264162	-.047769	-.026577	0.332882	0.240891
5M2P	0.257894	0.232801	0.134638	-.405753	0.153806
EAR	0.243163	0.199409	0.304013	-.110013	-.826730

Eigenvalues of the Covariance Matrix for skin data

	Eigenvalue	Difference	Proportion	Cumulative
PC1	291.159	265.591	0.861871	0.861871
PC2	25.567	17.722	0.075683	0.937554
PC3	7.845	1.860	0.023224	0.960778
PC4	5.985	2.404	0.017716	0.978494
PC5	3.581	.	0.010600	0.989094

Eigenvectors for skin data

	PC1	PC2	PC3	PC4	PC5
FA	0.436917	-.177662	0.007483	-.086968	-.112129
TL	0.286216	0.838009	0.032346	-.425519	-.058424
FT	0.131921	-.000564	-.011854	0.006849	0.289219
LT	0.225196	-.164422	-.019462	-.045728	0.619027
2Met	0.297813	-.231497	-.114306	-.252160	-.236267
3Met	0.280391	-.247885	-.157035	-.248075	-.311316
3M1P	0.170217	0.068958	0.059092	0.083375	0.323803
3M2P	0.282318	0.018436	0.593296	0.386236	-.190846
4Met	0.324035	-.112374	0.010306	-.025399	0.017004
4M1P	0.095237	-.062720	-.194659	-.223802	0.088361
4M2P	0.168455	0.090546	0.403284	0.208864	-.114035
5Met	0.348338	-.168407	0.053094	-.035630	0.080587
5M1P	0.101482	-.011961	0.042441	-.059414	-.023549
5M2P	0.155578	0.105969	0.004239	0.081638	0.423889
EAR	0.289912	0.232636	-.632500	0.650353	-.144137

APPENDIX 2

Appendix 2.

LIST OF SPECIMENS USED

1. *R. acuminatus* - skull (44): Java (3), USNM 456262, 156351, 155791; Sumatra (9), USNM 141012, 141014, 141015,141340, 141341, 141344, 141346, 241241, 241242; Borneo (2), USNM 292390, 449972; Philippine (8), USNM 477613, 477615-477620, 477623; Siam (5), USNM 84493, 254766, 254768, 254770, 355561; Thailand (17), AMNH 88016-88032; skin (17): Tailand (17), AMNH 88016-88032;

2. *R. adami* - skull (1):Cameroon (1), CMNH 13178; skin (1):Cameroon (1), CMNH 13178;

3. *R. affinis* - skull (75):Burma (3), USNM 279204, 279205, 18456; China (42), USNM 238849-238851, CMNH 88033-88036, 88551-88553, 88555, 88557, 92146, 92140-92142, 92143, FMNH 33806-33813, 33818, 33819, 75996-77999, 76001-76003, 76005-76012, 76015, 33924, 33922, 33923; Malysia (4), USNM 481057, FMNH 64089, 87345, 87351; Siam (3), 83538, 83571, 83540; Borneo (3), USNM 152045, 154402, 154406; Vietnam (9), USNM 320630, FMNH 32143-32146, 32149-32152; Assam (4), FMNH 75956, 75962, 82639, 82641; Borneo (7), FMNH 44154, 47076-47081; skin (27): China (15),CMNH 88033-88036, , 92140-92142, 92146, FMNH 33813-33816, 33818, 33819; Bornio (6), 47076-47081; Siam (6), 76007-76009, 76011, 76012, 76015;

4. *R. alcyon* - skull (27):Camerom (8), USNM 511918, 511919, AMNH 236298, 206955, 86880, CMNH 58295-58297, 41000; Ghana (1), USNM 414973; Sierra Leone (18), USNM 546967-546977, 546979, 546980, 546982-546984, 546986, 546987; skin (7): CMNH Camerom (7) 58295-58297, 41000; AMNH 86880, 206955, 236298;

5. *R. alticolus* - skull (17):Camerom (5), CMNH 5701, 42308, 58311, 58312, 58320; S. Africa (12), CMNH 58298-58309; skin (5):Camerom (5), CMNH 5701, 42308, 58311, 58312, 58320;

6. *arcuatus* - skull (24):Philippine (24), USNM 101093, 101964, 175798, 175803, 175817, 175820, 175824, 303960, 303952, 303965, 304354, 304355, 304357, 304359, 459451, 459452, 573282, 573283, AMNH 241805, 241807, 187134, 187136-187138; FMNH 140671-140678; skin (10):Philippine (10), FMNH 61229-61233, MCZ 35106-35108, 35110,035111;

7. *blassi* - skull (30):Burma (1), USNM 327990; Ethiopia (1), AMNH 48077; Palestine (2), AMNH 54413, 54414; Yugoslavia (2), AMNH 239591, 239591; Turkmenia (1), AMNH 245355; Fordan (6), CMNH 78840-78845; Afghanistan (11), FMNH 102271-102275, 102277-102281, 102369; Iran (16), FMNH 96608-96610, 96612, 11169, 11174,

96580-96584, 96563, 96566, 96567, 96570, 96572; skin (19): Afghan (19), CMNH 78841-78845, FMNH 102271-102275, 102277-102281, 102369;

8. *R. blyth* - skull (26):Burma (10), USNM 279206-279209, 279212-279214, 279216-279218; China (15), USNM 238855, 238857-238860, 238862, 260045, 279350, 238156, 238158-238160, 294812, AMNH 58311, 58461; Siam (1), USNM 296498; skin (10): China (10), MCZ 20291-20294, 7515-7517, 58293, 58464, 58474;

