Z. zool. Syst. Evolut.-forsch. 30 (1992) 142–160
© 1992 Verlag Paul Parey, Hamburg und Berlin
ISSN 0044-3808

Received on 15. March 1991

Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland, and Department of Biological Sciences, Texas Tech University, Lubbock, USA

Phylogenetic analyses of the bat family Rhinolophidae

By W. Bogdanowicz and R. D. Owen

Abstract

The 35 mensural traits of 62 species from the family Rhinolophidae were analyzed by the maximum likelihood method using data matrices after size-free and common-part-removed transformations. Of several groups of species recognized by most earlier researchers, only a few are well defined and supported phylogenetically. The majority, like the *philippinensis* group of Tate (1943), for example, do not represent natural assemblages. The results suggest south-east Asia as a centre of origin for the family. The extreme morphological similarity among horseshoe bats appears to reflect the monophyly of the genus *Rhinolophus*.

Key words: Rhinolophidae – Phylogenetic affinities – Centre of origin – Question of monophyly

Introduction

Rhinolophids can be found throughout the Old World from Europe and Africa, to south-east Asia and Japan, Philippines, New Guinea and Australia (Koopman 1982; Corbet and Hill 1986). Their fossils are known to occur during the late Eocene of Europe, the Miocene of Africa, and the Pleistocene of Asia (Friant 1963; Koopman and Jones 1970; Butler 1978; Russel et al. 1982; Hand 1984). The oldest bat fossil from Australia, recognized from a tooth in the middle Miocene Etadunna Formation, has been tentatively identified as a rhinolophid (Archer 1978).

The Rhinolophidae were first reviewed by Andersen (1905a, 1905b, 1918), who was the first to construct a phylogenetic tree for the family. Tate and Archbold (1939) and Tate (1943) provided a useful compilation of information from the literature of all described taxa, but they presented few new data and only slightly different interpretations. Most later authors (e. g., Hill and Yoshiyuki 1980; Hill and Schlitter 1982; Meester et al. 1986; Lekagul and McNeely 1988; Yoshiyuki 1989, 1990) have either accepted Andersen's point of view or have made only minor changes in his classification. The most recent research on phenetic affinities among 62 species greatly altered the currently accepted taxonomy of Rhinolophidae, primarily in separating Ethiopian and Palaearctic bats from Australian and Oriental ones (Bogdanowicz, in press). However, the question arises as to what extent phenetic clusters may reflect phylogenetic history? It is important to realize that phenetic analysis will lead to results similar to phylogenetic analysis only when taxa have diverged at constant evolutionary rates (Abbott et al. 1985). However, in most realistic cases evolutionary rates are not uniform, and a phylogenetic approach is necessary to discover evolutionary relationships among species.

The present study addresses the question of how recent rhinolophids are related to one another by analyzing morphological data with phylogenetic methods. We also evaluated two other problems of current interest: 1. the centre of origin for the family; 2. the monophyly of the genus *Rhinolophus*.

Received on 15. March 1991

Materials and methods

Species, specimens, and measurements

The analyses in this study were based on a sample of 903 skins and skulls of 62 species, including two samples of *R. ferrumequinum* (*R. f. ferrumequinum* from Europe and *R. f. nippon* from Japan), and two samples of *R. luctus* (from India and Ceylon, and south-east Asia). Our goal was to examine at least 5 adult specimens of each species. In some instances 5 specimens were not available, but in several more than 10 animals were measured. Most bats were complete and intact, with no missing characters. Only animals with fully ossified metacarpal-phalangeal joints were used in the analysis (Appendix).

Measurements were taken by the senior author with dial calipers to the nearest 0.05 mm and 0.1 mm for cranial and external dimensions, respectively. A necessary emphasis has been placed on characters of the cranium and body. A total of 35 (19 cranial and 16 external) characters was used as listed in Table 1 (BOGDANOWICZ, in press).

Data transformations

OWEN (1988) was generally followed for data transformation and phenetic procedures. All values were transformed to their natural logarithms. The arithmetic mean of each character was then calculated for each species. The common-part-removed transformation was used to remove the portion of the variance accounted for by the estimate of the common part (WOOD 1983b). In this study, the vector of character values for each species was regressed on that for *Aselliscus tricuspidatus*. In the light of immunological research *A. tricuspidatus* is much closer to *Rhinolophus* than to *Hipposideros*, and about the same distance from *Hipposideros* as is *Rhinolophus* (PIERSON 1986; cf. QUMSIYEH et al. 1988). For each species, the vector of residual values was retained. These vectors were combined and used in further calculations in the form of the transformed data matrix. This method is described and developed more fully in WOOD (1983a). Another method used was a "size-out" procedure. After averaging the ln-transformed values, a character variance-covariance matrix was calculated, and a principal component analysis was performed on the matrix. From this, the matrix of projections of each species of each component was calculated based on unstandardized data. The first principal component was then deleted from the matrix, and the remaining principal component scores were taken to be character-state values for a newly created suite of characters; thus, the effect of principal component I was removed from the matrix. In the case of the transformation described above, this component primarily reflected size relationships. Character loadings were scaled by dividing the eigenvectors by the standard deviation of the characters and multiplying the quotient by the square root of the eigenvalue (VAN ZYLL DE JONG 1984).

Phylogenetic analyses

The resultant matrices were subjected to a maximum likelihood procedure written for continuous characters (procedure CONTML of PHYLIP – FELSENSTEIN 1988). This algorithm, used primarily for genetic distance data, makes four assumptions concerning the data: 1. the lineages evolve independently; 2. after lineages separate, their genetic (or, in the present case, morphometric) evolution proceeds independently; 3. drift, rather than selection, is the cause of evolutionary change; and 4. each character drifts independently. These assumptions are discussed more thoroughly in FELSENSTEIN (1981).

Although it may be argued that none of these assumptions are met absolutely in our study (or probably in any phylogenetic study), we believe that both our transformation methods result in reasonable agreement of the data with the assumptions. In both transformed data sets, the character vectors are statistically independent. This absence of correlation among character vectors serves to simulate different aspects of biological independence that the four assumptions address. In the PHYLIP manual, FELSENSTEIN (1988) recommends that "If you are going tu use CONTML to model evolution of continuous characters, then you should ... remove genetic correlations between the characters (usually all one can do is remove phenotypic correlations by transforming the characters ...)". By using the principal component scores (size-out method) and residuals vectors (common-part-removed), we have in both cases removed correlations among the characters, while retaining what we believe to be phylogenetically useful information in the data sets.

For both analyses, *Aselliscus tricuspidatus* was included to provide a root for the tree (PIERSON 1986). In the common-part-removed data, *Aselliscus* was represented by a vector of zeros (the

vector of residuals that would result from regression of each *Aselliscus* character vector upon itself). Also for both analyses more than 120 000 tree topologies were compared.

For each branch on the final tree, CONTML calculates and reports a branch length and its approximate confidence limits (mean plus or minus one standard error). A negative lower confidence limit for a branch length indicates that an alternate topology may be acceptable, and we therefore collapsed that branch to a zero length, resulting in an unresolved node. By this method of removing the less certain branching information, we are able to generate a maximally robust phylogenetic tree.

To ascertain the areas of agreement between the two trees, we calculated an Adams-2 consensus tree (Adams 1972). As noted by Owen (1987), calculation of an Adams-2 tree is an operational method of phylogenetic hypothesis testing, in which the falsified (contradicted) portions of the component trees are reconstructed in accordance with the extent of congruence between the trees. The non-falsified parts (areas where there is agreement among the component trees) are retained in the consensus tree.

Table 1. **Character loadings and percent variance for the first five principal components from principal components analysis based on the character variance-covariance matrix**

Analysis of 64 taxa of *Rhinolophus* sp. plus *Aselliscus tricuspidatus*

Character	Principal components				
	I	II	III	IV	V
Greatest skull length	0.989	0.110	0.074	0.003	0.011
Condylocanine length	0.989	0.114	0.064	0.000	0.012
Breadth of braincase	0.976	0.055	0.157	0.051	0.057
Mastoid breadth	0.981	0.083	0.070	0.089	0.061
Zygomatic breadth	0.977	−0.006	0.166	−0.054	0.013
Least interorbital breadth	0.663	−0.126	−0.232	−0.245	0.358
Breadth of nasal swellings	0.984	−0.016	0.057	0.077	0.010
Height of braincase	0.946	0.228	0.193	−0.075	−0.036
Length of maxillary toothrow	0.958	0.047	0.251	−0.089	0.009
Width across upper canines	0.949	0.063	0.270	−0.106	−0.008
Width across upper third molars	0.950	0.155	0.058	−0.099	0.053
Supraorbital length	0.835	0.377	−0.115	0.147	−0.191
Palatal length	0.806	0.232	−0.485	0.053	0.111
Breadth of foramen magnum	0.941	−0.099	0.127	0.074	0.167
Bullar width	0.951	0.144	0.017	0.179	0.042
Greatest length of mandible	0.979	0.131	0.130	−0.043	−0.014
Length of mandibular toothrow	0.969	−0.073	0.059	−0.074	−0.002
Coronoid-angular distance	0.982	−0.092	0.075	−0.032	0.034
Height of mandibular ramus	0.942	0.214	0.215	−0.092	−0.031
Forearm length	0.976	−0.010	−0.042	−0.047	0.117
Third digit, metacarpal length	0.925	0.134	−0.014	−0.123	0.197
Third digit, first phalanx length	0.953	−0.138	−0.151	−0.030	−0.066
Third digit, second phalanx length	0.910	−0.336	0.073	0.164	0.069
Fourth digit, metacarpal length	0.976	−0.005	−0.015	0.033	0.076
Fourth digit, first phalanx length	0.770	0.348	−0.165	−0.395	0.018
Fourth digit, second phalanx length	0.888	−0.398	0.032	0.200	0.055
Fifth digit, metacarpal length	0.983	0.003	−0.007	0.003	0.066
Fifth digit, first phalanx length	0.928	−0.072	−0.142	−0.149	0.186
Fifth digit, second phalanx length	0.921	−0.165	−0.154	0.096	−0.225
Total length	0.942	−0.229	−0.055	−0.142	−0.027
Tail length	0.776	−0.456	−0.257	−0.261	−0.176
Ear length	0.886	0.121	−0.244	0.238	0.052
Greatest breadth of horseshoe	0.849	0.434	−0.059	0.087	−0.111
Tibia length	0.964	0.069	0.088	0.077	−0.086
Hindfoot length	0.951	−0.021	0.077	0.058	−0.080
Variance explained (%)	85.01	5.11	3.04	1.84	1.04

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l components		
III	IV	V
0.074	0.003	0.011
0.064	0.000	0.012
0.157	0.051	0.057
0.070	0.089	0.061
0.166	−0.054	0.013
-0.232	−0.245	0.358
0.057	0.077	0.010
0.193	−0.075	−0.036
0.251	−0.089	0.009
0.270	−0.106	−0.008
0.058	−0.099	0.053
-0.115	0.147	−0.191
-0.485	0.053	0.111
0.127	0.074	0.167
0.017	0.179	0.042
0.130	−0.043	−0.014
0.059	−0.074	−0.002
0.075	−0.032	0.034
0.215	−0.092	−0.031
-0.042	−0.047	0.117
-0.014	−0.123	0.197
-0.151	−0.030	−0.066
0.073	0.164	0.069
-0.015	0.033	0.076
-0.165	−0.395	0.018
0.032	0.200	0.055
-0.007	0.003	0.066
-0.142	−0.149	0.186
-0.154	0.096	−0.225
-0.055	−0.142	−0.027
-0.257	−0.261	−0.176
-0.244	0.238	0.052
-0.059	0.087	−0.111
0.088	0.077	−0.086
0.077	0.058	−0.080
3.04	1.84	1.04

Results

Size-free-analysis

The first principal component of the ln-transformed morphometric data explains 85.0% of the variation, and all characters have positive loadings on this component (Table 1). The second through fifth components explain 5.1, 3.0, 1.8, and 1.0%, respectively. The remaining components each account for less than 1.0% of the variance. After removal of the first-component projections, the maximum likelihood analysis was conducted on vectors from the remaining 34 components.

The size-out tree indicates that the Taiwanese *R. monoceros* should be treated as a basal taxon for all horseshoe bats (Fig. 1). This species is followed by a group of small and medium sized rhinolophids known from south-east Asia and Japan which form five (or possibly six) separate clades. One of them is created by *R. madurensis, R. virgo, R. cognatus, R. subbadius, R. gracilis,* and *R. sedulus*. The last species is the most divergent member of the clade. Within this group, *R. madurensis, R. celebensis, R. simplex, R. malayanus, R. feae,* and *R. keyensis* seem to be most closely related phylogenetically. The results suggest that *R. pearsonii* and *R. yunanensis* have close affinities with *R. borneensis, R. megaphyllus, R. robinsoni,* and *R. toxopei*. The next most basal group contains three different clades with both Asiatic and African species which arose from ancestors with morphological features much like the present-day *R. silvestris*. In the first branch, *R. stheno, R. shameli, R. coelophyllus, R. arcuatus, R. subrufus, R. euryotis,* and *R. creaghi* appear to constitute a natural group together with the less-derived species *R. acuminatus, R. rouxii, R. thomasi, R. sinicus,* and *R. affinis*. As shown by the second branch, *R. fumigatus, R. eloquens, R. hildebrandtii, R. luctus, R. trifoliatus, R. rufus, R. maclaudi, R. philippinensis, R. macrotis,* and *R. marshalli* all arose from morphologically similar ancestors, and all (especially *R. macrotis* and *R. marshalli*) have evolved considerably since. The third clade of this group is monotypic and contains *R. alcyone* only. All the remaining species on the cladogram come from the Ethiopian and Palaearctic Regions. *R. clivosus, R. bocharicus, R. f. ferrumequinum,* and *R. f. nippon* share a common ancestor with *R. darlingi*. *R. euryale* is most closely associated with *R. mehelyi*, and together they comprise a clade with *R. landeri* and *R. guineensis*. *R. hipposideros* seems to be widely divergent from the species most closely related to it, *R. denti* and *R. swinnyi*.

Common-part-removed analysis

Linear regressions of character vectors of each of the species on that of the outgroup (*Aselliscus tricuspidatus*) revealed that the portion of the vector variance, accounted for by the outgroup ranged from 93.6% (*R. mehelyi*) to 97.5% (*R. megaphyllus* and *R. thomasi*; Table 2). Thus, the maximum likelihood analysis was performed on residuals vectors representing from 6.4% to 2.5% of the original variance in the data from each species.

A number of similarities occur between this tree (Fig. 2) and the one previously described from the size-free data (Fig. 1). This involves some assemblages suggested by both cladograms. Such is the case for, among others, two groups of species: 1. *R. stheno, R. shameli, R. coelophyllus, R. arcuatus, R. subrufus, R. euryotis, R. creaghi,* and 2. *R. darlingi, R. clivosus, R. f. ferrumequinum,* and *R. f. nippon*. The two cladograms, however, differ substantially in the position of individual species. In the common-part-removed tree, Australian and New Guinean *R. megaphyllus* is the closest taxon to the root. *R. philippinensis, R. macrotis, R. marshalli,* and widely divergent *R. cognatus* appear to be isolated from the rest of the horseshoe bats, forming a sister clade to the other species studied. Within the remaining taxa of the more basal rhinolophids, some species are relatively divergent from the centre of the groups to which they belong. Such is the case of *R. gracilis* and *R. osgoodi*

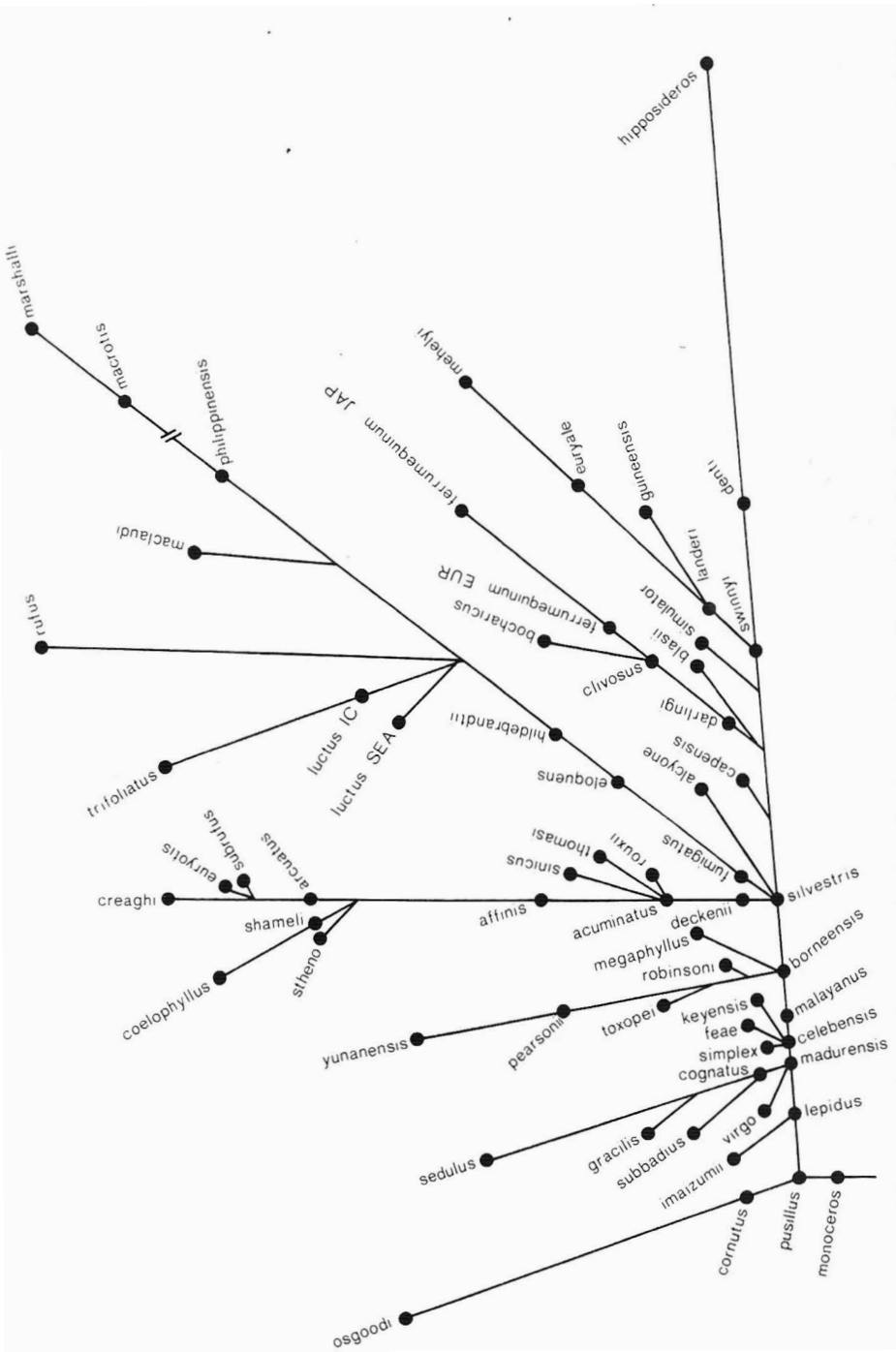
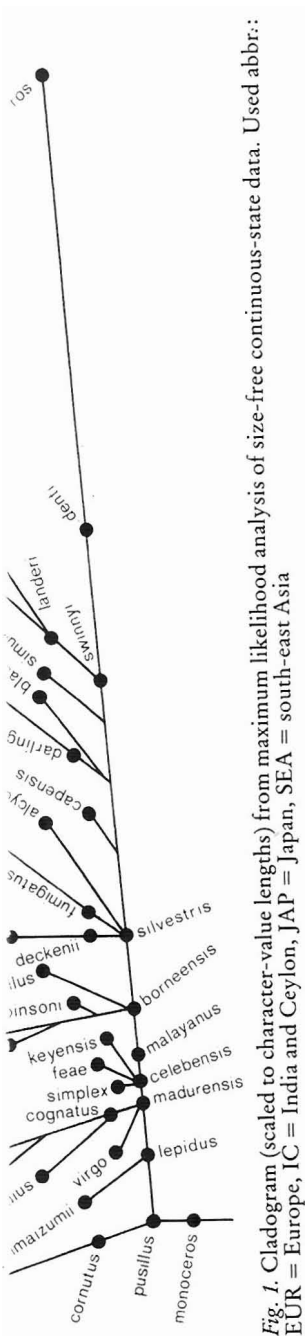


Fig. 1. Cladogram (scaled to character-value lengths) from maximum likelihood analysis of size-free continuous-state data. Used abbr.: EUR = Europe, IC = India and Ceylon, JAP = Japan, SEA = south-east Asia