9. *R. borneensis* - skull (21):Natuna (4), USNM 140751-140752, 107755, FMNH 640950; Indonasia (4), USNM 521820, 145611, 145612, 145699; Malaysia (1), USNM 449973; Borneo (1), AMNH 106844; Timor (4), AMNH 153511, 237759, 237760, 237777; Java (Bali) (2), AMNH 107887, 107888; Noesa (2), AMNH 107958, 107959; Sulawesi (3), 102231, 102360, 102246; skin (10): Borneo(8), AMNH 102230-102233, 102360, 102366, AMNH 103918, MCZ 36081; Celebes (1) AMNH 106844; Malaya (1), USNM 449973;

10. *R. capensis* - skull (9):Africa (9), USNM 342583-342588, CMNH 46787-46789; skin ():Africa (10), CMNH 46787-46789, MCZ 17899, 37226, 37227, 37049-37051;

11. *R. celebensis* - skull (3):Sulawesi (3), USNM 217464, 219379, 219383; skin (2): USNM 217463, 217464;

12. *R. chaseni* - skull (8):VietNam (8), USNM 357010-357013, 357094, 357096, 357257, 357351; skin (6):VietNam (6), USNM 357010-357013, 357257, 357258;

13. *R. clivosus* - skull (66):Africa (36), USNM 381538-381541, 381544-381550, 381552-381555, CMNH 40669-40672, 46793, 46796, 93167, 93169, 52642-52650, FMNH 38137-38140; Egypt (12), USNM 282406, 282478, 312514, CMNH 42356, 78854, 78855, FMNH 78780, 78783, 78821, 78822, 123219, 123220; Liberia (1), AMNH 265710; Libya (1), CMNH 78856; Sudan (7), FMNH 77648, 77649, 78470, 78474, 108146-108148; Ethiopia (3), FMNH 28775, 28777, 79289; Kenya (6), FMNH 67897-67902; skin (11): Africa (11) CMNH 40669-40672, 46793, 46796, 93167, 93169, 78854, 78855, 62356;

14. *R. coelophyllus* - skull (16):Siam (6), USNM 267260, 296824, 296825, 296827, 296828, 356305; Japan (2), USNM 278722, 278723; Borneo (2), USNM 198947, 198948; Malaysia (3), AMNH 216856, 216857, 216861; Thailand (3), CMNH 88037-88039; skin (6):Thailand (3), CMNH 88037-88039; ; Malaysia (3), AMNH 216856, 216857, 216861;

15. *R. cornutus* - skull (2):Japan (2), AMNH 244343, FMNH 73678; skin (7): Japan (7) USNM 728722, 728722, 23691, 23692, 23694-23696;

16. *R. creaghi* - skull (7):Timor (2), AMNH 237784, 237787; Borneo (5), FMNH 47071-47075; 64094; skin (11):Timor (6), AMNH 237784-237787, 237801, 237802; Borneo (5), FMNH 47071-47075;

17. *R. darlingi* - skull (13):Bechwana (3), USNM 382645, 365203, 470252; S. Africa (9), AMNH 257157-257161, 257163, CMNH 93168, 93170, 40675; Tanganyika (1), AMNH 188272; skin (): Africa (8) MCZ 34093-34097, CMNH 93168, 93170, 40675;

18. *R. denti* - skull (23):Bechwana (21), USNM 322855-322862, 322864, 322869-322871, 322874, 322876-322882, 322890; S. Africa (1), CMNH 36015; Cameroom (1), CMNH 58313; skin (10): Bechwana (6) USNM 322875-322878, 322883, 367683; Ivory Coast (2) FMNH 105206, 105325; Africa (2) CMNH 93171, 58313;

19. *R. deckeni* - skull (3):Kenya (2), USNM 247386, FMNH 48827; Tanganyida (1), AMNH 208341;

20. *R. eloquens* - skull (26): Zaire (1), AMNH 82392; Kenya (12), CMNH 10704, 97940-97943, 79746-97949, 102165, FMNH 67916, 67917; Sudan (4), FMNH 56291, 66665-66667; S. Africa (5), 97932-97935, 102164; Zaire (4), FMNH 25600, 67497, 68063, 68068; skin (12): Kenya (12), CMNH 93171, 10704, 97940-97943, 79746-97949, 102165;

21. *R. euryale* - skull (26):France (1), USNM 38351; Greece (1), USNM 153596; Italy (4), USNM 105790, 105792, 86586, 86588; Spain (1), USNM 260652; Czechoslovakia (1), USNM 540777; Morocco (4), USNM 476274, 476267-47629; Algeria (4), CMNH 78857-78859, 78869; Iran (9), FMNH 96540, 96544, 96545, 11170-11173, 11175, 11176; Lebanon (1), FMNH 99556; skin (20): Algeria (5), CMNH 78857-78859, 78869, 89477; Iran (15), FMNH 96540-96542, 96544, 96547-96551, 11170-11173, 11175, 11176;

22. *R. euryotis* - skull (24):Indonasia:Moloccas (2), USNM 543263, 543264; Sulawesi (6), USNM 501515-501517, 501519-501521; Bismarcks (1), AMNH 195249; New Guinea (9), AMNH 109956, 109957, 101940, 101941, 195248, 157400, 158462, 158470, 190270; Mulaccos (2), AMNH 54432, FMNH 34051; Sulawesi (4), AMNH 196475, 102236, 102239, 102241; skin (15): Sulawesi (8), AMNH 196475, 196476, 102236-102239, 102241, 102241; Malayasia (7), USNM 198371-198373, 198375-198378;

23. *R. ferrumequinum* - skull (56):Frace (3), USNM 154221, 154525, 154526; Italy (2), USNM 38198, 38343; Spain (2), USNM 172123, 172129; Japan (2), USNM 291737, 291739; Morocco (2), USNM 476307, 470606; B.EA?? (4), USNM 182665, 182667, 162499, 182668; Kenya (15), USNM 350880-350882, 350884-350887, 436583-436586, 436596, 436598, 436599, 436602; Jordan (15), CMNH 78876, 78877, 62112-62115, 62120-62124, 78872-78875; China (1), CMNH 92167; Afghanistan (10), FMNH 102370-102379; skin (15): Jordan (15), CMNH 62112-62115, 62119-62124, 78872, 78874, 78876, 78877, 92167;

24. *R. fumigatus* - skull (30): Kenya (17), USNM 350889-350894, 436519-436522, 436531, 436533-436536, 436538, 436540-436542; Namibia (3), CMNH 93172, 93173, 61476; Algeria (10), CMNH 97930, 97931, 97950, 97951, 67971, 93174, 94985-94987, 98531; skin (13): Namibia (2), CMNH 93172, 93173; Algeria (11), CMNH 61476, 97930, 97931, 97950, 97951, 67971, 93174, 94985-94987, 98531;

25. *R. guineensis* - skull (3):Liberia (3), AMNH 257046, 265719, 265738;

26. *R. hildebrandti* - skull (17):ABA (1), AMNH 49102; Mozambique (7), AMNH 245158, 216206, 216208-216212; Tanganyika (1), AMNH 161308; Zimbabwe (2), AMNH 213048, 213049; Kenya (1), AMNH 161917; S. Africa (1), CMNH 93175; Sudan (3), FMNH 78196, 79553, 79554; S. Africa (1), FMNH 95148; skin (10): S. Africa (1), CMNH 93175; Sudan (4), FMNH 78196, 79553, 79554, 95148, 95149; Africa (5) MCZ 22790, 22791, 38923, 38982, 43764;

27. *R. hipposideros* - skull (34):Iran (6), USNM 350138, FMNH 96667, 111183, 111184, 111188, 111190; France (1), 172121; Germany (3), USNM 152530, 67540, 67541; Spain (2), USNM 172122, 172126; Italy (3), USNM 38347, 152527, 38192; Switzerland (3), USNM 121183, 124393, FMNH 44123; Morocco (1), USNM 476320, 476321; Austria (1), AMNH 150439; Germany (1), AMNH 217131; Poland (1), AMNH 212186; Georgia (1), AMNH 245359; Algeria (1), CMNH 62111; Poland (1), CMNH 45292; Jordan (1), CMNH 78905; Afghanistan (6), FMNH 102410-102413, 102415, 102424; Egypt (1), FMNH 74476; Lebanon (1), FMNH 9956; skin (18): Africa (4), CMNH 45292, 62111, 78905, 78906; Afghanistan (7) FMNH 102409, 102411-102415, 102424; Iran (7), FMNH 96656, 96657, 111183-111185, 111189-111190;

28. *R. hirsutus* Philippine (1), USNM 125487;

29. *R. imaizumii* - skull (1):Japan (1), AMNH 241142; skin (): Japan (7), AMNH 241137-241143;

30. *R. inops* - skull:Philippine (21), USNM 125314, 458607-458612, 459494, 573289, 458580-458587, 458590-458592, 458594; skin (12): USNM 458604, 458606, 458609-458612, 574818-574823;

31. *R. keyensis* - skull (2): Moluccas (2), AMNH 222739, 222741; skin (3): Moluccas (3), AMNH 222739-222741;

32. *R. landeri* - skull (42): Gambia (7), USNM 379388, 412004-412006, 412009, 412011, 412016; Nigeria (4), USNM 379508, 379513, 402708, 402710; Mozambique (4), USNM 365181, 365184, 3665187, 365191; West Africa (1), 185330; Ghana (1), AMNH 237419; Kenya (1), AMNH 114476; Congo (1), AMNH 49132; Botswana (2), AMNH 89174, 89175; Cameroom (13), CMNH16064, 16067, 16069-16073, 16077, 42309, 42310, 58314-58316, 59318; Kenya (1), CMNH 97952; Gabon (2), CMNH 90800, 90801; India (2), CMNH 92230-92234; Sudan (3), FMNH 67323, 79546, 79547; Ivery Coast (1),

FMNH 105236; skin (122): Cameroom (19), CMNH 7443, 16064-16073, 58314-59318, 42309-42311; Gabon (2), CMNH 90800, 90801; Kenya (1), CMNH 97952;

33. *R. lepidus* - skull (27):China (1), AMNH 84384; India (12), AMNH 236216, 208837, 174287, 247284, 216889, 216896, 216897, FMNH 82654, 82652, 82653, 82647, 82649, 82650; SN (6), CMNH 92235-92240; Afghanistan (8), FMNH 102283-12286, 102288, 102416-102418; skin (17): Afghanistan (8), FMNH 102283-12286, 102288, 102416-102418, India (4), FMNH 82651-82654; SN (5), CMNH 92230-92234;