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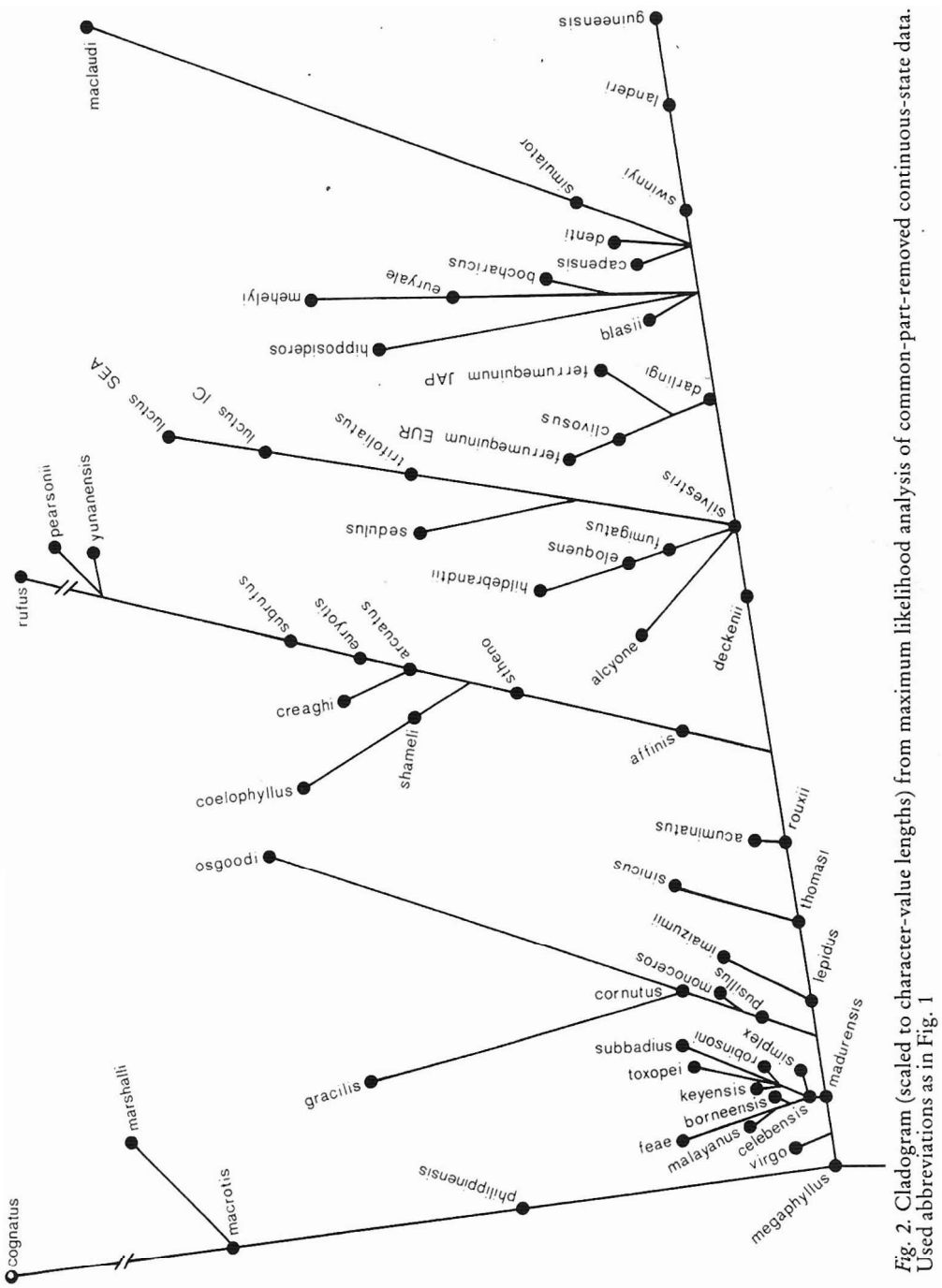

Fig. 2. Cladogram (scaled to character-value lengths) from maximum likelihood analysis of common-part-removed continuous-state data. Used abbreviations as in Fig. 1

Table 2. **Coefficient of determination (R^2) values adjusted for degrees of freedom from linear regression of each study taxon (Rhinolophus sp). on an outgroup (Aselliscus tricupidatus)** Values (when multiplied by 100) indicate percentage of original variance for each taxon data vector explained by outgroup

Taxon	R^2	Taxon	R^2
acuminatus	0.964	*luctus* (SE Asia)	0.939
affinis	0.955	*luctus* (India, Ceylon)	0.941
alcyone	0.945	*maclaudi*	0.952
arcuatus	0.950	*macrotis*	0.969
blasii	0.966	*madurensis*	0.970
bocharicus	0.953	*malayanus*	0.971
borneensis	0.972	*marshalli*	0.955
capensis	0.958	*megaphyllus*	0.975
celebensis	0.968	*mehelyi*	0.936
clivosus	0.955	*monoceros*	0.971
coelophyllus	0.944	*osgoodi*	0.970
cognatus	0.971	*pearsonii*	0.954
cornutus	**0.968**	***philippinensis***	**0.972**
creaghi	0.939	*pusillus*	0.971
darlingi	0.958	*robinsoni*	0.964
deckenii	0.954	*rouxii*	0.966
denti	0.953	*rufus*	0.951
eloquens	0.950	*sedulus*	0.954
euryale	0.941	*shameli*	0.953
euryotis	0.944	*silvestris*	0.951
feae	0.967	*simplex*	0.967
ferrumequinum (Europe)	0.957	*simulator*	0.959
ferrumequinum (Japan)	0.957	*sinicus*	0.971
fumigatus	**0.949**	***stheno***	**0.948**
gracilis	**0.953**	***subbadius***	**0.959**
guineensis	0.945	*subrufus*	0.941
hildebrandtii	0.949	*swinnyi*	0.957
hipposideros	0.954	*thomasi*	0.975
imaizumii	0.973	*toxopei*	0.973
keyensis	0.964	*trifoliatus*	0.950
landeri	0.950	*virgo*	0.970
lepidus	0.971	*yunanensis*	0.951

sharing a common ancestor with *R. cornutus*, and *R. rufus* which seems to be related with *R. shameli, R. coelophyllus, R. arcuatus, R. creaghi, R. euryotis*, and *R. subrufus*. The group of "typical" Ethiopian and Palaearctic bats (i. e., without *R. cornutus* and *R. lepidus*) is more homogenous and only *R. maclaudi* is widely divergent from its congeners. All these species together with Oriental *R. luctus, R. trifoliatus*, and *R. sedulus* arose from ancestors with morphological characters much like the present-day *R. deckenii*.

Consensus tree

An Adams-2 consensus tree combines the information of the size-out and common-part removed cladograms. As can be expected from a consensus tree based on rather different component trees (Figs. 1 and 2), a number of unresolved nodes occur on this cladogram (Fig. 3). In general, the consensus tree recognizes the poor resolution in several taxa placed close to the root (among others in the cases of *R. monoceros* and *R. megaphyllus*; *R. virgo* and *R. pusillus*; *R. madurensis, R. lepidus*, and *R. imaizumii*), and suggests that the focal question concerns the origin of Rhinolophidae. However, in each instance, Asian, not African, species appear to be most basal in the phylogeny of the family Rhinolophidae.

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	R^2
	0.939
lon)	0.941
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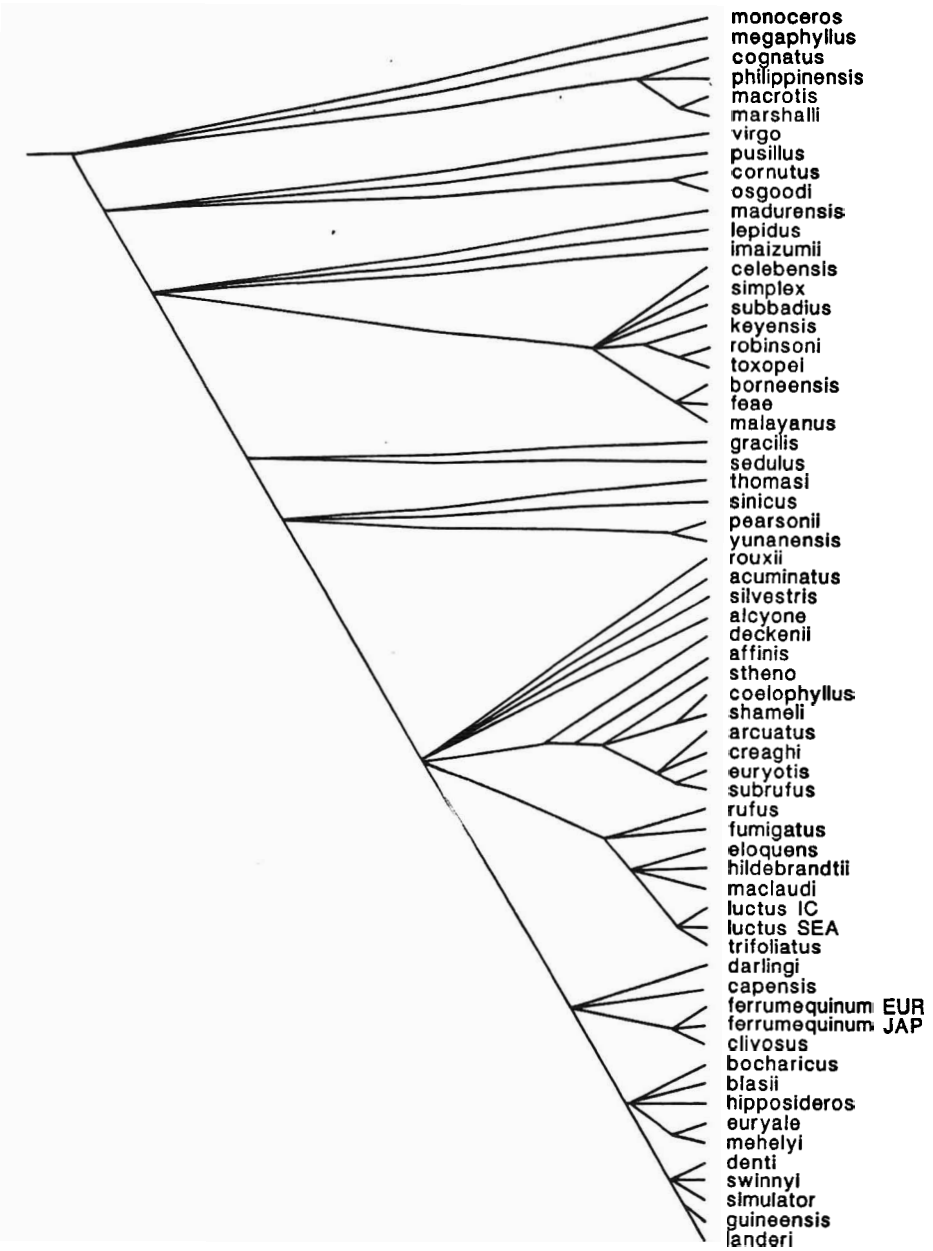

Fig. 3. Adams-2 consensus cladogram from size-free cladogram (Fig. 1) and common-part-removed cladogram (Fig. 2). Used abbreviations as in Fig. 1. Determination of branch lengths is not possible for a consensus tree

Discussion

Evolutionary relationships among horseshoe bats

A consensus tree was produced to illustrate the most robust phylogenetic hypothesis based on all data considered in this study. However, a number of unresolved nodes occur on this tree and we were not particularly convinced that it was the best estimation of rhinolophid phylogeny. Probably one of the two original cladograms (size-out or common-part-removed) should be selected as the best working hypothesis of phylogenetic relationships within the Rhinolophidae.