34. *R. luctus* - skull (33):Borneo (4), USNM 292387, 292388, 300837, 300838; Taiwan (8), USNM 358199-358202, 332843-332845, 294141, 358198; Siam (2), USNM 296829, 296830; Thailand (3), USNM 528271, AMNH 167933, CMNH 88040; Indochina (1), AMNH 87311; Java (1), AMNH 107853; Borneo (3), AMNH 106834-106836; Malaysia (7), CMNH 88041-88046, 98681; India (3), FMNH 82646, 48497, 85046; Indochina (1), FMNH 46539; skin (9): India (8), FMNH 82646, 48497, 85046, 99466, 46539, 73005, 76016, 98681; Thailand (1), CMNH 88040;

35. *R. maclaudi* - skull (4):Liberia (1), AMNH 265708; Uganda (1), AMNH 245634; Uganda (2), FMNH wts595, jck1966; skin (1): Uganda (1), AMNH 245634;

36. *R. macrotis* - skull (13):India (2), USNM 399303, FMNH 47403; Malaysia (4), AMNH 243057, 216864, 84382, 57161; Indochina (4), FMNH 32142, 32127, 32215, 38992A; China (1), FMNH 33892; Vietnam (2), FMNH 38992, 32142; skin (10): China (3), AMNH 84888, 56894, 56897; Malaya (2), 216864, 216870; Indochina (5), FMNH 32142, 32127, 32215, 33892, 47403;

37. *R. malayanus* - skull ():Thailand (), USNM 528272-528277; Vietnam (), USNM 260043; Indochina (), AMNH 87300-87302, 216875, FMNH 32117, 32119, 32121, 32126, 32139, 32217, 32218, 32225, 33768; skin (): Thailand (16), FMNH 32117, 32119, 32121, 32126, 32138, 32139, 32217, 32218, 32225, 33768; CMNH 88041-88046;

38. *R. megaphyllus* - skull (15):Australia (10), AMNH 194238, 160288, 154594, 183446, 154626, 183514, 162663, 154627-154629, FMNH 64398; Papua (5), AMNH 157391, 158652-158654, 158674; skin (10): Australia (10), FMNH 60851, 60852, 60853, 64398, MCZ 29087, 27928, 27930-27933;

39. *R. mehelyi* - skull ():Egypt (), USNM 312517, 312518, FMNH 79082, 79088, 79089; Sardinia (), USNM 86536; Morocco (), USNM 476213, 476215, 476223, 476232-476234; Dagestan (USSR), AMNH 245361; Azerbaijan (USSR), AMNH 245360; Trnisia (), AMNH 217132; Algeria (), CMNH 78884, 78885, 78893-78897; Libya (), CMNH 78898-78904; Sudan (), CMNH 89625-89632; Iran (), FMNH 111129-111132, 96614, 96616-96619, 96621;

40. *R. milutilus* - skull (2): Indonesia (1), USNM 101770; Siam (1), USNM 254763; skin (7): Malaya (2), AMNH 234060; Thailand (4), USNM 528278, 528279, 528280, 528281; Siam (2);USNM 260606, 260607;

41. *R. monoceros* - skull (22):Taiwan (22), USNM 294142, 294143, 330053, 332849, 332850, 358144, 358145, 358151, 358152, 38154, 38155, 358174-358179, 358181, 358193-358196; skin (11): Taiwan (11), 215770, 215777, 215784, 215786; USNM 330052, 332850, 358149-358153;

42. *R. nereis* - skull (1):Philippine (1), USNM 101714; skin (1):Philippine (1), USNM 101714;

43. *R. osgoodi* - skull (4):China (4), AMNH 45046, 44547, FMNH 33295, 33689; skin (): China (), 45052-45055, 45074, 45078, 45838, 45089, FMNH 33295, 33297;

44. *R. pearsoni* - skull (13):China (4), AMNH 84862, 58282, FMNH 33839, 33840; Thailand (3), AMNH 250003, 250004, 167935; Malaysia (1), AMNH 234063; Burma (1), AMNH 112910; Assam (4), FMNH 75963, 75966, 75968, 75969; India (3), FMNH 82643-82645; skin (8): China (3), AMNH 84862, 58281, MCZ 249339; Thailand (3), AMNH 250003, 250004, 167935; Burma (2), AMNH 112908, 112910;

45. *R. philoppinensis* - skull (4): Philippine (1), USNM 459469; Australia (2), AMNH 157069, 157071; Sulawesi (1), AMNH 102348; skin (11): Sulawesi (9), 35007-35009, 35098, 35099, AMNH 102348-102351; Negris Id. (2), USNM 459496, 459497;

46. *R. pusillus* - skull ():Thailand (), USNM 528278; China (), AMNH 56910, 56922, 57156, 57160, 58294, CMNH 88047-88049, 33829, 33831; Vietnam (), FMNH 32220; *R. refulgens* - skull (): Thailand (), USNM 528280;

47. *R. rex* - skull (3):China (3), AMNH 84381, 56893, FMNH 39548; skin (4): China (4), AMNH 84891, 56893, 56970, MCZ 20286;

48. *R. robinsoni* - skull (2):Malaysia (1), AMNH 236201; Thailand (1), CMNH 88050; skin (2): Malaysia (1), AMNH 236201; Thailand (1), CMNH 88050;

49. *R. rouxi* - skull (38):Srilanda (1), USNM 540556; China (25), USNM 238834, 238836, 238838-238844, 279352, 279353, AMNH 84848, 84855, 84857, 84859, 44682, 44694, 60217, 56935, 60225, CMNH 92144, 92145, FMNH 33823, 33824, 33896; India (3), CMNH 92241, FMNH 82634, 82635; Assam (8), FMNH 75958, 75959, 75965, 76063-76026, 76013; Ceylon (2), FMNH 99465, 35376; skin (10): India (4), CMNH 92241, FMNH 82634, 82635, 32632, 32633; Ceylon (3), FMNH 99465, 35375, 35376; China (3),CMNH 92144, 92145, 92241;

50. *R. rufus* - skull (10): Philippine (10), USNM 303953, 458613-458616, 573588, FMNH 61220-61222, 49275; skin (11): Pilippine (11), MCZ 35086, 35088-35090, 35092, 35166, 35167, FMNH 61220-61222, 49275;

51. *R. sedulus* - skull (6): Malaysia (6), USNM 115494, 449975, 449976, AMNH 235576, 247289, FMNH 87277; skin (8): Burma (5), 106801, 235576, 234788-234790; Malaya (3), AMNH 234088-234090;

52. *R. shameli* - skull (1):Thailand (1), USNM 528285-528287;

53. *R. silvestris* -skull (1):Gabon (1), FMNH 73827;

54. *R. simplex* - skull (3): Lesser Sundas 1(), AMNH 54861; skin (3): Lesser Sundas (3), AMNH 54861, 54862, 54868;

55. *R. simulator* - skull (33):Mozambique (5), USNM 365193, 365198-365201; S. Africa (18), USNM 376755, 368607, AMNH 168149-168155, CMNH 46077-46082, 46084-46086, 40686; Liberia (1), AMNH 265746; S. Africa (9), AMNH 168241, 245213, 245214, 257165-257170; skin (11): CMNH 46076-40686;

56. *R. stheno* - skull (10):Thailand (2), USNM 528288, 88051; vietnam (2), USNM 320629, 320631; Malaysia (6), AMNH 235577, 216905, 216909, 216929, 216931, FMNH 64090; skin (11): Malaysia (11), AMNH 216921, 216923-216928, 216930, 216931-216934, CMNH 88051;

57. *R. subbadius* - skull (7): India (1), USNM 398802; Vietnam (3), FMNH 32216, 32209, 32266; Assam (3), FMNH 76018-76020; skin (): India (1), USNM 398802; Vietnam (3), FMNH 32216, 32219, 32226; Assam (3), FMNH 85062, 75976,76019;

58. *R. subrufus* - skull (12):Philippine (8), USNM 303901, 303903, 303907, 303908, 125315, 573286-573288, AMNH (4), 241804, 241808, 241810, FMNH 49274; skin (8): Philippine (8), FMNH 49274, MCZ 35010-35014, 35094-35096;

59. *R. swinnyi* - skull (6): Africa (3), USNM 344268, CMNH 93176, 36971, 98532; Botswana (2), AMNH 207416, 115827; Mozambique (1), USNM 365202; skin (6): Africa (6), USNM 344268, 365202, 368608, CMNH 93176, 36971, 98532;

60. *R. thomasi* - skull (15): China (9), USNM 258019, 260044, FMNH 33680, 33286-33290; Burma (3), 142553, 142554, AMNH 115567; Indochina (3), FMNH 32140, 32141, 32231; skin (): Indochina (3), FMNH 32140, 32141, 32231; Burma (1), AMNH 115567; China (), AMNH 45040, 45041, 45059, 45075;

61. *R. trifoliatus* - skull (25):Borneo (12), USNM 142384, 153962, 198951, 449977-449979, AMNH 106838, 103825, 103826, FMNH 8241-, 33029, 64092; Sumatra (2), USNM 141091, 143323; Malaysia (8), AMNH 216937, USNM 283687, 481059-481061, FMNH 87274, 87275, 64091; Siam (3), USNM 86787, 83537, 258950; skin (10): Borneo (10),

AMNH 106837, 106838, 103825, 103826, 106242, 106243, 103875, 216937; FMNH 8241-, 33029;

62. *R. virgo* - skull (16):Philippine (15), USNM 463869, 463873-463875, 477624, 477627-477629, 477633-477636, 477638, 477685, 483692, AMMH 207522; Palawan (Philippine) (1), FMNH 63633; skin (10): Philippine (10), USNM 303954-303958, 303961, FMNH 63632-63634, MCZ 35017;

63. *R. yunanensis* - skull (1): Thailand (1), USNM 528298; skin (3): Thailand (3), AMNH 167934, 67937, USNM 528289;

LIST OF REFERENCES

LIST OF REFERENCES

Andersen, K. 1905a. On some bats of the genus *Rhinolophus*, with remarks of their mutual affinities, and descriptions of twenty-six new forms. *Proc. zool. Soc. Lond.*, 2:75-145.

Andersen, K. 1905b. A list of the species and subspecies of the genus *Rhinolophus*, with some notes on their geographic distribution. *Ann. Mag. Nat. Hist.*, (7), 16:648-662.

Andersen, K. 1905c. Further descriptions of new *Rhinolophi* from Africa. *Ann. Mag. Nat. Hist.*, (7), 15:70-76.

Andersen, K. 1905d. On the bats of the *Rhinolophus arcuatus* group, with description of five new forms. *Ann. Mag. Nat. Hist.*, (7), 16:281-288.

Andersen, K. 1905e. On the bats of the *Rhinolophus macrotis* group, with descriptions of two new forms. *Ann. Mag. Nat. Hist.*, (7), 16:289-292.