ANDERSEN (1905b) regarded the following features as primitive for Rhinolophidae: unshortened palate, retention of P^2 and P_3 in line with toothrows, subequal metacarpals (4th a trifle longer), three mental grooves. Some of these traits can be treated as primitive also on the basis of palaeontological research. For instance, within the *ferrumequinum* group from about 6 million years ago, from early Pliocene (*R. kowalskii*) to recent Holocene (*R. ferrumequinum*), the palate has become reduced by about 20%, yet the rate of process fluctuated considerably. The shortening of the palate was relatively rapid in the first half of the Pliocene, slowing down somewhat in the latter half of this period, to accelerate considerably in the Pleistocene (WOŁOSZYN 1987). A considerable reduction of the jaw apparatus in a comparatively short geological period was also observed. The process involved both the small premolars and the postdental part of the mandible and probably also of the skull. In a further stage of evolution, small premolars began to reduce their crown area and to project labially from the toothrow (SIGÉ 1978; WOŁOSZYN 1987). On the basis of the above traits, the following are the most primitive of the extant Rhinolophidae species: *R. simplex, R. megaphyllus, R. keyensis, R. celebensis, R. borneensis, R. virgo, R. malayanus* (ANDERSEN 1905a: 652, 1905b: 120), *R. lepidus* (ANDERSEN 1905b: 135, 138), and *R. philippinensis* (ANDERSEN 1905c: 654–655). Of three obtained phylogenetic trees the common-part-removed cladogram (Fig. 2) was closest to the results expected based on these considerations. All of the most primitive species are close to the root.

The relationship between the remaining species also appeared to be more probable in the common-part-removed tree. This is especially visible in bats from the *philippinensis* group of TATE and ARCHBOLD (1939). All these species are characterized by an unusually large and complicated noseleaf structure and their call frequencies are at the bottom margin of distribution (HELLER and v. HELVERSEN 1989). HELLER and v. HELVERSEN (1989) suggest that in this case a related group may have a once-acquired apomorphic feature in common. TATE and ARCHBOLD (1939), on the basis of ANDERSEN's research (1905a, 1905c), divided Oriental representatives of the *philippinensis* group into three subgroups: *philippinensis* (*R. philippinensis, R. mitratus*), *sedulus* (*R. sedulus*), and *trifoliatus* (*trifoliatus* and *luctus*). Later, the Oriental rhinolophids *R. macrotis, R. rex, R. coelophyllus* (with *shameli*), *R. paradoxolophus*, and *R. marshalli* were also added to the *philippinensis* subgroup (TATE 1943; HILL 1972; THONGLONGYA 1973; cf. BOGDANOWICZ, in press). It has been suggested that these bats are the most primitive members of the whole *philippinensis* group (TATE and ARCHBOLD 1939). According to ANDERSEN (1905c: 254), in all the most important points, cranial and external, *R. philippinensis philippinensis* and *R. p. achilles* (= *R. achilles*) are either much like or quite on the same level as other primitive Rhinolophidae. *R. marshalli*, although clearly related to *R. rex* and *R. paradoxolophus*, seems further removed from these than they are from each other and in certain its features *R. marshalli* tends particularly towards *R. philippinensis* (THONGLONGYA 1973). On the common-part-removed cladogram the most primitive bats of the *philippinensis* group of TATE and ARCHBOLD (1939), as can be expected, are close to the root, in the cluster of "typical" Australian and Oriental rhinolophids. A separate clade is composed of morphologically similar (nose-leaf) *R. sedulus, R. trifoliatus*, and *R. luctus* sharing a common

ancestor with African *R. silvestris, R. fumigatus, R. eloquens, R. hildebrandtii,* and *R. alcyone*. It is interesting that the results of recent phenetic research indicate that the *philippinensis* group of TATE and ARCHBOLD (1939) is more heterogenous than thought to date (BOGDANOWICZ, in press). *R. luctus* and *R. trifoliatus*, in respect to overall morphological similarity, clearly differ from *R. philippinensis, R. macrotis*, and *R. marshalli*. The first two species phenetically are in the cluster of Ethiopian and Palaearctic rhinolophids, while *R. philippinensis, R. macrotis*, and *R. marshalli* are more or less typical members of Australian and Oriental bats. The assumption, that highly derived, south-east and south Asian species from the *philippinensis* group are more closely related to Ethiopian than to Oriental rhinolophids, seems not very probable. However, the results of size-out analysis are even worse (Fig. 1). In the size-free cladogram, *R. rufus* and all studied members of the *philippinensis* group (except *R. sedulus*) arose from morphologically similar ancestors, and all (especially *R. macrotis* and *R. marshalli*) have since evolved considerably. All these horseshoe bats and highly derived *R. fumigatus, R. eloquens*, and *R. hildebrandtii* diverged from the same common ancestor.

Practically, only in the case of *R. bocharicus* and *R. cognatus* phylogenetic affinities suggested by the size-free cladogram seem more likely than those in the common-part-removed tree. *R. bocharicus* is treated by some as a subspecies of *R. clivosus* (GAISLER 1971; KOOPMAN 1982). Its baculum, in dorsal view, is like an arrow-head with convex external borders of body (HANÁK 1969). Within the Rhinolophidae only *R. ferrumequinum* and *R. clivosus* are characterized by similar bacular morphology (TOPÁL 1958, 1975; LANZA 1959; HANÁK 1969; YOSHIYUKI 1989). *R. cognatus* is thought to be closely related to *R. subbadius, R. monoceros*, and *R. imaizumii* (HILL and YOSHIYUKI 1980; YOSHIYUKI 1989; cf. Figs. 1 and 2). *R. cognatus* and its allies are Asian members of the *pusillus* group, and are characterized by an erect, narrow horn-like connecting process (HILL and YOSHIYUKI 1980).

Especially interesting is the phyletic position of African *R. maclaudi*, which in general is treated as an Ethiopian offshoot of the *philippinensis*-type, more highly developed than *R. philippinensis* at least in dentition, wing-structure, and mental grooves (ANDERSEN 1905c). Of the bats from this group, *R. maclaudi* is phenetically closer to *R. trifoliatus* and *R. luctus* than to *R. philippinensis* or *R. marshalli* (BOGDANOWICZ, in press). LAURENT (1940) presented an entirely different position. He felt that *R. maclaudi* should be treated as an African type isolated from other Asiatic bats. The initial results of bacular morphology analysis appear to agree with this suggestion (BOGDANOWICZ, unpubl. data). Such a phylogenetic position of *R. maclaudi* is recommended by the common-part-removed cladogram.

Fossil evidence, perhaps surprisingly, may be of rather little use in determining cladograms or phylogenies (ABBOTT et al. 1985). In the *ferrumequinum* group, TOPÁL (1979) distinguished two phyletic lines. He derived the first line from the Miocene *R. delphinensis* and the second line from *R. lemanensis* of the oldest Miocene of France. TOPÁL (1979) was of the opinion that the recent *R. ferrumequinum* may have evolved within the second line. ANDERSEN (1905b) traces the *ferumequinum* "section" back to *R. affinis* of the *simplex* group, whose dentition has several primitive features. However, a very short palate in *R. affinis*, shorter than in *R. ferrumequinum*, is in opposition to the evolutionary trend observed within the group. *R. affinis* probably represents a separate branch and not "the base of the *ferrumequinum* section" (TOPÁL 1979). This suggestion agrees with common-part-removed and size-free cladograms presented here.

Centre of origin and monophyly of the family

To date it has been accepted that the family originated somewhere in the Old World tropics, probably in Africa or southern Asia (KOOPMAN 1970; HALL 1989). In both original cladograms (Figs. 1 and 2), morphologically primitive Australian-Oriental species

were found close to the root, while highly derived Ethiopian-Palaearctic species were located at the top (some distortions can be observed in the size-free cladogram). The most basal rhinolophid (*R. megaphyllus*) on the common-part-removed cladogram recently is known from New Guinea, New Ireland, New Britain, and Australia (CORBET and HILL 1986). However, it is generally assumed that Chiroptera entered Australia from Asia (HAMILTON-SMITH 1975; FLANNERY 1989) by way of the Indonesian Archipelago and New Guinea (TATE 1946; HAMILTON-SMITH 1974; HAND 1984). Nowadays only two rhinolophids, *R. megaphyllus* and *R. philippinensis*, occur in Australia. Their presence in the forests of the eastern part of this continent evidently represents a relatively recent arrival from New Guinea probably via northeastern Queensland, perhaps in the Pliocene or Pleistocene (ARCHER et al. 1989). The middle Miocene Australian rhinolophid of ARCHER (1978) is unfortunately known only from an isolated tooth. Because most isolated bat teeth are of limited taxonomic value, this tooth has not been yet certainly assigned to any particular bat family (HAND 1984). Other species close to the common ancestor are *R. virgo* from the Philippines, *R. madurensis* from Madura, *R. celebensis* from Sulawesi and Java, and *R. simplex* from the Lesser Sunda Islands (KOOPMAN 1982; CORBET and HILL 1986). Thus, these results indicate that the family most probably originated in south-east Asia, not in Africa. From fossil evidence, it appears that Rhinolophidae entered Africa at a relatively late date (Mio-Pliocene of North Africa) although further research may well disprove this (BUTLER 1978). The oldest African rhinolophid, *Rhinolophus mellali*, has been recovered from later Miocene deposits of Beni Mellal in Morocco. This species may be closely related to Europe's *Rhinolophus ferrumequinum* (LAVOCAT 1961; but see SIGÉ 1976).

The oldest fossils from the genus *Rhinolophus* are known from the late Eocene of Europe (e. g., RUSSELL et al. 1982; SIGÉ and LEGENDRE 1983; HAND 1984; REMY et al. 1987). However, assuming that rhinolophids originated in Africa it is somewhat surprising that for 40 and more million years they were not able to get to Madagascar. One reason for this may be the fact that Madagascar is an island dating at least from the Paleocene or late Cretaceous (SAVAGE and RUSSELL 1983; HAND 1984; BRIGGS 1989), and rhinolophids are not capable of crossing broad water gaps (KOOPMAN 1970; HALL 1989). It is likely that the colonization of Malagasy by Chiroptera involved a large number of invasions. Unfortunately, there is no pre-Pleistocene record of bats on Madagascar (HAND 1984). On the other hand as many as five rhinolophid species are known today on the Japanese islands (YOSHIYUKI 1989), which separated from the Asian continent between the late Eocene and the early Oligocene (SAVAGE and RUSSELL 1983). It is interesting to note that in Australia accidental or waif dispersal, such as on floating vegetation mats, is postulated as the method of arrival for most of terrestrial Asian emigrants, including songbirds, varanid lizards, rodents, and others. One of the hypotheses suggests that Australia's first bat colonists were storm-blown to shores of this continent (HAND 1989). Nowadays rhinolophids are widespread in the continental portions of the Eastern Hemisphere with several species extending well into the Palearctic Region (Ireland, England, Central Europe, Japan). The sister family Hipposideridae, with very strict microhabitat requirements, is more restricted to the tropics and extends only marginally into the Palearctic. Nevertheless, a few species of large and medium sized hipposiderids have reached both Madagascar and the Japanese islands (KOOPMAN 1970, 1982; HILL 1982; CORBET and HILL 1986; YOSHIYUKI 1989).