Andersen, K. 1905f. On the bats of the *Rhinolophus philippinensis* group, with descriptions of five new species. *Ann. Mag. Nat. Hist.*, (7), 16:243-257.

Andersen, K. 1918. Diagnosis of new bats of the families Rhinolophidae and Megadermatidae. *Ann. Mag. Nat. Hist.*, (9), 2:374-384.

Ando, K., Yasazuma, F., Tagawa, T. and Ushida, T.A. 1983. Further study on the karyotypic evolution of the genus *Rhinolophus* (Mammalia: Chiroptera). *Caryologia*, 36:101-111.

Archie, J.W. 1985. Methods for coding variable morphological features for numerical taxonomic analysis. *Syst. Zool.*, 34(2): 326-345.

Bogdanowicz, W. and Owen, R. D. 1992. Phylogenetic analysis of the bat family Rhinolophidae. *Z. zool. Syst. Evolut. Forsch.*, 30:142-160.

Bogdanowicz, W. 1992. Phenetic relationships among bats of the family Rhinolophidae. *Acta Theriol.*, 37(3): 213-240.

Brenon, P. 1972. The geology of Madagascar. In *Biogeography and ecology in Madagascar*. eds. Battistini, B. and Richard-Vindard, G., Dr. W. Junk B.V., Publishers, The Hague.

Briggs, J.C. 1984. *Center of origin in biogeography.* Biogeographical Monographs 1. Univ. of Leeds Printing Service.

Briggs, J.C. 1987. *Biogeography and plate tectonics*. Elsevier, Amsterdam, Oxford, New York and Tokyo.

Bryant, H.N. 1989. An evaluation of cladistic and character analysis as hypothetico-deductive procedures, and the consequences for character weighting. *Syst. Zool.*, 38(3): 214-227.

Corbet, G.B. and Hill, J.E. 1981. *A world list of mammalian species*. British Mus. (Nat. Hist.), London, Comstock.

Corbet, G.B. and Hill, J.E. 1992. *The mammals of the Indomalayan region*. Nat. Hist. Mus. Pub., Oxford Univ. Press. Oxford.

Cracraft, J. 1988. Deep-history biogeography: retrieving the historical pattern of evolving continental biotas. *Syst. Zool.* 37:221-236.

Cranbrook, E. 1981. The vertebrate faunas. In *Wallace's line and plate tectonics*. ed. Whitmore, T.C., pp. 57-69. Clarendon Press, Oxford.

Craw, R. 1988 Continuing the synthesis between panbiogeography, phylogenetic systematics and geology as illustrated by empirical studies on the biogeography of New Zealand and the Chatham Islands. *Syst. Zool.*, 37(3):291-310.

Darlington, P.J.Jr. 1958. Area, climate, and evolution. *Evolution.*, 13:488-510.

Dawson, M.R. and Krishtalda, L. 1984. Fossil history of the families of resent mammals. In *Orders and families of recent mammals of the world*. eds. Anderson, S. and Jones, J.K.Jr., pp11-58. John Wiley & Sons. New York.

DeBlase, A.F. 1980. The bats of Iran: systematics, distribution, ecology. *Fieldiana* Zool., No. 4. pp1-424.

Dransfield, J. 1981. Palms and Wallace's line. In *Wallace's line and plate tectonics*. ed. Whitmore, T.C., pp. 43-56. Clarendon Press, Oxford.

Dubes, R.C. and Jain, A.K. 1991. *Pattern recognition*. Notes for CPS808, Computer Science Department, Michigan State University, East Lansing, Michigan. pp 1-322.

Duncan, T. and Stressy, T.F. 1984. *Cladistics: Perspective on the Reconstruction of Evolutionary History*. Columbia University Press. New York.

Dulic, B. and Mutere, F.A. 1974. The chromosomes of two bats from East Africa: *Rhinolophus clivosus* Cretzchma 1928 and *Hipposideros caffer* (Sundevall, 1946). *Period. Biol.*, 76:31-34.

Eldredge, N. 1979. Cladism and common sense. In *Phylogenetic analysis and paleontology.* eds. Cracraft. J and Eldredge, N, pp165-198. Columbia University Press, New York.

Ellerman, J.R., Morrison-Scott, T.C.S. and Hayman, R.W. 1953. *Checklist of southern African mammals.* British Mus. (Nat. Hist.), London.

Ellerman, J.R. and Morrison-Scott, T.C.S. 1966. *Checklist of Palaearctic and Indian mammals.* British Mus. (Nat. Hist.), London.

Farris, J.S. 1969. A successive approximations approach to character weighting. *Syst. Zool.*, 18:374-385.

Felsenstein, J. 1988. Phylogenies and Quantitative characters. *Syst. Zool.* 45:445-471.

Findley, J.S. 1972. Phenetic relationships among bats of the genus Myotis. *Syst. Zool.*, 21:31-52.

Freeman, P.W.1981. A multivariate study of the family Molossidae (Mammalia, Chiroptera): morphology, ecology and evolution. *Fieldiana* Zool., n.s., no.7, vii + 173p.

Geske, J.G. 1992. *Theory of Algorithms.* Course notes for CPS834. Department of Computer Sciences, Michigan State University, East Lansing, Michigan. pp 1-259.

George, W., 1981. Wallace and his line. In *Wallace's line and plate tectonics.* ed. Whitmore, T.C., pp. 3-8. Clarendon Press, Oxford.

Garey, M.R. and Johnson, D.S. 1991. *Computers and intractability: A guide to the theory of NP-completeness.* W.H. Freeman and Company, New York.

Goodwin, R.E. 1979. The bats of Timor: Systematics and ecology. *Bull. Amer. Mus. Nat. Hist.*, 163(2): 77-122

Gressitt, J.L. 1956. Some distribution patterns of Pacific Island faunae. *Syst. Zool.* 5:11-32.

Hall, L.S. 1989. Rhinolophidae. In *Fauna of Australia.* Vol. 1. Mammalia. eds. Walton, D.W. and Richardson, B.J., pp. 857-863. Govern. Pub. Service. Canberra.

Harada, M., Minezawa, M., Takada, S., Yenbutra, S., Nunparkdee, P. and Ohtani, S. 1982. Karyological analyses of 12 species of bats from Thailand. *Caryologia.*, 35: 269-278.

Harada, M., Yenbutra, S., Yosida, T.H. and Takada, S. 1985. Cytogenetical study of *Rhinolophus* bats (Chiroptera, Mammalia) from Thailand. *Proc. Jpn. Acad.* Ser. B., 61:455-458.

Hayman, R.W. and Hill, J.E. 1971. Part 2, Order Chiroptera. In *The mammals of Africa:*

an identification Manual. eds. Meester, J. and Setzer, H.W., pp1-73. Smithsonian Institution Press. Washington, D.C.

Heaney, L.R., Gonzales, P.C. and Alcala, A.C. 1987. An annotated checklist of the taxonomic and conservation status of land mammals in the Philippines. *Silliman J.*, 34:32-66.

Hecht, M.K. and Edwards, J.L. 1977. The methodology of phylogenetic inference above the species level. In *Major patterns in vertebrate evolution*. eds. Hecht, M.K., Goody, P.C. and Hecht, B.M., pp 3-51. NATO Advanced Study Institute Series A. Volume 14. Plenum Press. New York and London.

Hill, J.E. 1963. A revision of the genus *Hipposideros*. *Bull. Brit. Mus. (Nat. Hist.) Zool.*, 11:1-129.

Holloway, J.D. and Jardine, N. 1968. Two approaches to zoogeography: a study based on the distributions of butterflies, birds, and bats in the Indo-Australian area. *Proc. Linn. Soc. London.*, 179:153-188.

Honacki, J.H., Kinman, K.E. and Koeppl, J.W. (eds.) 1982. *Mammal species of the world: A taxonomic and geographic reference*. Allen Press and the Assoc. Syst. Collec., Lawrence, USA.

Hutchinson, C.S. 1989. *Geological Evolution of South-east Asia*. Clarendon Press. Oxford

Humphries, J.M., Bookstein, F.L., Chernoff, B., Smith, F.R., Elder, R.L. and Poss, S.F. 1981. Multivariate discrimination by shape in relation to size. *Syst. Zool.*, 30(2):291-308.

Huxley, T.H. 1868. On the classification and distribution of the Alectoromorphae and Heteromorphae. *Proc. zool. Soc. Lond.* 1868:294-319.

Jepson, G.L. 1970. Bat origins and evolution. In *Biology of bats*. ed. Wimsatt, W.A. Acad. Press. New York and London.

Kalayeh, H.M. and Landgrebe, D.A. 1983. Predicting the required number of training samples. *IEEE Transactions on Pattern Analysis and Machine Intelligence*. Vol. Pam-5, No 6. pp. 664-667.

Koopman, K.F. 1965. Status of forms described or recorded by J.A. Allen in "American Museum Congo Expedition collection of bats". *Am. Mus. Novit.*, 2219:1-34.

Koopman, K.F. 1966. Taxonomic and distributional notes on southern African bats. *Puku, Occ. Papers Dept. Game and Fisheries*, Zambia, no. 4.

Koopman, K.F. 1970. Zoogeography of bats. In *About bats: A chiropteran biology symposium*. eds. Slaughter, B.H. and Walton, D.W., pp 29-50. Southern

Methodist Univ. Press. Dallas.

Koopman, K.F. 1975. Bats of Sudan. *Bull. Amer. Nus. Nat.* 154: 353-444.

Koopman, K.F. 1984. Bats. In *Orders and families of recent mammals of the world.* eds. Anderson, S. and Jones, J.K.Jr., pp. 145-186. John Wiley & Sons. New York.

Koopman, K.F. 1989. Distributional patterns of Indo-Malayan bats (Mammalia: Chiroptera). *Amer. Mus. Novit.* 2942:1-19.

Koopman, K.F. 1992. Order Chiroptera. In *Mammal species of the world: A taxonomic and geographic reference*. eds. Wilson, D.E. and Reeder, D.M. Smithsonian Institution Press. Washington and London.

Koopman, K.F. and Jones, J.K., Jr. 1970. Classification of bats. In *About bats: A chiropteran biology symposium*. eds. Slaughter, B.H. and Walton, D.W., pp 22-28. Southern
Methodist Univ. Press. Dallas.

Lekagul, B. and McNeely, J.A. 1977. *Mammals of Thailand.* Sahakarnbhat, Bangkok. pp1-758.

Lomolino, M.V. 1994. Species richness of mammals inhabiting near-shore archipelagoes: area, isolation, and immigration filters. *J. Mamm.* 75(1):39-49.

Lydekker, R. 1896. *A geographical history of mammals.* Cambridge University Press.

Luginbuhl, R.C. and Schlotzhauer, S.D. 1987. *SAS/STAT Guide for Personal Computers, Version 6 Edition.* SAS institute Inc. Cary, NC.