The question of monophyletism in bats of the family Rhinolophidae deals with one known "modern" type of *Rhinolophus*. The sole fossil genus, *Palaeonycteris*, is known from the Miocene of Europe (HELLER 1936; SIGÉ and LEGENDRE 1983; HAND 1984; cf. SIMPSON 1945 and HALL 1989). In light of immunological research, based on microcomplement fixation transferrin distances, it seems that *Rhinolophus* forms a monophyletic unit. Australasian *R. megaphyllus* is 19, 24, and 28 units from Indo-Malayan *R. creaghi*,

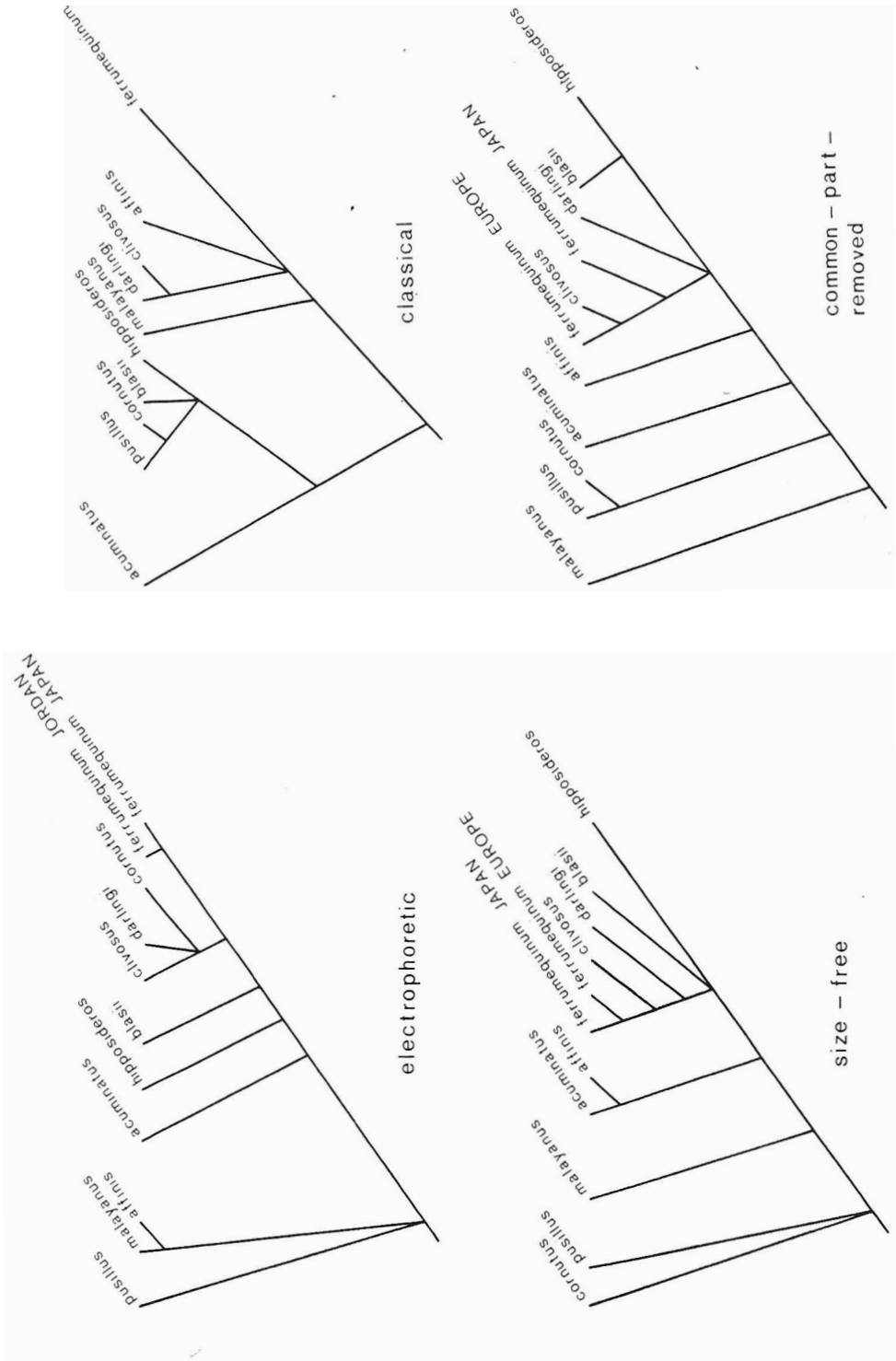

Fig. 4. The best estimate of phylogenetic affinities among 10 rhinolophid species, based on electrophoretic (QUMSIYEH et al. 1988), and morphological data (classical: ANDERSEN 1905b: 120, 138; size-free and common-part-removed: present study)

African *R. swinnyi*, and African *R. hildebrandtii*, respectively (PIERSON 1986). The morphological data appear to reflect the monophyly of the genus, although they also are reflective of the extreme phenetic similarity of horseshoe bats. This similarity is particularly indicated by the exceptionally low variances remaining from the common-part-removed transformation (2.5–6.4 %, mean = 4.2 %, range = 3.9 %). For 64 species of the stenodermatine bats of the family Phyllostomidae this ranged from 1.3 to 13.8 % (mean = 3.6 %, range = 12.5 %; OWEN 1987). Final results concerning monophyly can be obtained after comparing species from the genus *Rhinolophus* to other, more or less closely related genera.

The best estimate of rhinolophid phylogeny

In the instance of the morphometric data used it is clearly evident that the presented phylogenetic relationships, in a very drastic way, depend on the initial assumptions. However, in actuality it seems that an analysis done with the common-part-removed method better than the size-free cladogram and Adams-2 consensus tree, reflects evolutionary affinities among horseshoe bats. Certain clades on the common-part-removed cladogram are also supported by the karyological data. Such is the case with *R. trifoliatus* (diploid number 2n = 32, fundamental number FN = 60; YONG H. S. and M. VOLLETH, in litt.), *R. luctus morio* (2n = 32, FN = 60; HOOD et al. 1988), *R. l. perniger* (2n = 32, FN = 60; HARADA et al. 1985), *R. l. beddomei* (2n = 32, FN = 60; NAIDU und GURURAJ 1984), and *R. formosae* (2n = 52, FN = 60; ANDŌ et al. 1980, 1983) which are characterized by a relatively low diploid number of chromosomes with the same number of autosomal arms. *R. sedulus* (2n = 28, FN = 52; YONG H. S. and M. VOLLETH, in litt.) seems to be also connected with this group. Most of the remaining species can be divided into two large groups that agree with their zoogeographic classification: Australian-Oriental bats (usually 2n = 62; FN = 60) and Ethiopian-Palaearctic (usually 2n = 56, 58; FN = 60, 62, 64; reviewed by BOGDANOWICZ, in press).

On the other hand, the proposed phylogenetic relationships within the Rhinolophidae based on morphological characters are in many aspects discordant with those based on electrophoretic criteria (Fig. 4). Evidently, the results of morphological and allozymic data may not be comparable at all levels in the phylogeny (see also QUMSIYEH et al. 1988). Resolution at different evolutionary levels by albumin, electrophoretic, chromosomal, and morphological characters was shown by ARNOLD et al. (1982) in a study on phyllostomoid bats.

It has to be emphasized that the construction of phylogenetic relationships should be based on the analysis of data drawn from as many different character sets as possible: morphological, chromosomal, and biochemical. The phylogenetic relationships arrived at in the present study are supported primarily by metric morphological data and should be considered tentative, as a working hypothesis. It would, therefore, be premature at this time to translate the results into a phylogenetic classification. Suffice it to say, for the moment, that hypothesized phylogenetic relationships among rhinolophids in general support recently suggested phenetic classification of the family (BOGDANOWICZ, in press).

Appendix

Specimens examined

Museum acronyms for specimens used in this study are defined in the acknowledgements section. Number in parentheses after localities indicates the number of specimens examined from that locality. Number in parentheses after species name indicates total number examined.

Rhinolophus acuminatus (24) – Indonesia (16): BMNH 9.1.5.156–157, 9.1.5.159–167, 9.1.5.169–171, 97.4.18.16; NMW 28259. Kampuchea (1): BMNH 70.1038. Malaysia (2): BMNH 73.609–610. Thailand (5): BMNH 70.1465–66, 70.1468, 78.2306; OCUMS 21.11.1979.

R. affinis (26) – Burma (4): BMNH 21.1.17.1, 50.410, 87.3.4.11, 90.4.4.7. China (1): BMNH 8.1.30.7. Hongkong (1): BBM HK65098. India (6): BMNH 21.1.6.21–23, 98.1.1.1, HNHM 773, 781. Indonesia (2): BMNH 10.4.7.6, 97.4.18.13. Malaysia (4): BMNH 0.7.3.2, 67.1552, 67.1554, 67.1559. Thailand (5): 70.1461, 78.2302–03, 78.971; OCUMS 1258. Vietnam (3): HNHM 371, 1364–65.

R. alcyone (17) – Cameroon (4): BMNH 68.888; MHNG 913.70–71; KMMD 7318M–129. Fernando Poo (1): KKMD RG20.432. Ghana (8): BMNH 10.10.23.1, 10.10.23.6, 11.2.14.1–3, 65.481, 65.751, 66.6242. Liberia (1): IRSNB 16783. Sudan (1): IRSNB 13666. Togo (2): BMNH 55.376–77.

R. arcuatus (16) – Borneo (4): BMNH 59.12, 59.190–91, 64.511. Sumatra (1): BMNH CH58a. Papua New Guinea (1): 83.271. Philippines (10): BMNH 70.1470, 74.5.27.5, 79.5.3.13; USNM 303968–73, 303976.

R. blasii (18) – Iran (4): BMNH 77.820–23. Israel/Jordan (11): BMNH 22.3.9.3–4, 22.4.2.1–4, 22.12.20.2–4; HZM 2.3152, 12.8655. Oman (3): HZM 10.8612, 11.8613, 13.8752.

R. bocharicus (10) – USSR (10): MGU S140535, S140538, S140540–3, S140545, S140547–9.

R. borneensis (incl. *importunus*) (8) – Borneo (6): BMNH 11.1.18.4, 65.5.9.15–6, 94.9.28.29; HZM 1.7461; SMF 52053. Java (1): RNHL 15320. Vietnam (1): BMNH 21.10.8.3.

R. capensis (33) – South Africa: BMNH 73.521, 75.8.9.9, 75.8.9.11–14; HZM 1.4733, 2.4734, 3.4735, 4.6710, 5.7129; KMSA 1774, 1785, 1811–12, 1814–15, 1820, 1830, 8983, 20171, 21185, 23853; TM 29063–65, 29067, 29069–70, 29072, 29077, 29080–81.

R. celebensis (incl. *javanicus*) (10) – Java (3): BMNH 9.1.5.173–5. Sulawesi (7): BMNH 55.52, 97.1.3.19, 1982.36–37, 1982.39–40, 1982.50.

R. clivosus (30) – Egypt (1): HZM 5.3227. Namibia (6): BMNH 25.1.2.85–90. Saudi Arabia (6): HZM 6.3793, 8.3796, 9.3797, 10.3803, 12.3817, 13.3826. South Africa (17): BMNH 4.5.1.2–4, 4.5.1.6–7, 4.5.1.9, 4.10.1.2–5, 4.10.1.7–8, 4.12.5.1, 5.5.1.3–4, 14.5.4.4, 98.4.4.2.

R. coelophyllus (10) – Laos (2): BBM LA41616, LA41617. West Malaysia (4): AMNH 216857, 216861; BMNH 68.821–22. Thailand (4): OCUMS 1291; USNM 296824–25, 356305.

R. cognatus (3) – Andaman Islands (3): BMNH 6.12.1.12, 9.4.4.7–8.

R. cornutus (23) – Japan (23): BMNH 2.10.7.2, 2.10.7.18, 7.2.7.2, 7.8.8.16–20, 25.9.3.5–6, 28.1.11.9, 80.3.20.8, 92.3.20.1; KM 501, 534–6, 614; OCUMS 4.12.1983a–b, 18.1.1984a–b, 23.7.1986.

R. creaghi (14) – Borneo (10): BMNH 51.128, 57.454–8, 96.7.30.1; HZM 1.7462; OCUMS 30.3.1979a–b. Java (3): BMNH 9.1.5.183–5. Madura (1): BMNH 10.4.7.5.

R. darlingi (25) – Botswana (1): HZM 6.4382. Namibia (1): LACM 58985. South Africa (12): BMNH 6.8.2.32; TM 35987–9, 35991–2, 36058, 36063, 36093–4, 36096, 4001. Tanzania (2): BMNH 51.390, 64.1501. Zimbabwe (9): BMNH 48.403, 48.231, 95.7.1.6, 95.8.27.1; HZM 1.3370, 2.3709, 3.3907, 5.4245, 7.6295.

R. deckenii (19) – Kenya (5): BMNH 9.6.12.10, 75.2460–63. Tanzania (13): AMNH 208341; BMNH 55.205, 55.208–9, 55.222; HZM 1.2619, 2.2797, 3.2798, 4.2799, 5.2800, 8.3974, 8.4721, 10.4723. Uganda (1): LACM 31834.

R. denti (16) – Botswana (1): HZM 1.4311. Namibia (4): BMNH 23.8.8.1, 25.1.2.5, 28.9.11.10–11. South Africa (11): TM 35993, 35996–9, 36002–3, 36006–7, 36010, 36016.

R. eloquens (28) – Kenya (22): BMNH 1.2013, 2.2045, 6.2953, 7.3041, 8.2702, 75.2489–90, 75.2492–4, 75.2496–97, 25.2499–501, 75.2503; HZM 1.2013, 2.2045, 5.2891, 6.2953, 7.3041, 8.2702. Tanzania (5): BMNH 64.1495–97, 64.1499; IRSNB 1561?b. Uganda (1): BMNH 99.8.4.4.

R. euryale (18) – France (5): BMNH 70.754–8. Hungary (4): BMNH 7.9.16.7; HNHM 56.531, 63.36.5, 66.35.1. Italy (2): BMNH 6.8.4.10–11. Yugoslavia (7): HNHM 66.237.1, 66.237.6–7, 66.237.9, 66.237.12–13, 66.237.15.

R. euryotis (26) – Amboina (2): BMNH 10.7.25.2, 11.7.12.15. Aru (1): BMNH 23.4.3.14. Buru (1): BMNH 25.6.5.22. Ceram (1): BMNH 10.3.4.12. Kei (4): BMNH 10.3.1.24–6, 99.12.4.4. New Guinea (2): AMNH 195248; BMNH 33.6.1.2. Sulawesi (15): BMNH unreg., 1982.51, 1982.55, 1982.78–82, 1982.84–8, 1982.90, 1982.98.

R. feae (1) – Burma (1): BMNH 7.1.9.16.

R. ferrumequinum (29) – Japan (5): KM 3112-14, 3116; OCUMS 29.8.1983. France (6): BMNH 6.4.1.2–6, 67.221. Great Britain (1): HZM 6.823. Hungary (1): HZM 38.3097. Italy (10): BMNH 7.9.16.1–6; 66.4306–9. Spain (3): HZM 26.2084, 28.2086, 29.2087. Switzerland (3): BMNH 2.8.4.1–3.

R. fumigatus (31) – Cameroon (2): BMNH 61.85; MHNG 1063.60. Ethiopia (5): BMNH 23.3.26.5, 37.2.24.3–5, 70.464. Kenya (3): BMNH 10.7.2.5; HZM 5.2885, 6.3027. Nigeria (10): BMNH 13.2.5.1, 56.90; HZM 1.1921, 4.1924, 43.11942, 44.11943, 45.11944, 46.11945; LACM 72829–30. Senegal (1): BMNH 19.7.7.2774. Sierra Leone (1); BMNH 61.5. Tanzania (7): HZM 2.2482, 3.2488, 4.2743, 7.3092, 8.3100, 9.3109, 10.311. Zimbabwe (2): BMNH 66.5447; HZM 1.2430.

R. gracilis (1) – India: BMNH 73.4.16.2.

R. guineensis (15) – Guinea (1): MAK 59.177. Sierra Leone (14): BMNH 47.591–8, 53.50–3, 56.36–7.

R. hildebrandtii (23) – Kenya (5): BMNH 4.2.5.1, 10.4.1.9–10, 75.2502, 75.2504. Malawi (1): BMNH 22.12.17.4. Mozambique (1): BMNH 8.4.3.15. Tanzania (5): BMNH 60.95–6, 64.1492; IRSNB 15622; MHNG 921.14. Zaire (5): IRSNB 6282, 14428, 14431; KMMD 23816; MHNG 1046.69. Zambia (1): BMNH 68.998. Zimbabwe (5): BMNH 2.2.7.3–4, 10.8.17.2, 51.630, 59.354.

R. hipposideros (15) – Great Britain (15): BMNH 39.213, 39.215, 39.217, 39.219–20, 39.222–3, 39.225–7, 39.231–2, 39.236–8.

R. imaizumii (4) – Iriomote Isl. (4): AMNH 241442; BMNH 80.465–6; OCUMS 25.1.1984.

R. keyensis (5) – Ceram (2): BMNH 20.7.26.2, 70.2516. Goram (1): BMNH 61.12.11.10. Kei (2): AMNH 222739; BMNH 10.3.1.73.

R. landeri (27) – Kenya (12): BMNH 10.6.2.33, 10.6.2.35, 10.7.2.6–10, 10.7.2.12, 75.2487–8; LACM 71170–1. Malawi (3): BMNH 22.12.17.5, 22.12.17.7, 96.10.28.12. Mozambique (3): BMNH 8.4.3.9, 8.4.3.11, 8.4.3.14. South Africa (1): TM 38131. Sudan (7): BMNH 28.1.11.8–10, 28.1.11.13, 28.1.11.15–6, 47.5.27.49. Zaire (1): BMNH 26.7.6.111.

R. lepidus (29) – Burma (10): BMNH 18.8.3.1, 21.1.17.21–7, 21.1.17.29–30. India (8): BMNH 12.11.29.16–7, 21.1.17.15, 21.1.17.17–8, 30.5.24.56, 30.5.24.59, 79.11.21.151. Malaysia (7): AMNH 95294; BMNH 67.1571–2, 67.1578, 67.1580, 67.1583, 98.11.29.2. Thailand (4): BMNH 8.2.5.26–7, 78.230, 78.235.

R. luctus (20) – India (3): BMNH 11.3.16.1, 12.11.28.5, 82.3.3.1. Sri Lanka (1): BMNH 18.8.3.3. Borneo (4): 59.183, 76.9.20.12, 89.1.8.4, 92.2.7.3. Burma (6): BMNH 21.1.6.1–3, 21.1.6.5, 50.396–7. Malaysia (1): BMNH 1.3.9.3. Singapore (1): BMNH 40.5.14.36. Thailand (4): BMNH 9.10.11.2, 70.1463, 78.2309–10.

R. maclaudi (14) – Uganda (3): BMNH 55.1187; LACM 57774, 57776. Zaire (11): IRSNB 15966; 60.99–101; KKMD RG35170, RG35173, RG35206, RG35208, RG35211, RG35217–8.

R. macrotis (13) – India (2): BMNH 79.1121143–4. Malaysia (7): AMNH 234057; BMNH 7.1.9.1, 67.1595–9. Nepal (1): BMNH 78.286. Philippines (1): SMF 27038. Sumatra (1): BMNH 6.12.1.22. Thailand (1): BMNH 78.2313.

R. madurensis (5) – Kangean Isl. (2): ZMA 21.828, 22.459. Madura (2): BMNH 10.4.7.9–10. Timor (1): BMNH 79.1394.

R. malayanus (15) – Malaysia (6): AMNH 216875; BMNH 68.812–6. Thailand (9): BMNH 3.2.6.83, 8.2.5.24–5, 70.1462, 78.973, 78.2295–7; OCUMS 11.11.1979.

R. marshalli (2) – Thailand (2): OCUMS 1246, 1251.

R. megaphyllus (28) – Australia (27): AMNH 194238; BMNH 3.8.3.3–6, 23.1.5.1–2; LACM 68743–4, 68746, 68749, 68752, 68758–9, 68763–5; MVM C3519, C3575–6, C3617, C3624, C3716–7, C3720, C3723–4. Louisiade Archipelago (1): BMNH 98.4.1.1.

R. mehelyi (11) – Algeria (10): ISEZ 278–9, 438–41, 525–6, 828, 830. Turkey (1): BMNH 62.238.

R. monoceros (15) – Taiwan (15): AMNH 115630; OCUMS T19, T21; USNM 358145–6, 358151–2, 358154–6, 358164, 358167, 358169, 358171–2.