MacArthur, R.H., and Wilson, E.O. 1967. *The theory of island biogeography.* Princeton Univ. Press, Princeton, New Jersey.

Maddison, W.P., Donoghue, M.J. and Maddison, D.R. 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33(1):83-103.

Maddison, W.P. and Maddison, D.R. 1992. *MacClade: Analysis of Phylogeny and Character Evolution, version 3.0.* Sinauer Associates, Sunderland, Mass.

Michevich, M. F. and Johnson, M.F. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. Syst. Zool. 25:260-270.

Miller, G.S., Jr. 1907. The families and genera of bats. *Bull. U.S. Natl. Mus.* 57:1-282.

Neff, N.A. 1986. A rational basis for *a priori* character weighting. *Syst. Zool.* 35:110-123.

Nelson, G. and Platnick, N.I. 1981. *Systematics and biogeography: Cladistics and vacariance.* Columbia Univ. Press. New York.

Ness, H.V. 1979. On the effects of dimension in discrimanant analysis for unequal covariance populations. *Technometrics* 21(1):119-127.

Pelseneer, P. 1904. La ligne de Weber, linite zoologique de l'Asie et de l'Australie. *Bull. Acad. r. Belg., Cl. Sci.* 1904:1001-1022.

Ride, W.D.L., Sabrosky, C.W., Bernardi, G. and Melville, R.V. 1985. *International Code of Zoological Nomenclature. Third edition.* International Trust for Zoological Nomenclature, British Museum (NH), London; University of California Press, Berkeley and Los Angeles.

Qumsiyeh, M.B., Owen, R.D. and Chesser, R.K. 1988. Differential rates of genic and chromosomal evolution in bats of the family Rhinolophidae. *Genome*, 30:326-335.

Rosevear, D.R. 1965. *The bats of west Africa.* Brit. Mus. (Nat. Hist.). London.

Savage, D.E. an Russell, D.E. 1983. *Mammalian palaeofaunas of the world.* Addison and Wesley Publication. London.

Sharkey, M.J. 1989. A hypothesis-independent method of character weighting for cladistic analysis. *Cladistics.* 5:63-86.

Slaughter, B.H. 1970. Evolutionary trends of Chiropetan dentition. In *About bats: A chiropteran biology symposium.* eds. Slaughter, B.H. and Walton, D.W., pp 51-83. Southern Methodist Univ. Press. Dallas.

Smithers, R.H.N. 1983. *The mammals of southern African subregion.* Univ. Pretoria, pp 1-736.

Sneath, P.H.A. and Sokal, R.R. 1973. *Numerical taxonomy: The principles and practice of numerical classification.* W.H. Freeman, San Francisco.

Straney, D.O. 1981. The stream of heredity: genetics in the study of phylogeny. In *Mammalian population genetics.* eds. Smith, M.H. and Joule, J., pp. 100-138. Univ. Georgia Press, Athens, Georgia.

Straney, D.O. 1984. The nasal bones of Chiroderma (Phylostomatidae). *J. Mamm.* 65(1):163-165.

Strauss, E.R. and Bookstain, F.L. 1982. The truss: body form reconstructions in morphometrics. *Syst. Zool.*, 31(2):113-135.

Swofford, D.L, and Begle, D.P. 1993. PAUP: *Phylogenetic Analysis Using Parsimony. User's Manual*. Smithonian Institution.

Tate, G.H.H. and Archbold, R. 1939. Results of the Archbold expeditions. No. 24. Oriental *Rhinolophus*, with special reference to material from the Archbold collections. *Am. Mus. Novit.* 1036:1-12.

Tate, G.H.H. 1943. Results of the Archbold expeditions. No.49. Further notes on the *Rhinolophus philippinensis* group (Chiroptera). *Amer. Mus. Novit.* no. 1219.

Tate, G.H.H. 1946. Geographical distribution of the bats in the Australasian Archipelago. *Amer. Mus. Novit.* 1323:1-21.

Vail, P.R. and Mitchum, R.M., Jr. 1979. Global cycles of relative change of sea level from seismic stratigraphy. *Geological and geophysical investigations of continental margins*, American association of petroleum geologists memoir, 29:496-72.

Van Valen, L., 1979. The evolution of bats. *Evolutionary Theory*. 4:103-121.

Walker, E.P. 1964. *Mammals of the world*. Johns Hopkings Press. Baltimore. pp. 1-1500.

Wallace, A.R. 1860. On the zoological geography of the Malay Archipelago. *J. Linn. Soc. (Zool.)*, 4:172-184.

Watrous, L.E. and Wheeler, Q.D. 1981. The out-group comparison method of character analysis. *Syst. Zool.* 30(1):1-11.

Wilkinson, L., Hill, M., Miceli, S., Birkenbeuel. G. and Vang E. 1992. *Systat: Graphics*. Systat, inc. Evanston.

Wiley, E.O. 1988a. Parsimony analysis and vicariance biogeography. *Syst. Zool.*, 37(3):271-290.

Wiley, E.O. 1988b. Vacariance biogeography. In *Annual Review of Ecology and Systematics*. Vol. 19. eds. Johnston, R.F., Frank, P.W. and Michener, C.D., pp.513-542. Annual Reviews Inc. Palo Alto, California.

Zima, J. 1982. Karyotypes of three species of horseshoe bats from Czechoslovakia. *Lynx* (Prague). 21:121-124.