R. osgoodi (1) – China (1): AMNH 44547.

R. pearsonii (14) – China (2): BMNH 98.11.1.2; MAK 50.219. India (6): BMNH 20.11.1.20, 21.1.6.11–15. West Malaysia (1): AMNH 234063. Nepal (1): BMNH 21.5.1.4. Thailand (3): BMNH 78.2317–8, 78.975. Vietnam (1): BMNH 33.4.1.25.

R. philippinensis (9) – Australia (3): AMNH 157069; HZM 1.12098; LACM 69700. Borneo (3): BMNH 47.1435, 51.130, 67.1427. Kei Isl. (2): BMNH 10.3.1.23, 99.12.4.5. Philippines (1): BMNH 55.12.26.270.

R. pusillus (19) – China (8): BMNH 11.2.1.2, 11.2.1.4, 11.9.8.3–5, 13.1.26.3, 13.5.17.3, 13.5.17.5. India (8): BMNH 18.8.3.2, 21.1.17.3–4, 21.1.17.8–9, 21.1.17.11, 21.1.17.13, 98.1.1.2. Madura (1): BMNH 10.4.7.8. Thailand (2): BMNH 78.23.29; OCUMS 1283.

R. robinsoni (6) – Malaysia (4): BMNH 18.8.2.2, 61.1712, 67.214, 74.326. Thailand (2): LACM 70320, 70322.

R. rouxii (29) – India (25): BMNH 0.4.1.8, 11.7.18.1, 11.7.18.3–4, 12.6.29.16–19, 12.11.28.6, 12.11.28.8, 12.11.28.11, 12.11.28.13–15, 18.8.3.19, 18.8.3.21, 30.5.24.44–6, 30.5.24.48–51, 30.5.24.53–4, 65.10. Sri Lanka (4): BMNH 9.11.18.2–4, 66.5516.

R. rufus (1) – Philippines (1): SMF 30201.

R. sedulus (3) – West Malaysia (2): AMNH 247289; BMNH 65.334. Borneo (1): BMNH 7.1.1.292.

R. shameli (6) – Kampuchea (1): BMNH 70.1037. Thailand (5): BMNH 70.1464, 76.1815, 78.2330–2.

R. silvestris (3) – Congo (2): MNHN 1985–1187, 1985–1518. Gabon (1): MNHN 1985–1519.

R. simplex (3) – Komodo (1): AMNH 54861. Lombok (1): BMNH 97.4.18.14. Sumatra (1): SMF 11945.

R. simulator (28) – Botswana (2): HZM 15.5505, 16.5506. Ethiopia (6): BMNH 71.2448–53. Kenya (1): BMNH 11.4.23.1. South Africa (1): TM 3936. Tanzania (4): HZM 5.2174, 6.3254, 18.6262, 22.7161. Zambia (8): BMNH 66.5444, 68.999, 68.1001–2; CASSF 16164–7. Zimbabwe (6): BMNH 2.2.7.10, 59.355, 95.7.1.5; HZM 8.3895, 10.3901, 14.5386.

R. sinicus/rouxii (4) – China (1): BMNH 99.3.1.6. Nepal (3): HZM 1.16291, 4.16294, 5.16295.
R. stheno (13) – Java (4): BMNH 9.1.5.179–82. West Malaysia (7): BMNH 67.1492, 67.1494, 67.1497, 99.3.13.1; CASSF 15151–2; MVZ 137236. Thailand (2): BMNH 78.974; OCUMS 1294.
R. subbadius (1) – Nepal (1): HZM 1.16287.
R. subrufus (13) – Philippines (13): BMNH 58.3.29.3–4, 98.11.3.10; USNM 303901–3, 303905, 303907, 303909, 303911–2, 303914–5.
R. swinnyi (29) – South Africa (10): HZM 7.1290, 7.1296, 8.1292, 10.5360; KMSA 24286–7, 24290–1, 24293, 24301; TM 36938. Tanzania (7): BMNH 55.228–34. Zambia (3): BMNH 68.600; HZM 13.11474, 14.11475. Zimbabwe (8): BMNH 64.478–80; HZM 2.3857, 4.3906, 6.3919, 11.5485, 12.7195.
R. thomasi (5) – Burma (1): BMNH 90.4.7.10. Thailand (4): BMNH 78.972, 78.2333–5.
R. toxopei (2) – Buru (2): BMNH 25.6.5.23–4.
R. trifoliatus (12) – Borneo (5): BMNH unreg., 7.1.1.293, 92.10.2.2, 94.7.2.49–50. Burma (1): BMNH 85.8.1.110. Malaysia (3): BMNH 6.10.4.8, 65.337; SMF 50507. Thailand (2): BMNH 78.2311–2. Singapore (1): BMNH 4.8.23.1.
R. virgo (15) – Philippines (15): AMNH 207522; SMF 31327, 31331; USNM 477624, 477626, 477629, 477632–6, 477638–9, 477649, 477661.
R. yunanensis (12) – Burma (3): BMNH 50.398–9, 50.402. China (1): BMNH 9.4.4.3. India (1): BMNH 21.12.5.2. Thailand (7): BMNH 78.2319–22, 78.2324, 78.976. OCUMS 1250.
Aselliscus tricuspidatus (13) – Ceram (5): ZMA 16.773–7. New Guinea (8): RNHL 36206, 36208–10, 36212–3, 36215–6.

Acknowledgements

The first author is very grateful to P. Bates, Earl of Cranbrook, J. Fairon, A. Frenkiel, Z. Frenkiel, D. L. Harrison, J. E. Hill, V. Hobbs, and A. M. Hutson for their help during his stay in Great Britain and Belgium. Dr. C. Smeenk helped with rare and old publications. Dr. G. Hartl translated the abstract into German. The PHYLIP analyses, which required many hours of mainframe CPU time for the global rearrangement comparisons, were completed while the second author was a member of the graduate faculty of Texas Tech University. We thank The Museum, Department of Biological Sciences, and College of Arts and Sciences of that university for providing the necessary access to computer equipment and facilities. Our appreciation is extended to Drs. M. Volleth and K.-G. Heller who made many useful suggestions regarding an earlier version of this manuscript.

The following persons and institutions are gratefully acknowledged for use of their specimens: American Museum of Natural History, New York, USA (AMNH); Bishop Museum, Honolulu, USA (BBM); British Museum (Natural History), London, Great Britain (BMNH); California Academy of Sciences, San Francisco, USA (CASSF); Hungarian Natural History Museum, Budapest, Hungary (HNHM); Harrison Zoological Museum, Sevenoaks, Great Britain (HZM); Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium (IRSNB); Institute of Systematic and Experimental Zoology PAS, Kraków, Poland (ISEZ); Kishio Maeda, Hozumi, Japan (KM); Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium (KMMD); Kaffrarian Museum, King William's Town, South Africa (KMSA); Natural History Museum of Los Angeles County, Los Angeles, USA (LACM); Museum Alexander Koenig, Bonn, Germany (MAK); Zoological Museum of Moscow University, Moscow, USSR (MGU); Muséum d'Histoire naturelle Genève, Switzerland (MHNG); Muséum national d'Histoire naturelle, Paris, France (MNHN); Museum of Victoria (Natural History and Anthropology), Melbourne, Australia (MVM); Museum of Vertebrate Zoology, University of California, Berkeley, USA (MVZ); Naturhistorisches Museum Wien, Austria (NMW); Masashi Harada, Osaka City University Medical School, Osaka, Japan (OCUMS); Rijksmuseum van Natuurlijke Historie, Leiden, Holland (RNHL); Senckenberg Museum, Frankfurt am Main, Germany (SMF); Transvaal Museum, Pretoria, South Africa (TM); National Museum of Natural History, Smithsonian Institution, Washington, USA (USNM); Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam, Holland (ZMA).

This study was made possible by the Royal Society of London (WB), Polish Academy of Sciences (WB), and Texas Tech University (RDO).

Zusammenfassung

Phylogenetische Untersuchungen an Fledermäusen aus der Familie Rhinolophidae

Bei 62 Arten der Familie Rhinolophidae wurden 35 metrische Merkmale mittels der Maximum-likelihood-Methode analysiert. Durch Transformationen wurden die Datenmatrizen vorher von gemeinsamen Größenfaktoren unabhängig gemacht. Von mehreren, in früheren Untersuchungen ermittelten Artengruppen sind nur wenige gut definierbar und durch phylogenetische Untersu-

chungen zu belegen. Die Mehrheit, wie etwa die *philippinensis* Gruppe von TATE (1943), spiegelt keine natürlichen Gruppierungen wider. Die Ergebnisse deuten auf Südostasien als Zentrum des Ursprunges für die Familie hin. Der extreme hohe morphologische Ähnlichkeitsgrad unter den Hufeisennasen scheint den monophyletischen Ursprung der Gattung *Rhinolophus* zu bestätigen.

References

ABBOTT, L. A.; BISBY, F. A.; ROGERS, D. J., 1985: Taxonomic analysis in biology. Computers, models, and databases. New York: Columbia University Press.

ADAMS, E. N., III, 1972: Consensus techniques and the comparison of taxonomic trees. Syst. Zool. 21, 390–397.

ANDERSEN, K., 1905a: A list of the species and subspecies of the genus *Rhinolophus*, with some notes on their geographical distribution. Ann. Mag. nat. Hist. 7, 16, 648–662.

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

– 1905c: On the bats of the *Rhinolophus philippinensis* group, with descriptions of five new species. Ann. Mag. nat. Hist. 7, 16, 289–292.

– 1918: Diagnoses of new bats of the families Rhinolophidae and Megadermatidae. Ann. Mag. nat. Hist. 9, 2, 374–384.

ANDŌ, K.; TAGAWA, T.; UCHIDA, T. A., 1980: Karyotypes of Taiwanese and Japanese bats belonging to the families Rhinolophidae and Hipposideridae. Cytologia 45, 423–432.

ANDŌ, K.; YASUZUMI, F.; TAGAWA, A.; UCHIDA, T. A., 1983: Further study on the karyotypic evolution in the genus *Rhinolophus* (Mammalia: Chiroptera). Caryologia 36, 101–111.

ARCHER, M., 1978: Australia's oldest bat, a possible rhinolophid. Proc. R. Soc. Qd 89, 23.

ARCHER, M.; GODTHELP, H.; HAND, S. J.; MEGIRIAN, D., 1989: Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. Aust. Zool. 25, 29–65.

ARNOLD, M. L.; HONEYCUTT, R. L.; BAKER, R. J.; SARICH, V. M.; JONES, J. K., JR., 1982: Resolving a phylogeny with multiple data sets: a systematic study of phyllostomoid bats. Occ. Pap. Mus. Tex. Tech Univ. 77, 1–15.

BOGDANOWICZ, W.: Phenetic relationships among bats of the family Rhinolophidae. J. Mammalogy (in press).

BRIGGS, J. C., 1989: The historic biogeography of India: isolation or contact? Syst. Zool. 38, 322–332.

BUTLER, P. M., 1978: Insectivora and Chiroptera. In: Evolution of African mammals. Ed. by V. J. MAGLIO and H. B. S. COOKE. London: Harvard University Press. 56–68.

CORBET, G. B.; HILL, J. E., 1986: A world list of mammalian species. 2nd ed. New York: Facts on File Publications and British Museum (Nat. Hist.).

FELSENSTEIN, J., 1981: Evolutionary trees from gene frequencies and quantitative characters: finding maximum likelihood estimates. Evolution 35, 1229–1242.

– 1988: PHYLIP (Phylogeny Inference Package) Version 3.1 Manual. Univ. of Washington, Seattle.

FLANNERY, T. F., 1989: Origins of the Australo-Pacific land mammalian fauna. Austr. Zool. Rev. 1, 15–24.

FRIANT, M., 1963: Les Chiroptera (Chauves-Souris). Révision des Rhinolophidae de l'époque tertiaire. Acta zool. Stockholm 44, 161–178.

GAISLER, J., 1971: Systematic review and distinguishing characters of the bats (Chiroptera) hitherto recorded in Afghanistan. Zool. Listy 17, 41–48.

HALL, L. S., 1989: Rhinolophidae. In: Fauna of Australia. Mammalia. Vol. 1B. Ed. by D. W. WALTON and B. J. RICHARDSON. Canberra: Australian Government Publishing Service. 857–863.

HAMILTON-SMITH, E., 1974: The present knowledge of Australian Chiroptera. J. Aust. mamm. Soc. 1, 95–108.

– 1975: Gondwanaland and the Chiroptera. J. Aust. mamm. Soc. 1, 382–383.

HANÁK, V., 1969: Zur Kenntnis von *Rhinolophus bocharicus* Kastchenko et Akimov, 1917 (Mammalia: Chiroptera). Věst. Čsl. Spol. zool. 33, 315–327.

HAND, S., 1984: Bat beginnings and biogeography: a southern perspective. In: Vertebrate zoogeography and evolution in Australia. (Animals in space and time). Ed. by M. ARCHER and G. CLAYTON. Carlisle: Hesperian Press. 853–904.

– 1989: On the winds of fortune. Austr. Nat. Hist. 23, 131–138.

HARADA, M.; YENBUTRA, S.; YOSIDA, T. H.; TAKADA, S., 1985: Cytogenetical study of *Rhinolophus* bats (Chiroptera, Mammalia) from Thailand. Proc. Japan Academy, Ser. B 61, 455–458.

HELLER, F., 1936: Eine oberpliozäne Wirbeltierfauna aus Rheinhessen. Neues Jb. Miner. Geol. Paläont. 76, 99–160.

HELLER, K.-G.; v. HELVERSEN, O., 1989: Resource partitioning of sonar frequency bands in rhinolophoid bats. Oecologia **80**, 178–186.

HILL, J. E., 1972: A note on *Rhinolophus rex* Allen, 1923 and *Rhinomegalophus paradoxolophus* Bourret, 1951 (Chiroptera: Rhinolophidae). Mammalia **36**, 428–434.

– 1982: A review of the leaf-nosed bats *Rhinonycteris*, *Cloeotis* and *Triaenops* (Chiroptera: Hipposideridae). Bonn. zool. Beitr. **33**, 165–186.

HILL, J. E.; SCHLITTER, D. A., 1982: A record of *Rhinolophus arcuatus* (Chiroptera: Rhinolophidae) from New Guinea, with the description of a new species. Ann. Carneg. Mus. **51**, 455–464.

HILL, J. E.; YOSHIYUKI, M., 1980: A new species of *Rhinolophus* (Chiroptera, Rhinolophidae) from Iriomote Island, Ryukyu Islands, with notes on the Asiatic members of the *Rhinolophus pusillus* group. Bull. natn. Sci. Mus., Tokyo, Ser. A (Zool.) **6**, 179–189.

HOOD, C. S.; SCHLITTER, D. A.; GEORGUDAKI, J. I.; YENBUTRA, S.; BAKER, R. J., 1988: Chromosomal studies on bats (Mammalia: Chiroptera) from Thailand. Ann. Carneg. Mus. **57**, 99–109.

KOOPMAN, K. F., 1970: Zoogeography of bats. In: About bats. A chiropteran biology symposium. Ed. by B. H. SLAUGHTER and D. W. WALTON. Dallas: Southern Methodist University Press. 29–50.

– 1982: Rhinolophidae. In: Mammal species of the world: a taxonomic and geographic reference. Ed. by J. H. HONACKI, K. E. KINMAN, and J. W. KOEPPL. Lawrence: Allen Press and The Association of Systematic Collections. 136–148.

KOOPMAN, K. F.; JONES, J. K., JR., 1970: Classification of bats. In: About bats. A chiropteran biology symposium. Ed. by B. H. SLAUGHTER and D. W. WALTON. Dallas: Southern Methodist University Press. 22–28.

LANZA, B., 1959: Notizie sull'osso peniale dei Chirotteri Europei e su alcuni casi di parallelismo morfologico. Monitore zool. ital. **67**, 3–14.

LAURENT, P., 1940: Le crâne de *Rhinolophus maclaudi* Pousargues. Bull. Mus. natn. Hist. nat. Paris **2**, 12, 224–231.

LAVOCAT, R., 1961: Le gisement de vertébrés miocènes de Beni Mellal (Maroc). Etude systématique de la faune des mammifères et conclusions generales. Notes Mém. Serv. Mines Carte géol. Maroc. **155**, 29–94.

LEKAGUL, B.; MCNEELY, J. A., 1988: Mammals of Thailand. Second ed. Bangkok: Darnsutha Press.

MEESTER, J. A. J.; RAUTENBACH, I. L.; DIPPENAAR, N. J.; BAKER, C. M., 1986: Classification of southern African mammals. Transvaal Mus. Monograph **5**, 1–359.

NAIDU, K. N.; GURURAJ, M. E., 1984: Karyotype of *Rhinolophus luctus* (ord.: Chiroptera). Curr. Sci. **53**, 825–826.

OWEN, R. D., 1987: Phylogenetic analyses of the bat subfamily Stenodermatinae (Mammalia: Chiroptera). Spec. Publs. Mus. Tex. Tech Univ. **26**, 1–65.

– 1988: Phenetic analyses of the bat subfamily Stenodermatinae (Mammalia: Chiroptera). J. Mammalogy **69**, 795–810.

PIERSON, E. D., 1986: Molecular systematics of the Microchiroptera: higher taxon relationships and biogeography. Ph. D. dissert. Berkeley: The University of California.

QUMSIYEH, M. B.; OWEN, R. D.; CHESSER, R. K., 1988: Differential rates of genic and chromosomal evolution in bats of the family Rhinolophidae. Genome **30**, 326–335.

REMY, J. A.; CROCHET, J.-Y.; SIGÉ, B.; SUDRE, J.; DE BONIS, L.; VIANEY-LIAUD, M.; GODINOT, M.; HARTENBERGER, J.-L.; LANGE-BADRÉ, B.; COMTE, B., 1987: Biochronologie des phosphorites du Quercy: mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. Münchner Geowiss. Abh., Geol. Paläont., Ser. A, **10**, 169–188.

RUSSELL, D. E.; HARTENBERGER, J.-L.; POMEROL, CH.; SEN, S.; SCHMIDT-KITTLER, N.; VIANEY-LIAUD, M., 1982: Mammals and stratigraphy: the Paleogene of Europe. Palaeovertebrata, Mém. Extraord. 1982, 1–77.

SAVAGE, D. E.; RUSSELL, D. E., 1983: Mammalian palaeofaunas of the world. London: Addison-Wesley Publication.

SIGÉ, B., 1976: Les insectivores et chiroptères du Paléogène moyen d'Europe dans l'histoire des faunes de mammifères sur ce continent. Paléobiol. contin. **7**, 3, 1–25.

– 1978: La poche à phosphate de Ste-Néboule (Lot) et sa faune de vertébrés du Ludien supérieur. 8. – Insectivores et chiroptères. Palaeovertebrata **8**, 243–268.

SIGÉ, B.; LEGENDRE, S., 1983: L'histoire des peuplements de chiroptères du bassin méditerranéen: l'apport comparé des remplissages karstiques et des dépôts fluvio-lacustres. Mém. Biospéol. **10**, 209–225.

SIMPSON, G. G., 1945: The principles of classification and a classification of mammals. Bull. Amer. Mus. nat. Hist. **85**, 1–350.

TATE, G. H. H., 1943: Results of the Archbold expeditions. No. 49. Further notes on the *Rhinolophus philippinensis* group (Chiroptera). Am. Mus. Novit. 1219, 1–7.

– 1946: Geographical distribution of the bats in the Australian Archipelago. Amer. Mus. Novit. 1323, 1–21.
Tate, G. H. H.; 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.
Thonglongya, K., 1973: First record of *Rhinolophus paradoxolophus* (Bourret, 1951) from Thailand, with the description of a new species of the *Rhinolophus philippinensis* group (Chiroptera, Rhinolophidae). Mammalia **37**, 587–597.
Topál, G., 1958: Morphological studies on the os penis of bats in the Carpathian Basin. Annls hist.-nat. Mus. natn. hung., Ser. Nov. **9**, 50, 331–342.
– 1975: Bacula of some Old World leaf-nosed bats (Rhinolophidae and Hipposideridae, Chiroptera: Mammalia). Vertebr. hung. **16**, 21–53.
– 1979: Fossil bats of the *Rhinolophus ferrumequinum* group in Hungary (Mammalia: Chiroptera). Fragm. Min. Palaeont. 9, 61–101.
Van Zyll de Jong, C. G., 1984: Taxonomic relationships of Nearctic small-footed bats of the *Myotis leibii* group (Chiroptera: Vespertilionidae). Can. J. Zool. **62**, 2519–2526.
Wołoszyn, B. W., 1987: Pliocene and Pleistocene bats of Poland. Acta palaeont. pol. **32**, 207–325.
Wood, D.S., 1983a: Character transformations in phenetic studies using continuous morphometric variables. Syst. Zool. **32**, 125–131.
– 1983b: Phenetic relationships within the Ciconiidae (Aves). Ann. Carneg. Mus. **52**, 79–112.
Yoshiyuki, M., 1989: A systematic study of the Japanese Chiroptera. Tokyo: National Science Museum.
– 1990: Notes on Thai mammals. 2. Bats of the *pusillus* and *philippinensis* groups of the genus *Rhinolophus* (Mammalia, Chiroptera, Rhinolophidae). Bull. natn. Sci. Mus., Tokyo, Ser. A. (Zool.) **16**, 21–40.

Authors' addresses: Dr. Wiesław Bogdanowicz, Mammal Research Institute, Polish Academy of Sciences, PL-17-230 Białowieża, Poland; Dr. Robert D. Owen, Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA