A PATKÓSDENEVÉREK RENDSZERTANA

TAXONOMY OF THE HORSESHOE BATS OF THE WORLD

(CHIROPTERA: RHINOLOPHIDAE)

Doktori (PhD) értekezés

Csorba Gábor
Debreceni Egyetem
Természettudományi és Technológiai Kar
Debrecen, 2008

Ezen értekezést a Debreceni Egyetem TTK Biológia Doktori Iskola Biodiverzitás programja keretében készítettem a Debreceni Egyetem TTK doktori (PhD) fokozatának elnyerése céljából.

Debrecen, 2008

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Tanúsítom, hogy Csorba Gábor doktorjelölt 2005-2008 között a fent megnevezett Doktori Iskola Biodiverzitás programjának keretében irányításommal végezte munkáját. Az értekezésben foglalt eredményekhez a jelölt önálló alkotó tevékenységével meghatározóan hozzájárult. Az értekezés elfogadását javasolom.

Debrecen, 2008

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1. INTRODUCTION

The extension and improvement of our taxonomic knowledge is rendered urgent by the biodiversity crisis which threatens to destroy much of the evidence of evolutionary history before it could be documented. This is especially emphasized in the case of mammals, a flagship group of the animal kingdom in the fields of conservation biology, phylogenetic classification, ecological and behavioural studies. The second most numerous order of mammals is that of the bats (Chiroptera), with over 1200 known living species. Due to the high number of taxa and their cryptic life-style bats are relatively poorly know. This might explain the fact that new species are described regularly from the tropical and even the temperate areas of the globe (the number of species has increased by approximately 20 per cent in the last decade) and a significant part of the bat literature is focused on their faunistics and taxonomy. The family of horseshoe bats (Rhinolophidae) is well-defined taxonomic unit with exclusively insectivorous species. The highest number of co-existing species can be found in mature tropical forests and extensive limestone cave systems of the Old World, in biotops, which are among the most threatened ones on the Earth. Specimens of many species are rarities in the collections and scattered in many countries. Our ability to differentiate the species is complicated by their uniform appearance, where differences between the species are mainly found in the complex anatomical parts, which are difficult to describe verbally (the shape of the noseleaf and the nasal swellings), and in differences in size. Moreover, in the last 100 years no serious attempt was made to provide a thorough revision and an overview of relevant literature. Neither the old species descriptions nor the new identification keys and comprehensive works give enough anatomical details or adequate quantity of measurements. Hence, the knowledge regarding the identification of these species - that forms the basis for all the other research such as ecological, physiological or conservation-oriented studies - was fairly difficult to gather. The aim of this work was therefore twofold: 1) Careful examination of specimens available in collections, information recorded as exact and repeatable measures and comparable illustrations (drawings and digital images). 2) re-organising and evaluating existing publications on various morphological characters (including external, cranial and dental features), taxonomy and systematics. By producing this database with the knowledge gained by the processes described in 1), my goal was to write a practical monography on taxonomy of this beautiful family of bats.

Due to this principal task **my dissertation is focusing exclusively on taxonomy**, although, during the data collecting period huge amount of information were gathered on aspects of horseshoe bat biology in general, including distribution, habits, feeding, breeding, echolocation, conservation status, phylogeny and biogeography. These fields are out of the scope of this work but presented in the book of Csorba et al. (2003).

2. LITERATURE OVERVIEW

The overview presented here is based on the compilation of Guillen et al (2003) published in the book of Csorba et al. (2003) and deals only with the systematics of the family above the species-level. The overview of the species-level taxonomy can be found in the 'species accounts' section under the heading 'Taxonomic remarks'. These historical parts are based on, according to my best knowledge, all the information published between 1903-2002 and different taxonomic opinions related to each species are provided. This is supplemented by my critical comments and by the interpretation of taxonomic actions applied in the dissertation including lectotype designations and revisions.

Beginning with the introduction of the genus name *Rhinolophus* by Lacépède (1799), most authors have included all extant horseshoe bats in a single genus, although some alternatives have been proposed. Leach (1816) proposed the genus name *Phyllorhina* for *Vespertilio minutus* Montagu, 1808 (now called *R. hipposideros minutus*; see Hill 1963). Initially, the genus *Rhinolophus* also included the species of *Hipposideros* known at that time. Gray (1847, 1866), based on differences in the noseleaves, proposed the genus *Aquias* for the Indomalayan species *R. trifoliatus* and *R. luctus* and *Phyllotis* for the indomalayan-australasian species *R. philippinensis*, while keeping all other species of horseshoe bats in the genus *Rhinolophus*, from which he excluded the hipposiderid bats. Peters (1867) proposed the genus *Coelophyllus* for *Rhinolophus coelophyllus*. Dobson (1876) returned all Asiatic horseshoe bats to *Rhinolophus* and ignored generic and subgeneric partitions proposed previously. He also separated rhinolophid and hipposiderid bats in two different subfamilies, Rhinolophinae and Phyllorhininae. Matschie (1901) described *Rhinolophus mehelyi* under the subgenus *Euryalus*, together with *R. euryale*. Miller (1907) elevated the subfamilies erected by Dobson (1876) to family rank. Iredale and Troughton (1934) introduced *Rhinophyllotis* with the type being *R. megaphyllus*. These additional genera were obviated by subsequent authors, and *Rhinolophus* was kept as the only genus. Bourret (1951) described the highly characteristic *R. paradoxolophus* as belonging to the genus *Rhinomegalophus*. But Hill (1972) brought it back into *Rhinolophus*, noting the close similarity of this species with *R. rex* and other species previously included in the genus.

Besides describing many new species and forms of *Rhinolophus*, Andersen (1905a, 1905b, 1905c, 1905d, 1905e, 1905f, 1918) reviewed the family in a classical fashion and advanced the first phylogenetic hypotheses on the evolution and biogeography of the group. Because horseshoe bats vary little in major skeletal structures, Andersen (works cited above) used few characters for establishing his systematic arrangement. Many of these characters are probably plesiomorphic or prone to homoplastic change. They included the size and degree of displacement from the toothrow of minor teeth (variable even within the same species), size and shape of noseleaves and ears, length of palate (characters involved in echolocation and prone to adaptive evolution), and relative length of finger bones of the wing (involved in adaptive flight morphology). According to the custom at the time, he also used non-objective methods of phylogenetic reconstruction and models of character evolution, regarding without clear justification some features (long palate, three mental grooves, subequal metacarpals) as primitive Andersen (1905a).

In his 1905 papers, Andersen arranged the species of *Rhinolophus* into six groups, named after the species: *R. simplex*, *R. lepidus*, *R. midas, R. philippinensis, R. macrotis* and *R. arcuatus*, some containing a number of sections. He also sketched the

putative phylogenetic relationships among and within groups. In a later paper presented by Oldfield Thomas under the authorship of Andersen (1918), who by then had disappeared under mysterious circumstances, newly described forms were added to some of the former groups. The five groups of Andersen that were discussed in this paper were renamed, presumably to comply with the precedence of species names. Tate and Archbold (1939) reviewed the Oriental species of the genus, incorporating newly described forms into Andersen's group names of 1905, although breaking the precedence rule (except in their renaming of the *R. simplex* group as the *R. ferrumequinum* group). They also split Andersen's (1905a, 1905b, 1918) *R. simplex* group into several "subgroups", as they called Andersen's "sections". Although they claimed to keep Andersen's synoptic classification, they also moved Andersen's *R. macrotis* group as a subgroup into the *R. philippinensis* group. However, they were seemingly not fully convinced of this latter change. In their table, they wrote 'group' after *R. macrotis* with font and paragraphing as other subgroups but displayed a *R. macrotis* 'group' in a graphical arrangement of the phylogenetic relationships among groups (pp. 3 and 5). Tate (1943) further discussed the *R. philippinensis* group, rearranging and renaming the subgroups, which he then referred to as "sections." He merged the *R. macrotis* and *R. philippinensis* subgroups into a single *R. philippinensis* "section" from where he excluded the highly characteristic *R. pearsoni*, which Andersen (1905a, 1905d, 1918) had included in his *R. macrotis* group. Awkwardly and without clear justification, he moved *R. coelophyllus* from Andersen's *arcuatus* group, which contains morphologically similar species, into this *R. philippinensis* section, integrated by very different species. He merged Andersen's *R. trifoliatus* and *R. sedulus* sections into his second section *R. trifoliatus*, excluding *R. luctus* because of differences in the skull. As a gross error, *R. pearsoni* was now included as conspecific with the latter species in a third *R. luctus* section.

Later authors have further changed names of the groups, modified slightly some of them, and incorporated the newly described forms into them. Ellerman and Morrison-Scott (1951) added Palaearctic and Indian taxa to the arrangement left by Tate and Archbold (1939) and Tate (1943). They used Andersen´s (1918) nomenclature, except for changing the name of the *R. luctus* group to *R. trifoliatus* group, because the latter name had precedence. Aellen and Brosset (1968) added some African species into the *R. ferrumequinum* group and created within this a new subgroup, *R. capensis*, comprising a number of characteristic Ethiopian forms. Koopman (1975) updated the arrangement with the new African taxa, but showed reserve on Tate's (1943) fusion of the *R. macrotis* and *R. philippinensis* groups, based on the distinctiveness of the African species putatively belonging to them. He also doubted that the species within the *R. capensis* subgroup belonged in the *R. ferrumequinum* group. Hill (in Corbet and Hill 1992) based his systematic arrangement of Indomalayan *Rhinolophus* on Andersen (1905a) mostly, but followed Tate (1943) in merging the group *R. macrotis* into *R. philippinensis*. He also moved *R. pearsoni* and the similar Indomalayan *R. yunanensis*, together with the Ethiopian *R. fumigatus* and allies, into a new *R. fumigatus* group. Koopman (1994) incorporated the group structure as it was left by Tate and Archbold (1939) and Tate (1943), although keeping the position of *R. coelophyllus* and allies into the *R. euryotis* group as Andersen (1918) did.

The latest and most comprehensive work on the systematics of the horseshoe bats was that of Bogdanowicz (1992), who combined previous taxonomic results with his phenetic ordination and clustering analyses to organize the genus into groups and subgroups. The resulting arrangement was broadly similar to Andersen´s organization,

but also showed major differences. The most important of these was that most Ethiopian and Palaearctic species grouped together in his phenograms. The new analyses provided Bogdanowicz a basis for defining, by depth in the phenograms, a number of groups (*R. capensis, R. ferrumequinum, R. fumigatus* and *R. euryale*) made up of species from these regions only. The remaining groups were composed only of Asian species. The Palaearctic species *R. hipposideros* was found to be quite distinct, and was left in a separate monotypic group, following previous authors since Andersen (1905b). Species in the *R. philippinensis* group defined by Hill (in Corbet and Hill 1992) were found to be very heterogeneous phenetically. The Indomalayan species *R. trifoliatus* and *R. luctus*, sometimes joined by *R. sedulus*, formed a distinctive cluster, closer to the Ethiopian cluster than to other Asian groups. Acknowledging their clear homologies and distinctiveness, Bogdanowicz (1992) placed these three taxa in a group of their own. The long-eared and large-noseleaved Asian species previously included in the *R. macrotis* and *R. philippinensis* subgroups of the *R. luctus* group were the most distinctive of all *Rhinolophus.* These clustered together outside all other species, sometimes adjoined by the Ethiopian long-eared form *R. maclaudi*. Bogdanowicz (1992) placed all these Asian species in an exclusive group (*R. philippinensis*) while keeping the only Ethiopian species in an *incertae sedis* category acknowledging zoogeographic and phenetic contradictions. The remaining Asian taxa formed a phenetic cluster, with four well-defined subclusters. One of them comprised *R. pearsoni* and *R. yunanensis*, revalidating their removal from the *R. luctus* group by Hill (1992), but not their allegiance with the Ethiopian taxa in the *R. fumigatus* group as Hill had proposed. This justified the creation of a new *R. pearsoni* group. All species in the previous *euryotis* group clustered together, with the addition of *R. stheno* and *R. affinis*. Bogdanowicz (1992) kept the classical ensemble, adding *R. stheno* on the basis of morphological similarities, but trusting more the classical ideas and the ordination than the cluster analyses in excluding *R. affinis*. Surprisingly, Bogdanowicz (1992) included *R. toxopeusi*, from the islands of Buru and Ambon (Moluccas; Hinton 1925, Flannery 1995), in this *R. euryotis* group, although his own analyses and other authors Flannery (1995) suggest that this form is actually a relative of *R. borneensis* and *R. celebensis*. All remaining species belonged in Andersen's (1918) *R. megaphyllus* and *R. pusillus* groups, which Andersen (1905a) considered very close to each other. However, Bogdanowicz´s (1992) analyses showed an outermost cluster containing the species in Tate and Archbold's (1939) *R. rouxi* subgroup, plus *R. acuminatus*, which Andersen (1918) included alone in a special subgroup within his *R. pusillus* group. Bogdanowicz (1992) proposed a new group *R. rouxi* for these species, also including *R. affinis* based on proximity in the space defined by his ordination analysis. The last ensemble of species split more or less cleanly into those left from the *R. megaphyllus* and *R. pusillus* groups of Andersen (1918), and Bogdanowicz (1992) kept these as subgroups within a *R. megaphyllus* group.

Lately, Kock *et al.* (2000) described the new species *R. maendeleo*. They established the new group *R. adami* to include this species and *R. adami*, which was formerly included in the *R. capensis* subgroup within the *R. ferrumequinum* group by Aellen and Brosset (1968).

In my dissertation I proposed changes in the arrangement of groups by Bogdanowicz (1992), adding some species not recognised or considered by the latter author and discarding others based on evident phenetic relationships. **The arrangement**

presented here has the more practical purpose of facilitating determination rather than trying to reflect phylogenetic relationships among species.

3. MATERIALS AND METHODS

3.1. THE FAMILY RHINOLOPHIDAE

The genus *Rhinolophus* as understood here, is the only genus in the family Rhinolophidae, horseshoe bats. Rhinolophidae, along with the families Rhinopomatidae, Craseonycteridae, Megadermatidae and its sister-group Hipposideridae belongs to the superfamily Rhinolophoidea Gray, 1825.

The family is characterised by the solid thoracal ring of bone, formed by the fusion of presternum, first and partly the second rib, seventh cervical and first thoracic vertebrae. The lumbar vertebrae are not fused. The trochiter of humerus is fairly large and definitely articulating with scapula. The ischium and pubis are reduced in size so that the space between them is reduced. Except for hallux, each toe has three phalanges. The baculum is elongated with conical basal part; the tip is never forked.

In the skull the premaxillae represented by projecting narrow palatal branches only; these two bones are partly cartilaginous and are not fused with each other or with the maxillae. Postorbital processes absent; the palate is deeply incised both anteriorly and posteriorly. The tympanic bullae are relatively small but the cochleae are well developed. The skull is always with rostral inflations. The basic dental formula is 1123/2133 but the anterior upper premolars and the middle lower premolars are often missing. The upper incisors are very small but usually well formed; the lower incisors are trifid. The molariform teeth do not show any particular modification, M^1 and M^2 without hypocone, M^3 almost always with three commissures.

The rhinarium is showing very characteristic and complex modifications which consist of an erect posterior lancet, a lower horizontal horseshoe-shaped expansion surrounding the nostrils and partly or fully covers the upper lip, and a perpendicular median sella and connecting process. The ears are moderate to large and lack a tragus. The tail is well developed and is completely enclosed in the uropatagium. Beside the two functional mammae on the chest, there are two additional teat-like processes not connected to mammary gland found on the abdominal region of adult females.

3.2. MATERIAL INVESTIGATED

During the five-years period of data collecting, beside the material housed in the Hungarian Natural History Museum, many other collections had been visited in Europe, North America and Asia in order to study their holdings in the spot. Important materials (including types) were also loaned. More than 4.000 individuals (conserved in different ways) were investigated and measurements were taken from approximately 2.000 specimens. The species identity in all cases were checked and no previous identification was accepted without careful re-examination of the material.

So far it was possible the drawings were made from the type specimens depicting the noseleaf (lateral and frontal views) of a wet specimen, left side of skull and left anterior (C-P4) upper and lower dentitions. Where the conditions of the types were not appropriate (dry study skins, damaged skulls, missing teeth or mandibles etc.) other specimens were selected possibly obtained from close to the *terra typica*.

The museums and other institutions visited and/or their acronyms used in this work are as follows:

AMNH - American Museum of Natural History, New York
BMNH - Natural History Museum, London; formerly British Museum (Natural History)
FMNH - Field Museum of Natural History, Chicago
HNHM - Hungarian Natural History Museum, Budapest
HZM - Harrison Institute, Sevenoaks; formerly Harrison Zoological Museum
IEBR - Institute of Ecology and Biological Resourches, Hanoi
MHN - Museum d'Historie Naturelle, Geneve
MNB - Museum für Naturkunde, Berlin
MNCN - Museo Nacional de Ciencias Naturales, Madrid
MNHN - Muséum National d'Histoire Naturelle, Paris
NMNS - National Museum of Natural Science, Taichung
NMW - Naturhistorisches Museum, Vienna
RMNH - National Museum of Natural History, Leiden;
SMF - Forschungsinstitut Senckenberg, Frankfurt a. M.
SMN - Staatliches Museum für Naturkunde, Stuttgart
TISTR - Thailand Institute of Scientific and Technological Research, Bangkok
USNM - United States National Museum of Natural History, Washington
ZMMU - Zoological Museum of Moscow State University, Moscow

3.3. DEFINITION OF MEASUREMENTS AND TECHNICAL TERMS

External measurements and terminology
In the text the range of several measurements (ear length, horseshoe breadth, tail and wing bones length) is given, partly based on my data, partly obtained from publications. These data are usually considered by me as less useful in the determination, however often cited in the literature. Since the ear measurement is subject to considerable error (Goodwin 1979) and in the field usually can be taken with difficulties, it is of frequently limited use in comparing different taxa, especially when the measurements are not all taken by the same investigator. For this reason, along with the absolute values the relative ear length (as compared to the head) is also given.

In the tables provided for each species for convenience the external measurement (forearm length) is given first followed by the internal ones.

Forearm From the extremity of the elbow to the extremity of the carpus with the wings folded

Ear length From the lower border of the external auditory meatus to the tip of pinna, not including any tuft of hair. Beside the ear length expressed in mm, I applied the relative ear length as related to the head according to the following terms: small - the ear by far does not reach the tip of nose when laid forward; medium - the ear reaches the nose or close to it; large - the ear extending far beyond the muzzle; enormous - the ear exceptionally developed

Noseleaf (Fig. i.)

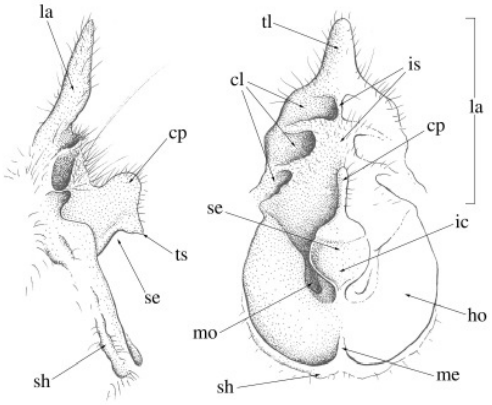

Fig. i. Lateral and front views of noseleaf of *Rhinolophus.*

cl: cells of lancet
cp: connecting process
ho: horseshoe
ic: internarial cup
is: intercellular septa
la: lancet
me: median emargination
no: nostril
se: sella
sh: secondary horseshoe (or supplementary leaflet)
tl: tip of lancet
ts: tip of sella

Craniodental measurements (Fig. ii.)

The following standard cranial and dental measurements - if were available at all from the material investigated - are included in each species accounts: skull length (SL), upper toothrow length (CM^3L), zygomatic width (ZW), mastoid width (MW), mandible length (ML) and lower toothrow length (CM_3L). All values are given in millimetres. In the tables I compiled the extreme values of forearm length obtained from different sources (own data, literature) therefore no sample size or other basic statistical details are given. The cranial and dental measurements were choosed as the taxonomically most informative and most easily measurable ones and are based exclusively on my own data set to avoid the differences derived from methodological variances. These measurements were taken under stereomicroscope by digital caliper (Mitutoyo ABSolute Digimatic Caliper) with 0.01 mm accuracy. Only data taken from fully grown adult specimens are included. For these measurements the mean, minimum and maximum values, standard deviation and the sample size are given. To cover the intraspecific variations an attempt was made to study and measure specimens from all over the range of the species, including as many subspecies as possible.

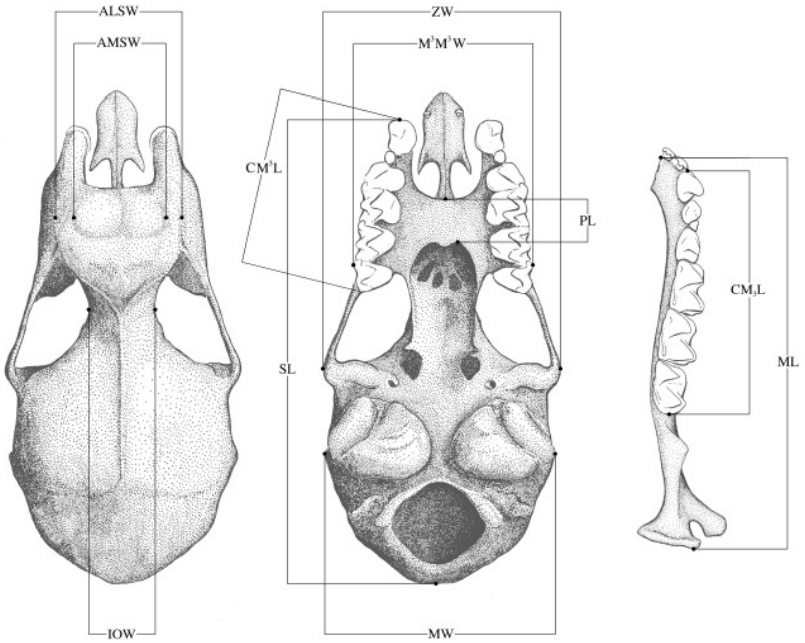

Fig. ii. Dorsal and ventral views of skull of *Rhinolophus.*

Cranial and dental terminology (Fig. iii.)

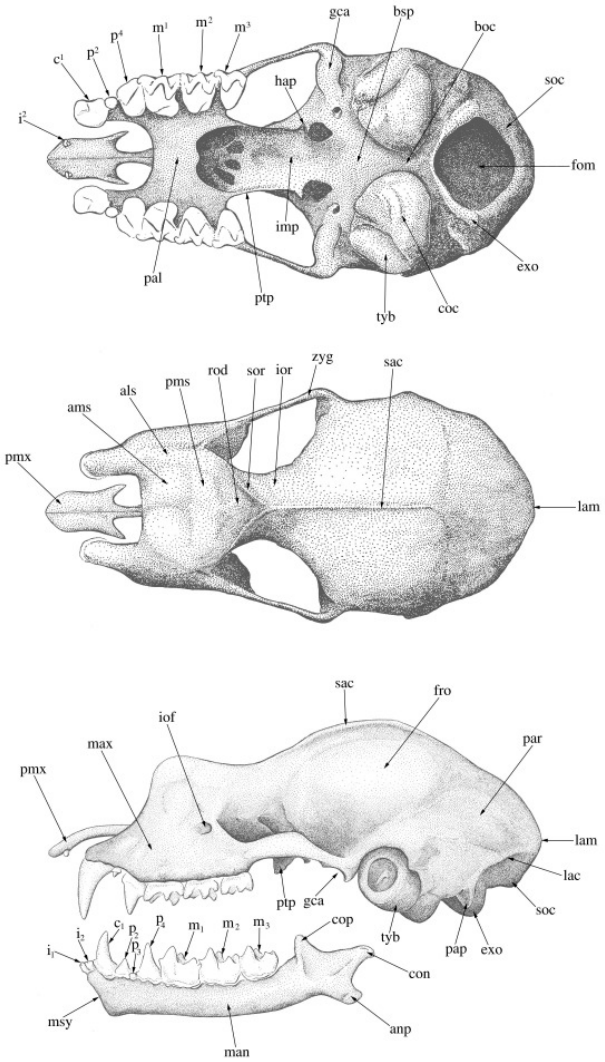

Fig. iii. Ventral, dorsal and lateral views of skull of *Rhinolophus*

SL: skull length, the greatest length from the occiput to the front of canine
ALSW: the greatest width of the anterior lateral swellings in dorsal view
AMSW: anterior median swellings width in dorsal view
IOW: interorbital width, the least width of the interorbital constriction
ZW: zygomatic width, the greatest distance across the zygoma
M^3M^3W: rostral width, measured between outer crowns of M^3
PL: palatal length, measured without the posterior spike
MW: mastoid width, the greatest distance across the mastoid region
CM^3L: upper toothrow length, the crown lentgth from the anterior of the upper canine to the posterior of the third upper molar
ML: mandible length, the distance from the most posterior portion of the articular process to the anteriormost edge of the alvelolus of the first lower incisor
CM_3L: lower toothrow length, the crown length from the anterior of the lower canine to the posterior of the third lower molar

als: anterior lateral swelling
ams: anterior median swelling
anp: angular process
boc: basioccipitale
bsp: basisphenoid
c^1: upper canine
c_1: lower canine
coc: cochlea
con: condyle
cop: coronoid process
exo: exoccipital condyle
fom: foramen magnum
fro: frontale
gca: glenoid cavity
hap: hamular process
i^2: upper incisor
$i_{1,2}$: lower incisors
inp: interpterygoid
iof: infraorbital foramen
ior: interorbital region
lac: lambdoid crest
lam: lambda
m^{1-3}: upper molars
m_{1-3}: lower molars
man: mandible
max: maxilla
msy: mandibular symphysis
$p^{2, 4}$: upper premolars
p_{2-4}: lower premolars
pal: palate
pap: paroccipital process
par: parietal
pms: posterior median swelling
pmx: premaxilla
ptp: pterygoid plate
rod: rostral depression
sac: sagittal crest
soc: supraoccipital
sor: supraorbital ridge
tyb: tympanic bulla
zyg: zygoma

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4. RESULTS

4.1. EVALUATION OF TAXONOMIC CHARACTERS

In his important and fundamental series of studies on *Rhinolophus* bats Andersen (1905a, 1905b, 1905c, 1905d, 1905e, 1905f, 1906a, 1906b) compiled the chief criteria of the classification of the genus. He used the forearm measurement, shape and size of nasal foliations, size of ears and antitragus, proportions of wing bones, number of mental grooves, palatal length, development of nasal inflations, position and height of supraorbital and sagittal crests and the size and position of the small upper and lower premolars as the most informative characters. Although Andersen's phylogenetic hypotheses based on these features seems to be immature and unreliable in the light of our present knowledge and therefore is not applicable to reveal the evolutionary relationships within the genus, most of the features recognised by him are quite useful key characters in the determination of species. The critical evaluation of the characters widely used in the classical taxonomy of the family is given below.

Forearm length From all the measurable characters the forearm length is the most commonly published one, which is measurable by a standard way. According to the study of Herr *et al*. (2000) there were no significant differences among the mean values taken by different investigators, although measurements taken by single investigators are more reliable.

The lengths of forearm of many pairs of sympatric bat species (representing a wide range of microchiropteran bat families) are used as diagnostic character in taxonomic keys often relying on differences of 1 mm only.

Ear and tail length Due to the methodological differences and the difficulties of measuring live animals or dry study skins, the ear and tail lengths are subjects of significant errors. Rautenbach (1986) found the external mensural characters generally unacceptably variable and used only the wing bones' values in his statistical analyses. Corbet and Hill (1992: 10) also stated that any measurements wich is notoriously difficult to take in a standardized way should be treated as very approximate.

Although the absolute tail length is subject to less error it is often not clear whether the anus or pelvis had been used as origin. E.g. the mensural data of tail length for the small bodied *R. lepidus* (forearm 37.0-43.0 mm) compiled from a wide range of literature is given as between 12.2 mm and 28.0 mm, which is widely overlapping with that of the considerably smaller *R. subbadius* (forearm 33.5-38.0 mm) and also with that of the much bigger *R. affinis* (forearm 47.0-55.5 mm). Therefore, I conclude, that ear and tail measurements are for general information only, and their taxonomic usefulness is highly questionable.

Wing shape Numerous authors have used the wing shape as discriminating character between species of horseshoe bats, described by the relative length either of metacarpals or phalanges of different digits. The wing shape definitely has taxonomic value in several cases (e. g. Happold and Happold 1989, Paunovic and Stamenkovic 1998) but sometimes however, of limited value. Based on detailed comparisons of series of some species-pairs (once thought as taxonomically informative) the results were not reliable e.g. *R. stheno* - *R. malayanus* (McFarlane and Blood 1986, Csorba and Jenkins 1998) and *R. euryale* - *R. mehelyi* (DeBlase 1972).

Noseleaf structure Although there are some individual variations in the shape of tip of lancet, the form of connecting process and sella, and sometimes strange aberrations are also known to occur (see account on *R. inops*), due to its complex anatomy the nasal foliations bearing the taxonomically most informative external characters. Beside the usage of the noseleaf shape in the determination of species (or sometimes subspecies), the earlier systematic arrangements of the family were also largely based on these characters (e.g. Andersen 1905a, Tate and Archbold 1939, Corbet and Hill 1992).

The particulars of the noseleaf which are well useable in determination include the absolute and relative size of horseshoe, shape and pilosity of sella, length and shape of lancet, outline of connecting process and development of and additional lobes on internarial region. The presence or absence of secondary horseshoe seems to be less informative as was accepted earlier (e.g. Lekagul and McNeely 1977).

Mental grooves The number of mental grooves are almost always standard within species and only few exceptions are known. In the case of *R. ferrumequinum* the number of these grooves varies, either one or three, or the lateral ones are obliterated. Andersen (1905a) commented that in the case of the above species the lateral grooves often more or less reduced in the eastern races of the species, but in the western races constantly only the central groove is present. In other cases (several African species) the lateral grooves are hardly visible by naked eye.

Skull shape The general shape of skull is frequently very informative at the first glance. The skull is said to be slender if the mastoid width is exceeds the zygomatic breadth, and robust if the zygomatic width is the greater. In most cases the species is clearly characterised by its slender or robust skull, but in some species (e.g. *R. simulator*) the difference between the two measurements is not so well expressed and the mastoid breadth can be either slightly greater or narrower than the zygomatic width. The development and length of supraorbital and sagittal crest, the shape of rostral depression and the form of infraorbital region are also informative. A rarely considered but sometimes useful character is the structure of interpterygoid region (see account on *R. maendeleo*).

Nasal swellings Perhaps the most important skull character is the development of the nasal swellings, the structure directly involved in the species-specific ultrasound emission. The nasal swellings are composed of pairs of anterior median, anterior lateral and posterior (median) compartments, the shape and relative size of which are typical of the species and usually only very little variable. In those cases where there is some intraspecific variation in the formation of nasal swellings, the taxonomic significance (if there is any) of this phenomenon not fully understand yet.

Palatal bridge The length of the palatinum is an important group-character, but usually can not be applied to separate species within a given group. The palatal length is expressed in percentage of the length of the upper toothrow (CM^3) and is said to be short under 30% of the upper toothrow, moderate at about one-third, and long when over 37-38%.

Teeth The vestigial upper incisors are usually not considered as taxonomically important, although Corbet and Hill (1992) evidenced the differences found on these teeth when compared *R. luctus* and *R. trifoliatus*. The size of canines (mainly the upper

canines are important from this point of view) frequently used characters, providing clues to separate closely related taxa as *R. imaizumii-R. cognatus* and *R. lepidus-R. shortridgei*. The absolute and relative length and the diameter of the basal area of canines are equally important. The taxonomic usefulness of premolars is different according to the species-group and also different in the upper and lower toothrow. As Koopman (1975) evidenced the occurence of the vestigial first upper premolar in *R. clivosus* is "however so variable that I don't think any taxonomic significance should be attached to it". Indeed, the very small, extruded P^2 of the *ferrumequinum* and *fumigatus* groups is often missing at all, and its presence or absence having no taxonomic value. But in those groups, where the anterior upper premolar is better developed and is situated within the row or only partly extruded, this character is stable and well useable in the course of determination. In the case of *R. macrotis*, according to our present knowledge the development and position of P^2 is distinguishing character even at subspecific level. Nevertheless, in any of the species-groups investigated the position of middle lower premolars (P_3) are subject of significant individual variations. The relative size of premolars and canines are also informative, although the age-dependent tooth-wearing must be taken into consideration. The structure of posterior premolars and the three molars show no important modifications, except the distinct fourth commissure of the last upper molar of *R. hipposideros*.

Baculum The baculum (os penis) of *Rhinolophus* species is morphologically much less diverse than that of Hipposiderids. In the bone (which itself occupies a large part of the penis with its tip in the glans), despite the size, the ventral or dorsal bend of shaft and tip, the flattening of shaft and the dorsal and ventral incisions of the basal cone provide taxonomic information (Topál 1958, 1975). However, the shape of baculum as distinguishing character, must be used with great caution due to the significant structural differences between adult and subadult specimens (see age-related features).

Craniodental measurements Among the several widely used measurements the longitudinal ones are used more frequently in determination keys of rhinolophid bats. In the case of condylocanine length, condylobasal length, greatest length of skull etc. the separation of species often relying in differences of 0.5 mm; in those measurements which reflect smaller distances (e.g. toothrow length, molar length, anterior median swellings width) the specific differences can be as small as 0.1 mm.

But even the so-called standard measurements are interpreted differently. According to Ingle and Heaney (1992) the maxillary toothrow length was taken from the posterior (crown) edge of the last molar to the bone line of the alvelolus of C^1; Rautenbach (1986) defined the upper toothrow length as alveolar length but in the accompanying drawing figured it as measurable between the crowns of C^1 and M^3; Harrison and Bates (1991) determined the same length as from the front of canine to the back of the crown of the last molar.

Dulic and Felten (1964) draw the attention that in the case of Rhinolophids the condylobasal length measurable by a different way as in vesper bats since the premaxillae (bearing the upper incisors) of horseshoe bats are frequently lost or deformed during preparation, and suggested the front of the upper canines as the most anterior point. In connection with the investigation of subspecies of *R. ferrumequinum*, they also pointed out that different cranial measurements were published by different authors taken from the very same specimens. In spite of their opinion, Ingle and Heaney (1992) measured the condylobasal length from the posterior edge of the occipital

condyles to the anterior tip of the premaxillae; Bates and Harrison (1997) from the occipital condyles to the alveolus of the upper incisor and Miric (1960) from the condyles to the alveolus of the upper canine. However, several authors e.g. Hill (1986), Kock (1996), Topál and Csorba (1992), Yoshiyuki (1990) followed the protocoll suggested by Dulic and Felten (op. cit.) and dropped the premaxilla as measuring point, at all. These investigators applied the term condylocanine length and also used the front of upper canine as the most anterior point of the greatest skull length.

The palatal length is measurable by two different ways, with or without the posterior spine of the bone. Some authors further distinguish palatal length (its anterior point is at the posterior alveolar line of the upper canine) and palatal bridge length (its anterior point is at the middle of the anterior palatal emargination).

Age-related features The age of bats can be estimated by the degree of ossification of the joints in the digits of the wing. In juvenile bats the joints are swollen and tapered, whereas in adult bats the joints are knobby and more distinct from the bone shaft. Although the fully volant immature and subadult horseshoe bats already show several characteristics of the adult ones (noseleaf structure, main features of dentition and skull shape) some other characters important in the determination of species changing significantly during ontogeny. The colouration is usually more greyish; the measurements (both external and internal) are slightly below or close to the lower limits typical of the species. The sagittal and supraorbital crests are less developed than in adults; the baculum is notably shorter and narrower, the emarginations of the basal cone are much less expressed (Yoshiyuki 1989). Investigating *R. ferrumequinum* in England, Ransome (1968) found that the abdominal false teats of the females and the testes of the males can not be observed in immature bats, and individuals bearing these external sexual features are at least three years old.

Sexual dimorphism Felten *et al*. (1977) and Iliopoulou-Georgudaki and Ondrias (1986) found that sexual dimorphism is minimal or detected no statistically significant differences in *R. ferrumequinum*. By multivariate analyses of forelimb and cranial characters Paunovic & Stamenkovic (1998) found no differences between sexes of *R. euryale* and *R. blasii*. The sexual variations of eight cranial dimensions were examined in *R. cornutus* by Maeda (1988), who found no clear sexual dimorphism in any character until two months of age. Differences appeared thereafter in most dimensions i.e. those of males increased more rapidly; however, the dimorphism disappeared again at age group III (classified by the degree of wear in the first upper molar, and including specimens approximately one year old). Thomas (1997) run multivariate tests on series of *R. ferrumequinum*, *R. clivosus*, *R. bocharicus*, *R. rouxii* and *R. affinis* which showed there to be no significant variation between sexes.

Nevertheless, Koopman (1982) made a short note on the on the fairly pronounced difference in skull size between males and females of *R. euryotis*, but on the basis of a limited sample and his statement was not supported with statistical analyses. Goodwin (1979) remarked that the horseshoe width of *R. celebensis parvus* appears to be correlated with sex, males tending to have broader horseshoes on average. Rautenbach (1986) recorded significant variation between sexes in five (external and cranial) measurements in *R. denti* and suggested that statistically comparing different samples, males and females should be treated independently.

4.2. TAXONOMIC CHANGES

The taxonomic changes listed here and explained in the appropriate species accounts are new opinions related to the comprehensive systematic works of Corbet and Hill (1992) and Koopman (1994).

Definitions of terms of taxonomic changes:
- new synonymy - later established (junior) name of the given taxon (here species or subspecies) which, according to my opinion, used to denote the same taxon given in parentheses;
- revised status - re-establishment of the original status of a species or subspecies name which subsequently was not generally accepted;
- new status - newly established specific status of a name established as a subspecies or subspecific status of a name established as a species;
- new combination - the first combination of a species name and a previously established subspecies name.

R. anderseni Cabrera, 1909 **new synonymy** (= *R. arcuatus* Peters, 1871)
R. beddomei Andersen, 1905 **revised status**
R. euryale barbarus Andersen and Matschie, 1904 **new synonymy** (= *R. e. euryale* Blasius, 1853)
R. euryale meridionalis Andersen and Matschie, 1904 **new synonymy** (= *R. e. euryale* Blasius, 1853)
R. formosae Sanborn, 1939 **revised status**
R. hipposideros vespa Laurent, 1937 **new synonymy** (= *R. h. escalerae* Andersen, 1918)
R. megaphyllus klossi Andersen, 1918 **new synonymy** (= *R. m. robinsoni* Andersen, 1918)
R. montanus Goodwin, 1979 **new status**
R. pearsoni chinensis Andersen, 1905 **new synonymy** (= *R. p. pearsoni* Horsfield, 1851)
R. ruwenzorii Hill, 1942 **revised status**
R. ruwenzorii hilli Aellen, 1973 **new status**
R. shortridgei Andersen, 1918 **new status**
R. sinicus Andersen, 1905 **new status**
R. sinicus septentrionalis Sanborn, 1939 **new combination**
R. thomasi latifolius Sanborn, 1939 **new synonymy** (= *R. t. thomasi* Andersen, 1905)

4.3. KEY TO THE GROUPS AND SPECIES OF GENUS *RHINOLOPHUS*

When compiling the species accounts the basic idea was to use phenetic groups established by Bogdanowicz (1992) to make the determination and comparisons easier. I depart from this principle only where Bogdanowicz put question mark aside the particular species indicating uncertain affinities. The species not investigated by Bogdanowicz were grouped phenetically based on the most important taxonomic features. The groups follow one another in alphabetic order and the species within the given groups are also placed accordingly. It is important to note, that I do not regard this arrangement as phylogenetically reliable mirroring the evolutionary relationships within the family. The modern molecular phylogeny (Guillén *et al.*, 2003) resulted in a grouping sometimes basicly different from our opinion which relying fundamentally on classical taxonomical methods. Nevertheless, for practical reasons there is a justification of the grouping followed by us.

In the group keys, the characters given to the groups in a particular geographic area are not necessarily valid for all the existing species of the group, but for the species occuring within the area in question. Throughout the keys external and internal characters are used alternatively since due to the relatively uniform appearence of horseshoe bats it was not possible to provide a reliable determination key based exclusively on external or on craniodental features.

The limits of the zoogeographical regions mentioned in the key are according to Udvardy (1975) except the Indomalayan Region where I followed the delineation of Corbet and Hill (1992). Where - due to the lack of recognisable taxonomic features - the determination at least partly depends on geographical distribution and a more detailed distinction was necessary within the given region I used common geographical names to avoid the usage (and map presentation) of the several divisions and subdivisions.

1(10) Specimen from the Palaearctic Region
2(3) Connecting process forming a continuous arch (Fig. 44.1) - ***pearsoni*-group** (*R. pearsoni*)
3(2) Connecting process different
4(5) Connecting process high and bluntly rounded (Fig. 18.1) – ***ferrumequinum*-group** (*R. bocharicus, R. clivosus, R. ferrumequinum*)
5(4) Connecting process different
6(9) Connecting process pointed, triangular in profile (Fig. 7.1)
7(8) Sella wedge-shaped – ***landeri*-group** (*R. blasii*)
8(7) Sella parallel sided – ***euryale*-group**
9(6) Connecting process low, rounded, its tip pointed downwards (Fig. 29.1) – ***hipposideros*-group**
10(1) Specimen outside the Palaearctic Region
11(24) Specimen from the Afrotropical Region
12(15) Anterior upper premolar (P^2) fully external, small or missing
13(14) Sella hairy, connecting process low, forming a continuous arch (Fig. 26.1); general colour greyish – ***fumigatus*-group**
14(13) Sella naked, connecting process higher; general colour not greyish – ***ferrumequinum*-group** (*R. clivosus, R. darlingi, R. deckeni, R. hillorum, R. sakejiensis, R. silvestris*)
15(12) Anterior upper premolar (P^2) in toothrow or at most half-external
16(19) Sella widening at base; anterior median swellings bulbous
17(18) Connecting process very low, internarial septum expanded into a cup-like structure (Fig. 34.1) – ***maclaudi*-group**
18(17) Connecting process well developed, internarial septum not expanded (Fig. 1.1) – ***adami*-group**
19(16) Sella normal; anterior median swellings moderate
20(21) Connecting process low, rounded, its tip pointed downwards (Fig. 29.1); the anterior half of the zygomatic arch weak, almost parallel-sided (Fig. 29.2) – ***hipposideros*-group**
21(20) Connecting process well developed, its tip pointed more or less forward; the zygomata more robust, medio-laterally flattened
22(23) Connecting process triangular in profile (Fig. 30.1) – ***landeri*-group**
23(22) Tip of connecting process rounded – ***capensis*-group**
24(11) Specimen from the Indomalayan, Oceanian and Australian Regions
25(26) Sella with lateral projecting lappets at its base – ***trifoliatus*-group**
26(25) Sella lacking lateral basal lappets
27(32) Connecting process pointed
28(31) Anterior median swellings moderately low, protruding anteriorly (Fig. 8.2)
29(30) Sella parallel-sided – ***euryale*-group** (*R. mehelyi*)
30(29) Sella wedge-shaped – ***landeri*-group** (*R. blasii*)
31(28) Anterior median swellings higher, directing upwards (Figs 52.2, 61.1) – ***pusillus*-group**
32(27) Connecting process rounded, not pointed
33(34) Connecting process low, rounded, its tip pointed downwards (Fig. 29.1); the anterior half of the zygomatic arch weak, almost parallel-sided (Fig. 29.2) – ***hipposideros*-group**
34(33) Connecting process usually more developed, its tip pointed more or less forward; the zygomata more robust, medio-laterally flattened

35(38) Connecting process forming a continuous arch or obsolete (Figs 10.1, 44.1)
36(37) Lower lip with one mental groove, internarial region not expanded– ***pearsoni*-group**
37(36) Lower lip with three mental grooves, internarial region expanded – ***euryotis*-group**
38(35) Connecting process not forming a continuous arch (Figs 37.1, 47.1)
39(40) Sella long and wide; palatal bridge more than 1/3 length of maxillary toothrow (CM^3) – ***philippinensis*-group**
40(39) Sella shorter and narrower, palatal bridge less than 1/3 length of maxillary toothrow (CM^3)
41(42) Connecting process high and rounded (Fig. 18.1); anterior upper premolar (P^2) when present always minute and fully external to toothrow – ***ferrumequinum*-group** (*R. bocharicus, R. ferrumequinum*)
42(41) Connecting process lower and rounded (Fig. 36.1); anterior upper premolar (P^2) larger, usually in row or only slightly extruded, very rarely totally external
43(44) Lancet abruptly narrowed at centre, its lateral margins strongly concave – ***rouxii*-group**
44(43) Lancet triangular, lateral margins more or less straight – ***megaphyllus*-group**

Remark: the only known specimen of *R. mitratus* (with uncertain affinites) has not been examined. According to the description given by Sinha (1973) it comes to the *pearsoni*-group in the key given here.

Key to the *adami*-group
1(2) Tip of lancet longer, with convex sides - ***R. adami***
2(1) Tip of lancet shorter, with nearly straight sides - ***R. maendeleo***

Key to the *capensis*-group
1(2) Skull length over 20 mm, CM^3 length over 7.2 mm – ***R. capensis***
2(1) Skull and upper toothrow length shorter
3(4) The sides of lancet straight or nearly so – ***R. denti***
4(3) The sides of lancet concave
5(6) Sella relatively broad, CM^3 length 6.3-7.0 mm – ***R. simulator***
6(5) Sella narrow, CM^3 length 5.8-6.7 mm – ***R. swinnyi***

Key to the *euryale*-group
1(2) The sides of lancet straight – ***R. euryale***
2(1) Lancet abruptly narrowing to a linear tip – ***R. mehelyi***

Key to the *euryotis*-group
1(4) Base of lancet densely pilose
2(3) Hairs at base of lancet forming a dense, bristly sub-conical tuft – ***R. creaghi***
3(2) Hairs at base of lancet long, dispersed – ***R. canuti***
4(1) Base of lancet at most sparsely haired
5(8) Lancet thickened and folded to form a vertical fissure enclosing rear of connecting process
6(7) Width across anterior lateral swellings less than 5.5 mm, supraorbital ridges well developed (Fig. 11.3) – ***R. coelophyllus***

7(6) Width across anterior lateral swellings more than 5.5 mm, supraorbital ridges weaker – ***R. shameli***
8(5) Lancet not folded, rear of connecting process not enclosed
9(10) Horseshoe with two parallel swollen ridges extending to internarial region and terminating in a small, tooth-like median projection – ***R. euryotis***
10(9) Horsehoe with only a narrow groove reaching less than halfway to internarial region
11(12) Forearm 66-74 mm, skull length over 28 mm – ***R. rufus***
12(11) Forearm maximum 57 mm, skull length shorter than 26 mm
13(14) Forearm 52-57 mm, CM^3 length 9.5-10.5 mm – ***R. subrufus***
14(13) Forearm under 53 mm, CM^3 length less than 9.9 mm
15(16) Skull length over 22,5 mm, CM^3 length 9.3-9.9 mm – ***R. inops***
16(15) Skull length shorter than 22,5 mm, CM^3 length shorter than 9 mm – ***R. arcuatus***

Key to the *ferrumequinum*-group
1(6) Specimen from the Palaearctic Region
2(3) Forearm over 53 mm, skull length over 20.5 mm – ***R. ferrumequinum***
3(2) Forearm under 53 mm, skull length under 20.5 mm
4(5) Specimen from Central Asia – ***R. bocharicus***
5(4) Specimen from North Africa and Arabia – ***R. clivosus*** (part)
6(1) Specimen from the Afrotropical Region
7(12) Connecting process high, pointed or rounded (Fig. 18.1)
8(9) Skull length under 23 mm – ***R. clivosus*** (part)
9(8) Skull length over 23 mm
10(11) Connecting process pointed – ***R. sakejiensis***
11(10) Connecting process blunt – ***R. hillorum***
12(7) Connecting process lower, rounded (Fig. 20.1)
13(16) Horseshoe width more than 9 mm, skull length over 22 mm
14(15) Sides of lancet nearly straight – ***R. deckeni***
15(14) Sides of lancet more or less concave – ***R. silvestris***
16(13) Horseshoe width less than 9 mm, skull lenght under 21 mm – ***R. darlingi***

Key to the *fumigatus*-group
1(2) Forearm over 60.5 mm – ***R. hildebrandti***
2(1) Forearm under 60.5
3(4) Skull length over 24.5 mm – ***R. eloquens***
4(3) Skull length under 24.5 mm – ***R. fumigatus***

Key to the *hipposideros*-group
The group contains a single species only – ***R. hipposideros***

Key to the *landeri*-group
1(2) Sella wedge-shaped, connecting process narrow and pointed – ***R. blasii***
2(1) Sella broadly rounded off above, connecting process a broadly-based triangle
3(4) Forearm 49-54 mm, skull length over 21 mm – ***R. alcyone***
4(3) Forearm under 49 mm, skull length shorter than 21 mm
5(6) Skull length over 19.3 mm – ***R. guineensis***
6(5) Skull length under 19.3 mm – ***R. landeri***

Key to the *maclaudi*-group

1(2) Skull length over 26 mm, mastoid width less or subequal to the zygomatic width **– *R. maclaudi***

2(1) Skull length less than 25 mm, mastoid width exceeds the zygomatic width – ***R. ruwenzorii***

Key to the *megaphyllus*-group

1(2) Skull length over 21 mm – ***R. affinis***

2(1) Skull shorter than 21 mm

3(6) Anterior rostral swellings very large, inflated, strongly elevated

4(5) Posterior median swellings inflated, in profile median anterior swellings shallowly concave posteriorly; interorbital width over 2 mm – ***R. malayanus***

5(4) Posterior median swellings uninflated, in profile median anterior swellings very sharply concave posteriorly; interorbital width less than 2 mm - ***R. stheno***

6(3) Anterior rostral swellings moderate, less inflated

7(8) Facial part of skull elongate, the supraorbital crest combining at a point behind the centre of the orbital cavity – ***R. megaphyllus***

8(7) Facial part of skull shorter, the supraorbital crest combining at a point above or in front of the centre of the orbital cavity

9(10) Skull length 20.87 mm, CM^3 length 8.50 mm – ***R. nereis***

10(9) Skull length less than 19.5 mm, CM^3 length less than 7.5 mm

11(12) Noseleaf very small and narrow – ***R. virgo***

12(11) Noseleaf moderate, wider

13(14) Skull length usually over 18 mm, CM^3 length usually over 7 mm – ***R. borneensis***

14(13) Skull usually shorter than 18 mm, CM^3 length usually less than 7 mm – ***R. celebensis***

Key to the *pearsoni*-group

1(2) Forearm 47-56 mm; skull length under 24.5 mm, CM^3 length less than 10 mm – ***R. pearsoni***

2(1) Forearm 51.5-64 mm; skull length over 24.5 mm, CM^3 length over 10 mm – ***R. yunanensis***

Key to the *philippinensis*-group

1(2) Internarial region not expanded, its width not exceeding that of the sella – ***R. macrotis***

2(1) Internarial region expanded, much wider than sella

3(6) Lateral margins of internarial expansion passing beneath base of sella

4(5) Forearm more than 56 mm, CM^3 length over 8 mm – ***R. rex***

5(4) Forearm less than 57 mm, CM^3 length less than 8 mm – ***R. paradoxolophus***

6(3) Lateral margins of internarial expansion integral with margins of sella

7(8) Internarial expansion trapezoid with projecting lateral wings – ***R. marshalli***

8(7) Internarial expansion subcircular

9(10) Forearm 49-56 mm, skull length over 20 mm – ***R. philippinensis***

10(9) Forearm 43.5-46.0 mm, skull length 18.45 mm – ***R. montanus***

Key to the *pusillus*-group

1(2) Forearm over 46 mm; CM^3 length over 20 mm – ***R. acuminatus***
2(1) Forearm under 46 mm; CM^3 length less than 19 mm
3(4) Lancet strongly rounded off, its outline convex – ***R. convexus***
4(3) Sides of lancet concave or nearly straight
5(8) Lancet long, its tip spatulate, connecting process always a long, narrow horn
6(7) Upper canines slender, posterior palatal emargination wider than anterior palatal emargination – ***R. cognatus***
7(6) Upper canines massive, posterior palatal emargination narrower than anterior palatal emargination – ***R. imaizumii***
8(5) Lancet shorter, its tip narrower, connecting process shorter, usually more triangular
9(10) Upper canines long, wide-based, skull length over 17 mm; sagittal crest well developed in its full length – ***R. shortridgei***
10(9) Upper canines shorter, skull length usually under 17 mm; sagittal crest weaker posteriorly
11(12) Forearm 41-46 mm, CM^3 length under 6 mm – ***R. osgoodi***
12(11) Forearm usually shorter, if longer than 41 mm the CM^3 length over 6 mm
13(14) Rostrum narrower, M^3- M^3 width less than 5 mm – ***R. subbadius***
14(13) Rostrum wider, M^3- M^3 width over 5 mm
15(16) CM^3 length usually over 6 mm – ***R. lepidus***
16(15) CM^3 length usually under 6 mm
17(18) Specimen from Taiwan – ***R. monoceros***
18(19) Specimen outside of Taiwan
19(20) Specimen from Japan – ***R. cornutus***
20(19) Specimen outside of Japan – ***R. pusillus***

Key to the *rouxii*-group

1(2) Upper canines small, CM^3 length 6.82-7.67 mm – ***R. thomasi***
2(1) Upper canines longer and stronger
3(4) Specimen from Peninsular India and Sri Lanka; CM^3 length 7.88-9.24 mm – ***R. rouxii***
4(3) Specimen outside the above territories; CM^3 length 7.04-8.40 mm – ***R. sinicus***

Key to the *trifoliatus*-group

1(8) Forearm over 48 mm; skull length over 21 mm
2(3) Noseleaf and ears yellowish; skull length under 25 mm – ***R. trifoliatus***
3(2) Noseleaf and ears dark brown or blackish; skull length usually over 25 mm
4(5) Skull length usually over 28 mm, CM^3 length over 10.5 mm – ***R. luctus***
5(4) Skull length under 28 mm, CM^3 length usually under 10.5 mm
6(7) Specimen from South India and Sri Lanka – ***R. beddomei***
7(6) Specimen from Taiwan – ***R. formosae***
8(1) Forearm under 48 mm, skull length less than 21 mm – ***R. sedulus***

4.4. SPECIES ACCOUNTS

ADAMI-GROUP

***Rhinolophus adami* Aellen and Brosset, 1968**
Adam's horseshoe bat
R. adami Aellen and Brosset, 1968 (Kouilou, Congo Republic)

Recognised subspecies: All specimens referred to the nominate form.

External characters: This is a medium sized *Rhinolophus*. The ears are large, (25-26 mm in height); they are brown in colour, slightly darker at the tips. The noseleaf is also large, almost covering the muzzle, with a breadth of 8.5-9 mm. There is a well defined notch on the anterior border of the horseshoe. The sella is large and broad, slightly narrower at the rounded tip and constricted in the middle. The connecting process forms a more or less continuous arch. The lancet is long, its outline is convex or nearly so, with its tip rounded. The lower lip is with three grooves. The tail is very long, 25.0-28.0 mm. In the wings the third metacarpal (32.0-33.5 mm) is equal to, or slightly exceeds 90% of the length of the fourth and fifth metacarpal which are subequal in length (34.5-37.0 mm). The pelage colour is light to darker brown on the head and back. It is usually grey-brown on the belly although in one individual it was whitish on the lower abdomen.

Cranial and dental characters: The skull is slender, the mastoid width greatly exceeds the zygomatic breadth. The anterior median swellings are well developed, the posterior swellings are reduced. The sagittal crest is weak, the frontal depression is long and moderately deep. The supraorbital ridges are well defined. The palatal bridge is long, 42-44 % of the upper toothrow length (CM^3).
The upper canines are moderately developed. The first upper premolar is large and stands in the toothrow, clearly separating the canine (C^1) from the second premolar (P^4). It slightly exceeds the height of the cingulum of C^1. The lower canine is slender. The second lower premolar (P_3) is slightly displaced externally from the toothrow. It separates the first premolar (P_2) from the third (P_4). It is less than half the height of P_4.

Bacular morphology: The basal cone of the heavily built bone is short, with shallow ventral and dorsal incisions. The shaft is thick and dorsoventrally flattened in its distal half.

Similar species: *R. adami* differs from it closest relative *R. maendeleo* by the shape of lancet (longer in *R. adami* with convex sides) and by its larger measurements of palatal bridge length (2.99-3.23 mm), interorbital width (2.64-2.81 mm), and mastoid width (9.47-9.88 mm). Another externally similar horseshoe bat is *R. simulator alticolus* which is smaller in cranial measurements and also differs by its less globular anterior median swellings. The ratio of skull length to zygomatic breadth is 2.14-2.24:1 in the case of *R. adami* and 2.00-2.13:1 in the case of *R. s. alticolus*. *R. s. simulator* beside its generally smaller measurements, differs by its smaller noseleaf and hastate lancet.
The other cranially similar sized species either have a very small (or missing), fully extruded anterior upper and middle lower premolars (*R. clivosus*, *R. darlingi*) or have a

shorter rostrum and frontal depression and much smaller nasal inflation (*R. landeri*, *R. guineensis*).

Taxonomic remarks: Aellen and Brosset (1968) considered *R. adami* to be most closely related to *R. simulator* and *R. bembanicus* (subsequently included in *R. simulator*). It was placed by them in a sub-group of the *ferrumequinum*-group along with *capensis*, *alticolus*, *denti*, *swinnyi*, *simulator* and *bembanicus*. This view was followed by Koopman (1994). Previously, Hayman and Hill (1971) suggested that *adami* might be conspecific with *simulator*. However, a range of external and craniodental features (large sella, slender skull and long palatal bridge) suggest a different clade within the African Rhinolophids. This was named the *adami*-group by Kock *et al*. (2000).

Fig. 1.1. Lateral and frontal views of noseleaf of *R. adami* (MNHN 1968.408 - holotype) from Congo. Scale = 3 mm.

Fig. 1.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. adami* (MHN 1129.84 - paratype) from Congo. Scale = 3 mm.

Table 1. ***R. adami***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		46.0	50.0		
SL	20.09	19.77	20.60	0.30	7
CM^3L	7.34	7.13	7.55	0.14	7
ZW	9.17	8.96	9.36	0.16	6
MW	9.76	9.47	9.88	0.14	7
ML	13.19	12.96	13.33	0.14	6
CM_3L	7.64	7.42	7.87	0.16	6

***Rhinolophus maendeleo* Kock, Csorba and Howell, 2000**
Tanzanian horseshoe bat
Rhinolophus maendeleo Kock, Csorba and Howell, 2000 (Amboni Cave Forest, 05º05'S, 39º02'S, 0-80 m, Mkulumuzi River Gorge, 2.5 km W of Tanga, Tanga Distr., NE Tanzania)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium size species of horseshoe bats. The ears are large, 24.0-24.5 mm in height. The horseshoe is relatively wide (8.2-8.4 mm), almost covering the muzzle. The sella is naked, wide at its base rising from a rather well developed narial cup and constricted in the middle. The connecting process is forming a continuous arch and its basal part is almost parallel to the sella. The tip of lancet is nearly straight-sided. Three mental grooves are in lower lip. The tail is 23.0-25.8 mm in length. In the wings the third metacarpal is shortened (32.1-34.6 mm), the fourth is the longest (36.1-38.1

mm), and the fifth metacarpal is medium long, 35.1-36.2 mm. The pelage is dorsally brownish, ventrally beige turning to whitish on lower abdomen; there is a darker brown collar around the lower neck and upper chest.

Cranial and dental characters: The skull is slender with a long rostral part and a well marked depression in front of the occipital region. The mastoid width equals or slightly exceeding zygomatic width. The anterior median swellings are bulbous, wide and long; the posterior swellings are less developed. The sagittal crest is weak; the frontal depression is moderately deep, flanked by strong supraorbital ridges. The palatal bridge is long 37-39% of the CM^3 length.
The upper canine is moderately developed, but considerably exceeding P^4 in height. The first upper premolar is medium sized, in toothrow and widely separating the upper canine and the posterior premolar. The lower middle premolar small and partly extruded but the adjoining premolars (P_2 and P_4) are not in contact.

Bacular morphology: The dorsal part of the basal cone is deeply incised and projecting proximally forming two long wings; the ventral incision is less deep. The distal part of the bone strongly flattened dorsoventrally.

Similar species: *R. maendeleo* externally can be distinguished from the closely related *R. adami* by the shape of lancet, which is longer in *R. adami* with convex sides; the large ears, wide sella, straight sided lancet, three mental grooves and the forearm length separate *R. maendeleo* from the other African species of the genus.
Cranially, *R. maendeleo* is further characterised by the peculiar open foramen infraorbitale where the bony bar is missing (although, this feature is rarely occur in other species as well). *R. adami* is greater in several measurements, and the interpterygoid groove is distinctly constricted near the proximal end (the walls of the groove run parallel in *R. maendeleo*). *R. simulator* is smaller than the recently known two specimens of *R. maendeleo*, but also differs by its less inflated nasal swellings and shorter rostrum. The similar sized *R. darlingi* has very small (sometimes missing) and fully extruded anterior upper and middle lower premolars.

Taxonomic remarks: This recently described species is showing close affinities to *R. adami* only. The two species are forming the newly established *adami*-group (Kock *et al*. 2000) which characterized by features regarded primitive by Andersen (1905a) (large ears, wide nasal appendages, long palate, narrow skull, P^2 in toothrow). These features in the Indomalayan Region are typical for the species of the *philippinensis*-group, and in the Ethiopian Region for the members of the *maclaudi*-group.

Fig. 2.1. Lateral and frontal views of noseleaf of *R. maendeleo* (SMF 79.643 - holotype) from Tanzania. Scale = 3 mm.

Fig. 2.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. maendeleo* (SMF 79.643 - holotype) fromTanzania. Scale = 3 mm.

Table 2. ***R. maendeleo***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		48.2	49.1		
SL	20.05	20.03	20.07	0.03	2
CM^3L	7.23	7.20	7.25	0.04	2
ZW	9.36	9.35	9.37	0.01	2
MW	9.41	9.39	9.42	0.02	2
ML		13.08			1
CM_3L	7.53	7.43	7.62	0.13	2

CAPENSIS-GROUP

***Rhinolophus capensis* Lichtenstein, 1823**
Cape horseshoe bat
R. capensis Lichtenstein, 1823 (Cape of Good Hope)
R. auritus Sundevall, 1860 (Belvedere, near Knysna, Cape of Good Hope)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized species of the genus. The ears are medium, 21.0-25.0 mm in height. The horseshoe is relatively narrow, does not cover the whole muzzle; a rudimentary secondary horseshoe may present. The sella is with more or less parallel sides, rarely slightly constricted at the middle. The connecting process is high, rounded, covered with long, sparse hairs; the lancet is distinctly hastate. The lateral mental grooves of the lower lip are obliterated. The tail length is 20.0-32.0 mm. In the wings, the third metacarpal strongly shortened (32.2-35.0 mm), the fourth and fifth metacarpals are subequal, 34.0-38.0 mm in length. The upperparts are darker or paler brown in colour, the individual hairs are cream coloured at their bases; underparts are light fawn-grey.

Cranial and dental characters: The skull is strong, the zygomatic width is always exceeds the mastoid width. The anterior median swellings are moderately developed, the posterior compartments are also well defined. The sagittal crest is moderate. The frontal depression is shallow, bordered with weak, ill-defined supraorbital crests. The palatal bridge is medium, 33-39% of upper toothrow length. The upper canine is massive, widely based, but relatively short. The first upper premolar is medium or small, usually slightly displaced, sometimes almost fully external but the adjoining teeth (C^1 and P^4) are not in contact (in typical cases widely separated). P_3 is small, fully or partly crowded out of row, P_2 is barely half the height of P_4.

Similar species: Within the distribution area of *R. capensis* the only taxon with similar external appearence (high and rounded connecting process) and size is *R. clivosus augur*. Based on large series of both species the size measurements are overlapping (albeit with greater mean values in the case of *R. clivosus*), but the more swollen anterior median nasal swellings resulted a distinctly concave rostral profil in *R. capensis*,

contrary to the almost horizontal rostral line of *R. clivosus*. In the dentition, the upper canine is not in contact with the posterior premolar (P^4) in *R. capensis*. The shape of sella (constricted at the middle in *R. clivosus* but practically parallel sided in *R. capensis*) another distinguishing feature, although much more individual variation can be expected here.
R. simulator is distinguishable from *R. capensis* by its smaller size and more prominent anterior median swellings. In the dental measurements of *R. capensis* there is a slight overlap with the larger *R. fumigatus*, but this latter species has a very small (frequently missing) upper premolar.

Taxonomic remarks: Although Andersen (1904a) concluded that *R. simulator* "in fact, has nothing to do with *Rh. capensis*", Bogdanowicz (1992) placed the two species in the same phenetic group. However, the wide sella and more pronounced nasal swellings of *R. simulator* separate the species from the other members of the group and linked it to a some extent to the *adami*-group.
Andersen (1904b) analysed the description of *auritus*, and found it indistinguishable from *R. capensis*. He also evidenced that Sundevall had for comparison with his *auritus* two specimens of *R. augur*, instead of *R. capensis* as Sundevall thought. Andersen (1904a, 1904b) gave detailed comparisons of *R. capensis* and *R. augur* (= *R. clivosus*) and listed the differences (external and cranial measurements, nasal swelling characteristics) between the two.
The position of the upper anterior premolar is given by most of the authors as in the toothrow. In contrast, Andersen (1905a) characterised the species with "P^2 is generally external but still a quite distinct interspace between the canine and P_4 indicating its former place". The investigation of series of the species from different localities supports Andersen's view. Neverthless, the shape of connecting process and the position of the small upper premolar raise the possibility of a closer relationship between *R. capensis* and *ferrumequinum*-group.

Fig. 3.1. Lateral and frontal views of noseleaf of *R. capensis* (BMNH 75.8.9.9) from South Africa. Scale = 3 mm.

Fig. 3.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. capensis* (HZM 3.4735) from South Africa. Scale = 3 mm.

Table 3. ***R. capensis***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		45.5	52.0		
SL	20.48	20.01	21.07	0.26	20
CM^3L	7.47	7.20	7.84	0.14	21
ZW	10.27	10.00	10.60	0.17	19
MW	9.77	9.60	10.02	0.12	18
ML	13.46	13.11	14.12	0.24	19
CM_3L	7.98	7.83	8.26	0.11	21

***Rhinolophus denti* Thomas, 1904**
Dent's horseshoe bat
R. denti Thomas, 1904 (Kuruman, Bechuanaland)
R. d. knorri Eisentraut, 1960 (Nyembaro, Salung-Plateau, 12 km W of Kolenté)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *denti* from Namibia and Zimbabwe to the Cape Province; *knorri* in Guinea, Ivory Coast, Ghana.

External characters: A small species of its genus. The ears are medium, 14.0-21.0 mm in height. The horseshoe is large covering most of the muzzle, its anterior edge sharply notched in the centre. The sella is almost parallel sided or slightly narrowing towards the tip, only very slightly constricted in the middle; its summit is broadly rounded off. The connecting process is high and rounded. The lancet is relatively short, evenly converging upwards, covered with fine fur. The lower lip is with three mental grooves. The tail is 17.0-24.0 mm in length. In the wings, the third metacarpal is short (26.9-32.0 mm), the fourth is subequal to, or slightly longer (28.3-34.0 mm) than the fifth metacarpal (27.5-32.0 mm). The colour of the upperparts is pale grey, pale brown or pale cream; the individual hairs are very soft and broadly white at their bases, the underparts are off-white. The colours are usually darker in *R. d. knorri*.

Cranial and dental characters: The skull is delicately built, the zygomatic width is subequal to or only slightly exceeds the mastoid width. The anterior median swellings are medium developed, the posterior inflation is well marked; the rostral profile is definitely but not sharply concave. The crista sagittalis is usually weak, the frontal depression is shallow bordered with less pronounced supraorbital ridges. The palatal bridge is 30-35% of the upper toothrow length.
The upper canine is moderate, the anterior upper premolar small or very small, lies in the toothrow or only half-way extruded. The upper canine and the posterior premolar are close to each other but not in contact. In the lower jaw the middle premolar is very small to minute, quite external to the toothrow, the cingula of the neighbouring teeth are touching each other.

Similar species: On average the smallest species of horseshoe bats in the Ethiopian Region. Both externally and cranially the most similar species is *R. swinnyi*, which has a more uniformly coloured fur on the dorsal side and the sides of the lancet are concave; the two species are indistinguishable by cranial characters. *R. landeri* overlaps in forearm length, but has a triangular, more pointed connecting process and strongly concave lancet.
By cranial measurements the smallest specimens of *R. blasii* and *R. landeri* are similar to *R. denti*. *R. blasii* is separable by its shorter upper canine and the anteriorly protruding median swellings which are longer than wide; *R. landeri* looks alike but its zygomatic width is always exceeds the mastoid width.

Taxonomic remarks: Hill and Carter (1941) suggested that *R. angolensis* is the same as *R. denti* over which it would have priority; nevertheless, *angolensis* was subsequently synonymised with *R. landeri* (Hayman and Hill 1971).
The possibility that *R. swinnyi* is conspecific with *R. denti* is frequently considered but mentioned as such only by Shortridge (1934) who treated *swinnyi* as synonym of *R.*

denti and ranking *piriensis* as subspecies of the latter. Rautenbach (1986) evidenced that *R. denti* and *R. swinnyi* are karyologically identical in all respects and consequently this parameter does not offer any clues to the specific distinctness of these two taxa (see also comments under *R. swinnyi*).
R. d. knorri is on average slightly smaller than *R. d. denti* (especially in the length of ears and tibia), but with darker colours and heavier dentition (Eisentraut 1960). In spite of this view, Rosevear (1965) treated the average differences „so slight that a new subspecies scarcely seems justified on the existing evidence". Meester *et al*. (1986) retained *knorri* as separate subspecies, if only on geographic ground.

Fig. 4.1. Lateral and frontal views of noseleaf of *R. denti* (USNM 322840) from Botswana. Scale = 3 mm.

Fig. 4.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. denti* (BMNH 4.4.8.2 - holotype) from Botswana. Scale = 3 mm.

Table 4. ***R. denti***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		37.0	44.0		
SL	16.93	16.40	17.34	0.29	23
CM^3L	6.03	5.83	6.28	0.12	25
ZW	8.41	7.66	8.85	0.31	21
MW	8.36	7.82	8.61	0.20	18
ML	10.94	10.61	11.28	0.21	25
CM_3L	6.39	6.05	6.59	0.14	22

***Rhinolophus simulator* Andersen, 1904**
Bushveld horseshoe bat
R. simulator Andersen, 1904 (Mazoe, Mashonaland, Rhodesia)
R. bembanicus Senna, 1914 (Lake Bengueolo, Rhodesia)
R. alcyone alticolus Sanborn, 1936 (Mt. Cameroon, Cameroon Mandate, 5800 ft)

Recognised subspecies: After Koopman (1994) the following subspecies are recognised - *alticolus* in Guinea, Liberia, Nigeria and Cameroon; *simulator* in eastern Africa from Ethiopia to Natal.

External characters: A medium sized horseshoe bat. The ears are large, 18.0-24.0 mm in height. The horseshoe is 7.0-8.3 mm wide, a secondary leaflet is present. The sella is high and relatively broad (especially in *R. s. alticolus*); its lateral margins are subparallel in their upper half, the summit is broadly rounded off. The connecting process is rounded, well-haired. The margins of lancet usually abruptly narrowed, the tip of lancet behind constriction is with nearly parallel sides; the margins of the lancet are less concave and sometimes almost straight in *R. s. alticolus*. The lower lip is with three mental grooves but the lateral ones rarely ill-defined. The tail is 18.8-30.0 mm in length.

In the wings, the third metacarpal is the shortest (29.0-33.0 mm), the fourth (31.5-35.0 mm) is slightly longer than, or subequal to the fifth (32.0-35.3 mm). The upper parts are dark brown in colour, the individual hairs are lighter brown towards their base; under parts are greyish-white, tinged brown on the flanks.

Cranial and dental characters: The skull is moderately built, the zygomatic width is less than or sometimes subequal to the mastoid with. The anterior median swellings are not especially broad but prominent, the posterior compartments are medium; the facial portion of the skull is distinctly concave. The crista sagittalis is weak, the frontal depression is only moderately deep but well defined. The cristae supraorbitales are prominent but the ridges are not always sharp. The palatal bridge is usually 29-34% (in *R. s. alticolus* up to 38%) of the upper toothrow length.
The upper canine is moderately developed. The small or medium sized anterior upper premolar is in the toothrow and has a minute cusp; the upper canine and P^4 are distinctly separated from each other. The cusp of P^4 is reaching more than half the height of C^1. The middle lower premolar (P_3) is small or minute and squeezed out externally to the toothrow or rarely fully missing.

Similar species: *R. simulator* differs from *R. capensis* by its lower (but similarly broadly rounded) connecting process and relatively wider sella. Cranially, *R. simulator* is smaller and has more prominent anterior nasal swellings than that of *R. capensis*. The anterior median swellings of *R. blasii* are more elongated, extending anteriorly beyond the anterior border of the lateral swellings; *R. blasii* is further characterised by its shallow or very shallow frontal depression. *R. landeri* is also similar cranially, but *R. simulator* separable from this species by its longer rostrum, more elongated, narrower and deeper frontal depression and more globular anterior median swellings. In the overlapping range of the measurements the separation of *R. swinnyi* and *R. simulator* is sometimes difficult, but *R. simulator* has a generally larger nasal foliation (see the horseshoe measurements) and more inflated anterior nasal swellings. The western African subspecies *R. s. alticolus* has a similar noseleaf than that of *R. adami*, but smaller in cranial measurements and its anterior median swellings are not so inflated. *R. darlingi* is separable on the base of its broad rostrum and reduced fully external anterior upper premolar.

Taxonomic remarks: The taxonomic position of *alticolus* is questionable. It was originally described as a small subspecies of *R. alcyone*, and was compared only with that species. Allen (1939) and Rosevear (1953) also listed it as *R. alcyone alticolus*. Eisentraut (1956) has shown that it is sympatric with *alcyone* but is clearly distinguishable from both that species and *R. landeri* by the shape of the connecting process. Eisentraut found no axillary sac and tuft in any of over a hundred males examined, wich is obvious because this feature never occurs outside the *landeri*-group. Since the taxon evidently differs from *R. alcyone* at specific level, it was long considered as full species (Eisentraut 1963, Rosevear 1965, Hayman and Hill 1971, Hill 1968). In the key given by Hayman and Hill (op. cit.) *alticolus* is separated from *simulator* by the relative length ("notably shortened" against "not notably shortened") of the first phalanx and the metacarpal of fourth finger, which is a doubtful taxonomic character. The possibility, that *alticolus* is belongs to *R. simulator* was first suggested by Koopman (1975) and finally accepted by subsequent authors (e.g. Grubb *et al*. 1998, Kock *et al.* 2000). Although *alticolus* is cranially almost indistinguishable from

simulator, the sella of the former is definitely wider and the connecting process is less pronounced; as a whole, the shape of noseleaf connected *alticolus* to the *adami*-group to some extent. Koopman *et al*. (1995) measured specimens from Liberia and Cameroon and found that *R. s. alticolus* tends to be somewhat larger, at least as shown by the length of the maxillary toothrow. Based on the different nasal foliation and on average longer palatal bridge there is possibility that *alticolus* will proved to be a distinct species.
Allen (1939) listed as separate species, but Ellerman *et al* (1953) and Hayman and Hill (1971) provisionally included *bembanicus* as a synonym of *simulator*. Ansell (1978) noted, that the type of *bembanicus* was never re-examined and directly compared with *simulator*. Since the type no longer exists, its status is indeterminable though it may continue to be regarded as a probable synonym of *simulator*.

Fig. 5.1. Lateral and frontal views of noseleaf of *R. simulator* (BMNH 2.2.7.10 - holotype) from Zimbabwe. Scale = 3 mm.

Fig. 5.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. simulator* (BMNH 2.2.7.10 - holotype) from Zimbabwe. Scale = 3 mm.

Table 5. ***R. simulator***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		40.0	49.0		
SL	18.44	17.27	19.25	0.40	60
CM^3L	6.63	6.31	7.08	0.17	62
ZW	8.92	8.51	9.32	0.24	57
MW	9.00	8.26	9.33	0.19	56
ML	11.99	11.32	12.69	0.26	60
CM_3L	7.01	6.66	7.40	0.17	62

***Rhinolophus swinnyi* Gough, 1908**
Swinny's horseshoe bat
R. swinnyi Gough, 1908 (Ngqeleni, District W Pondoland)
R. s. piriensis Hewitt, 1913 (Pirie, near King William's Town, eastern Cape Colony)
R. s. rhodesiae Roberts, 1946 (Bezwe River, Wanetsi River, Southern Rhodesia)

Recognised subspecies: According to Koopman (1994) all specimens referred to the nominate form.

External characters: A small species of its genus. The ears are pale grey or pale brown, small or medium long in relation to the head; 15.0-20.1 mm in height. The horseshoe does not cover the muzzle, 6.8-7.4 mm wide. The sella is slightly constricted at the middle; the connecting process is rounded, sparsely haired. The lancet is with concave sides, its tip is relatively elongated. The lower lip is with three mental grooves but the lateral ones are frequently obliterated. The tail is 18.0-29.0 mm in length. In the wings

the third metacarpal is the shortest (27.8-31.8 mm), the fourth is subequal to, or sometimes slightly longer (30.5-35.4 mm) than the fifth (30.0-34.7). The upper parts vary in colour from pale drab grey to pale brown, the white or creamy bases of individual hairs showing through to accentuate the general pale colour; under parts off-white or cream, tinged brown or grey. A bright orange phase is known, and it does appear that the orange phase has become fixed in the topotypical population of *rhodesiae*.

Cranial and dental characters: The skull is delicate, the zygomatic and mastoid width are subequal. The anterior median swellings are semicircular in outline, moderately developed; the posterior ones are also well inflated. The sagittal crest is less developed or medium, the frontal depression is shallow, sometimes almost flat. The supraorbital crests are weak. The palatal bridge is 30-34% of the maxillary toothrow length.
The upper canine is widely based; the anterior upper premolar medium or small sized and lies in the toothrow or slightly extruded but always separating the canine and the second premolar. The middle lower premolar minute and external. The first lower premolar (P_2) is barely half the height of the last premolar (P_4); these teeth are close to or in most cases contacting each other.

Similar species: *R. denti* is said to have individual hairs broadly white at their bases and an almost straight sided lancet; but the two species cranially indistinguishable. *R. simulator* is also closely related and the separation of the larger specimens of *R. swinnyi* from this species may be problematic; but *R. simulator* has broader horseshoe and sella and more prominent anterior swellings. *R. landeri* is externally characterised by its broadly triangular, pointed connecting process and cranially by the broad zygomata which is exceeds the mastoid breadth by at least 0.3-0.4 mm. *R. capensis* is similar in appearence but larger in every (external and craniodental) respects.

Taxonomic remarks: Hewitt (1913) suggested that *swinnyi* might represent a smaller eastern taxon of *R. capensis*. Since that time more specimens of both taxa have been collected and the mensural data have failed to support Hewitt's idea (Kock and Howell 1988).
Already Roberts (1914) indicated that *swinnyi* is possibly a synonym or subspecies of *R. denti*. Koopman (1966) and Hayman and Hill (1971) again suggested that the two taxa are very closely related and possibly conspecific, but the problem remained unresolved and all subsequent authors listed them as separate species. Nevertheless, the external differences between the two are very small and Kock and Howell (1988) found no skull character to specifically differentiate between *R. swinnyi* and *R. denti*. Bronner (1990) reported a specimen from Natal identified on the base of its noseleaf characters and standard karyotype, but the fur was lightish basally as in *R. denti* instead of unicoloured as in *R: swinnyi*. As he stated, the two species are so similar in size, morphology and echolocation characteristics that only subspecific distinction between them may be warranted (see also comments under *R. denti*).
Roberts (1951) recognised three subspecies of *R swinnyi* (*swinnyi*, *piriensis* and *rhodesiae*) which were synonymised by Ellerman *et al*. (1953). Koopman (1966) compared specimens of *rhodesiae* and *piriensis* obtained from close to the type localities. He found that the size characters mentioned by Roberts certainly did not hold and the two forms can only be maintained on colour but did not take a stand to assess the alleged subspecies. Ansell (1967) still maintained *rhodesiae* as valid subspecies on

the base of its smaller skull and longer tail, and also noted that too much importance should not be attached to the colour. Upon subsequent examination by Ansell (1969, 1978) no clearly separating characters could be demonstrated between the nominate subspecies and *rhodesiae*. Later on *R. swinnyi* was treated as monotypic by Hayman and Hill (1971), Meester *et al*. (1986) and Koopman (1994).

Fig. 6.1. Lateral and frontal views of noseleaf of *R. swinnyi* (BMNH 95.264) from Malawi. Scale = 3 mm.

Fig. 6.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. swinnyi* (BMNH 64.478) from Zimbabwe. Scale = 3 mm.

Table 6. ***R. swinnyi***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		40.0	44.5		
SL	17.43	17.00	18.18	0.35	15
CM^3L	6.19	5.87	6.73	0.19	20
ZW	8.62	8.25	9.04	0.25	16
MW	8.57	8.19	8.91	0.22	16
ML	11.18	10.84	11.55	0.22	18
CM_3L	6.58	6.31	7.02	0.16	18

EURYALE-GROUP

***Rhinolophus euryale* Blasius, 1853**
Mediterranean horseshoe bat
R. euryale Blasius, 1853 (Milan, Italy)
?R. algirus Loche, 1867 (Algeria; unidentifiable name)
R. meridionalis Andersen and Matschie, 1904 (Algeria)
R. barbarus Andersen and Matschie, 1904 (Tangiers, Morocco)
R. judaicus Andersen and Matschie, 1904 (Cave of Adullam, Jerusalem, Palestine)
R. toscanus Andersen and Matschie, 1904 (Caverna di Parignana, Mt. Pisani, Italy)
R. atlanticus Andersen and Matschie, 1904 (St. Paterne, Indre-et-Loire, France)
R. cabrerae Andersen and Matschie, 1904 (Alcalá de Henares, Madrid, Spain)
R. euryale nordmanni Satunin, 1912 (Pavlovsk, Sukhum, Transcaucasia)

Recognised subspecies: The following subspecies are recognised - *euryale* in northwestern Africa, southern Europe east to Turkmenia and Iran, Mediterranean Islands; *judaicus* from Syria and south Iraq to Israel.

External characters: A medium sized horseshoe bat. The ears are medium or large, their length is 18.5-23.0 mm. The horseshoe does not cover the muzzle, its breadth is 5.4-6.7 mm. The sella is almost parallel sided, the summit is broadly rounded. The connecting process is elevated into an acutely pointed horn-shaped projection, the

borders of which are nearly straight. The sides of the lancet is gradually narrowed to a blunt tip. The lower lip is with three grooves. The tail is 16.2-31.0 mm in length. In the wings the third metacarpal is notably shortened (32.0-34.8 mm), the fourth (34.5-37.0 mm) is usually shorter than or sometimes subequal to the fifth (35.2-38.8 mm). The pelage is soft and dense; the colour shows a comparable range of individual variation. Some individual are more greyish others a warm fulvous brown. The underparts are lighter, dull drab, brownish or greyish according to the tint of the back.

Cranial and dental characters: The skull is lightly built, the rostrum is narrow. The ratio of the zygomatic and mastoid width is variable; in most cases they are subequal, but sometimes the zygomatic breadth is either greater or smaller than the mastoid breadth. The anterior median swellings are small, but the posterior ones also less inflated so the rostral profile is definitely concave. The sagittal crest is hardly developed at all. The frontal depression is shallow, the supraorbital crests are weak but visible. The palatal bridge is 31-35% of the maxillary toothrow.
The upper canine is less robust and slender. The small upper premolar (P^2) is situated just in the toothrow, compressed in a narrow gap between the canine and the second premolar (P_4). The small lower premolar (P_3) occupies a position in the outer part of the toothrow, but there is a distinct gap between P_2 and P_4. The first lower premolar is much smaller than the third premolar (P_4).

Bacular morphology: The base of the basal cone is approximately a circle. There are knobs on its outer surface, mainly on the two sides of the ventral incision. The first half of the shaft is cylindrical becoming dorsoventrally flattened at approximately the middle of the bone. The shaft bends only sligthly down.

Similar species: As compared to *R. blasii*, *R. euryale* externally is characterised by its widely rounded sella. Cranially, in *R. euryale*, there is a marked contrast between the crown areas of the anterior and posterior lower premolars, P_2 is about half the area of P_4; while in *R. blasii*, P_2 is almost as large as P_4. The braincase is more globular in *R. euryale*, without the marked depression at the occipital region of *R. blasii*.
Externally *R. euryale* is distinguished from *R. mehelyi* by the shape of the lancet, which is essentially triangular in shape, whilst in *R. mehelyi* there is marked concavity in the sides, and the distal half of it is narrow. The connecting process of *R. euryale* also difffers being more pointed and narrower than that of *R. mehelyi*. The two species is almost indistingushable by craniodental characters.

Taxonomic remarks: *R. euryale* and *R. mehelyi* have long been confused. DeBlase (1972) summarised the various criteria used to distinguish the two species (forearm length, ratio of phalanges of the fourth digit, horseshoe shape and size, toothrow and skull lenghts) and found that out of these lancet shape and zygomatic width are the most reliable characters. However, according to our dataset, there is a certain overlap in all the cranial and dental measurements (including the zygomatic breadth) investigated. Felten *et al*. (1977) found the scatterplots of skull indices and probably the structure of humeral epiphyses of use to tell apart the two species.
R. blasii is another species having been frequently mis-identified as *R. euryale*. Paunovic and Stamenkovic (1998) conducted multivariate analysis based on three wing-shape (phalanges of fourth finger and forearm) and two cranial characters

(condylocanine length and zygomatic breadth), and found powerful discrimination among the two taxa.
The several species described by Andersen and Matschie (1904) are frequently cited as *Euryalus* species, but the authors introduced *Euryalus* as a proposed subgeneric name; therefore these species are mentioned here under the name *Rhinolophus*. Koopman (1994) recognised two of them namely *meridionalis* and *barbarus* in northwestern Africa as valid subspecies but without distinction in their distribution. Corbet (1978) is of the opinion that all European and North African populations belong to the nominate subspecies and Kowalski and Rzebik-Kowalska (1991) also found the distinction between these subspecies very doubtful.
Harrison (1964) considered Egyptian material examined by him to be indistinguishable from specimens of *judaicus* (from Israel) and the latter he thought to be hardly separable from typical *euryale*; Harrison and Bates (1991) provisionally referred specimens from Arabia to *R. e. judaicus* but questioned again the validity of this subspecies.

Fig. 7.1. Lateral and frontal views of noseleaf of *R. euryale* (HNHM 66.247.5.) from Croatia. Scale = 3 mm.

Fig. 7.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. euryale* (MNHN 1932.4035) from Italy.

Table 7. ***R. euryale***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		42.5	51.0		
SL	18.73	17.71	19.75	0.40	43
CM^3L	6.39	5.90	7.02	0.18	43
ZW	9.52	9.02	10.52	0.29	43
MW	9.51	9.09	9.87	0.20	41
ML	11.91	11.42	13.04	0.30	42
CM_3L	6.80	6.36	7.50	0.17	42

***Rhinolophus mehelyi* Matschie, 1901**
Mehely's horseshoe bat
R. mehelyi Matschie, 1901 (Bucharest, Rumania)
R. carpetanus Cabrera, 1904 (Madrid, Spain)
R. euryale tuneti Deleuil and Labbe, 1955 (El Haouaria, Cap Bon, Tunisia)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *mehelyi* in Europe and western Asia; *tuneti* in northern Africa.

External characters: A relatively large species. The ears are medium, 18.0-23.0 mm in height. The horseshoe is narrow, its width is 4.9-6.7 mm. The sella is practically parallel sided and widely rounded at the top. The connecting process is an elongated triangle with more or less pointed tip. The lancet is abruptly narrowing to a linear tip. The tail is 16.2-37.0 mm. In the wings, beside the shortest third metacarpal (34.0-37.5 mm) the

fourth (35.2-39.8 mm) and fifth (35.8-40.7 mm) are subequal or the fourth is slightly shorter. The dorsal pelage is light brown, the individual hairs are mostly tipped with darker brown, except the unicoloured hairs around the neck and along the flanks, which giving a lighter impression. There are well marked dark brownish patches under each eye. The ventral pelage is more lighter greyish brown or even purely white.

Cranial and dental characters: The skull is moderately built, the zygomatic width well exceeds the mastoid width. The anterior median swellings are relatively low, but protruding anteriorly; the posterior swellings are also less inflated. The crista sagittalis is medium, the frontal depression is shallow or almost flat; the supraorbital crests are ill defined. The palatal bridge 32-33% of the maxillary toothrow (CM^3) length.
The upper canine is strong, moderately long. The small upper premolar is more or less out of the row but the upper canine and the posterior upper premolar is separated by a distinct (sometimes narrow) gap. In the lower jaw, the middle lower premolar (P_3) is minute or even almost invisible, the crown area of the first premolar (P_2) is much smaller than that of the last premolar (P_4); these teeth are touching each other.

Similar species: *R. euryale* and *R. mehely* is frequently confused, and indeed the only definite distinguishing character is the shape of the lancet which is clearly hastate in *R. mehelyi* but straight sided in *R. euryale*. *R. mehelyi* also has a shorter, less pointed and more widely based connecting process.
R. blasii has a wedge shaped connecting process and almost straight sided (not hastate) lancet; the crown area of P_2 is equal to or only slightly smaller than that of the P_4 (much smaller in *R. mehelyi*). There is a wide overlap in the toothrow lengths of *R. lepidus* and *R. mehelyi*, but the former species is always smaller in the skull length and has relatively higher, anteriorly not protruding anterior median swellings.

Taxonomic remarks: Cabrera (1904) described *R. carpetanus* based on Spanish specimens, but later (1914) considered this form to be a subspecies of *R. mehelyi*, distinguishable from the nominate subspecies by its larger size. Kahmann (1958) analysed the external and cranial measurements of *R. m carpetanus* and *R. m. mehelyi*, and concluded that there is no subspecific variation within the species. Felten *et al*. (1977) and Palmeirim (1990) also found no reason to retain Cabrera's subspecies. Cockrum (1976) described the history of the name *R. euryale tuneti* and based on the original description and photographs (as well as forced by the fact, that subsequently only *R. mehelyi* specimens were collected at the type locality) concluded that the taxon is should stand as the subspecies of *R. mehelyi*. Since not only the type specimen but all others examined by Deleuil and Labbe appear to have been lost, Cockrum designated a neotype for the taxon, which he found a valid subspecies of *R. mehelyi* on the base of its longer tails, ears, fourth metacarpal and shorter tibia as compared with the typical race. Felten *et al*. (1977) stated that the taxonomic position of *tuneti* can not be determined, but on the other hand, Gaisler (1983) designated the Algerian population to *R. m. tuneti*.
Strinati and Aellen (1958) have shown that the name *mehelyi* is quite probably based upon specimen of *R. euryale* in which case *R. carpetanus* would be the prior name of this species. But as Corbet (1978) pointed out, such a change would cause needless confusion since *mehelyi* has been used consistently for this species since the two names were synonymized by Miller (1912).
(For the comparisons of *R. mehelyi* and *R. euryale* see also comments under *R. euryale*.)

Fig. 8.1. Lateral and frontal views of noseleaf of *R. mehelyi* (RMNH) from Romania. Scale = 3 mm.

Fig. 8.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. mehelyi* (HNHM 2714.2) from Romania. Scale = 3 mm.

Table 8. ***R. mehelyi***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		47.0	53.0		
SL	19.81	18.88	20.36	0.31	44
CM^3L	6.88	6.22	7.22	0.20	48
ZW	10.48	10.02	10.90	0.21	47
MW	9.83	9.59	10.22	0.16	42
ML	12.79	11.84	13.20	0.29	50
CM_3L	7.35	6.94	7.67	0.18	46

EURYOTIS-GROUP

***Rhinolophus arcuatus* Peters, 1871**
Arcuate horseshoe bat
R. arcuatus Peters, 1871 (Luzon I. Philippines)
R. a. exiguus Andersen, 1905 (Zamboanga, Mindanao, Philippines)
R. a. beccarii Andersen, 1907 (Bua Cave, Upper Padang, Sumatra)
R. anderseni Cabrera, 1909 (type locality unknown, probably Luzon I., Philippines)
? *R. anderseni equalis* Allen, 1922 (Puerto Prusse, Palawan I., Philippines)
R. toxopei Hinton, 1925 (Buru I., Moluccas, 1400 m)
R. a. angustifolius Sanborn, 1939 (Wetter I., Southwest Islands, Flores Sea, Moluccas)
R. a. proconsulis Hill, 1959 (Bungoh Cave, Bau, 1st. Division, Sarawak, Borneo)
R. a. mcintyrei Hill and Schlitter, 1982 (4 km ENE Telefomin, W Sepik Province, Papua New Guinea, 05º06'S, 141º41'E)

Recognised subspecies: Following Hill and Schlitter (1982) the following subspecies are recognised - *beccarii* in Sumatra; *proconsulis* in Borneo; *arcuatus* in northern Philippines; *exiguus* in southern Philippines; *toxopei* in Buru and Ambon; *angustifolius* in Wettar, Southwest Island, Flores Sea; *mcintyrei* in New Guinea.

External characters: A medium sized *Rhinolophus* species. The ears are medium, 17.2-22.0 mm in height. The horseshoe is relatively wide, almost covering the muzzle, with slight median emargination, 7.7-10.0 mm in width. The sella is broadly ovate, wide at its base and for much of its length only slightly narrower than the internarial cup, tapering slightly in its upper part to a rounded tip; the internarial cup is strongly angular. The connecting process is arcuate, forming a semicircle. The lancet is straight sided, its tip pointed. The lower lip is with three grooves. The tail is relatively short, 15.0-21.0 mm in length. In the wings, the third metacarpal is the shortest (29.0-39.5 mm), the fourth is

29.0-41.5 mm; the fifth is sometimes subequal to the fourth or (usually) slightly longer (30.0-41.7 mm). The colour above is slightly reddish brown or dark brown, lighter at the base of hairs; that of the belly is buff to gray brown.

Cranial and dental characters: The skull is relatively slender with an elongate, slightly inflated braincase, the interorbital region abruptly narrowed. The zygomatic width is usually exceeds the mastoid width or sometimes subequal (more typical in the Philippine populations). The anterior median swellings are well developed, circular in outline; the posterior swellings are defined but less pronounced, so the rostral profil is distinctly concave when viewed laterally. The crista sagittalis is moderate. The frontal depression is very variable in depth, being shallow, moderately deep or deep. The supraorbital crests are slightly or well developed. The palatal bridge is short, 22-28% of the upper toothrow length.
The canines are relatively slender and slightly curved. The first upper premolar is small or medium with well developd cusp, wholly in the toothrow and separating the upper canine and the posterior upper premolar. The second lower premolar is sometimes missing, if present small or very small and crowded entirely out of row. P_2 and P_4 are in contact or nearly so, their cingula almost always overlapping each other.

Similar species: Although externally and cranially very similar, *R. arcuatus* and *R. euryotis* may be separated by the structure of the noseleaf, which in *R. arcuatus* is characterised by a narrow anterior emargination, extending less than halfway to the internarial region. *R. euryotis* has a shallow emargination, its margins thickened, the tickening extending posteriorly as narrow parallel ridges. *R. creaghi* is also very similar cranially and can be tell apart by noseleaf characteristics. *R. arcuatus* is separable from its closest relative *R. inops* by craniodental measurements only.
The cranially similar sized *R. sedulus* is characterised by its long, deep frontal depression which bordered by high, sharp supraorbital ridges; *R. philippinensis* has longer rostrum, anteriorly elongated median swellings and the P^2 is widely separated from the adjoining teeth. *R. affinis* is usually larger, its skull is more robust and has a less pronounced nasal swellings and stronger, more massive upper canine. *R. acuminatus* is separable by its shorter rostrum and not so deeply concave rostral profile. *R. canuti* and *R. creaghi* have smaller posterior nasal swellings and usually more prominent frontal depression. *R. coelophyllus* and *R. shameli* also separable by the shape of the frontal depression, which is very long in these two species.

Taxonomic remarks: The taxon *R. anderseni* was described by Cabrera (1909) based on a single specimen from unknown locality (from the Philippines, probably Luzon, see Taylor 1934). As Cabrera stated, the species belongs to the *simplex*-group of Andersen and discussed its relationship only to *R. stheno* and *R. nereis*. In the key given by him (op. cit.) and later applied by Taylor (1934) for the Philippine horseshoe bats, he separated *anderseni* from the majority of the species by the shape of sella being slightly concave or parallel sided. Beside the works of Cabrera (1909) and Taylor (1934), the measurements of the holotype of *R. anderseni* were also given by Ibanez and Fernández (1989) but by lapsus, with wrong value for the maxillary toothrow length (5.8 mm instead of 8.5). The type specimen (deposited in the Museo Nacional de Ciencias Naturales, Madrid) was not investigated by subsequent researchers and Cabrera's original designation of the species to the *simplex* (= *ferrumequinum*) group was generally accepted (Corbet and Hill 1992, Koopman 1994). Lawrence (1939) remarked,

that *R. anderseni* is of the same size as *R. arcuatus* and both the external and cranial measurements are fall within the limits of variation of *R. arcuatus*, but without examining Cabrera's type it is impossible to say in what relation these forms stand to each other. Subsequently, Ingle and Heaney (1992) - based on the personal communication of J. E. Hill - thought possible that some specimens referred to *R. arcuatus* may be *R. anderseni*. By examination of the recently prepared detailed drawings (made by the courtesy of Conservator of Vertebrates, MNCN) of the skull and noseleaf of the holotype, however, it became evident that *anderseni* is a member of the *euryotis*-group and is obviously not connected to the *ferrumequinum*-group. This view is supported by the structure of the internarial cup, connecting process and nasal swellings. Within the Philippine members of *euryotis*-group, *anderseni* fall into the size-class of *arcuatus*, and is virtually indistinguishable from that species. Therefore, we consider *anderseni* as the synonym of the latter species. The form *R. anderseni aequalis* was said to corresponds fairly well with Cabrera's careful description (Allen 1922) but slightly differs in the proportion of metacarpals. From the characters provided by Allen its affinities can not be determine; the type is not seen and the taxon is of uncertain relationship (Heaney *et al*. 1998).

As Heaney *et al*. (1991) and Ingle and Heaney (1992) noted, Philippine bats previously identified as *R. arcuatus* appear separable to two morphotypes; the smaller one (forearm 43-46 mm, maxillary toothrow 6.7-7.5 mm) is typically found in lowland caves or disturbed habitat, and the larger one is usually found in primary upland forest. The shape of the nasal swellings and the frontal depression of different populations is also variable. Heaney *et al* (1998) also noted subtle but consistent differences between populations on each pleistocene island of the Philippines. According to the measurements, the *„R. arcuatus*-small" of Ingle and Heaney (1992) and the type of *R. anderseni* agreeing with the type of *R. arcuatus*; hence the „*R. arcuatus*-large" form of Ingle and Heaney may represent a still undescribed taxon.

Hinton (1925) allied his new species *R. toxopei* to *R. arcuatus*, which was for long acccepted as separate species (Honacki *et al*. 1982, Corbet and Hill 1986), but later on regarded as conspecific with *R. arcuatus* (e.g. Corbet and Hill 1992, Flannery 1995).

Hill and Schlitter (1982) provided an overview of the accepted subspecies but probably due to the relatively few specimens at hand, with no mention of the questionable taxonomic position of the different Philippine populations. They also noted, that at present no proper assessment of geographic variation of the species can be made. According to Hill (1988) a specimen from Sulawesi seems likely to be most like *R. a. proconsulis* from Borneo, differing in a slightly wider and more ovate sella, slightly longer rostrum and higher anterior median swellings.

Fig. 9.1. Lateral and frontal views of noseleaf of *R. arcuatus* (MNB 2531.2 - cotype) from the Philippines. Scale = 3 mm.

Fig. 9.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. arcuatus* (MNB 2531.1 - cotype) from the Philippines. Scale = 3 mm.

Table 9. ***R. arcuatus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		42.0	53.5		
SL	20.64	18.93	22.03	0.74	49
CM^3L	8.14	7.17	8.91	0.39	53
ZW	9.75	8.77	10.97	0.52	53
MW	9.65	8.92	10.35	0.37	49
ML	13.89	12.47	15.16	0.63	52
CM_3L	8.61	7.56	9.52	0.41	52

***Rhinolophus canuti* Thomas and Wroughton, 1909**
Canuti horseshoe bat
R. canuti Thomas and Wroughton, 1909 (Kalipoet-jang, Tji-Tangoei R., S Java)
R. creaghi timorensis Goodwin, 1979 (Lia Hoo Cave, near Fatu Maca Village, 7 miles S of Baucau, Timor I., c. 550 m)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *canuti* in Java; *timorensis* in Timor.

External characters: A fairly large species of horseshoe bats. The ears are large, their heights is 21.0-24.1 mm. The horseshoe is wide, about 11 mm in breadth across. The sella is gradually narrowing to a rounded tip; the tuft of hairs between the sella and the lancet is diffuse and sparse its colour is reddish brown (*timorensis*) or straw-yellow (*canuti*). There is a fringe of hairs along the edge of the connecting process, which is very low but slightly better developed in *timorensis*. The lancet is with concave sides. There are three mental grooves on the lower lip. The tail is 16.4-24.0 mm in length. In the wings, the third metacarpal is the shortest, the fourth and fifth are subequal in length (about 36.7, 39.4 and 39.5 mm, respectively). The hair is long and fine, exhibits considerable variation in colour. The uppersides varied from dark red to wood brown, the hairs of the dorsal surface are paler basally. The ventral pelage is from wood brown to light drab.

Cranial and dental characters: The skull is heavily built, the zygomatic width is slightly exceeds the mastoid width. The anterior median swellings are well inflated and extended posteriorly, the lateral swellings are also prominent; the posterior swellings are relatively reduced, so the rostral profil is sharply concave. The crista sagittalis is strong, the frontal depression is greatly or moderately developed. The crista supraorbitalis is with sharp ridges. The palatal bridge is short, 24-27% of the maxillary toothrow.
The upper canine is moderately strong and long, the posterior upper premolar (P^4) is well developed. The first upper premolar is relatively large, included in the toothrow but shows a tendency to be crowded slightly out of line. In the mandible the second premolar is small and completely out of the row or rarely missing. The first (P_2) and third (P_4) lower premolars touching each other.

Similar species: Externally the only similar species is *R. creaghi*, which can be tell apart by its rudimentary connecting process and more compact tuft of hairs at the base of lancet. *R. creaghi* is essentially the same cranially, as well, but has a smaller, subcircular anterior median swellings and narrower interpterygoid groove.
The skull of *R. trifoliatus* also similar, but its anterior median swellings do not reach anteriorly the border of the nasal orifice, the rostrum is lower and the sagittal crest is much better developed. *R. arcuatus* is separable by its more inflated posterior swellings and usually shallower frontal depression. The rostral part of the skull of *R. euryotis* is longer, caused by the elongated and narrow frontal depression; the upper canine of this species is longer and heavier at its base. *R. philippinensis* has a slender skull with the zygomatic width is less than the mastoid width and very long palate.

Taxonomic remarks: The close relationship of *R. creaghi* and *R. arcuatus* has long been recognised (Andersen 1905e) and the morphological gap between these two species is further narrowed by the intermediate character of *R. canuti* and especially that of *R. c. timorensis*. Thomas and Wroughton (1909) allied their species closely to *R. creaghi*, but clearly distinguished from that taxon by the different development of connecting process. Hill (1958) and Goodwin (1979) considered *canuti* and *creaghi* belonging to the same species, but Goodwin (op. cit.) when described *timorensis* characterised its noseleaf as most similar to that of *canuti*. Subsequently Hill and Schlitter (1982) listed *creaghi* and *canuti* as separate species, allying *timorensis* to the latter. Goodwin (op. cit.) noted the interesting inverse correlation between the degree of specialization of the facial tuft and the degree of development of the connecting process in *creaghi*, *canuti* and their subspecies.

Fig. 10.1. Lateral and frontal views of noseleaf of *R. c. canuti* (HNHM 66.4.1.) from Java. Scale = 3 mm.

Fig. 10.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. canuti* (BMNH 9.1.5.183 - holotype) from Java. Scale = 3 mm.

Table 10. ***R. canuti***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		47.0	53.0		
SL	21.79	20.76	22.73	0.60	14
CM^3L	8.66	8.08	9.22	0.31	14
ZW	10.47	9.91	11.03	0.32	13
MW	10.15	9.70	10.54	0.27	14
ML	14.83	14.11	15.44	0.40	14
CM_3L	9.19	8.61	9.71	0.30	14

***Rhinolophus coelophyllus* Peters, 1867**
Croslet horseshoe bat
R. coelophyllus Peters, 1867 (Salween R., Burma)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized horseshoe bat. The ears are medium, 16.5-23.0 mm in height. The horseshoe is 8.7-10.8 mm wide; a rudimentary secondary noseleaf is present. The sella is short, its sides are almost parallel or continously convergent, with rounded summit. The arched connecting process is proximally inserted into a densely haired vertical fissure in the lancet, which is very thick and short, its outline is convex. The lower lip is with three grooves. The tail is 16.5-24.5 mm in length. In the wings, the third metacarpal is the shortest (31.0-31.6 mm), the fourth (32.2-32.3 mm) is slightly longer than or almost equal with the fifth metacarpal (31.5-32.8 mm). The upperparts are brown; the fur on the belly is paler and more greyish, the individual hairs being whitish with brown tip; a red phase (although less frequent) and a wide range of intermediate forms are also known.

Cranial and dental characters: The skull is moderately built, the zygomatic width is only slightly greater than mastoid width. The anterior median nasal swellings are high but short antero-posteriorly; the lateral and posterior compartments are also well defined. The sagittal crest is moderate or well developed. The frontal depression is prominent, moderately deep, enclosed by sharp, well developed supraorbital crests. The palatal bridge is short or very short, 23-27% of the maxillary toothrow.
The upper and lower canines are slender. The moderately large anterior upper premolar is in the toothrow, and clearly separates the adjoining teeth. The posterior upper premolar (P^4) is relatively large, reaching almost height of the canine. The lower second premolar is small and external to a different extent; P_2 and P_4 are in contact.

Similar species: The closest and most similar species is *R. shameli*, which is about the same size by forearm measurements but its horseshoe is wider; cranially, the width across the anterior lateral swellings is more than 5.5 mm, and the shallow frontal depression is flanked by low supraorbital ridges in *R. shameli*.
The species of the *pusillus*-group are either smaller or larger (*R. acuminatus*) cranially than *R. coelophyllus*. *R. stheno* and *R. arcuatus* have a much shorter frontal depression. This difference is less pronounced but still useable as distinguishing character in the case of *R. borneensis* and *R. megaphyllus*; these two species also have anteriorly less protruding median swellings. Both *R. creaghi* and *R. canuti* have similarly shaped skulls, but they are larger by craniodental measurements. *R. macrotis* is characterised by its slender skull and very long palatal bridge.

Taxonomic remarks: *R. shameli* was originally described as a subspecies of *R. coelophyllus* based on its considerably larger size and more brilliant colouration (Tate 1943). However, there are two colour phases in the former species (Hill and Thonglongya 1972) and based on larger series the measurements overlap in several dimensions in the two species. The depth of the frontal (rostral) depression, the shape and developement of the supraorbital ridges as distinguishing characters (Corbet and Hill 1992) are well usable in most cases, although there is some individual variation.

The rostral depression of *R. shameli* is not typically short as mentioned by Koopman (1994).

Fig. 11.1. Lateral and frontal views of noseleaf of *R. coelophyllus* (MNB 3143 - holotype) from Myanmar. Scale = 3 mm.

Fig. 11.2. Lateral view of the rostral part of the skull (MNB 3143 – holotype) and occlusal view of the upper (left) and lower (right) left anterior dentition (BMNH 98.10.1.1) both from Myanmar of *R. coelophyllus*. Scale = 3 mm.

Table 11. ***R. coelophyllus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		40.0	46.0		
SL	19.06	18.39	19.85	0.38	33
CM^3L	7.31	6.99	7.67	0.18	28
ZW	9.34	9.16	9.53	0.10	23
MW	9.16	9.02	9.32	0.10	23
ML	12.52	12.06	13.07	0.29	29
CM_3L	7.67	7.33	8.03	0.18	24

***Rhinolophus creaghi* Thomas, 1896**
Creagh's horseshoe bat
R. creaghi Thomas, 1896 (Sandakan, Sabah, Borneo)
R. pilosus Andersen, 1918 (Marengan, Soemenep, E. Madura I., off NE Java)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *creaghi* in Borneo; *pilosus* in Madura.

External characters: A relatively large species of the genus. The ears are small or medium, 18.8-25.0 mm in height. The horseshoe is moderately wide, 9.8-11.4 mm in width; a rudimentary secondary leaflet is present. The base of sella is constricted at the narial cup, its outline above is more or less ellipsoid. The species is virtually without connecting process, but there is a highly specialised tuft at the base of lancet, in which the long hairs are gathered into a dense, dark brown conical mass. In *pilosus* the hairs themselves are strangely modified by having their distal halves flattened and expanded in bladelike fashion. The lancet is relatively long with only slightly concave sides. The lower lip is with three mental grooves. The tail is relatively short, its length is 11.1-16.0 mm. In the wings, the third metacarpal is shortened, 34.6-35.5 mm in length; the fourth (35.5-37.4 mm) is shorter than or subequal to the fifth metacarpal (37.2-38.5 mm). The upperparts are usually dark brown to olive brown; the underparts are paler.

Cranial and dental characters: The skull is heavily built, the zygomatic width is slightly greater than or subequal to mastoid width. The anterior median swellings are high and bulbous, the lateral ones are also well developed. The posterior compartments are less developed, the rostral profile is distinctly concave. The crista sagittalis is

moderate or strong, the frontal depression is deep. The bordering cristae supraorbitales are prominent, frequently with sharp ridges. The palatal bridge is very short or short, 22-28% of the upper toothrow.
The upper canine is moderately strong, but long; the prominent posterior upper premolar reaches two-third of its length. The first upper premolar is well developed, slightly extruded. The middle lower premolar is minute, fully external or sometimes lacking, the adjoining premolars are in contact.

Similar species: *R. canuti* has better developed connecting process (especially in the subspecies *timorensis*) and antero-posteriorly elongated, more inflated anterior swellings and broader interpterygoid groove. *R. arcuatus* is similar cranially but characterised by its more prominent posterior swellings and usually less deep frontal depression. In the case of *R. trifoliatus*, the upper edge of the nasal orifice is formed by a bony rim, the median swellings are not extending anteriorly to the edge; the anterior median swellings itself is less prominent. *R. euryotis* is recognisable on the base of the long rostral part of skull and the very strong, widely based upper canine. *R. acuminatus* has a much shorter, shallower frontal depression; *R. philippinensis* is characterised among others by its narrow skull and very long palate.

Taxonomic remarks: Andersen (1905e) related the species very close to the Philippine *R. arcuatus*. Thomas and Wroughton (1909) based on the cleaned skull made corrections to the original description and noted that the second lower premolar (P_3) of the type is not „entirely absent" but present on one side, though excessively minute. The taxon *pilosus* once described as separate species was mentioned at first by Chasen (1940) as a probable subspecies of *R. creaghi*, the opinion fully accepted by the subsequent authors.

Fig. 12.1. Lateral and frontal views of noseleaf of *R. creaghi* (BMNH 78.2489) from Borneo. Scale = 3 mm.

Fig. 12.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. creaghi* (BMNH 96.7.30.1 - holotype) from Borneo. Scale = 3 mm.

Table 12. ***R. creaghi***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		46.0	52.0		
SL	21.79	20.98	23.03	0.52	28
CM^3L	8.76	8.38	9.23	0.24	29
ZW	10.74	9.85	11.36	0.35	27
MW	10.55	10.06	10.99	0.21	26
ML	14.85	14.11	15.57	0.38	29
CM_3L	9.28	8.81	9.85	0.26	29

***Rhinolophus euryotis* Temminck, 1834**
Broad-eared horseshoe bat
R. euryotis Temminck, 1834 (Ambon I., Moluccas)
R. e. timidus Andersen, 1905 (Bacan I., Moluccas)
R. e. praestans Andersen, 1905 (Kai Is)
R. e. aruensis Andersen, 1907 (Aru I.)
R. e. burius Hinton, 1925 (Lehsoela, Buru I., Moluccas)
R. tatar Bergmans and Rozendaal, 1982 (Moinakom R., Dumoga Nature Reserve, N. Sulawesi, 0º41'N, 124º3'E, 525 m)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *tatar* in Sulawesi; *timidus* from northern Moluccas through New Guinea to the Bismarcks; *burius* in Buru; *euryotis* from Ceram to Timorlaut; *praestans* in Keis; *aruensis* in Arus.

External characters: A large species of its genus. The ears are medium, 20.5-24.6 mm in height. The horseshoe is concealing the muzzle and even projecting slightly beyond it and divided in front by a longitudinal groove with raised edges extending from the median edge to the internarial region; the breadth of the horseshoe is 10.2-13.0 mm. The horseshoe is darkly pigmented except for the whitish stripe of the median longitudinal groove. The sella is wide but relatively short, almost parallel sided, its terminus is convex in outline. The lancet is more or less straight sided, densely haired. The lower lip is with three grooves. The tail is short, 13.5-25.7 mm in length. In the wings, the third metacarpal is the shortest (38.2-40.8 mm), the fourth is medium in length (38.8-42.5 mm) and the fifth is the longest (40.3-43.2 mm). The colour of the upperparts is brown, the base of the individual hairs are lighter drab; the underside is lighter brownish or wood brown.

Cranial and dental characters: The skull is large, but relatively slenderly built. The zygomatic width is usually exceeds the mastoid width, but in the subspecies *R. e. tatar* they are subequal. The anterior median swellings are prominent, bulbous; the posterior nasal swellings are reduced. The frontal depression is extending anteriorly to the median swellings, elongated and moderately deep. The supraorbital crests are well defined, but not especially sharp; the crista sagittalis is medium developed. The palatal bridge is short, 25-28% of the upper toothrow (CM^3) length.
The upper canine is long and strong, the posterior upper premolar is also well developed. The anterior upper premolar (P^2) is medium sized, situated in the axis of the toothrow, or at most halfway extruded. In the lower jaw, the middle premolar is small and fully out of row or sometimes entirely missing. The adjoining teeth (P_2 and P_4) are close to each other or their cingula are overlapping.

Similar species: The special noselaef characteristics are distingusihing the species externally from its congeners. Cranially, among the similar sized species, *R. creaghi* and *R. canuti* have shorter rostrum, with wider and somewhat shorter frontal depression; *R. affinis* is characterised by its much lower anterior nasal swellings. *R. arcuatus* is usually smaller, and has a distinctly shorter frontal depression; *R. acuminatus* differs from *R. euryotis* by its less developed upper canines, short rostrum and short frontal depression. *R. trifoliatus* is separable on the base of the shape of median swellings and the much

better developed sagittal crest. *R. philippinensis* and its allies have generally more slender skull, a very long palatal bridge and weaker upper canine.

Taxonomic remarks: According to Andersen (1905b, 1907a) the nominotypical race differs from *timidus* by its broader braincase, longer mandible and toothrows and wider horseshoe; *praestans* has very wide horseshoe (about 13 mm in width) and nasal swellings; *aruensis* is very similar to *timidus* but smaller. Tate and Archbold (1939) introduced a series of the species from Celebes (Sulawesi) and noted their short forearm length (48-51 mm) as compared with other material from New Guinea (forearm length 54-56 mm, referred to *R. e. timidus*). The authors found probable, that the subspecific name *euryotis* is applicable to the short-winged forms and the specimens from Celebes must be so identified. Later on, Hill and Schlitter (1982) remarked, that „the Sulawesian population [of *R. euryotis*] is currently under description by the senior author as a distinct subspecies", but Hill never published this paper. Instead, Bergmans and Rozendaal (1982) introduced *R. tatar* from that island (and remarked its close relation to *R. arcuatus*) but as Hill (1983) stated „comparison with all but *angustifolius* among *R. arcuatus*, and with all of the described forms of *R. euryotis* leads me to the conclusion that *tatar* is best considered a subspecies of this latter". The earlier described races of *R. euryotis* are very close to each other (Andersen 1907a, Hinton 1925) and can be tell apart chiefly by their localities only. As Koopman (1982) noted on the basis of samples from New Guinea (*timidus*) compared with two Moluccan subspecies (*euryotis* and *praestans*), he is therefore skeptical of the validity of the currently recognised subspecies. However, later on Koopman and Gordon (1992) noted that based on topotype specimens *timidus* is distinct from the nominotypical form.

Fig. 13.1. Lateral and frontal views of noseleaf of *R. euryotis* (BMNH 11.7.12.15) from Ambon, Indonesia. Scale = 3 mm.

Fig. 13.2. Lateral view of the rostral part of the skull (BMNH 86.11.3.4) and occlusal view of the upper (left) and lower (right) left anterior dentition (RMNH 35198 – cotype) of *R. euryotis* both from Ambon, Indonesia.

Table 13. ***R. euryotis***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		49.0	59.5		
SL	23.98	22.05	25.35	0.83	32
CM^3L	9.57	8.69	10.27	0.38	35
ZW	11.73	10.55	12.62	0.58	33
MW	11.13	10.13	11.72	0.35	31
ML	16.53	15.09	18.04	0.74	34
CM_3L	10.21	9.40	10.98	0.43	35

***Rhinolophus inops* Andersen, 1905**
Philippine forest horseshoe bat
R. inops Andersen, 1905 (Mt. Apo, Todaya, Davao, Mindanao, Philippines, 1,325 m)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A moderately large species of *Rhinolophus*. The ears are medium or large, about 23 mm in height. The horseshoe is wide, concealing the muzzle, its width is about 13 mm. The sella of the holotype is highly modified into a small triangular pouch, turning the opening downwards; in the case of other specimen without this peculiar feature, its outline is approximately ovate or nearly parallel sided. The connecting process is strongly arcuate, almost semicircular in outline, covered with sparse, stiff hairs. The lancet is moderately high, its sides are straight. The tail is relatively short, about 16 mm in length. In the wings, the fifth metacarpal is the longest, the fourth is medium long and the third metacarpal is the shortest. The colour is deep dark brown or slightly reddish-brown both in the upper and undersides; the ventral aspect is frequently lighter.

Cranial and dental characters: The skull is relatively strong; the zygomatic width is greater than the mastoid width. The anterior median and lateral swellings are well inflated, the posterior swellings are less developed. The sagittal crest is strong or very strong; the frontal depression is clearly defined, moderately or very deep especially proximally. The cristae supraorbitales are well defined, strong and thick. The palatal bridge is short, 28-31% of the maxillary toothrow (CM^3) length.
The upper canine is medium developed, the anterior upper premolar (P^2) is moderate, situated in the axis of the tootrow, always separating the adjoining teeth (C^1 and P^4). The lower middle premolar (P_3) is small or rarely medium sized, and external to different extent; P_2 and P_4 usually in contact.

Similar species: Within the distribution area of the species the form of the connecting process and the general size; cranially the size and the wide zygomatic arch separate *R. inops* from the majority of the Philippine horseshoe bats, except *R. arcuatus* and *R. subrufus*. These three species are strikingly similar in every respect and even there is a certain overlap in their measurements (see also taxonomic remarks under each species).
Outside the Philippines, *R. pearsoni* looks alike externally, but this latter species is different having only one mental groove and the sella distinctly constricted below the middle; cranially, *R. pearsoni* has smaller anterior median nasal swellings, lower rostrum and relatively longer palatal bridge.

Taxonomic remarks: The peculiar triangular pouch (with its greatest depth of 1.5 mm) at the summit of sella of the holotype specimen was thought to be the most important diagnostic feature of the species (Andersen, 1905b, Corbet and Hill 1992, Taylor 1934). But as Ingle and Heaney (1992) remarked, this modified sella is not found in any other specimen that has been referred to *R. inops*. Since a specimen of *R. megaphyllus keyensis* (RMNH 27886) also shows a similar modification, it most probably represent an aberration found in only one individual of the species. As Taylor (1934) remarked *R. inops* intermediate in size between *R. arcuatus* and *R. subrufus*; Ingle and Heaney (1992) evidenced that the *inops-subrufus* species-group may be broken into at least two morphs (based solely on size) and referred the range of smaller bats to *R. inops* and that

of the larger ones to *R. subrufus*. Ingle and Heaney (op. cit.) further noted, that the size variation of the specimens derived from different islands and assigned to *R. inops* made possible that each morph represents a distinct species.

Fig. 14.1. Lateral and frontal views of noseleaf of *R. inops* (USNM 459462) from the Philippines. Scale = 3 mm.

Fig. 14.2. Lateral view of the rostral part of the skull and occlusal view of the left upper (left) and right lower (right) anterior dentition of *R. inops* (USNM 125314 - holotype) from the Philippines. Scale = 3 mm.

Table 14. ***R. inops***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		46.5	53.0		
SL	23.63	22.88	24.11	0.34	17
CM^3L	9.59	9.34	9.87	0.15	17
ZW	11.38	10.89	11.83	0.29	17
MW	10.85	10.48	11.19	0.23	17
ML	16.40	15.86	16.71	0.27	17
CM_3L	10.24	9.96	10.61	0.22	17

***Rhinolophus rufus* Eydoux and Gervais, 1836**
Large rufous horseshoe bat
R. luctus var. *rufus* Eydoux and Gervais (1836; Manila, Luzon, Philippines)
Aquias eudoxii Fitzinger, 1870 (Manila, Luzon, Philippines)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A very large species of its genus. The ears are medium, their heights is 29.0-34.0 mm. The horseshoe extends to almost cover the upper lip. The sella is parallel margined or slightly but gradually narrowing upwards, widely rounded at the apex and scarcely expanded at the base. The connecting process is strongly arcuate, and starting from the very tip of the sella. The lancet is moderately long, straight-sided. The lower lip is with three mental grooves. The tail is 24.0-30.0 mm in length. In the wings, the fifth metacarpal is the longest, the third and fourth are subequal or the third is the shortest. The species has two, not very well marked colour phases. In the one the dorsal fur is „Vandyke brown" at the tips shading gradually at the bases; the other extreme is much warmer coloured, ochraceous-tawny washed with dark. In both cases the ventral aspect is of about the same colour as the upperside.

Cranial and dental characters: The skull is enormous, very strongly built. The zygomatic width is considerably greater than the mastoid width. The anterior median swellings are large and strongly projecting, the anterior lateral and the posterior swellings are less developed. The sagittal crest is high or very high; the supraorbital

ridges are very pronounced, with a deep frontal depression between them. The palatal bridge is medium long, 31-33% of the upper toothrow length.
The upper canine is strong, moderately long. The anterior upper premolar (P^2) is small and closely wedged between the canine and the second upper premolar (P^4) but situated in the axis of the row. The middle lower premolar is minute, scarcely as high as the cingulum of P_2 and partly or fully extruded from the toothrow. The first (P_2) and third (P_4) lower premolars are separated by a slight place or are barely in contact with each other.

Similar species: The only other species in the genus with similarly huge measurements is *R. luctus*. Externally, their noseleaves are very different; cranially *R. rufus* may be separated from this species by its shorter frontal depression, which is not extending posteriorly beyond the mid-orbit, by the shape of the well inflated anterior nasal swellings which are forming the upper part of the nasal orifice and by its widely separated, minute upper incisors.

Taxonomic remarks: Eydoux and Gervais (1836) mentioned *R. luctus* var. *rufa* from Manila, which is said to be like *R. luctus* but with different colour. The authors provided neither detailed diagnoses nor measurements or figures and their description could not be applied with certainty to any known species. Andersen (1905c) showed that no bat of the *luctus* type has been found in the Philippines and speculated that *R. luctus* var *rufus* is nothing but *R. philippinensis*. According to Taylor (1934) the name „might even more probably apply to *R. rufus* of Peters, which certainly does occur at Manila". Nevertheless, Peters' species is much smaller than the form described by Eydoux and Gervais (and is a junior primary homonym of the latter) and conspecific with *R. subrufus* Andersen 1905. *R. rufus* Eydoux and Gervais was redescribed in details by Lawrence (1939) who based on further specimens evidenced its specific distinctness and discussed its relation to the above mentioned other taxa.

Fig. 15.1. Lateral and frontal views of noseleaf of *R. rufus* (USNM 459501) from the Philippines. Scale = 3 mm.

Fig. 15.2. Lateral view of the rostral part of the skull and occlusal view of the left upper (left) and right lower (right) anterior dentition of *R. rufus* (USNM 303953) from the Philippines. Scale = 3 mm.

Table 15. ***R. rufus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		66.5	74.0		
SL	29.80	28.68	31.81	0.89	13
CM^3L	12.39	11.91	13.29	0.33	13
ZW	14.34	13.85	14.71	0.27	13
MW	13.00	12.68	13.44	0.25	13
ML	21.44	20.53	22.79	0.63	13
CM_3L	13.33	12.50	14.19	0.44	12

***Rhinolophus shameli* Tate, 1943**
Shamel's horseshoe bat
R. coelophyllus shameli Tate, 1943 (Koh Chang I., off SE Thailand)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized species. The ears are small or medium, 18.0-20.0 mm in height. The horseshoe is wide, covering the whole muzzle, about 9.0 mm in width. A secondary noselaed is present but concealed from above. The sella with parallel sides in its full length. The connecting process is a continuous arch, terminating at the very tip of the sella and proximally inserted into the fissure of the thickened lancet. The vertical fissure is covered with short, dense hairs. The lancet is a low, broadly based triangle, with slightly convex sides. The lower lip is with three mental grooves. The tail is 15.2-19.0 mm in length. In the wings, beside the shortest third metacarpal, the fourth and the fifth are subequal in length. Two colour phases are known; the dorsal surface is bright golden brown or brown, with the individual hairs are pale greyish white at base. The ventral surface is paler, orange buff or pale buff, much paler than the back; the hairs are creamy white at base and tipped with buff or buff brown.

Cranial and dental characters: The skull is moderately built, the zygomatic width is always greater than the mastoid width, but the difference is sometime small. The anterior median and lateral swellings are prominent, the rostrum is high; the posterior swellings are less developed. The sagittal crest is weak, the frontal depression is shallow. The supraorbital crests are low and obtuse. The palatal bridge is excessively short, 23-27% of the upper toothrow (CM^3) length.
The upper canine is moderately strong. The anterior upper premolar is medium, lying in the axis of the toothrow, but only barely reaching beyond the cingula of the posterior premolar. In the lower jaw, the canine has a wide base but the tooth itself is quite slender. The middle lower premolar is medium or small, extruded outside the row. The neighbouring teeth are usually separated, but are very close to each other.

Similar species: The closely related *R. coelophyllus* has narrower horseshoe; cranially the shallow frontal depression with ill-defined supraorbital crests of *R. shameli* separates it from *R. coelophyllus*, where the deep frontal depression is formed by strong, beaded supraorbital ridges developed from the forward extension and division of the sagittal crest; the width across the lateral swellings is over 5.5 mm in *R. shameli* but less in *R. coelophyllus*.
R. borneensis and *R. megaphyllus* are usually smaller, and are cranially separable by their anteriorly less protruding median nasal swellings and shorter frontal depression. *R. creaghi* and *R. canuti* are very similar in skull proportions, but have deeper frontal depression and narrower, more expressed interpterygoid groove (this latter part of the skull of *R. shameli* is only with a shallow depression, without well defined ridges). *R. arcuatus* is distinguishable by its much shorter frontal depression.

Taxonomic remarks: Shamel (1942) referred two specimens from Thailand to *R. coelophyllus* and described them individually. These specimens, however, differed sufficiently from each other in several characters, and subsequently Tate (1943) recognising the differences in size and colouration considered one of them as separate

subspecies, *R. c. shameli*. Based on more material from Thailand and Cambodia, Hill and Thonglongya (1972) suggested that *shameli* represents a distinct species, distinguishable chiefly by its larger size and differently shaped rostral part of skull.

Fig. 16.1. Lateral and frontal views of noseleaf of *R. shameli* (BMNH 70.1037) from Cambodia. Scale = 3 mm.

Fig. 16.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. shameli* (BMNH 78.2330) from Thailand. Scale = 3 mm.

Table 16. ***R. shameli***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		42.00	46.5		
SL	20.45	19.30	21.57	0.55	17
CM^3L	8.15	7.60	8.51	0.25	17
ZW	10.05	9.65	10.46	0.25	16
MW	9.73	9.32	10.21	0.26	17
ML	13.82	12.96	14.30	0.41	18
CM_3L	8.57	8.07	8.88	0.25	17

***Rhinolophus subrufus* Andersen, 1905**
Small rufous horseshoe bat
R. rufus Peters, 1861 (Paracali, Luzon, Philippines) (preoccupied by *R. rufus* Eydoux and Gervais, 1836)
R. subrufus Andersen, 1905 (Manila, Luzon, Philippines)
R. bunkeri Taylor, 1934 (Saub, Cotabato, Mindanao, Philippines)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *subrufus* in northern and central Philippines; *bunkeri* in Mindanao.

External characters: A relatively large species of horseshoe bats. The ears are medium, 22.9-25.5 mm in height. The horseshoe is relatively wide (11.8-13.3 mm), covering the muzzle; a secondary noseleaf is present. The sella is long, its sides very slightly narrowing upwards. The connecting process is semicircular, started at the very tip of the sella and lined with long hairs. The lancet is nearly straigth sided, tapering regularly to summit and densely haired. The lower lip is with three mental grooves. The tail is 17.2-25.0 mm in length. In the wings, the third metacarpal is 37.2-39.4 mm long, the fourth and fifth are longer (39.0-42.1 mm) and subequal with each other in length or sometimes the fourth is shorter. The fur on the head is reddish, on the back is cinnamon-rufous, rarely dark brown with no trace of the reddish colour; the base of individual hairs orange-rufous. The pelage below is similar, slightly more brownish.

Cranial and dental characters: The skull is large and heavily built, the zygomatic width always exceeds the mastoid width, but difference is sometimes slight. The

zygomatic arch itself is robust, highly flared, especially in the case of *R. s. bunkeri*. Beside the bulbous lateral and prominent median nasal swellings, the posterior ones are less inflated; the rostral profil is distinctly concave. The sagittal crests is high or very high, extending posteriorly for some length. The frontal depression is distinct, sometimes quite deep (typical form) sometimes shallow (*bunkeri*); the supraorbital crest are well defined. The palatal bridge is short or moderate, 27-33% of the upper toothrow (CM^3) length.
The upper premolar is quite long, the first upper premolar small and in the tootrow. The posterior premolar is moderately developed in relation to the canine, just reaching beyond the half of its length. The middle lower premolar (P_3) is small or medium, external to the tootrow; the first (P_2) and third (P_4) premolars are in contact or sometimes slightly separated.

Similar species: In the Philippines, by size, external and cranial characters the only similar species is *R. inops* which is usually smaller but there is a certain overlap between the two species. *R. subrufus* resembles to *R. pearsoni* in size and in the shape of the connecting process, but has three mental grooves and its sella is without the distinct constriction below the middle, a typical feature of *R. pearsoni*. The skull of *R. subrufus* differs from *R. pearsoni* by its more prominent nasal swellings and relatively longer palatal bridge.

Taxonomic remarks: Dobson (1878) suggested, that *R. arcuatus* differs from *R. rufus* Peters (= *R. subrufus*) in size only and is probably a local form of the same (see also comments under *R. rufus*). The separation of *R. subrufus* and *R. inops* is problematic, and as Ingle and Heaney (1992) noted the two morphs can be separated by size only; they referred the larger form to *R. subrufus*, but the forearm and craniodental measurements are overlapping between the two species.
R. bunkeri is said to be greater in body length, with wider horseshoe, more robust skull and dentition but the forearm and tibia measurements are not larger than that of *R. s. subrufus* (Taylor 1934). As later on Lawrence (1939) remarked, the difference in colour (the fur only scarcely paler at the roots and having a very pronounced silvery seen), large molars and the absence of the frontal depression readily distinguish *bunkeri* from *R. subrufus*; however, the size, general shape of the skull and the proportions of wing bones are too similar to warrant its its recognition as a full species.

Fig. 17.1. Lateral and frontal views of noseleaf of *R. subrufus* (MNB 2532 – holotype of *R. rufus* Peters) from the Philippines. Scale = 3 mm.

Fig. 17.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. subrufus* (BMNH 58.3.29.4 - holotype) from the Philippines. Scale = 3 mm.

Table 17. ***R. subrufus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		52.0	57.0		
SL	24.45	23.08	25.49	0.55	35
CM^3L	9.97	9.54	10.45	0.24	39
ZW	11.76	10.87	13.55	0.48	38
MW	11.17	10.31	11.73	0.27	37
ML	17.05	16.20	18.35	0.44	38
CM_3L	10.66	10.23	11.10	0.28	38

FERRUMEQUINUM-GROUP

***Rhinolophus bocharicus* Kastschenko and Akimov, 1917**
Bukharan horseshoe bat
R. bocharicus Kastschenko and Akimov, 1917 (Murghab River, S. Russian Turkestan)

Recognised subspecies: All specimens are referred to the nominate form.

External characters: A medium sized *Rhinolophus* species. The ears are medium, 19.3-24.0 mm in height. The horseshoe does not cover the whole muzzle, its breadth is 5.4-7.3 mm. The sella is narrow and constricted at the middle. The connecting process is tall and distinctively rounded in side view; the lancet is hastate. The lateral mental grooves of the lower lip are very weak, indistinct. The tail is 22.0-32.0 mm in length. In the wings, the third metacarpal is notably shortened (32.9-37.8 mm), the fourth and fifth are subequal (36.9-42.2 mm in length) or the fourth is sometimes longer than the fifth. The general colour of the fur is pale; the dorsal pelage is smoky grey-brown, darker on the shoulders; the base of the individual hairs are whitish. The underparts are whitish-grey throughout the full length of the hairs.

Cranial and dental characters: The skull is small but heavily built, the zygomatic width greatly exceeds the mastoid width. The anterior median swellings are very small in every dimensions, the posterior swellings are relatively large. The crista sagittalis is moderately developed, the frontal depression is shallow or very shallow. The supraorbial crests are low, but sometimes with more or less sharp edges. The palatal bridge is short, approximately 29-30% of the CM^3 length.
The upper canine is short and massive. The first upper premolar is minute (occasionally fully absent), fully displaced laterally from the toothrow; the adjoining C^1 and P^4 are in contact. P_3 is minute and entirely crowded out from row, P_2 and P_4 are always in contact with each other.

Bacular morphology: The structure of the bone is essentially the same as that of the *R. ferrumequinum* but in typical cases without strong protuberances on the ventral side of the basal cone; the lancet of the shaft is usually longer as compared to *R. ferrumequinum* (Strelkov 1971). (In his work Strelkov depicted the bacula of the two species but the captions of the Figs 5 and 6 had been confounded.) According to Hanák (1969) the shaft

is flattened almost in its full length and the whole bone is relatively thicker and larger than that of *R. ferrumequinum*.

Similar species: The only species with similar external and craniodental characteristics (high and rounded connecting process, very small anterior median swellings, fully displaced upper and lower premolars) near the distribution area of the species is *R. ferrumequinum* which is larger in every respects (but see taxonomic remarks below).

Taxonomic remarks: The morphological similarity of *R. bocharicus*, *R. clivosus* and *R. ferrumequinum* has led to a number of differing taxonomic conclusions and *R. bocharicus* was considered either as a subspecies of *R. ferrumequinum* (e.g. Bobrinskii 1925, Ognev 1927), or a subspecies of *R. clivosus* (e.g. Aellen 1959b, Bauer 1963, Koopman 1994), or a separate species (e.g. Hanák 1969, Felten *et al*. 1977, Corbet and Hill 1992). Recognising the close similarity in size and shape of all taxonomically important anatomical characters, Aellen (op. cit.) first suggested the conspecifity of *bocharicus* and *clivosus*. However, the detailed morphological, morphometric and molecular analyses undertaken by Thomas (1997) confirm this taxon is representing a discrete species. Thomas (op. cit.) also concluded that *R. bocharicus* (and *R. clivosus*) may have evolved from populations of *R. ferrumequinum* as a result of allopatric speciation occurring during periods of climatic change in the Pliocen and Pleistocene.
During the investigation of extensive material from Turkmenia, Strelkov (1971) found that sympatric populations of *R. ferrumequinum* and *R. bocharicus* are readily distinguishable by external and craniodental measurements (the limit between the two taxa in the case of the upper toothrow length is given as 7.4 mm) but a small population from the inner Karakumy Desert showed intermediate features of which the specific designation was not possible.
Koopman (1994) listed the taxon *rubiginosus* from Azerbaydzhan as valid subspecies, which apparently would be the only datum of *R. bocharicus* from that country. However, Pavlinov and Rossolimo (1987) mentioned *R. bocharicus rubiginosus* as synonym of *R. ferrumequinum* and in the literature there is no mention of *R. bocharicus* from Azerbaydzhan or from anywhere else in the Caucasus region (e.g. Kuzyakin 1950, Hanák 1969, Gromov and Baranov 1981).

Fig. 18.1. Lateral and frontal views of noseleaf of *R. bocharicus* (HNHM 97.116.1.) from Uzbekistan. Scale = 3 mm.

Fig. 18.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. bocharicus* (HZM 1.26890) from Uzbekistan. Scale = 3 mm.

Table 18. ***R. bocharicus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		47.5	53.0		
SL	19.64	19.04	20.22	0.25	38
CM^3L	7.00	6.71	7.20	0.13	38
ZW	10.27	9.75	10.81	0.23	38
MW	9.41	9.12	9.65	0.12	38
ML	12.92	12.40	13.39	0.22	37
CM_3L	7.60	7.34	7.85	0.13	37

***Rhinolophus clivosus* Cretzschmar, 1828**
Geoffroy's horseshoe bat
R. clivosus Cretzschmar, 1828 (Mohila, W. Arabia)
? R. geoffroyii Smith, 1829 (South Africa) (unidentifiable name)
R. acrotis Heuglin, 1861 (Keren, Eritrea)
R. augur Andersen, 1904 (Kuruman, Bechuanaland)
R. andersoni Thomas, 1904 (Wadi Alagi, Egyptian Desert)
R. augur zuluensis Andersen, 1904 (Jususic Valley, 20 miles NW Eshove, Zululand)
R. augur zambesiensis Andersen, 1904 (Fort Hill, North Nyasa)
R. acrotis brachygnathus Andersen, 1905 (Ghizeh, Lower Egypt)
R. keniensis Hollister, 1916 (Mount Kenia, British East Africa)
R. acrotis schwartzi Heim de Balsac, 1934 (Djanat, Algeria)

Recognised subspecies: After Thomas (1997) and Koopman (1994) the following subspecies are recognised - *clivosus* from Yemen and Saudi Arabia; *brachygnathus* from Egypt and Israel to northeastern Libya and northern Sudan; *schwartzi* southeastern Algeria and southwestern Libya; *acrotis* in Ethiopia, most of central and southern Sudan, Somalia; *keniensis* in southeastern Sudan, Uganda, Kenya, northern Tanzania; *zuluensis* in coastal South Africa; *augur* in southern Tanzania, Malawi, Zimbabwe, Botswana and northern South Africa.

External characters: The size is from medium to fairly large. The ears are transparent brown, small or medium in relation to the head, 10.0-24.0 mm long. The horseshoe is 5.6-8.3 mm in width accross, and not covering the whole muzzle. The sella is distinctly constricted in the middle. The connecting process is high and rounded, sparsely haired; the lancet is definitely hastate. The lower lip is with one distinct mental groove, the lateral ones obliterated. The tail is 18.0-41.0 mm in length. The third metacarpal is characteristically short (27.0-41.1 mm), the fourth is slightly shorter (29.7-45.3 mm) than or subequal with the fifth (30.0-45.8 mm). The general colour is greyish or reddish brown, the individual hairs are pale buffy with brown tips; the underparts are paler, the individual hairs are uniform pale greyish-brown. However, significant differences can occur between the extremes of the very dark, almost uniformly brown *R. c. zuluensis* and the very pale *R. c. schwarzi*.

Cranial and dental characters: The skull is robustly built, the zygomatic breadth much greater than the mastoid breadth. The anterior median swellings are very reduced in every dimensions but the posterior compartments are well developed resulting a nearly horizontal rostral profil. The anterior part of the rostrum is low in relation to the braincase. The sagittal crest is medium or well developed, the frontal depression is very shallow. The crista supraorbitalis is low but usually well defined. The palatal bridge is short, 25-31% of the CM^3 length.
The upper canine is strong and massive. The first upper premolar is small, minute or frequently missing; when present is fully external and placed in the outer angle formed by C^1 and P^4. The last upper premolar (P^4) is reaching the two-third of the upper canine. The second lower premolar is minute (as high as the cingulum of P_4) or missing, always totally out of row the adjoining premolars are in contact.

Bacular morphology: The general morphology of the bacula is essentially similar to that of *R. ferrumequinum*. The shaft is flattened laterally and expanded in dorsal view, and narrow in the lateral view. The shaft is constricted before the base, which is expanded. The tip is simple and unexpanded (Thomas 1997).

Similar species: In the sub-Saharan Africa two more species have similarly high and rounded connecting process, but they are differ in the following characters: *R. capensis* is characterised by its large anterior upper premolar wich is lying in the toothrow or only half-way extruded, and has more swollen anterior median swellings; *R. hillorum* of West Africa is similar in skull and dental proportions but much larger in all external and craniodental dimensions. *R. sakejiensis* (sympatric with *R. clivosus zuluensis*) has a more pointed connecting process and distinctly larger in every respects (Cotterill 2002).
The following species also have very small and extruded or even missing P^2 and P_3 but differ in the following features: *R. silvestris* and *R. deckeni* are almost always larger; *R. darlingi* and *R. fumigatus* are similar in size but all four have well inflated anterior median swellings with characteristically concave rostral profile. Despite its differently shaped connecting process *R. alcyone* cranially separable from *R. clivosus* by its larger anterior upper and middle lower premolars, and more pronounced anterior nasal swellings. *R. blasii* is easily distinguishable by its slender upper canines and subequal zygomatic and mastoid width.

Taxonomic remarks: The publication date of Cretzschmar's original description is variously given by different authors. It appeared between 1826 and 1830; here we follow Koopman (1994).
As Koopman (1966) noted there were three explanations of the taxonomic status of the large southern African representative of *ferrumequinum*-group. Roberts (1951) would place these forms in an endemic southern African species under the name *R. geoffroyii* (described from Cape Province); Ellerman *et al*. (1953) regarded the southern African forms as a subspecies of *R. clivosus* (described from Arabia) and the third is regarded these forms as a subspecies of *R. ferrumequinum* (Harrison 1959, Ansell 1960). As it was pointed out by Koopman (1966), where *R. ferrumequinum* and *R. clivosus* occur sympatrically or nearly so, the latter is represented by small bodied subspecies (*clivosus*, *brachygnathus*, *swartzi*); whereas in the more southern African localities where only *R. clivosus* occur, the specimens are indistinguishable from *R. ferrumequinum*. Thomas (1997) confirmed that specimens of *R. clivosus* from Yemen to South Africa showing an average increase in forearm length and skull measurements. Dulic and Mutere (1974)

differentiated *R. clivosus* and *R. ferrumequinum* on chromosomal ground, but as Rautenbach (1986) noted their conclusions as based solely on karyology appears to be incorrect and the two species are karyologically identical. However, the results of phenetic analysis and DNA sequencing (Thomas op. cit) showed that *R. clivosus* and *R. ferrumequinum* are specifically distinct throughout their ranges.

Andersen (1904b) stated, that *acrotis* is decidedly the same species as *andersoni* and the certain size differences may be due to the fact that the type of *andersoni* is an immature individual. Kock (1969) came to the conclusion that *andersoni* is consubspecific with *brachygnathus* but based in part, at least, on the presence or absence of the anterior upper premolar. Koopman (1975) speculated that probably *andersoni* is a synonym of *R. c. clivosus*, but in the absence of adults from the region, it seems impossible to say with certainty. The taxon *brachygnathus* was separated within *R. acrotis* by its shorter upper and lower toothrows (Andersen 1905f). The same author (1906) tell apart *R. clivosus* from *R. acrotis* by its larger, broader skull, and the presence of P^2 but based on a very limited sample. Allen (1939) listed all *acrotis*, *clivosus* and *geoffroyi* (this latter including *augur*, *keniensis*, *zambesiensis* and *zuluensis*) as separate species. Although the name *geoffroyii* antedates *augur* (Roberts 1919), Ellerman *et al*. (1953) pointed out that the description does not identify *geoffroyii* and the type is apparently lost, therefore they proposed that the name be discarded as unidentifiable; the authors furthermore regarded *augur* as a subspecies of the northern *R. clivosus*.

According to the opinion of Aellen (1959b) the forms united under the name *R. clivosus* are two different kinds; the Ethiopian forms are characterised by their shorter third metacarpal and the appropriate name for these forms should be *R. augur*, while the Palaearctic races (*clivosus, acrotis*, *andersoni*, *brachygnathus*, *schwartzi*) with the third metacarpal exceeds 90% of the fifth metacarpal length are best differentiated at specific level. The skull of the type of *R. clivosus* was prepared out long after its description and was investigated at first by Harrison (1964) who found no even a trace of the first upper or the middle lower premolars. As he noted, the separation of *acrotis* as a distinct species by reason of the absence of these vestigial teeth certainly can not be maintained. Harrison (op. cit.) characterised *acrotis* as probably averages larger and rather darker than *clivosus*, but first mentioned the former as a subspecies of the latter. Koopman (1975) discussed the distribution patterns of subspecies of *R. clivosus*, and noted the occurence in south-central Kenya of specimens of intermediate size, between the large *R. c. keniensis* and small *R. c. acrotis*, and pointed out that each distinct population differed to a greater or lesser extent from every other. On the other hand, Aggundey and Schlitter (1984) tentatively referred all records in Kenya to *R. c. keniensis*. The two subspecies currently recognised in southern Africa (Skinner and Smithers 1990) seem to be based chiefly in colour, the paler *R. c. augur* occuring in the drier western regions and the darker *R. c. zuluensis* (including *zambesiensis*, see Ellerman *et al*. 1953, Meester *et al*. 1986) in the wetter eastern areas. *R. c. schwartzi* was mentioned only from southeastern Algeria by Koopman (1994), but Setzer (1957) assigned material from Fezzan (southwestern Libya) to this subspecies, as well. Hanák and Elgadi (1984) remarked that this determination most likely was based on its geographical location.

The subspecific allocations accepted and presented here are based on the work of Thomas (1997) who examined the intra-specific relationships of *R. clivosus* by using classical taxonomic methods, univariate and multivariate statistical analysis. However, the wide range of all the measurements within the species suggest that probably one or more cryptic species are involved, e.g. the very small, pale coloured and geographically marginal subspecies *R. c. schwarzi* may represent a separate species. In connection with

the description of a new species (*R. sakejiensis*) Cotterill (2002) revised the *clivosus*-complex and shows that *hillorum* originally described as subspecies of *R. clivosus* is specifically distinct.

Fig. 19.1. Lateral and frontal views of noseleaf of *R. clivosus* (HNHM 2648.12) from Tanzania. Scale = 3 mm.

Fig. 19.2. Lateral view of the rostral part of the skull and occlusal view of the left upper (left) and right lower (right) anterior dentition of *R. clivosus* (SMF 4371 - holotype) from Saudi Arabia. Scale = 3 mm.

Table 19. ***R .clivosus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		45.5	56.0		
SL	20.72	18.06	22.82	1.34	57
CM^3L	7.59	6.53	8.39	0.49	63
ZW	10.75	9.29	12.36	0.79	60
MW	9.64	8.52	10.96	0.64	57
ML	13.88	11.87	15.98	1.01	64
CM_3L	8.20	7.02	9.27	0.53	64

***Rhinolophus darlingi* Andersen, 1905**
Darling's horseshoe bat
R. darlingi Andersen, 1905 (Mazoe, Mashonaland, Rhodesia)
R. d. barbertonensis Roberts, 1924 (Louw's Creek, Barberton district, southeastern Transvaal)
R. d. damarensis Roberts, 1946 (Oserikari, Okahandja, Damaraland, Namibia)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *darlingi* from Tanzania to Angola and the Cape Province; *damarensis* in Namibia.

External characters: A medium sized species of the genus. The ears are translucent light brown, and are medium length (17.0-30.0 mm) related to the head. The horseshoe is narrower than 8.5 mm, but covering almost the whole of the muzzle; a supplementary leaflet is present. The sella is relatively wide, constricted at the middle, widely rounded at its terminus. The connecting process is broadly rounded, nearly semicircular; the lancet is with only slightly concave almost straight sides. The lower lip is with one mental groove. The tail is relatively long, 25.0-34.0 mm. In the wings the third metacarpal (28.5-35.0 mm) is shortened in relation to the fourth and fifth metacarpals which are subequal in length (32.0-39.5 mm). There is some variation in the colour of upperparts. The majority of specimens being drab grey but others are slightly browner; the underparts are much lighter in colour, usually light dove-grey.

Cranial and dental characters: The skull is relatively strongly built, the zygomatic width is exceeds the mastoid width. The anterior and lateral rostral swellings are moderately inflated, the rostral profil is concave but not very expressedly. The sagittal crest is medium. The frontal depression is shallow or moderate, flanked with well visible supraorbital crests. The palatal bridge is medium long, 30-35% of the CM^3 length.
The upper canine is massive and short, the well developed posterior premolar is almost reaching its tip. The first upper premolar is minute, fully outside and crowded into the recess between C^1 and P^4, or sometimes missing; C^1 and P^4 are in contact or very nearly so. P_3 is frequently missing, when present minute and totally extruded from the row; the cingula of P_2 and P_4 are overlapping.

Similar species: *R. darlingi* differs from the similar sized *R. simulator* by its short, broad rostrum, the supraorbital length less than or more rarely equal to the width of the rostrum across the anterior lateral rostral swellings, rather than considerably exceeding this width; by its frontal depression, which is about as wide as long, not longer than wide; and by its extruded P^2, which possibly on occasion may be lacking. *R. darlingi* can be tell apart from *R. clivosus* on the base of its lower connecting process; cranially by the shape of the rostrum, which is definitely concave in *R. darlingi* but nearly straight in *R. clivosus*. *R. fumigatus* is larger in every respects; *R. adami* and *R. maendeleo* have a large anterior upper and relatively well developed middle lower premolars. *R. capensis* externally distinguishable from *R. darlingi* by its higher connecting process and more hastate lancet; cranially on the base of its larger anterior upper premolar wich is usually at most half-way excluded from the row but always separating C^1 and P^4. *R. landeri* cranially differs from *R. darlingi* by its relatively large anterior upper premolar.

Taxonomic remarks: According to Koopman (1975) *R. deckeni* and *R. silvestris* resemble to *R. darlingi* in the greater degree of nasal inflation and narrow basisphenoid bridge and all three show some approach to the *fumigatus-eloquens-hildebrandti* complex.
Erasmus and Rautenbach (1984) had difficulty distinguishing specimens of *R. darlingi* from *R. capensis* on the bases of cranial and chromosome morphology. As Maree and Grant (1997) noted the morphological similarity between these species is unlikely due to retained ancestral characters states, because of the large genetic distance between them and the degree of morphological differentiation between other pairs of species with similar genetic distances.
Roberts (1951) characterised *barbertonensis* as being in colour like *darlingi*, but smaller in size; and *damarensis* as being paler drab grey than *barbertonensis* and in size larger. Hayman and Hill (1971) and Meester *et al*. (1986) regarded *barbertonensis* as consubspecific with the nominate form *R. d. darlingi*, but *damarensis* is widely accepted as valid subspecies. Hill *et al*. (1988) recorded specimens from Nigeria, and noted that their measurements are almost entirely within the size range of *R. d. darlingi* from the Transvaal, Zimbabwe and Malawi but clearly more material is needed to establish the subspecific status of the West African population.

Fig. 20.1. Lateral and frontal views of noseleaf of *R. darlingi* (BMNH 82.551) from Nigeria. Scale = 3 mm.

Fig. 20.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. darlingi* (BMNH 95.8.27.1 - holotype) from Zimbabwe. Scale = 3 mm.

Table 20. ***R. darlingi***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		44.5	49.0		
SL	19.32	18.43	20.50	0.56	15
CM^3L	7.07	6.76	7.48	0.21	18
ZW	10.12	9.70	10.66	0.28	14
MW	9.21	8.92	9.73	0.25	14
ML	12.97	12.43	13.91	0.42	15
CM_3L	7.56	7.23	8.03	0.25	16

***Rhinolophus deckeni* Peters, 1868**
Decken's horseshoe bat
R. deckeni Peters, 1868 (Zanzibar Coast)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A fairly large species of *Rhinolophus*. The ears are small or medium in relation to the head, about 23 mm in height. The horseshoe is wide (9.0-11.0 mm in width across), covering the whole muzzle. The sella is long, slightly constricted in the middle, widely rounded above. The connecting process is semicircular, sparsely haired. The lancet is relatively high with almost straight sides. The lower lip is with a single well-visible groove, the lateral grooves are very indistinct. The tail is about 29 mm in length. In the wings, the third metacarpal distinctly shortened (about 37 mm), the fourth and the fifth are subequal or the fifth is slightly longer (42.0-43.0 mm). The dorsal aspect of the pelage is greyish dull-brown, ventrally similarly coloured but lighter; a rarer cinnamon-brown phase is also known.

Cranial and dental characters: The skull is strongly built, the zygomatic width is always greatly exceeds the mastoid width. The anterior median and posterior swellings are all moderately developed. The sagittal crest is strong; the frontal depression is medium and flanked by well defined, more or less sharp supraorbital ridges. The palatal bridge is 29-34% of the maxillary toothrow length.
Theupper canine is massive, the posterior upper premolar (P^4) reaches two-third of its length. The anterior upper premolar (P2) is excessively minute (or missing), external to row or rarely only half-way extruded; the canine and the posterior premolar are usually separated by a very narrow gap. In the lower jaw, the middle lower premolar (P_3) is missing, the neighbouring teeth and crowded to each other.

Similar species: *R. silvestris* is essentially the same in all particulars as *R. deckeni* and the separation is based on their geographic distribution only. Although by forearm measurements *R. clivosus* is similar, the connecting process of this species is higher, the

horseshoe breadth is less than 9 mm, usually smaller in craniodental dimensions and has less inflated nasal swellings. *R. fumigatus* is very similar cranially, the only (but also very slight) difference is the situation of the anterior upper premolar, which is in contact with the canine in *R. fumigatus*. These teeth are separated by a fine gap in *R. deckeni*.

Taxonomic remarks: The taxonomic position of *deckeni* was not entirely clear for long. Thomas (1913) apparently considered it related to *foxi* (= *R. fumigatus*) which is "evidently a western representative of *R. deckeni*". Aellen (1959) discussed *deckeni* in relation to his new *R. silvestris*. Harrison (1961) listed *R. deckeni* in Kenya as a species, but noted that only size (particularly the hind leg) separates it from *R. c. keniensis* and *R. c. zambesiensis* (= *R. c. zuluensis*). Hayman and Hill (1971) and Corbet (1978) considered *deckeni* as a synonym of *R. clivosus*, but Koopman (1975) considered it as a distinct species. This view is fully supported by the details of the noseleaf and is accepted by all subsequent authors (e. g. Aggundey and Schlitter 1984, Cockle *et al*. 1998, Kock *et al*. 2000). The relationship between *R. deckeni* and *R. silvestris* is still questionable, the latter is similar in all essentials to *R. deckeni* and probably represents a western subspecies of it.

Fig. 21.1. Lateral and frontal views of noseleaf of *R. deckeni* (MNB 3269 - holotype) from Tanzania. Scale = 3 mm.

Fig. 21.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. deckeni* (BMNH 1.5.1.8) from Tanzania. Scale = 3 mm.

Table 21. ***R. deckeni***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		48.0	56.0		
SL	23.35	22.56	24.12	0.51	19
CM^3L	8.87	8.33	9.41	0.33	20
ZW	12.14	11.45	12.64	0.38	18
MW	10.96	10.39	11.31	0.26	19
ML	16.34	15.46	17.19	0.53	19
CM_3L	9.63	9.04	10.21	0.39	20

***Rhinolophus ferrumequinum* (Schreber, 1774)**
Greater horseshoe bat
Vespertilio ferrumequinum (Schreber, 1774 (France)
Vespertilio equinus (Müller, 1776) (France)
Vespertilio solea (Zimmermann, 1777) (type loc. unknown)
Vespertilio perspicillatus (Blumenbach, 1779) (type loc. unknown)
Vespertilio ungula (Boddaert, 1785) (Burgundy, France)
Vespertilio ferrumequinum major (Kerr, 1792) (France)
Vespertilio hippocrepis (Schrank, 1798) (renaming of *V. ferrumequinum* Schreber, 1774)

Rhinolophus major (not of Kerr, 1792) (Geoffroy, 1803) (Burgundy, France)
Vespertilio unihastatus (Geoffroy, 1803) (France).
? *R. unifer* Kaup, 1829 (nomen nudum)
R. nippon Temminck, 1835 (Japan)
R. tragatus Hodgson, 1835 (Nepal)
R. f. germanicus Koch, 1863 (Wiesbaden, Germany)
R. f. italicus Koch, 1863 (Italy)
? *R. brevitarsus* Blyth, 1863 (Darjeeling, India) (nomen nudum)
R. unihastatus homorodalmasiensis Daday, 1885 (Homorodalmás Cave, Udvarhely) (nomen nudum)
R. f. homorodensis Daday, 1887 (renaming of *R. u. homorodalmasiensis* Daday, 1885)
R. f. obscurus Cabrera, 1904 (Valencia, Spain).
R. f. proximus Andersen, 1905 (Gilgit, Kashmir)
R. f. regulus Andersen, 1905 (Masuri, Kumaon, N.W. India)
R. f. insulanus Barrett-Hamilton, 1910 (Cheddar, Somerset, UK)
R. f. colchicus Satunin, 1912 (Abkhazia, Georgia)
R. f. irani Cheesman, 1921 (Shiraz, Iran, 5200 ft)
R. f. mikadoi Ognev, 1927 (Yokohama, Japan)
R. nippon pachyodontus Kishida and Mori, 1931 (Korea) (nomen nudum)
R. quelpartis Mori, 1933 (Kin-nei, Sai-shu-to, Korea)
R. f. korai Kuroda, 1938 (Shuronmen, Seisiu-gun, Keisho-hukudo, southern Korea)
R. fudisanus Kishida, 1940 (Mt. Fuji, Honshu, Japan)
R. kosidianus Kishida, 1940 (Murakami-mura, Iwafune-gun, Niigata-ken, Honshu, Japan)
R. norikuranus Kishida, 1940 (Mt. Norikura, Nagano-ken, Honshu, Japan)
R. ogasimanus Kishida, 1940 (Oga-pensula, Akita-ken, Honshu, Japan)
R. f. martinoi Petrov, 1941 (Trifunovicevo, Brdo, Pepeliste, Yugoslavia)
R. bocharicus rubiginosus Gubarev, 1941 (Shusha, Azerbaijan)
R. f. creticum Iliopoulou-Georgudaki and Ondrias, 1986 (Lasithi, Crete)

Recognised subspecies: After Thomas (1997) the following subspecies are recognised - *ferrumequinum* in Europe and northwestern Africa; *creticum* in Crete; *irani* in Iraq, Iran and Turkmeniya; *proximus* from Afghanistan and Uzbekistan east to Kashmir; *tragatus* from northern India to eastern China; *korai* in Korea; *nippon* in Japan and eastern China.

External characters: A fairly large horseshoe bat. The ears are brownish and semitranslucent, medium long, 18.0-28.5 mm in height. The horseshoe is relatively narrow and does not cover the whole muzzle, 6.5-9.9 mm in breadth; an additional secondary horseshoe is present but sometimes hardly visible. The relatively small sella is constricted in the middle, widened below and narrowed above. The connecting process is high but bluntly rounded. The lancet is hastate, its tip generally long and slender. The number of the mental grooves varied, either one or three, the lateral ones frequently reduced. The tail is well developed, its length is 25.0-44.0 mm. In the wings the third metacarpal is characteristically short (33.7-43.2 mm in length) 8.1-14.0% less than the fourth metacarpal (37.0-47.5 mm) and 9.0-16.0% shorter than the fifth (38.5-49.5 mm). The colour of the long and dense fur is variable; the upperside is from greyish drab (lighter on the neck) to mars-brown with drab tinge; underside is from very light drab to wood-brown. The desert-dwelling Irani population has the general colour above

pale fawn, bases of individual hairs pale drab darkening to pale fawn at the tip; underparts are pale drab.

Cranial and dental characters: The skull is robustly built, the zygomatic width exceeds the mastoid width. The anterior median swellings are low, less inflated, the posterior swellings relatively well developed; the rostral profile is only slightly concave, sometimes almost straight. The crista sagittalis is from medium to prominent. The frontal depression is shallow, the cristae supraorbitales are weak. The palatal bridge is 28-35% of the maxillary toothrow.
The upper canine is very broad related to its height. The minute anterior upper premolar is completely external, situated in the angle between the canine and second premolar; frequently absent altogether. The second upper premolar (P^4) is powerful, reaches three-quarter the heights of the canine. The first lower premolar (P_2) is half the height and crown area of the well developed P_4, with which it is in contact. The middle lower premolar is external, exceedingly small or very often lost.

Bacular morphology: The proximal part of the bone forming a dorsoventrally flattened basal cone, with the ventral incision somewhat deeper than the dorsal one; the rim of the cone thickened and forms a strong protuberance on both sides of the ventral incision. The shaft tapering and almost cylindrical to continue and end as a dorsoventrally strongly flattened lancet. The dorsal side of the lancet is flat and a median ridge runs on its ventral surface. The baculum of the Indian subspecies *proximus* is considerably bigger with a longer and more flattened basal cone than that of the nominate subspecies (Topál 1975). The baculum from specimens of Japanese *nippon* is particularly large, measuring over 20% more in length than that of the specimens from the rest of the range (Thomas 1997); the bone has a lateral expansion along the whole shaft, starting immediately after the basal cone (Wallin 1969).

Similar species: In *R. ferrumequinum* the first phalanx of the third metacarpal is relatively long, exceeding half the length of the metacarpal; in *R. rouxi* and *R. affinis*, it is less than 40% (Bates and Harrison 1997). *R. ferrumequinum* is further distingusihable from *R. affinis* by its higher connecting process and clearly hastate lancet (straight sided in *R. affinis*); cranially by its reduced, external upper premolar, more widely based upper canine and the slightly less globular anterior swellings. These cranial features distinguish *R. ferrumequinum* from *R. rouxi* and *R. sinicus*, as well. *R. ferrumequinum* is larger than *R. bocharicus* and *R. clivosus* specimens from the Palaearctic Region, but is virtually indistinguishable from the larger sub-Saharan subspecies of *R. clivosus* (see taxonomic remarks below).

Taxonomic remarks: Andersen (1905a) divided the races into „eastern" (*nippon*, *tragatus* and perhaps *regulus*) and"western" (*proximus*, *ferrumequinum*) forms. East of the line drawn somewhere between Musoorie and Gilgit the individuals are generally larger, with broader horseshoe and frequently with developed lateral mental grooves. Blanford (1891) separated *R. tragatus* from *R. ferrumequinum* on account of its three mental grooves but Andersen (1905a) commented that the lateral grooves very often more or less reduced in the eastern races of the species, and treated *tragatus* as a subspecies of *R. ferrumequinum*.
The taxon *nippon* was introduced as separate species but Dobson (1876) considered it to be conspecific with *R. ferrumequinum*. Andersen (1905a) stated that *nippon* on average

markedly smaller as compared with *tragatus* and *regulus* (here considered as synonym of *tragatus*) in toothrow lengths but the nasal swellings are nevertheless quite as broad; cranially no differences were found between *nippon* and the nominotypical race. Wallin (1969) synonymised Ognev's subspecies *mikadoi* with *nippon*. According to Yoshiyuki (1989) *R. f. nippon* is greater in the mean value of the noseleaf breadth (10.7 mm) than the other subspecies. She also investigated the types of Ognev and Kishida (see above) and considered them consubspecific with *nippon*. Recently, based on mitochondrial DNA analyses Thomas (1997) found very high (21.6-24.5%) sequence divergence between Japanese *nippon* and other subspecies of *R. ferrumequinum* and suggested that *nippon* may represent a discrete species. However, due to a lack of material from India, China and Japan particularly for use in molecular analyses, no formal taxonomic conclusions were drawn regarding the status of these populations. The Korean population was recognised by Ellerman and Morrison-Scott (1951) as valid subspecies *R. f. korai*, and Thomas' (op. cit) statistical analysis supports this view.

Specimens of *R. ferrumequinum* from Afghanistan, Pakistan and the surrounding region are referred to either the nominotypical form (Ognev and Heptner 1928) or *irani* (Gaisler 1970, Mirza 1965) or *proximus* (Meyer-Oehme 1965, Siddiqui 1961), but as Gaisler (op. cit.) remarked the „validity of this subspecies [*irani*] is disputable with respect to the earlier subspecies [*proximus*]". Aellen (1959b) stated, that *irani* can be separated from the nominate race by colouration only. Strelkov *et al*. (1978) checked the features (tail length, forearm measurement) stated diagnostic between *proximus* and *irani* (Aellen 1959b, Sinha 1973) and found them doubtful when determining Central Asian material. Nevertheless, DeBlase (1980) accepted *irani* as valid subspecies based on its colouration and smaller cranial (particularly in the condylobasal length) measurements than that of *f. ferrumequinum* from Arabian Peninsula and Turkey; Rybin *et al*. (1989) recently determined specimens from Kyrgyzstan as *R. f. irani*. *R. f. proximus* is usually pale coloured and smaller, with a forearm length of 53-59 mm (Chakraborty 1977), while specimens referrable to *tragatus* tend to be larger (forearm exceeding 60 mm), the pelage colour is usually dark; the taxon *regulus* is a synonym of *tragatus* (Bates and Harrison 1997, Sinha 1973). On the other hand, Thomas (1997) based on univariate and multivariate statistical analysis accepted all *irani*, *proximus* and *tragatus* as valid subspecies.

Despite some individual variation in colour Harrison and Bates (1991) referred all specimens from the eastern littoral of the Mediterranean to the nominate form, while specimens from Iraq were assigned to the pale subspecies *irani* by Nader and Kock (1983).

R. f. martinoi was long accepted as valid subspecies by different authors (Ellerman and Morrison-Scott 1951, Djulic and Miric 1967, Felten *et al.* 1977) based on its large cranial measurements. The geographic variation of the species in south-eastern Europe was investigated by Krystufek (1993) who based on multivariate statistical analyses concluded that the descibed size differences between the nominate form and *R. f. martinoi* are due to climatic factors and considered the latter as synonym. Specimens from Crete was considered as belong to *R. f. ferrumequinum* by Felten *et al* (1977) but subsequently under the name *R. f. creticum* was separated from the continental race by its smaller measurements and paler colour (Iliopoulou-Georgudaki and Ondrias 1986).

The form *obscurus* was described as separate subspecies from Spain and subsequently applied to the north African population as well. It was synonymised with the nominal subspecies by Ellerman and Morrison-Scott (1951) and Bauer (1957). Panouse (1953) maintained its separation as a subspecies of *R. ferrumequinum* which view was followed

by Hayman and Hill (1971). However, recognising the gradual nature of geographic size changes in this species and the broad contact between *R. f. obscurus* and *R. f. ferrumequinum* in Iberia, Palmeirim (1990) and Koopman (1994) did not accept the taxonomic distinctness of *obscurus*. On the other hand, Thomas (1997) found that specimens from north-west Africa were significantly different in size from those in Europa, but by DNA analysis specimens from Europe and Algeria were consistently resolved together and both populations were finally referred to *R. f. ferrumequinum.*

Fig. 22.1. Lateral and frontal views of noseleaf of *R. ferrumequinum* (BMNH 8.3.15.1) from France. Scale = 3 mm.

Fig. 22.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. ferrumequinum* (BMNH 19.7.7.1081) from France. Scale = 3 mm.

Table 22. ***R. ferrumequinum***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		53.0	62.5		
SL	23.32	20.82	24.91	0.94	128
CM^3L	8.69	7.88	9.67	0.40	144
ZW	11.98	10.73	13.30	0.52	121
MW	10.55	9.59	11.39	0.43	122
ML	15.80	14.24	17.60	0.73	127
CM_3L	9.35	8.50	10.56	0.44	142

Rhinolophus hillorum **Koopman, 1989**
Hill's horseshoe bat
R. clivosus hillorum Koopman, 1989 (Voinjama, NW Liberia)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A large species of *Rhinolophus*. The sella is parallel-margined for much of its length. The connecting process is high and rounded; the lancet very narrow terminally, the margins in its upper quarter more or less parallel and is liberally furnished with moderate hairs. The lower lip is with a single median groove.

Cranial and dental characters: The skull is heavily built, the zygomatic breadth greatly exceeds the mastoid breadth. The anterior median swellings are low, the posterior compartments are better developed resulting an almost horizontal rostral profile. The sagittal crest well-developed, the frontal depression is very shallow. The supraorbital crests are ill-defined.
The upper canine is strong and wide at base. The first upper premolar is always lacking. In the lower toothrow the middle premolar (P_3) is missing at all, P_2 and P_4 are in full contact.

Bacular morphology: The baculum (measured on two specimens) 2.9-3.1 mm long; the distal half of the shaft broadened, the apex flattened dorsoventrally (Cotterill 2002).

Similar species: In West Africa *R. maclaudi* is larger in every respects and has a markedly different appearence; *R. alcyone* overlaps in body dimensions but its connecting process pointed and smaller cranially, with more prominent narial inflations. *R. hillorum* is distinguishable from its closest relative *R. sakejiensis* by its rounded connecting process and smaller baculum; from the other Afrotropical species of the *ferrumequinum*-group by the combination of its large external and craniodental measurements and reduced anterior nasal swellings.

Taxonomic remarks: The first west African specimens of a bat representing the *clivosus*-complex were mentioned by Hill (1968, 1982) who intimated that they probably belong to a new subspecies. This form was described by Koopman (1989) as *R. clivosus hillorum* and he pointed out that even if the very similar *keniensis*, *zuluensis* and *augur* were combined into one subspecies, *hillorum* would still remain distinct. According to Koopman (1989) and Koopman *et al*. (1995) this very large-sized western African taxon probably most closely related to *R. c. zuluensis*. But for unknown reason, Koopman (1994) missed to list *R. c. hillorum* in his comprehensive work. However, the size differences are enormous between this taxon and the other subspecies of *R. clivosus*; and beside the measurements, based on bacular, cranial and noseleaf characters Cotterill (2002) concluded that *hillorum* represents distinct species more closely related to his new species *R. sakejiensis* and both taxa distinct from all other parts of the *clivosus* complex. Cotterill (op. cit) suggested that these rhinolophids diverged in the Pleistocene to form sister species.
The hastate lancet with narrow terminal part (typical for specimens of *clivosus*, *sakejiensis*, *ferrumequinum* and *bocharicus*) of the first known individual of *hillorum* was noted by Hill ((1968), but the BM(NH) 79.459 specimen was described as having an unusually short terminal portion, but perhaps through damage (Hill 1982). The drawing of AMNH 265710 specimen provided by Cotterill (2002) also shows a short tip of lancet.

Table 23. ***R .hillorum***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		52.0	57.5		
SL		24.63			1
CM^3L	9.12	9	9.37	0.21	3
ZW	13.22	12.9	13.4	0.27	3
MW		11.2	11.5		2
ML		16.79			1
CM_3L		9.8	10.2		2

***Rhinolophus sakejiensis* Cotterill, 2002**
Sakeji horseshoe bat

R. sakejiensis Cotterill, 2002 (Kavunda, between the Sakeji and Zambezi Rivers in the Ikelenge Pedicle, Mwinilunga District, N.W. Zambia)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A large species of horseshoe bats. The ears are medium long, 19.5-21.9 mm in length. The horseshoe is relatively small, less than 9 mm accross, not covering the muzzle. The sella is almost parallel sided and widely rounded at the top. The connecting process is high, pointed, sparsely haired; the lancet is long, very hastate with a narrow, elongated tip. The lower lip is with a single median groove, the lateral ones are obliterated. The tail is 29.2-31.4 mm in length. The third metacarpal is by far the shortest (37.4 mm), the fourth is slightly shorter (42.4 mm) than the fifth (44.4 mm). The colour of the pelage of all three known specimens is fulvous; an area of darker, brown fur surrounds the eye extending from noseleaf to ear. The body fur is relatively long, at least 7 mm on the venter and over 10 mm between the scapulas.

Cranial and dental characters: The skull is very strongly built, the zygomatic width is clearly exceeds the mastoid width. The anterior compartments of the nasal swellings are reduced, appear square-sided in vertical view. The posterior swellings better developed but the rostral profile still slightly sloping backwards. The crista sagittalis strong, very distinct, the frontal depression exceedingly shallow. The supraorbital crests are indistinct. The palatal bridge is approximately one-third of the upper toothrow length.
The upper canine is long and strong, the first upper premolar is entirely missing, C^1 and P^4 are in full contact. The middle lower premolar is missing at all, the well-developed adjoining first and third premolars are always in contact.

Bacular morphology: The large baculum (total length 3.9-4.5 mm) is distinctly curved and bow-shaped in lateral view. The spatulate shaft is dorsoventrally flattened in the apical portion; the tip broad and rounded. Medially the shaft is distinctly constricted (Cotterill 2002).

Similar species: *R. sakejiensis* is easily separable from the other Afrotropical species of its group by the following character-combination: very large external and craniodental measurements (forearm over 50 mm, SL over 23 mm), high connecting process and low anterior rostral swellings. In these features the only similar species within the *ferrumequinum*-group is *R. hillorum* which has a more rounded connecting process; generally narrower skull, narrower interorbital constriction (Cotterill 2002) and the males have much smaller bacula (2.9-3.1 vs. 3.9-44 mm total bacular length). *R. deckeni, R. silvestris*, *R. hildebrandti* and *R. eloquens* are all similar or overlap in size but have differently shaped noseleaf and more pronounced anterior rostral swellings.

Taxonomic remarks: According to Cotterill (2002) the bacular morphology, noseleaf and skull characteristics of *sakejiensis* places it in the *ferrumequinum*-clade of Bogdanowicz (1992), together with *hillorum* (as distinct species) and *clivosus*. These three species comprise the *clivosus*-complex.

Fig. 24.1. Lateral and frontal views of noseleaf of *R. sakejiensis* (HZM 1.32236 - paratype) from Zambia. Scale = 3 mm.

Fig. 24.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. sakejiensis* (HZM 1.32236 - paratype) from Zambia. Scale = 3 mm.

Table 24. ***R. sakejiensis***: External, cranial and dental measurements (mm).

	min	max	n
FA	52.5	55.2	
SL	25.11		1
CM^3L	9.71		1
ZW	13.43		1
MW	11.11		1
ML	16.74		1
CM_3L	10.23		1

***Rhinolophus silvestris* Aellen, 1959**
Forest horseshoe bat
R. silvestris Aellen, 1959 (N'Dumbu Cave, Latoursville, Gabon)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A fairly large species of its genus. The ears are medium, 21.9-23.2 mm in height. The horseshoe is 9.5-10.0 mm in width across, covering the whole of the muzzle. The sella is naked, wide, constricted at the middle and widely rounded off at its terminus. The connecting process widely rounded and in some cases slightly directed downwards; the lancet is more or less an equilateral triangle, its sides are slightly concave. The lower lip is with one distinct central and ill-defined lateral grooves. The tail 26.1-32.0 mm in length. In the wings, the third metacarpal (33.0-36.8 mm) is much shorter than the fourth (37.0-42.0 mm) and the fifth (38.0-42.0 mm), which are subequal in length or the fifth is slightly longer. The colour (based on wet specimens) is darker rufous-brown on the dorsal side, ventrally lighter; the individual hairs are unicoloured.

Cranial and dental characters: The skull is massive, the zygomatic width greatly exceeds the mastoid width. The nasal swellings are moderately developed, the anterior compartments are semicircular in outline. The crista sagittalis is prominent; the frontal depression is moderately developed and bordered by well-defined supraorbital ridges. The palatal bridge is 31-34% of the upper toothrow length.
The upper canine is short, strongly built, and close to or just in contact with the posterior upper premolar (P^4). The first upper premolar is reduced and outside the toothrow. The first (P_2) and third (P_4) lower premolars are also in contact; the middle lower premolar is minute, extruded from the row or sometimes missing.

Similar species: The cranially similar sized *R. alcyone* has longer and more slender upper canine, much larger P^2 which is situated in the row or only slightly extruded, and a very shallow rostral depression. *R. clivosus* is usually smaller and its rostral profil is nearly straight. There is no recognisable differences in the skulls of *R. silvestris* and *R. deckeni*. Another cranially very similar species is *R. fumigatus*; the only recognisable (although very small) difference is the always contacting position of the upper canine and posterior premolar (P^4) of *R. fumigatus*; these teeth are usually slightly separated in *R. silvestris*. However, the two species is readily distinguishable by external features. *R. fumigatus* has densely pilose sella, the connecting process is lower and terminating at the tip of sella, and greyish fur.

Taxonomic remarks: The taxonomic position of this taxon is questionable. According to Allen (1959) the first specimen of the species was investigated by Sanborn (1953) who determined it as *R. fumigatus*. Aellen (op. cit.) compared his new *R. silvestris* with *R. fumigatus* in details, and remarked the considerable differences between them. He suggested that *R. silvestris* may be a western forest representative of the larger *R. deckeni* but noted it probably will only be the subspecies of the latter as more material become available. Aellen and Brosset (1968) still found the differences between the two species well-established, but speculated that the probable intervening populations should be intermediate in characters. Hayman and Hill (1971) listed it as a subspecies of *R. clivosus*; and Koopman (1994) although recognised it as full species, remarked that it probably only a subspecies of *R. deckeni*. As it was already stated by Koopman (1975) the shape of the nasal swellings and basisphenoid bridge is clearly separate *R. silvestris* and *R. deckeni* from *R. clivosus* and this separation is supported by the structure of the noseleaf. The differences between *R. silvestris* and *R. deckeni* are, however, very slight.

Fig. 25.1. Lateral and frontal views of noseleaf of *R. silvestris* (MHN 965.40 - holotype) from Gabon. Scale = 3 mm.

Fig. 25.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. silvestris* (MHN 965.40 - holotype) from Gabon. Scale = 3 mm.

Table 25. ***R. silvestris***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		49.5	54.5		
SL	23.12	22.29	23.68	0.66	5
CM^3L	8.83	8.52	9.20	0.27	5
ZW	11.94	11.51	12.25	0.31	5
MW	10.83	10.52	11.07	0.27	5
ML	15.91	15.38	16.69	0.59	4
CM_3L	9.45	9.14	9.98	0.39	4

***Rhinolophus eloquens* Andersen, 1905**
Eloquent horseshoe bat
R. hildebrandti eloquens Andersen, 1905 (Entebbe, Uganda)
R. hildebrandti perauritus De Beaux, 1922 (Territory of the Rahanuin, southern Somaliland)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *perauritus* in southern Somalia; *eloquens* from southern Sudan to eastern Zaire and northern Tanzania, Pemba and Zanzibar.

External characters: A fairly large species of horseshoe bats. The ears are medium or large, about 27 mm in height. The horseshoe is very broad, covering the whole muzzle; its breadth is about 11 mm. The sella is suddenly emarginated after its proximal third, parallel sided above; its margins and front face are clothed with long hairs. The connecting process is a continuous arch, terminating near the tip of sella. The lancet is moderately long, almost straight sided. The lower lip is with one mental groove. The tail is comparatively short, 21.0-24.8 mm. In the wings, the third metacarpal is short (39.8-42.0 mm), and beside the longer fourth (42.5-44.3 mm), the fifth metacarpal is the longest (44.0-45.2 mm). The upperside is tinged with wood brown, paler beneath. The base of the hairs both on the upper and under sides is dark smoke grey.

Cranial and dental characters: The skull is robustly built, the zygomatic width is much greater than the mastoid width. The anterior median and lateral swellings are well inflated, the posterior ones are shifted to a more lateral position. The crista sagittalis is strong, the frontal depression is moderately deep or sometimes shallow. The supraorbital crests are low, but well defined. The palatal bridge is relatively long, 32-37% of the upper toothrow length.
The canines are massive basally, medium long. The first upper premolar (P^2) is exceedingly small or absent altogether; if present always fully extruded from the row, C^1 and P^4 is contact. The middle lower premolar is almost always wanting, the cingula of the adjoining premolars are overlapping each other.

Similar species: Externally, the large size, greyish colouration, densely pilose sella and wide horseshoe separate *R. eloquens* from all other African species except *R. fumigatus* (from which is separable by cranial measurements) and *R. hildebrandti* which species is even larger by forearm length.
Cranially, the great skull and toothrow length values, the combination of the massive canines, missing or excessively minute anterior upper and middle lower premolars and the rather bulbous anterior swellings separate the species from its congeners; the craniodental measurements overlap only slightly with those of *R. hildebrandti*.

Taxonomic remarks: Both taxa recently accepted as races of *R. eloquens* was described as subspecies of the much larger *R. hildebrandti*. Andersen (1905f) remarked that the „largest specimens of *Rh. H. eloquens* fall short of the smallest individuals of the typical form". As he noted „until now, however, the very large *Rh. Hildebrandti* and its small counterpart, *Rh fumigatus*, have been without any intermediate link, widely separated in size as well as in geographical distribution. *Rh. H. eloquens* greatly reduces the gap

between the two species". Nevertheless, Andersen later on (1907a) listed *R. eloquens* as full species, which view was followed by Allen (1939). Subsequently, *eloquens* were transferred to the smaller *R. fumigatus* (see Hayman and Hill 1971), but Koopman (1965, 1966) distinguished *aethiops* as full species from *fumigatus* largely on size and recognised *eloquens* as its subspecies. Later on (Koopman 1975) he revised this opinion and remarked that it was erroneous associating the East African *eloquens* with the Southwest African *aethiops* (see also comments under *fumigatus*). Aellen (1957) still recognised *perauritus* as a subspecies of *R. hildebrandti* but at once remarked that its smaller size linked it to *R. fumigatus* rather than to *R. hildebrandti*. Koopman (1975) studied the type specimens of *perauritus* and concluded it is closely similar to *eloquens* but is somewhat larger, and may be retained as a subspecies of *R. eloquens*.

Fig. 26.1. Lateral and frontal views of noseleaf of *R. eloquens* (AMNH 82391) from Uganda. Scale = 3 mm.

Fig. 26.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. eloquens* (BMNH 99.8.4.4 - holotype) from Uganda. Scale = 3 mm.

Table 26. ***R. eloquens***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		54.0	60.5		
SL	25.40	24.78	26.23	0.32	36
CM^3L	9.22	8.56	9.58	0.24	38
ZW	12.91	12.25	13.48	0.28	37
MW	11.67	11.13	12.15	0.20	37
ML	17.39	16.77	18.02	0.30	39
CM_3L	9.87	9.25	10.26	0.25	39

***Rhinolophus fumigatus* Rüppell, 1842**
Rüppell's horseshoe bat
R. fumigatus Rüppell, 1842 (Shoa Province, Ethiopia)
R. aethiops Peters, 1869 (Otjimbingue, Southwest Africa)
R. macrocephalus Heuglin, 1877 (Adowa, Abyssinia)
R. antinorii Dobson, 1885 (Daimbi, Shoa)
R. fumigatus exsul Andersen, 1905 (Kitui, Kenya Colony)
R. foxi Thomas, 1913 (Kabwir, Bauchi plateau, northern Nigeria)
R. acrotis (not of Heuglin, 1861) Allen, 1914 (Magangani, Blue Nile Province, Sudan)
R. abae Allen, 1917 (Aba, Uele district, Congo Belge)
R. aethiops diversus Sanborn, 1939 (Bakel, Senegal, French West Africa)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *exsul* from central Sudan to Tanzania; *fumigatus* in Ethiopia; *abae* in northeastern Zaire; *foxi* from Central African Republic to Burkina Faso; *diversus* in

Guinea, Sierra Leone, Gambia and Senegal; *aethiops* from Zambia and Angola to the Cape Province.

External characters: A medium to fairly large species. The ears are small to medium, 20.0-28.0 mm in height. The horseshoe is wide (9.0-10.2 mm), alomst covering the whole of the muzzle; a secondary leaflet is present. The sella is broad, only sligthly emarginated below the middle, its lateral margins subparallel; the front face is densely pilose with long straight hairs. The connecting process is relatively low, broadly rounded off and terminating near the very tip of the sella. The lancet is almost straight sided. The lower lip is with a single median groove. The tail is 21.0-35.0 mm in length. In the wings, the third metacarpal is the shortest (34.5-42.5 mm), the fourth is longer (36.8-44.0 mm), and the fifth (38.0-45.0 mm) is usually subequal to or rarely longer than the fourth. The colour of upperparts is greyish-brown; the underparts are light grey the hairs on the chest and belly are with lighter tips.

Cranial and dental characters: The skull is quite massive, the zygomatic width is greatly exceeds the mastoid width. The anterior median swellings are prominent, the posterior ones less inflated. The sagittal crests are strong or very strong, the frontal depression is shallow or only moderately deep. The cristae supraorbitales are weak but well visible. The length of the palatal bridge is very variable, 28-37% of the maxillary toothrow.
The upper canine is short and strong. The first upper premolar is very frequently missing, if present exceedingly minute and totally external; the neighbouring C^1 and P^4 are always widely overlapping each other. The middle power premolar is only rarely present, the P_2 is tightly compressed between C_1 and P_4.

Similar species: *R. alcyone* is similar by cranial measurements, but characterised by the relatively large anterior upper and middle lower premolars and a very shallow rostral depression. *R. capensis* is usually greater in every craniodental measurements and has a relatively large, less external anterior upper premolar (P^2). *R. clivosus* has very low anterior nasal swellings and almost horizontal rostral profile. *R. darlingi* is smaller in every craniodental measurements. *R. deckeni* has a naked sella and differently shaped connecting process; cranially they are almost identical, but the upper canine and the anterior upper premolar is separated by a small gap in this species (these teeth are touching each other in *R. fumigatus*). By forearm measurements, *R. fumigatus* is almost same sized as *R. eloquens*, but the cranial and dental measurements are readily separate the two closely related species.

Taxonomic remarks: The taxonomic position of several described forms of the three recently accepted and closely related species *hildebrandti*, *eloquens* and *fumigatus* was long questionable. *R. fumigatus* and *R. macrocephalus* were regarded as „small forms of *Rh. ferrum-equinum* with dark coloured fur" by Dobson (1878, 1880) but Andersen (1904b) evidenced, that these two taxa were based upon conspecific individuals and „they are the same species as, later on, described by Dobson under the name *Rh. Antinorii*". *R. aethiops* was kept as separate species by Andersen (1907a), Allen (1939) and Roberts (1951). Ellerman *et al.* (1953) treated *aethiops* as a race of *fumigatus* and Aellen (1959a) also included *aethiops* in *fumigatus* as either a synonym or a subspecies. Koopman (1965, 1966) distinguished *aethiops* from *fumigatus* at specific level by its larger size and applied the name *aethiops* to those forms with a forearm of 55-60 mm.

The recently removed and cleaned skull of the type specimen of *aethiops* (MNB 3295) also shows very large cranial measurements as compared with the lectotype specimen (SMF 4372) of *fumigatus* (SL 23.57 mm vs. 21.86 mm, ML 16.25 mm vs. 14.99 mm). Hill (in Grubb *et al*. 1998) thought possible that *diversus* might be more properly regarded as a subspecies of *R. aethiops* if this taxon is specifically distinct from *R. fumigatus*. The forearm length of *diversus* is rather greater than in *fumigatus* and its close allies, and the dimensions of the skull are similar to those of *aethiops* as it was already noted by Rosevear (1965). Koopman (1975, 1994) finally listed *aethiops* as a subspecies of the smallest species of the group *R. fumigatus*. Thomas (1913) described *foxi* as new species and connected with *deckeni*; but Rosevear (op. cit.) evidenced its true relationship with *R. fumigatus*. The form *abae* was considered specifically distinct by Allen (1939), but Koopman (1965, 1975) discussed its allocation and stated it may stands as a subspecies of *R. fumigatus*, distinct from *R. f. exsul* on the bases of somewhat larger size.
The full size range of the species from *fumigatus* to *aethiops* is too wide for a single species (Rosevear 1965) and the inclusion of more than one species under the name *R. fumigatus* is possible. As Koopman (1975) noted, *R. fumigatus* appears to demonstrate character displacement, being most distinct from *R. eloquens* where it occurs with it in East Africa (*R. f. exsul*) and least distinct outside the range of *R. eloquens* (*abae*, *fumigatus*, *foxi*, *diversus*, *aethiops*). The exact geographic limits of the subspecies of *R. fumigatus* have never been worked out (Koopman 1994).

Fig. 27.1. Lateral and frontal views of noseleaf of *R. fumigatus* (HNHM 95.87.1.) from Ethiopia. Scale = 3 mm.

Fig. 27.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. fumigatus* (SMF 4372 – lectotype) from Ethiopia. Scale = 3 mm.

Table 27. ***R. fumigatus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		47.0	60.0		
SL	22.69	21.58	24.25	0.68	60
CM^3L	8.32	7.72	8.96	0.28	62
ZW	11.75	10.84	12.70	0.39	57
MW	10.56	9.68	11.28	0.34	57
ML	15.53	14.68	16.64	0.45	61
CM_3L	8.96	8.33	9.61	0.30	61

***Rhinolophus hildebrandti* Peters, 1878**
Hildebrandt's horseshoe bat
R. hildebrandti Peters, 1878 (Ndi, Taita, Kenya)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A large species of its genus. The ears are medium or large, 28.0-37.0 mm in height. The horseshoe is characteristically wide, covering the muzzle, 12.0-15.0 mm in width across. The sella is constricted at its proximal third, with slightly ovate or almost parallel sides above. Its front is densely pilose with long hairs. The lancet is relatively long, straight sided. The lower lip is with a single median groove. The tail length is 27.5-45.0 mm. In the wings, the third metacarpal is shortened (42.3-48.0 mm), the fourth is longer (44.2-49.0 mm) and the fifth (45.3-50.0) is the longest. The upperparts are greyish-brown, the individual hairs long and unicoloured; the underparts are about the same colour or very slightly paler.

Cranial and dental characters: The skull is large and heavily built, the zygomatic width is much greater than the mastoid width. The anterior median swellings are well inflatred, bulbous, longer than wide; the lateral and posterior swellings are moderately developed. The crista sagittalis is quite strong in its full length. The frontal depression is shallow or moderate, the bordering supraorbital crests are well defined but not always with sharp ridges. The palatal length is long or moderately long, 32-38% of the upper toothrow length.
The upper canine is large based, relatively long. The anterior upper premolar is usually missing, if present small or minute, but always fully outside of row. The upper canine and P^4 in most cases are in contact. In the lower jaw, the middle premolar (P_3) was wanting in all the investigated specimens, the anterior lower premolar is tightly compressed between the canine and the posterior premolar.

Similar species: The only similar species is *R. eloquens*, which is smaller in almost every respects, although there is a small overlap in the craniodental mesurements. The large size, greyish colouration, unmodified narial cup and connecting process, the reduced (or missing) and extruded anterior upper and middle lower premolars separate *R. hildebrandti* from the other Ethiopian *Rhinolophus*.

Taxonomic remarks: Andersen (1905f) when described *eloquens* (intermediate in size and geographical distribution between *R. hildebrandti* and *R. fumigatus*) speculated, “it is not improbable that when the region between Uganda and Abyssinia is better explored, we shall have to regard *Rh. Hildebrandti* and *Rh. fumigatus* no longer as distinct ’species’, but rather as peripheral forms of one species, bound together by races”.

Fig. 28.1. Lateral and frontal views of noseleaf of *R. hildebrandti* (BMNH 87.1073) from Malawi. Scale = 3 mm.

Fig. 26.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. hildebrandti* (BMNH 79.1.21.1 - cotype) from Kenya. Scale = 3 mm.

Table 28. ***R. hildebrandti***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		60.5	67.0		
SL	27.37	26.06	28.67	0.72	44
CM^3L	10.08	9.20	10.65	0.35	48
ZW	13.98	12.62	14.95	0.47	44
MW	12.50	11.58	13.23	0.39	40
ML	18.98	17.65	20.63	0.64	48
CM_3L	10.83	9.91	11.45	0.37	47

HIPPOSIDEROS-GROUP

***Rhinolophus hipposideros* (Bechstein, 1800)**
Lesser horseshoe bat
Vespertilio ferrum-equinum minor (Kerr, 1792) (preoccupied by *V. molossus minor* Kerr, 1792)
Noctilio hipposideros (Bechstein, 1800) (France)
Vespertilio minutus (Montagu, 1808) (Wiltshire, England)
R. bihastatus Geoffroy, 1818 (Europe)
? *R. bifer* Kaup, 1829 (nomen nudum)
R. minimus Heuglin, 1861 (Keren, Eritrea)
R. h. alpinus Koch, 1863 (Alps)
R. h. pallidus Koch, 1863 (Mediterranean region)
R. eggenhöffner Fitzinger, 1870
R. bihastatus kisnyiresiensis Daday, 1885 (Kisnyires Cave, Szolnok-Doboka) (nomen nudum)
R. h. troglophilus Daday, 1887 (renaming of *R. bihastatus kisnyiresiensis* Daday, 1885)
R. euryale helvetica Bretscher 1904 (Baar, Zug, Switzerland)
R. phasma Cabrera, 1904 (Madrid, Spain)
R. midas Andersen, 1905 (Jask, Persian Gulf)
R. h. majori Andersen, 1918 (Patrimonio, N. Corsica)
R. h. escalerae Andersen, 1918 (Ha-ha, Mogador, Morocco)
R. anomalus Söderlund, 1920 (Wildbad Gastein, Salzburg, Austria)
R. intermedius Söderlund, 1920 (Wildbad Gastein, Salzburg, Austria)
R. h. vespa Laurent, 1937 (Korifla, Morocco)
R. h. intermedius (not of Söderlund, 1920) Laurent, 1943 (Geneva, Switzerland)
R. moravicus Kostron, 1943 (Moravia)

Recognised subspecies: Partly after Koopman (1994) the following subspecies are recognised - *escalerae* in north Africa; *minimus* from southern Europe to the eastern end of the Mediterranean, including several islands and south to Ethiopia and Sudan; *majori* in Corsica; *minutus* in Britain and Ireland; *hipposideros* in continental Europe to the eastern end of Black Sea; *midas* from Transcaucasia and Iraq to Kazakhstan and Kashmir.

External characters: A relatively small sized species of *Rhinolophus*. The ears are small, 12.0-19.0 mm in height. The horseshoe almost covers the muzzle and measures 5.0-7.3 mm in width. The sella is long and narrow, lateral margins convergent, its tip pointed and projects downwards and forwards. The connecting process is low and rounded (sometimes very bluntly pointed). The lancet is long, narrow and cuneate, its tip bluntly pointed. The lower lip is with one mental groove. The tail is 17.5-36.0 mm long. In the wings, the third metacarpal is the shortest, 22.2-29.3 mm; the fourth is 23.0-31.9 mm, subequal in length to the fifth, which is 23.5-31.3 mm in length. The general colour above is light or dark brown, base of hairs ecru-drab; the underside is ecru-drab or greyish drab.

Cranial and dental characters: The skull is very delicately built; the braincase is relatively narrow, the zygomatic width is only slightly exceeds or subequal to the mastoid width. The shape of the zygomatic arch is unique within the genus being a very weak and slender bone, at its anterior half running nearly parallel to the toothrow. The rostrum is relatively low, the anterior median swellings are moderately inflated, the posterior ones are well developed. The sagittal crest is medium, but quickly flattened posteriorly. The frontal depression is shallow, flanked by weak supraorbital ridges. The palatal length is variable, usually 29-33 (very rarely up to 36) % of the maxillary toothrow.
The upper canine is delicate, its heights is barely exceeds the cusp of the corresponding last premolars. The first upper premolar is a well developed, functional tooth (the largest in the genus in relation to the upper canine) which lies entirely in the toothrow. The second lower premolar is very small, normally situated externally to the toothrow; the first and third lower premolars are in contact or separated by a small gap.

Bacular morphology: As compared with the body measurements the size of os penis is remarkably large. The ventral incision is deeper and always simple, the dorsal one is less deep and may have manifold lobes. There is a broad groove on the ventral surface of the basal cone bordered by knob-like protuberances. The median and distal parts of the bone bend upwards. The tip is with a button-like knob (Topál 1958).

Similar species: Contrary to *R. pusillus* the third upper molar possesses a distinct fourth comissure and a metastyle (Harrison 1964, Bates and Harrison 1997). The third metacarpal is considerably shorter (80.1-88.8%) than the combined length of its respective phalanges; in *R. pusillus*, *R. lepidus* and *R. subbadius* the third metacarpal is about equal to or exceeds the length of the phalanges. The second phalanx of the fourth finger is noticeable long in comparison to those of *R. pusillus* and *R. lepidus*. In *R. hipposideros*, it is 171-203% the length of the first phalanx; this ratio is only 104-143% in the other two species (Bates and Harrison 1997).
In general, by the small size, very low connecting process and high lancet; reduced canine but relatively very large anterior upper premolar and weak zygomata *R. hipposideros* is easily separable from all its congeners.

Taxonomic remarks: The very narrow basioccipital region (due to the large cochleae) was the base of the separation of the *midas*-group of Andersen (1905a) comprising the species *midas* and *hipposideros*. This feature is, however, slightly variable within the species; the cochleae are sometime almost in contact, in other individuals situated further from each other. Similar variation can be observed in *R. pusillus*, as well,

although the very narrow basioccipital much rarer in the latter species. Nevertheless, the placing of *R. hipposideros* in its own group is also supported by Bogdanowicz's (1992) phenetic analysis and by cranial characters.
The race *midas* named from Iran is distinguished by the form of the sella (Andersen 1905a), which is considerably broader accross its base (2.3 mm in the type) than those of *R. h. hipposideros* and *R. h. minimus* where the breadth of sella is less than half the height. DeBlase (1980) re-examined the holotype of *midas*, and as noted "cannot determined any method of measurement that will produce dimensions even approximating those of Andersen" and found no reliable differences in the sella shape when compared specimens from Europe, Turkey, Lebanon, Jordan and Iran. Reporting specimens from Afghanistan Gaisler (1970) considered the dental difference between *h. midas* and *h. hipposideros-h. minimus* to be significant; in all the Afghani specimens the first and third lower premolars are nearly or completely touching, while in some 100 specimens from the +nominate subspecies examined there is a distinct interspace between P_2 and P_4. DeBlase (op. cit.) again found this character very highly variable in populations in Iran. The subspecific status of the Turkmenian population was not determined by Strelkov *et al*. (1978). *R. h. minimus* is smaller in every respect than the nominate form, its forearm length is between 34.7-38.0 mm (Andersen 1905a). Felten *et al* (1977) restricted the distribution area of *minimus* to the type locality (Eritrea) and Crete only. Since the descriptions of the north African forms *escalerae* and *vespa* were based on very limited samples and both were described from Morocco, Panouse (1951) doubted their validity; he also mentioned that the type of *vespa* has disappeared. Although Koopman (1994) listed both *escalerae* and *vespa* as valid subspecies (but did not give information on their geographic limits within north Africa), it appears unjustified to retain two sympatric subspecies and *vespa* is considered here as junior subjective synonym of *escalerae*. According to Palmeirim (1990) *R. hipposideros* varies locally with climatic conditions and the size similarities along the Mediterranean do not reflect a close evolutionary relationship among the population of the area, and believe that no subspecies of *R. hipposideros* should be distinguished within continental Europe. The separation of the form *minutus* (in average also smaller than *R. h. hipposideros*) from the British Isles also seems to be unjustifiable (Blackmore 1964).
The date of the species (as *R. h. midas*) from Jammu and Kashmir, India (Topál 1975, Bates and Harrison 1997) is based on specimens belong to another taxon, more probably close to the Afghani population of *R. lepidus*.

Fig. 29.1. Lateral and frontal views of noseleaf of *R. hipposideros* (HNHM 2823.1) from Switzerland. Scale = 3 mm.

Fig. 29.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. hipposideros* (BMNH 601.c.3) from France. Scale = 3 mm.

Table 29. ***R. hipposideros***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		34.0	42.0		
SL	15.47	14.53	16.65	0.42	49
CM^3L	5.42	5.02	6.27	0.20	54
ZW	7.53	6.68	8.22	0.25	48
MW	7.40	7.05	8.01	0.19	47
ML	9.82	8.83	10.85	0.33	51
CM_3L	5.65	5.16	6.68	0.24	52

LANDERI-GROUP

***Rhinolophus alcyone* Temminck, 1852**
Halcyon horseshoe bat
R. alcyone Temminck, 1852 (Boutry River, Gold Coast)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized horseshoe bat. The ears are medium, 19.6-25.0 mm in height. The horseshoe is broad (8.8-10.5 mm), supplementary leaflet is present. The sella is almost parallel-sided, only slightly pandurate, its tip widely rounded; the front face is covered with extremely short white hairs. The connecting process is a usually bluntly, sometimes sharply pointed triangle. The lancet is straight sided or its lateral margins are only slightly emarginated. The lower lip is with one groove, rarely with indistinct lateral ones. The tail is relatively short, 17.1-32.0 mm in length. In the wings, the third metacarpal is distinctly shortened (34.8-40.2 mm), the fourth (38.7-44.5 mm) and the fifth (39.9-44.8 mm) are subequal or the fifth is slightly longer. There are two distinct colour phases; the upperparts is usually deep brown, the rufous phase is much rarer. The belly is almost as dark as the back. An intermediate form is also described, being mostly dark-brown, but had some orange-brown on the rump and on the shoulders above the scapule. The males sometimes possess bright orange axillary tuft.

Cranial and dental characters: The skull is storngly built, the zygomatic width is greatly exceeding the mastoid width. The anterior median swellings are globular, pronounced; the lateral and posterior swellings are medium. The crista sagittalis is moderately or strongly developed. The frontal depression is very shallow and flanked with weak supraorbital crests. The palatal bridge moderately long, 29-35% of the maxillary toothrow.
The upper and lower canines are strong and long. The well-developed first upper premolar is in the toothrow or maximum halfway extruded, separating the upper canine and the posterior upper premolar. This latter is reaching more than halfway the height of the canine. The lower middle premolar is medium or small, just reaching the cingula of the adjoining premolars; sometimes within, usually out of row. The first (P_2) and third (P_4) lower premolars are separated from each other.

Similar species: The other African species with similar triangular connecting process (*R. guineensis*, *R. landeri*) are smaller, at least cranially; *R. blasii* has a differently shaped, longer and narrow-based connecting process and also smaller in every craniodental measurements. The connecting process of some *R. clivosus* may be similar, but in this species the sides of the lancet are concave (not being almost straight as in *R. alcyone*).
Within the distribution area of *R. alcyone* the following species are fall into the same size class by cranial measurements: *R. fumigatus*, *R. clivosus* and *R. silvestris*. *R. fumigatus* differs from *R. alcyone* having an excessively minute anterior upper and lower premolar (if not missing at all) and a deep frontal depression. *R. clivosus* is distinguishable by its very low anterior median swellings and also by the fully displaced, minute P^2 and P_2. *R. silvestris* is characterised by its shorter, less curved and more massive upper canines, minute and more extruded anterior upper premolar, more bulbous anterior median swellings and slightly deeper frontal depression.

Taxonomic remarks: The description of the species was characterised by Andersen (1906) as being very vague and fragmentary that nobody has been able to identify the species with any degree of certainty. Based on a second specimen Andersen (op. cit.) provided a detailed description and allied the species close to, but separable by its much larger size from *R. landeri* and *R. lobatus* (this latter is recently accepted as subspecies of the former species).
Eisentraut (1964) reported specimens from Bioco being larger (mainly in the ear measurements) than the mainland population but refrained to separate them subspecifically.

Fig. 30.1. Lateral and frontal views of noseleaf of *R. alcyone* (BMNH 68.328) from Cameroon. Scale = 3 mm.

Fig. 30.2. Lateral view of the rostral part of the skull and occlusal view of the left upper (left) and right lower (right) anterior dentition of *R. alcyone* (RMNH 35892 - holotype) from Guinea. Scale = 3 mm.

Table 30. ***R. alcyone***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		49.0	54.0		
SL	22.28	21.00	23.29	0.59	30
CM^3L	8.63	8.09	9.07	0.24	32
ZW	11.61	10.96	12.12	0.30	30
MW	10.63	10.13	11.07	0.24	30
ML	15.46	14.39	16.42	0.42	31
CM_3L	9.26	8.45	9.80	0.32	31

***Rhinolophus blasii* Peters, 1866**
Peak-saddle horseshoe bat
R. clivosus Blasius, 1857 (Italy) (preoccupied by *R. clivosus* Cretzschmar, 1828)
R. blasii Peters, 1866 (replacement name for *R. clivosus* Blasius, 1857)
R. empusa Andersen, 1904 (Zomba, Nyasaland)
R. andreinii Senna, 1905 (Adi Ugri, Eritrea)
R. brockmani Thomas, 1910 (Upper Sheikh, British Somaliland, 4500 feet)
R. b. meyeroehmi Felten, 1977 (Pashtunkot, Grotte Zarmast, 1295 m, Fariab Prov., Afghanistan)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *blasii* in northwestern Africa, southern Europe and southwestern Asia; *meyeroehmi* in Iran, Turkmenia, Afghanistan and Pakistan; *andreinii* in Ethiopia, Somalia; *empusa* in southestern Africa from southern Zaire to Transvaal.

External characters: A medium sized species of *Rhinolophus*. The ears are medium (15.0-22.0 mm) and are translucent light brown. The horseshoe does not cover the muzzle, its width is 6.6-9.0 mm. The sella is wedge-shaped, its lateral margins converging towards the summit, which is subacutely pointed. The connecting process is a relatively long, erect (not curved) and pointed horn; the lancet is long, almost straight sided or only slightly concave. The lower lip is with three mental grooves. The tail is 15.4-35.0 mm. The third metacarpal is the shortest (28.5-33.5 mm), and beside the longer fourth (30.9-36.5 mm) the fifth metacarpal is the longest (32.6-38.5 mm). The colour is light brown or yellowish-brown above, greyish, white or creamy beneath. Individual hairs are long and soft, their base is cream coloured. From the shoulders to the base of tail they are tipped with brown, the hairs on the back of the neck showing very little tipping and giving the appearence of a lighter band. Sides of face are yellowish-white, with a marked dark brown patch under each eye. Within the subspecies *empusa* there are greyish and orange colour phases.

Cranial and dental characters: The skull is delicately built, the zygomatic and mastoid width is usually subequal. The anterior median swellings are moderately low, their anterior border protruding beyond anteriorly the lateral swellings. The crista sagittalis is usually weak, sometimes moderately developed. The frontal depression shallow or very shallow, the bordering supraorbital ridges are ill-defined. The palatal bridge is medium long, 32-35% of the upper toothrow length.
The upper canine is relatively short (but not weak), its height is only slightly exceeds that of the posterior upper premolar; the latter is well developed. The anterior upper premolar is moderate or relatively large (sometimes quite flat, without any central cusp, in other cases with a distinct cusp) and placed in the toothrow. The middle lower premolar (P_3) small or very small, its situation in the toothrow is variable. The first and third lower premolars are usually not in contact; the crown area of P_2 is equal to or only slightly smaller than that of the P_4.

Bacular morphology: The ventral incision of the basal cone is moderately deep, on the dorsal side is lacking emargination. The shaft is approximately cylindrical in cross section and clearly bend upwards. The tip of the shaft is without terminal knob.

Similar species: According to Happold and Happold (1989) the ratio of first phalanx to the metacarpal of the fourth finger important character for the distinction between *R. blasii* (ratio 1:3.1-3.9) and *R. landeri* (ratio 1:4.3-5.6). In the Palaearctic Region, *R. euryale* has a less sharply pointed but slightly more elongated connecting process and a much wider sella; *R. mehelyi* has a bluntly pointed connecting process and distinctly emarginated lancet.
Cranially, *R. blasii* is further characterised by a marked depression between the parietal and occipital region, so that the occipitale is distinctly demarcated from the rest of the braincase (Harrison 1964). The crown areas of the first and third lower premolars are nearly equal in *R. blasii* while P_2 is about half the area of P_4 in *R. euryale*. The skulls of *R. landeri* and *R. simulator* are similar, but is characterised by an antero-posteriorly shorter anterior nasal swellings and longer, more curved upper canine (this feature is usually more expressed in the former species). *R. clivosus* is readily separable by its more robust upper canine and wide zygomatic arch.

Taxonomic remarks: Discussing the affinities within his *lepidus* (= *pusillus*) group, Andersen (1904a , 1905a) noted, that *R. empusa* and *R. blasii* are two extremely closely allied species, that time separated by an enormous tract (between the Mediterranean and Nyasaland) where no relative appears to be occur. Similarly, Andersen (1905d, 1906) placed *R. andreinii* very close to *R. blasii* and separated the two by minor differences in the sella shape only. Thomas (1910) described *brockmani* as being close to *R. landeri* but Koopman (1975) studied the type and revealed that all the skull and tooth characters Thomas used to distinguish *brockmani* from *dobsoni* (= *R. landeri*) are actually characters that distinguish *R. blasii* from *R. landeri*. He concluded, that *brockmani* best considered a synonym of *R. b. andreinii*. Allen (1939) still regarded *andreinii*, *brockmani* (interestingly as members of the *simplex* group) and *empusa* as full species, but later (Ellerman *et al*. 1953, Hayman and Hill 1971) these taxa were considered conspecific. It appears that the broader horseshoe and more sharply cuneiform sella may separate *empusa* from the nominate race (Ansell 1978).
Felten (in Felten *et al*. 1977) found that specimens from Afghanistan and Iran are characterised by slightly larger cranial and forearm measurements and mainly by longer phalanges of the fourth finger and described them as a new subspecies *R. b. meyeroehmi*. This finding was anticipated by Aellen (1959b) who described specimens from the eastern part of the distribution area of the species as larger than those from south Europe.
As Kock (1988) pointed out, it was not determined if the Pakistani population (recorded by Roberts 1977) belong to *R. b. meyeroehmi*; later on Corbet and Hill (1992) referred it to the subspecies in question. Harrison and Bates (1991) provisionally referred all specimens from Arabia to the nominate subspecies, but the subspecific status of the Oman and Yemen populations not entirely clear and these notable pale specimens may represent a yet undescribed subspecies.

Fig. 31.1. Lateral and frontal views of noseleaf of *R. blasii* (HNHM 2498.2) from Albania. Scale = 3 mm.

Fig. 31.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. blasii* (HNHM 2964) from Yugoslavia. Scale = 3 mm.

Table 31. ***R. blasii***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		40.0	51.0		
SL	19.20	18.17	19.98	0.46	38
CM^3L	6.70	5.65	7.10	0.28	40
ZW	9.21	8.09	9.88	0.34	37
MW	9.17	7.97	9.61	0.29	37
ML	12.05	10.99	12.80	0.44	40
CM_3L	7.00	6.01	7.62	0.31	40

***Rhinolophus guineensis* Eisentraut, 1960**
Guinea horseshoe bat
R. guineensis Eisentraut, 1960 (Tahiré, foot of Kelesi Plateau, Guinea)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized species of its genus. The ears are small, 17.0-20.0 mm in height. The horseshoe is relatively narrow, about 9 mm in width across. The sella is narrow, straight sided, widely rounded off at its terminus. The connecting process is a broadly based, more or less acutely pointed triangle. The lancet is distinctly hastate. The lower lip is with one mental groove.The tail is 24.0-28.0 mm long. In the wings, the third metacarpal is the shortest (32.0-33.5 mm), the fourth (35.0-36.8 mm) and the fifth (34.4-36.2 mm) are subequal in length. The colouration in dorsal aspect is dark or lighter brownish-grey, rarely light reddish-brown; the ventral aspect is generally lighter. The axillary tuft of the adult males is whitish or reddish-brown.

Cranial and dental characters: The skull is moderately built, the zygomatic width is always but only slightly greater than the mastoid width. The anterior and lateral nasal swellings are well inflated, the rostral profil is distinctly concave. The sagittal crest is medium, sometimes strong, the frontal depression is shallow. The cristae supraorbitales are prominent but without sharp ridges. The palatal bridge is relatively short, 26-31% of the maxillary toothrow length.
The upper canine is medium, the posterior upper premolar is well developed, and widely separated from the canine. The small upper premolar (P^2) is relatively large, slightly extruded. The lower middle premolar is small or minute, does not reach the half height of the last premolar (P_4), rarely missing altogether. The adjoining P_2 and P_4 are in contact.

Similar species: The most closely related *R. landeri* is smaller cranially, but the external measurements of these two species are widely overlapping. *R. adami* is similar by cranial measurements, but having longer rostrum, frontal depression and much more inflated anterior median swellings. *R. clivosus* is distinguishable by its different connecting process, distinctly constricted sella; much lower anterior rostrum and reduced, frequently missing anterior upper premolar. Within the distribution area of *R.*

guineensis, *R. simulator* is represented by the subspecies *alticolus*, which has a characteristically wide sella and horseshoe and a shorter skull.

Taxonomic remarks: This taxon was described as a subspecies of *R. landeri* by Eisentraut (1960) who gave extensive measurements comparing it with *R. l. landeri* and *R. l. lobatus*. The sympatric occurence of *R. l. landeri* and *R. l. guineensis* was noted by Rosevear (1965) who mentioned that the range of measurements of *R. landeri* (including *guineensis* as subspecies) is much greater than was formerly supposed. This led to the speculation of Hayman and Hill (1971), that because hardly seems necessary to accept sympatric subspecies, *guineensis* is not even a subspecies but appear to be no more than a large variant of *R. landeri*. Contrary to this view, Böhme and Hutterer (1979) concluded that in view of sympatry, the two taxa should be considered separate species. The specimen they recorded had a reddish axillary tuft, and they noted that not known how the colour of this tuft is changing according to the physiology of males. Koopman (1989, 1994) further noted that due to the evident size differences *guineensis* is clearly specifically distinct from *R. landeri*.

Fig. 32.1. Lateral and frontal views of noseleaf of *R. guineensis* (BMNH 56.36) from Sierra Leone. Scale = 3 mm.

Fig. 32.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. guineensis* (SMN 6103 - holotype) from Guinea. Scale = 3 mm.

Table 32. ***R. guineensis***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		44.0	49.0		
SL	20.07	19.31	20.84	0.40	18
CM^3L	7.56	6.91	7.89	0.24	20
ZW	10.01	9.37	10.57	0.28	18
MW	9.54	9.25	9.90	0.19	18
ML	13.47	12.58	14.19	0.36	19
CM_3L	8.10	7.35	8.68	0.29	19

***Rhinolophus landeri* Martin, 1838**
Lander's horseshoe bat
R. landeri Martin, 1838 (Fernando Po)
R. lobatus Peters, 1852 (Sena, Tette, Mozambique)
R. angolensis Seabra, 1898 (Hanha, Angola)
R. dobsoni Thomas, 1904 (Kordofan, Anglo-Egyptian Sudan)
R. axillaris Allen, 1917 (Aba, Uele district, Congo Belge)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *landeri* from Gambia to Cameroon and south to the mouth of the Congo

river; *lobatus* from Sudan and Ethiopia south to Transvaal, Zanzibar; *angolensis* in western Angola and perhaps Namibia.

External characters: A small to medium sized horseshoe bat. The ears are relatively small, 14.0-22.0 mm in height. The horseshoe is narrow, does not cover the whole muzzle, its breadth is 6.0-7.8 mm. The sella is slightly narrowed in the centre, broader and rounded off above. The shape of the connecting process is variable, sometimes a relatively slender, acutely pointed triangle in other cases more broadly rounded off. The lancet is hastate, its sides are definitely concave. The lower lip is with one distinct median groove, the lateral ones are very ill defined. The tail is 18.0-31.0 mm in length. In the wings, the third metacarpal is shortened, its length 28.3-33.0 mm; the fourth is subequal to or sometimes slightly shorter or longer (32.0-37.0 mm) than the fifth (31.5-36.0 mm). Two contrasting colour phases are known. The upperparts are from buffy-brown to grey-brown, or bright reddish-brown; the underparts are lighter in colour. Both phases may occur in the same colony, but in one colony in Nigeria 99% were orange-brown. The reddish axillary tuft lying in a glandular sac and present in many adult males as a secondary sexual feature.

Cranial and dental characters: The skull is moderately built, the zygomatic width is slightly but always exceeds the mastoid width. The anterior median swellings are moderately inflated, the lateral ones are well developed. The sagittal crest is medium. The frontal depression is usually shallow, the bordering supraorbital crests are either obliterated or well visible but with ill defined ridges. The palatal bridge is variable in length, 28-37% of the upper toothrow (CM^3) length.
The upper canine is moderately developed, the posterior upper premolar is about two-third of its length. The anterior premolar (P^2) is medium or small, situated in the row or slightly external. The canine and P^4 not in contact. In the lower jaw, the middle premolar is small, crowded out of the row, the neighbouring teeth are touching each other or very nearly so.

Similar species: The ratio of first phalanx to the metacarpal of the fourth finger is 1:4.3-5.6 in *R. landeri* but only 1:3.1-3.9 in *R. blasii* (Happold and Happold 1989). *R. blasii* similar cranially, but has an anteriorly elongated median nasal swellings and shorter, less curved upper canine. *R. adami* is usually larger and its rostrum and frontal depression is longer, the anterior median swellings are well inflated. The skull of *R. swinnyi* resembles to that of *R. landeri*, but the zygomatic and mastoid width are subequal. *R. darlingi* is cranially separable from *R: landeri* by its reduced, frequently missing anterior upper premolar. *R. guineensis* is similar sized by external measurements, but cranially distinctly larger than *R. landeri*.

Taxonomic remarks: Already Andersen (1905d) pointed out the very close relationships between *lobatus*, *dobsoni* and *landeri*, although listed them as separate species. Later on (Andersen 1906) noted „it is not unlikely that, when a completer material is to hand we shall have to regard *Rh. landeri* and *lobatus* as western and eastern representatives of one species...I have some doubt that *Rh. dobsoni* is distinguishable from *Rh. lobatus*". As he also noted, the measurements and the shape of the noseleaf (after seeing Seabra's sketches) indicate that *angolensis* comes nearest to *R. landeri* (Andersen 1906). These remarks were apparently overlooked by Allen (1939) who regarded all *lobatus*, *angolensis*, *dobsoni* and *axillaris* as separate species. The

form *axillaris* was distinguished chiefly upon the presence of tufts of stiff hairs in the armpits of males but it had been discovered that these axillary tufts occur also in *landeri* and *alcyone* (Eisentraut 1963, Rosevear 1965).
Hill and Carter (1941) and Ellerman *et al*. (1953) also listed *angolensis* as a valid species. In the meantime, Ellerman *et al* (op. cit.) first regarded *lobatus* as a subspecies of the earlier named *R. landeri* which inhabiting all the mainland territories (except Angola, where in their opinion *R. angolensis* occurs), while the distribution of *R. l. landeri* is restricted to Fernando Po. Koopman (1975) regarded *dobsoni* as valid subspecies (although mentioned as quite similar to *lobatus*), but later (Koopman *et al*. 1995) following Eisentraut (1963) and Hayman and Hill (1971) included *axillaris* and *dobsoni* in the larger eastern subspecies *R. l. lobatus*.

Fig. 33.1. Lateral and frontal views of noseleaf of *R. landeri* (BMNH 84.1668) from Cameroon. Scale = 3 mm.

Fig. 33.2. Lateral view of the rostral part of the skull (USNM 412008) from Ghana and occlusal view of the left upper (left) and right lower (right) anterior dentition (BMNH 55.12.26.250 – holotype) from Fernando Poo of *R. landeri*. Scale = 3 mm.

Table 33. ***R. landeri***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		38.0	46.5		
SL	18.02	17.08	19.22	0.52	34
CM^3L	6.65	6.32	7.29	0.22	39
ZW	9.29	8.48	10.11	0.34	35
MW	8.87	8.40	9.59	0.25	33
ML	11.96	11.37	12.99	0.35	38
CM_3L	7.11	6.66	7.80	0.27	37

MACLAUDI-GROUP

***Rhinolophus maclaudi* Pousargues, 1897**
Maclaud's horseshoe bat
R. maclaudi Pousargues, 1897 (Conakri Island, French Guinea)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A very large species of the genus. The ears are enormous, 40.0-44.0 mm in height. The horseshoe is broad, almost covering the whole muzzle; a distinct ridge is running on its surface nearly parallel to the outer edge. There is no secondary horseshoe. A well developed, high and wide internarial cup is formed above the nostrils, the sides of it are integral with the base of sella. The sella itself is very broad, constricted at the narial cup but parallel margined above, the summit is broadly rounded-off. The connecting process is long, thin and very low. The lancet is peculiarly long, narrow and cuneate. The lower lip is with a single median mental groove. The tail is 38.0-43.0 mm

long. In the wings, the third metacarpal is not shortened. The pelage is soft, dense and short; the dorsal aspect is chestnut-brown or grey-brown, the ventral side is paler.

Cranial and dental characters: The skull is large, but rather slenderly built. The zygomatic width is slightly exceeds or subequal to the mastoid width. The anterior median swellings are highly domed, their outline is usually subcircular, sometimes narrowed anteriorly; the posterior swellings are less developed. The sagittal crest is moderate or strong, but flattened near the occiput. The frontal depression is very shallow, the supraorbital crests are weak. The palatal bridge is very long, 45-48% of the upper toothrow (CM^3) length.
The upper incisor is exceptionally large, its bulk is equal to or even exceeds that of the anterior upper premolar. The upper and lower canines are powerful; the anterior upper premolar is very small but stands in the toothrow or only slightly external to it. The middle lower premolar is also very reduced (or missing altogether) and situated externally to the main row. The first (P_2) and third (P_4) lower premolars are either in contact or close to each other.

Similar species: Because of its large size, elaborate noseleaf; prominent median swellings and small but at most only slightly extruded anterior upper premolar, the only similar species is *R. ruwenzorii* from which is separable by its greater skull measurements and relatively broader zygomata.

Taxonomic remarks: Andersen (1905c) regarded *R. maclaudi* as an Ethiopian offshot of the *philippinensis*-type, but more highly developed in the dentition (small P^2) and the mental grooves (only the median groove exists). Rosevear (1965) compared *R. maclaudi* and *R. ruwenzorii* and remarked that they correspond in nearly everything but size.
Hayman and Hill (1971) mentioned *maclaudi* and *ruwenzorii* as separate species, but noted that the reputed size difference is not so obvious that more material has been measured. Happold (1987) recognised no subspecies of *R. maclaudi*, therefore probably also accepted *R. ruwenzorii* as full species, but Koopman (1994) recognised only *R. maclaudi* as full species and retained *ruwenzorii* as its subspecies. According to our investigations the available mensural (although small but consistent) and cranial differences are all support the specific distinctness of these two forms (see also comments under *R. ruwenzorii*).

Fig. 34.1. Lateral and frontal views of noseleaf of *R. maclaudi* (MNHN 1987.981 - holotype) from Guinea. Scale = 3 mm.

Fig. 34.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. maclaudi* (SMN 6117) from Guinea. Scale = 3 mm.

Table 34. ***R. maclaudi***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		58.5	69.5		
SL	28.57	26.32	29.63	1.52	4
CM^3L	10.12	8.89	10.59	0.82	4
ZW	13.33	12.42	13.83	0.62	4
MW	13.14	12.38	13.46	0.51	4
ML	18.83	17.10	19.81	1.51	3
CM_3L	10.69	9.55	11.29	0.99	3

***Rhinolophus ruwenzorii* Hill, 1942**
Ruwenzori horseshoe bat
R. ruwenzorii Hill, 1942 (Vallée de Butahu, West Mt Ruwenzori, Zaire)
R. hilli Aellen, 1973 (Uwinka, Cyangugu, Rwanda, 1300 m)

Recognised subspecies: The following subspecies are recognised - *ruwenzorii* in Zaire and Uganda; *hilli* in Rwanda.

External characters: A fairly large species of the horseshoe bats. The ears are large or enormous (29.0-32.5 mm). The horseshoe is well developed, almost covering the muzzle, its breadth is 12.0-13.0 mm; a secondary noseleaf is present. A well visible but moderately high internarial cup is formed, its margin is connected to the base of sella. The connecting process is very low, the lancet is long, narrow at its terminal part, squared off at the tip. The lower lip is with one distinct mental groove, the lateral ones are frequently ill-defined. In the wings, beside the shortest third metacarpal (37.5-40.0 mm) the fourth and fifth are subequal or the fifth is slightly longer (41.5-44 and 42.0-46.8 mm, respectively). The fur is soft and dense, its colour is uniformly dark brown both above and below.

Cranial and dental characters: The skull is very large but slender, the mastoid width exceeds the zygomatic width. The anterior median swellings are relatively low, but elongated, narrowing anteriorly and extending beyond the upper rim of the nasal orifice. The posterior nasal compartments are less developed. The crista sagittalis is medium, the frontal depression is shallow, bordered by low supraorbital ridges. The palatal bridge is very long, 41-47% of the maxillary toothrow length.
The upper incisor is very large, subequal to the size of the small upper premolar (P^2). The canine is broad-based, relatively short. The first upper premolar is small and more or less external but widely separating C^1 and P^4 from each other. The middle lower premolar is small, does not reach the half height of P_4, external to the toothrow or sometimes missing. The P_2 and P_4 are in contact or close to each other.

Similar species: Because of its relatively large size, peculiar noseleaf; long and protruding median swellings, narrow skull and widely separated C^1 and P^4, the only similar but cranially readily separable species is *R. maclaudi*.

Taxonomic remarks: According to Hayman and Hill (1971) the small size differences - once thought to be diagnostic - does not support the separation of *maclaudi* and *ruwenzorii* and they considered them conspecific. When describing *R. hilli*, Aellen (1973) noted its close relationship *to R. ruwenzorii*, and recognised *maclaudi* and *ruwenzorii* as separate species, the view followed by Koopman (1975). Nevertheless, this opinion was not generally accepted and even Koopman (1994) synonymised all the three taxa under the name *R. maclaudi*. Kingdon (1974) and later on Kityo and Kerbis (1996) used again the name *R. ruwenzorii* but with no further comment. However, the different skull shape, the small but obvious mensural differences and the presence of the secondary noseleaf reportedly typical for most known specimens of the *ruwenzorii-hilli* taxa all support the separation of *maclaudi* and *ruwenzorii*.
Aellen (1973) stated *hilli* is distinguishable from *ruwenzorii* mainly by the greater development of the connecting process. According to our opinion, based on the very limited sample available for Aellen (single specimen from each taxon investigated) his taxonomic conclusion is premature and by this character perhaps the subspecific status is appropriate. Therefore, *hilli* is provisionally recognised here as a subspecies of *R. ruwenzorii*.

Fig. 35.1. Lateral and frontal views of noseleaf of *R. ruwenzorii* (BMNH 55.1187) from Uganda. Scale = 3 mm.

Fig. 35.2. Lateral view of the rostral part of the skull (BMNH 60.99) and occlusal view of the left upper (left) and right lower (right) anterior dentition (AMNH 82394 – holotype) both from Congo of *R. ruwenzorii*. Scale = 3 mm.

Table 35. ***R. ruwenzorii***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		55.5	60.5		
SL	24.41	23.30	24.86	0.51	8
CM^3L	8.36	8.16	8.60	0.14	8
ZW	10.96	10.64	11.27	0.22	8
MW	12.03	11.80	12.32	0.20	7
ML	15.58	15.21	15.97	0.21	8
CM_3L	8.73	8.53	8.84	0.11	8

***Rhinolophus affinis* Horsfield, 1823**
Intermediate horseshoe bat
R. affinis Horsfield, 1823 (Java)
R. andamanensis Dobson, 1872 (S. Andaman I.)
R. a. himalayanus Andersen, 1905 (Masuri, Kumaon, N.W. India)
R. a. macrurus Andersen, 1905 (Taho, Karennee, S.E. Burma)
R. a. tener Andersen, 1905 (Pegu, Burma)
R. a. superans Andersen, 1905 (Pahang, Malaya)
R. a. nesites Andersen, 1905 (Bunguran I., N. Natuna Is)
R. a. princeps Andersen, 1905 (Lombok, Lesser Sunda Is)
R. hainanus Allen, 1906 (Pouten, Hainan I., China)

Recognised subspecies: According to Koopman (1994) the following subspecies are recognised - *himalayanus* in northern India and Nepal across northern Myanmar to southwestern China; *macrurus* in southeastern China through Vietnam and Thailand to southeastern Myanmar; *hainanus* in Hainan Island; *tener* in southwestern Myanmar; *andamanensis* in Andaman Islands; *superans* in Malay Pensinsula, Sumatra, Mentawai Islands; *nesites* in Anamba and North Natuna Islands, Borneo; *affinis* in Java; *princeps* in Lombok, Sumbawa and Sumba.

External characters: A medium to fairly large *Rhinolophus*. The ears are small (14.0-25.0 mm), do not reach the tip of nose when laid forward. The horseshoe is 8.0-11.4 mm in width, relatively broad but not covering the whole muzzle. The sella is pandurate, slightly concave. The connecting process is rounded and sparsely haired; the lancet is always straight sided, its tip pointed. The lower lip is with three mental grooves. The tail is 17.1-30.2 mm in length. The third metacarpal is 35.2-41.9 mm (0.4-6.6% shorter than the fourth), the fourth (36.0-43.2 mm) is shorter than or subequal to the fifth which is 36.8-43.7 mm in length. The upperside is darker or lighter brown, sometimes ochraceous buff; the belly is from brown to cream-buff.

Cranial and dental characters: The skull is robust, with moderately long rostrum. The mastoid width is bigger than the zygomatic width. The anterior median swellings are relatively less inflated, semicircular in outline; the posterior swellings are well defined. The crista sagittalis is medium or strong, extending posteriorly almost to the lambda. The frontal depression is medium developed, the bordering crista supraorbitalis are well-defined ridges. The palatal bridge relatively short, 23-29% of the upper toothrow.
The upper canine is usually massive, its cingulum is not in contact with the posterior upper premolar (P^4). P^2 small or medium and in the toothrow or only sligthly displaced. P_3 small or very small, usually fully, rarely partly external. The first (P_2) and third (P_4) lower premolars are in contact or nearly so.

Bacular morphology: According to Topál (1975) the basal cone is deeply emarginated in the ventral margin but less so in the dorsal one. There are still smaller emarginations on the lateral sides. The shaft is roughly circular in cross sections and sligthly bends towards the ventral side in the subspecies *himalayanus*, and considerably shorter and more expressedly bent in the case of *macrurus*.

Similar species: Beside the differently shaped connecting process and lancet, the specimens of *R. affinis* are further distinguishable from *R. ferrumequinum* by the wing shape; the first phalanx of the third metacarpal is considerably less than half the length of the metacarpal (in the case of *R. ferrumequinum* this proportion is more than 50%) (Bates and Harrison 1997). *R. affinis* differs from *R. rouxi* and *R. sinicus* by the characteristically straight sided lancet and the long second phalanx of the third digit (66.3-80.4% of the length of the metacarpal); this bone is less than two-thirds of the metacarpal in *R. rouxi*.
Cranially, *R. affinis* is distinguishable from *R. ferrumequinum* by its anterior upper premolar (minute and fully extruded in the case of the latter species) and by its more inflated nasal swellings. Another similar sized species is *R. acuminatus* which has an even more pronounced anterior swellings and usually more slender upper canine. *R. rouxi* is cranially indistinguishable from *R. affinis* obtained from north India; *R. sinicus* also very similar but smaller (SL under 21.0 mm) than *R. affinis*. *R. pearsoni* is also similar by craniodental measurements, but its rostral part is longer and due to the less developed posterior swellings the rostral profil more expressedly concave from lateral view which is further reinforced by the strong sagittal crest. *R. arcuatus* is usually smaller, with more bulbous anterior swellings and weaker upper canines.

Taxonomic remarks: In the original description of the species Horsfield (1823) indicated no type specimen. Beside a specimen (labelled as holotype) stored in the BM(NH), Jentink (1887) listed two more specimens in the RMNH, Leiden marked as types. However, the two Leiden individuals (RMNH 25236 and 25237) represented by skulls only, proved to be *Hipposideros larvatus*. Since there was no holotype designation in Horsfield's work, these three specimens are regarded as syntypes; as a consequence, the BM(NH) specimen (BMNH 79.11.21.70) being the only *R. affinis* designated herein as lectotype.
Dobson (1878) did not make distinction between *R. affinis* and *R. rouxi*, and enumerated all the described forms of *rouxi* under *affinis*. As a consequence, he listed *R. affinis* from Ceylon; a similar mis-identification may resulted Blyth's (1863 in Sinha 1973) highly doubtful record of the species from that island (Bates and Harrison 1997).
The separation between the subspecies lying in the size differences of ears, noseleaf, tibia, tail and skull length. The subspecies *himalayanus* differs from others in having smaller ears and narrower noseleaf and the tail comparatively short; *macrurus* can be differentiated by its larger, broader noseleaf and longer ear; *tener* is mentioned having smaller ears and skull; *princeps* has the widest horseshoe. *R. andamanensis* was differentiated by Dobson (1872) from *R. affinis* by its broader horseshoe, but Andersen (1905a, 1905d) noted, that it seems to be a local representative of the *affinis* type. Ellerman and Morrison-Scott (1951) also listed it as separate species, but stated that the taxon may represent *R. affinis*. Subsequently, Sinha (1973) treated *andamanensis* as a subspecies of *R. affinis*, characterised by its longer ear and slightly longer upper and lower toothrows and longer mandible. When compared topotype specimens of *macrurus* with *himalayanus*, Osgood (1932) found only slight average differences and stated that the distincition of the two forms is rather difficult.
According to Andersen (1905a) considering the continental forms the more southern the subspecies the larger the measurements. Based on our database regarding the mean values of skull and toothrow lengths, the most southern form *R. a. superans* is really considerably larger than the northern taxa. This rule does not appear true for the populations occuring in the Sunda Islands and specimens from the Kangean Islands

appears to average smaller than any of the subspecies Andersen recognised (Bergmans and van Bree 1986). Based on multivariate statistical analysis Thomas (1997) also suggested that this population may represent a distinct subspecies.

Fig. 36.1. Lateral and frontal views of noseleaf of *R. affinis* (BMNH 0.7.3.2 – *R. a. superans* holotype) from Malaysia. Scale = 3 mm.

Fig. 36.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. affinis* (BMNH 79.11.21.70 - lectotype) from Java. Scale = 3 mm.

Table 36. ***R. affinis***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		46.0	55.5		
SL	22.52	21.15	23.70	0.52	60
CM^3L	8.96	8.36	9.73	0.26	62
ZW	11.15	9.87	11.82	0.35	59
MW	10.46	9.57	11.11	0.26	58
ML	15.51	14.36	17.11	0.46	62
CM_3L	9.55	8.93	10.44	0.27	61

***Rhinolophus borneensis* Peters, 1861**
Bornean horseshoe bat
R. borneensis Peters, 1861 (Labuan I., N. Borneo)
R. spadix Miller, 1901 (Sirhassen I., S. Natuna Is)
R. importunus Chasen, 1939 (Tjiawitali, near Wijnkoopsbaai, S. coast of W. Java)
R. chaseni Sanborn, 1939 (Pulo Condore, S. Vietnam)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *borneensis* in Borneo; *spadix* in South Natunas and Karimata; *importunus* in Java; *chaseni* in Cambodia, Laos, Vietnam and Malaysia.

External characters: A relatively small species of the genus. The ears are medium, 16.0-19.5 mm in heights. The skin of noseleaf and ears is brown. The horseshoe wide, almost covering the whole of the muzzle, its anterior margin bears a notch at the midpoint; its width is about 8.7 mm. A secondary horseshoe is visible. The sella is narrow, and after a slight constriction above the midpoint with its lateral margins parallel or nearly so. The connecting process is rounded, sparsely haired; the lancet is almost cuneate, moderately long. The lower lip is with three mental grooves. The tail is 18.0-26.0 mm in length. In the wings, the fourth and fifth metacarpals are subequal or the fifth is slightly longer (29.8-33.8 mm in length); the third metacarpal is the shortest (28.7-32.7 mm). Two colour phases are known. The fur of the upperparts is dark brown to bright reddish brown, more or less uniformly coloured or very slightly paler at the bases of the hairs. The underside is similar in colour but lighter.

Cranial and dental characters: The skull is small but relatively strongly built, the zygomatic width usually exceeds the mastoid width, only rarely subequal. The zygomata is highly arched. The anterior median swellings are bulbous but longer than wide, the lateral and posterior swellings are also well developed. The sagittal crest is weak or moderate. The frontal depression is medium and flanked by prominent, more or less sharp supraorbital ridges. The palatal bridge medium, 26-32% of the maxillary toothrow.
The upper canine is relatively slender and long. The first upper premolar is quite well developed and almost always in the toothrow, C^1 and P^4 never in contact. The middle lower premolar (P_3) is moderate or small and usually completely external. The P_2 and P_4 almost always in contact, rarely slightly separated.

Similar species: *R. borneensis* is hardly distinguishable externally from the other species of its group. Although usually larger than *R. malayanus* and *R. celebensis* there is an overlap in the forearm measurements. In these cases the cranial differences (beside the usually larger size, the relatively narrower anterior swellings than those of *R. malayanus*) help the identification. Several larger specimens of *R. celebensis* virtually indistinguishable from *R. borneensis* and the determination was based solely on geographical ground. *R. stheno* is separable externally from *R. borneensis* by the structure of its lancet where the median septa is wider than the middle pockets - although this feature is less obvious in the smaller subspecies *R. s. microglobosus*.
Cranially, *R. stheno* is characterised by its less developed posterior swellings and the very narrow interorbital constriction (its breadth is less than 2 mm). *R. lepidus* and *R. convexus* is smaller (albeit the differences are very slight), *R. shortridgei* is similar sized but all have less inflated nasal swellings. *R. coelophyllus* and *R. shameli* have longer frontal depression and anteriorly more protruding median swellings.

Taxonomic remarks: The confusing history of the name *borneensis* was reviewed in detail by Andersen (1905a) who described it as "accumulation of errors and wrong identifications" which resulted "*Rh. borneensis* has for many years been completely confused not only with several more or less closely related species, but also with the widely different *Rh. minor*" (= *R. pusillus*). For example, Dobson (1878) also synonymised *R. borneensis* with *R. minor*. One of the possible reason of the confusion should be the mis-matching of labels and/or skulls in the Museum für Naturkunde, Berlin (MNB). There are two skulls (in very bad condition) in the type collection of MNB (2533.1 and 2533.2) which certainly represent specimens of *R. borneensis* although both labelled as „*Rhinolophus minor*, type, Labuan, Java". On the other hand, the type of *R. minor* is housed in the BM(NH). Since the terra typica of *R. borneensis* is also Labuan (the Malayan island, off Borneo, not in Java) and according to Peters (1871) its type is deposited in the Berlin Museum, the MNB 2533.1 and 2533.2 specimens are undoubtedly the mis-labelled types of *R. borneensis*.
The species limit of *R. borneensis* and *R. celebensis* is not clear. They differ from each other chiefly only by size; in general, *R. borneensis* is larger in every respects but there is a certain overlap between *R. b. spadix* and *R. c. celebensis* or *R. c. javanicus* (see also comments under *R. celebensis*). As Chasen (1939) mentioned „although they [*javanicus*, *borneensis*, *importunus*] are so obviously very closely related, contrary to my usual costum, I am reluctant to unite any of the Bornean and Javan bats of this group in a trinominal nomenclature. It seems that they replace each other geographically, in Java decreasing in size from W to E, but actually we know very little about them".

Subsequently Hill (1983) studied one of the original specimens and concluded „that further examination leaves little doubt that *importunus* must be allied with *borneensis*". He also noted that *nereis* evidently represents *R. borneensis* but is considerably larger. When describing *R. spadix* as a new species, Miller (1901) compared it with *R. affinis* but not with *R. borneensis* which that time was regarded as conspecific with *R. minor* (= *R. pusillus*). Discussing the taxonomic position of *R. b. borneensis* and *R. b. spadix* Andersen (1905a) remarked that „I should not have separated these forms (if they be so) of *borneensis*...there is no tangible difference in the skull, not even in the measurements of them". According to Hill and Thonglongya (1972) *spadix* seems only barely separable from the Bornean subspecies by virtue of its very slightly larger ears. Phillips (1967) considered that on the basis of the published description it is probable that *R. chaseni* from Con Son Island (South Vietnam) will prove conspecific with *R. malayanus*. However, the examination of the holotype of *chaseni* showed it to belong with *R. borneensis* rather than with *R. malayanus* (Hill and Thonglongya 1972). Since only a few specimens of *R. borneensis* had been collected in the mainland Asia, the taxonomic allocation of these is highly problematic. Hill and Thonglongya (op. cit.) speculated that *chaseni* will prove to be the correct subspecific name for the mainland population(s), but Francis *et al.* (1999) pointed out that specimens from Laos are quite distinct in morphology and genetics from specimens of *R. borneensis* from Sabah. They appear to represent a distinct species and further study is required to determine whether *R. chaseni* is the correct name for this taxon.

Fig. 37.1. Lateral and frontal views of noseleaf of *R. borneensis* (BMNH 65.5.9.16) from Borneo. Scale = 3 mm.

Fig. 37.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. borneensis* (BMNH 65.5.9.15) from Borneo. Scale = 3 mm.

Table 37. ***R. borneensis***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		41.0	47.0		
SL	18.49	17.49	19.44	0.44	30
CM^3L	7.10	6.66	7.47	0.17	35
ZW	9.28	8.60	9.85	0.27	28
MW	8.96	8.61	9.43	0.21	27
ML	12.39	11.80	13.25	0.36	35
CM_3L	7.61	7.03	8.10	0.22	35

***Rhinolophus celebensis* Andersen, 1905**
Sulawesi horseshoe bat
R. celebensis Andersen, 1905 (Makassar, S. Sulawesi)
R. madurensis Andersen, 1918 (Soemenep, E. Madura I.,off N.E. Java)
R. javanicus Andersen, 1918 (Pangandaran, Dirk de Fries Bay, S. Java)
R. borneensis parvus Goodwin, 1979 (Lia Hoo Cave, near Fatu Haca village, 7 miles S of Baucau, Timor I., Lesser Sunda Is)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *celebensis* in Sulawesi; *javanicus* in Java and Bali; *madurensis* in Madura; *parvus* in Timor.

External characters: A small or medium sized Rhinolophid bat. The ears are small or medium, 14.6-20.0 mm in heights. The horseshoe is 7.1-8.4 mm in width across; the small secondary noseleaf is frequently concealed from above. The sella is almost parallel sided or only slightly constricted. The connecting process is rounded, with sparse, short hairs; the sides of lancet are nearly straight. The lower lip is with three mental grooves. The tail is 18.9-27.0 mm in length. In the wings, the third metacarpal is slightly shorter (30.5-31.5 mm) than the fourth and fifth which are subequal, 31.0-33.2 mm in length. The colour is uniform dull brown or deep brown with shade of drab above; somewhat lighter below. The colour of *parvus* is said to be unique having pale patches of fur behind the bases of the anterior edges of the ears.

Cranial and dental characters: The skull is of the general shape of the group, the zygomatic width is always greater than the mastoid width. The anterior median swellings are moderately developed, semicircular in outline, the posterior swellings are relatively well inflated. The sagittal crest is medium; the frontal depression is moderate, the bordering supraorbital crests are well visible. The palatinum is usually short, 27-30% (in one case 34%) of the upper toothrow length.
The upper canine is not especially massive, the posterior upper premolar is almost reaching its tip. The first upper premolar is medium sized and situated in the axis of the toothrow. The middle lower premolar is small, halfway external; the adjoining premolars are close to each other but not in contact.

Similar species: *R. celebensis* is hardly separable from its closest relatives in the *megaphyllus*-group by external features. The supraorbital crests of this species are usually meeting at a point in front of the middle of orbit and only rarely behind it; but even in these cases the frontal depression is maximum as wide as long thus the rostral part of the skull shorter than that of *R. megaphyllus*. Several specimens are overlapping in both external and craniodental measurements with the generally larger *R. borneensis* and virtually indistinguishable from that species. *R. stheno* has much less inflated posterior nasal swellings, therefore the anterior swellings are very elevated. *R. malayanus* is characterised by its very broad, laterally expanded anterior swellings.
R. lepidus is very similar to *R. celebensis* by cranial measurements and characteristics but has a somewhat smaller anterior median swellings, lower rostrum and relatively larger upper canines.

Taxonomic remarks: Goodwin (1979) recognised *parvus*, *borneensis*, *celebensis* and *javanicus* conspecific, but remarked that because of the differences in the nasal

swellings and with its more bulbous occipital area *borneensis* is the most different. This view was revised by Hill (1983) and based on measurements resulted the separation of *borneensis* and *celebensis* at specific level. Hill (op. cit.) also tentatively suggested that *madurensis* may be a subspecies of *R. celebensis* but at the same time observes that its very small size might justify its specific distinction. Bergmans and van Bree (1986) agreed that the two taxa are closely related, but regarded *madurensis* as a distinct species and listed *parvus* as its synonymy. These two taxa are separable by only slight differences in the narial inflations (Hill 1983). The forearm length of *madurensis* and *celebensis* is widely overlapping, but according to Bergmans and van Bree (1986) the differences in the development of the cingulum and position of the small premolars may prove to be of value in distinguishing the two taxa at specific level. Nevertheless, they used only one specimen of *celebensis* for direct comparison and knowing the variation of the morphology and position of the small premolars this opinion seems unsupported. Subsequently, both *parvus* and *madurensis* were listed by Corbet and Hill (1992) and Koopman (1994) as subspecies of *R. celebensis*.
Some specimens referred to *R. celebensis* on geographical ground are clearly within the size range of *R. borneensis* making the specific limits unclear. A series of the species from Bali (housed in SMF) is similar to *R. megaphyllus* in the form of supraorbital crests, although the frontal depression is about as long as wide.

Fig. 38.1. Lateral and frontal views of noseleaf of *R. celebensis* (BMNH 97.1.3.19 - holotype) from Sulawesi. Scale = 3 mm.

Fig. 38.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. celebensis* (BMNH 97.1.3.19 - holotype) from Sulawesi. Scale = 3 mm.

Table 38. ***R. celebensis***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		38.0	45.0		
SL	17.72	16.06	18.29	0.41	38
CM^3L	6.79	6.00	7.23	0.21	41
ZW	8.85	8.02	9.41	0.28	37
MW	8.53	7.97	8.93	0.16	37
ML	11.87	10.82	12.34	0.30	40
CM_3L	7.25	6.43	7.79	0.24	40

***Rhinolophus malayanus* Bonhote, 1903**
Malayan horseshoe bat
R. malayanus Bonhote, 1903 (Biserat, Patani, Thailand)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A relatively small species of the genus. The ears are medium, their heights is 12.7-22.0 mm. The horseshoe is almost covering the muzzle, its breadth

is 6.6-9.0 mm; a relatively well developed secondary horseshoe is present. The lateral margins of the relatively wide sella are almost parallel, its summit is rounded. The lancet is with concave or almost parallel lateral margins and an elongate tip. The lower lip is with three mental grooves. The tail is 17.6-26.3 mm in length. In the wings, the metacarpals are almost the same length, the third metacarpal is 28.3-31.0 mm, the fourth is 29.0-31.0 mm, and the fifth is 29.2-31.5 mm in length. Two colour phases are know; the upper part bright cinnamon or brown, the base of hairs much lighter; belly buff or whitish in contrast to the colour of the upper part.

Cranial and dental characters: The skull is moderately built; thezygomatic width is only slightly (but always) exceeds the mastoid width. The anterior median swellings are prominent, wider than long, their outer part forming the upper region of the lateral rostral wall. The posterior compartments are also well inflated. The sagittal crest is weak, the frontal depression is relatively long but shallow. The supraorbital crests are more or less demarcated. The palatal bridge is short, 27-30% of the maxillary toothrow length.
The upper canine is slender, the well developed posterior upper premolar reaching beyond its two-third. The anterior premolar is medium sized, has a distinct cusp and situated in the toothrow. The canine and P^4 not in contact. The second lower premolar is small, sligthly extruded or external.

Similar species: By external characters, *R. malayanus* is hardly distinguishable from the other small sized species of its group, but *R. stheno* is characterised by the wider median septa of lancet. *R. malayanus* cranially differs from *R. borneensis* and *R. celebensis* (and similarly from the species of the *pusillus*-group) chiefly in the form of the anterior nasal swellings; in the former the anterior median swellings are large and much inflated, extending laterally, so the lateral swellings are relatively small. In *R. borneensis* and *R. celebensis* the anterior median swellings are less developed, with the lateral swellings conspicuously larger than in *R. malayanus*. *R. stheno* has very small posterior nasal inflation, and the frontal depression is extending anteriorly to the rearof the anterior nasal swellings. *R. megaphyllus* is similar to several *R. malayanus* specimens in the shape of the frontal depression (the supraorbital crests being combined at a point behind the centre of the mid-orbit), but this former species has more reduced lateral swellings.

Taxonomic remarks: Lekagul and McNeely (1977) summarized the taxonomy of *R. malayanus* and *R. stheno* by distinguishing the two species on the basis of size, lancet shape and particularly the relative proportions of the first and second phalanges of the third digit. McFarlane and Blood (1986) checked all this features using relatively large series of *R. malayanus*, and found no reliable differences between the two species with regard the lancet shape, wing characteristics and colour. They also noted a probable overlap in the forearm measurements if more populations of these species will investigated. Instead, the shape of the rostrum and nasal swellings are clearly establish the distinction between them (Corbet and Hill 1992). Csorba and Jenkins (1998) provided further details to the cranial features (see also comments under *R. stheno*).

Fig. 39.1. Lateral and frontal views of noseleaf of *R. malayanus* (BMNH 3.2.6.83 - holotype) from Thailand. Scale = 3 mm.

Fig. 39.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. malayanus* (BMNH 3.2.6.83 - holotype) from Thailand. Scale = 3 mm.

Table 39. ***R. malayanus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		38.0	44.0		
SL	17.53	16.97	18.21	0.32	22
CM^3L	6.80	6.54	7.23	0.19	22
ZW	8.62	8.13	8.94	0.22	21
MW	8.25	8.04	8.50	0.12	22
ML	11.76	11.18	12.35	0.31	22
CM_3L	7.20	6.86	7.63	0.18	22

***Rhinolophus megaphyllus* Gray, 1834**
Eastern horseshoe bat
R. megaphyllus Gray, 1834 (Murrumbidgee R., E Australia)
R. truncatus Peters, 1871 (Bacan I., N Moluccas)
R. keyensis Peters, 1871 (Kai Is)
R. simplex Andersen, 1905 (Lombok I., Lesser Sunda Is)
R. nanus Andersen, 1905 (Goram I., S.E. of Seram I., Moluccas)
R. m. monachus Andersen, 1905 (St. Aignan's Island, Luisiade Archipelago)
R. fallax Andersen, 1906 (Ighibieri, Kemp Welch River, British New Guinea)
R. robinsoni Andersen, 1918 (Khao Nawng, Bandon, S. Thailand)
R. klossi Andersen, 1918 (Pulo Pemangil)
R. m. ignifer Allen, 1933 (Coen, Cape York, Queensland, Australia)
R. keyensis annectens Sanborn, 1939 (Wetter I., Southwest Islands, Flores Sea, Moluccas)
R. m. vandeuseni Koopman, 1982 (Bululogon plantation, east coast of New Ireland, Bismarck Archipelago)
R. robinsoni siamensis McFarlane and Blood, 1986 (Big House Cave, Aungkang Region, N. Thailand, 19º50'N, 99º10'E) (preoccupied by *R. macrotis siamensis* Gyldenstolpe, 1917).
R. megaphyllus thaianus Hill, 1992 (replacement name for *R. robinsoni siamensis* McFarlane and Blood, 1986).

Recognised subspecies: Following Corbet and Hill (1992) and Koopman (1994) the following subspecies are recognised - *simplex* from Lombok to Komodo; *megaphyllus* in eastern Australia; *fallax* in southeastern New Guinea and D'Entrecasteux islands; *monachus* in Luisiades; *vandeuseni* in northeastern New Guinea and Bismarck Archipelago; *truncatus* in Batchian islands; *nanus* in Ceram and the nearby islands; *keyensis* in Keis; *annectens* in Wetar; *robinsoni* in Malay Peninsula; *thaianus* in northern Thailand.

External characters: A small to medium sized species. The ears are medium, 16.0-26.0 mm in height. The horseshoe is wide (8.3-9.2 mm), almost covering the muzzle; the supplementary leaflet is visible (e.g. *simplex*) or almost completely concealed by the horseshoe (*fallax*). The shape of sella reportedly differs according to the subspecies being wide, but abruptly constricted in the middle, upper margin slightly convex (*megaphyllus*, *fallax*, *robinsoni*); narrower, constriction in the middle less distinct, not broader at the base than at the summit (*monachus*); narrow and parallel margined (*nanus*); broad and subparallel at the base and after a shallow constriction very slightly converging (*truncatus*). The sides of the quite long lancet are straight or slightly concave; the terminal part is with pointed or more or less blunt tip. The lower lip is with three mental grooves. The tail is 17.8-26.8 mm long. In the wings, the fifth and fourt metacarpals are subequal in length (29.4-37.8 mm) and both of them only slightly longer than the third which is 29.9-36.0 mm in length. The fur of upperside is dark drab, sometimes very dark brown, the base of hairs is more distinctly drab; the underside is essentially the same colour but lighter.

Cranial and dental characters: The skull is moderately built, the zygomatic width is slightly larger than or subequal to the mastoid width. There is some small variation in the shape and size of the nasal swellings, but the anterior swellings are moderately developed, semicircular in outline; the lateral compartments are well inflated, larger than the anterior ones. The sagittal crest is low, the clearly defined frontal depression is longer than wide. The supraorbital crests are joining the sagittal crest at a point more or less behind the mid-orbit; the rostrum is elongated. The palatal bridge is short or medium, 28-35% of the upper toothrow.
The upper canine is usually moderately developed, relatively slender. The anterior upper premolar is with a well developed cusp, and in the toothrow or a little towards the external side. The upper canine and the posterior premolar are widely separated. The position of the small-sized second lower premolar (P_3) varies individually, being completely in row, partially or wholly extruded.

Similar species: By external characters, *R. megaphyllus* is hardly separable from its closest relatives but in *R. borneensis* the sella is narrower, its lateral margins are always parallel or nearly so, and in *R. stheno* the median septa of the lancet is wide, wider than the middle lateral pockets. The chief character of *R. megaphyllus* is the long supraorbital region, but this feature is a little variable and some specimens are practically indistinguishable from *R. borneensis*. This latter species is cranially also characterised by its less globular, antero-posteriorly shortened anterior median swellings. The junction of the supraorbital crests of *R. celebensis* is sometimes also combined behind the mid-orbit, but the frontal depression of this species is shorter than wide. The form of the supraorbital crests may be similar in *R. malayanus* as well, but *R: malayanus* is recognisable by its wide anterior nasal swellings, which are forming the upper part of the lateral rostral wall.

Taxonomic remarks: As it was pointed out by Corbet and Hill (1992) the name *R. robinsoni siamensis* described by McFarlane and Blood (1986) was pre-occupied by *R. macrotis siamensis* and the replacement name *R. megaphyllus thaianus* was given by Hill. However, in the original description of this taxon the photo depicting the type specimen not unambigously shows the long facial part of the skull typical for the species (Andersen 1905a, Corbet and Hill 1992). Unfortunately, the table of measurements cited

by McFarlane and Blood is missing from the paper, and the authors did not provide any comparisons with other species. Therefore, there is a certain possibility that the holotype and the additional material referred, represent specimens of *R. borneensis*, which species since had been recorded from the nearby countries of Vietnam and Laos. It is worth to note, that the type specimen of *R. robinsoni* was tentatively identified as *R. borneensis* by Robinson and Kloss (1915). The importance of the shape of supraorbital crests in separating *borneensis* and the *keyensis-megaphyllus-simplex* complex was also discussed by Goodwin (1979). The situation is further complicated by the fact, that a small series of *Rhinolophus* from Cochinchina (South Vietnam) stored in the Paris Museum also possess the very long frontal (supraorbital) depression and the junction of crests situated far behind the middle of orbital cavity. As a consequence they are referable to *R. megaphyllus* and represent the first record of the species from that country.

As already Andersen (1905a) pointed out, some forms (e. g. *nanus*) "marks a further steps towards the *celebensis-borneensis* type". Hill (1972) also remarked that *R. robinsoni* (= *R. megaphyllus*) is evidently closely related to *R. borneensis* which in many respects it resembles. Indeed, a few mainland specimens showing intermediate features and can be determined by difficulties.

Several described forms recently listed under the name of *R. megaphyllus* were differentiated by only small variations of the shape of sella and the width of horseshoe and in many cases the subspecific allocation possible by the localities only. The subspecies *R. m. robinsoni* and *R. m. klossi* both from the Malay Peninsula were described in detail by Hill (1972) but the differences (e.g. the relative breadth of palate and mesopterygoid fossa) listed by him between the two are very slight and they are considered here as synonyms under the name *R. m. robinsoni* by line priority. The taxon *keyensis* was described and separated from *megaphyllus* by Peters (1871) from the Keis, but later he recorded only *megaphyllus* from that islands (Andersen 1906). Andersen (op. cit.) gave a detailed description and separated *keyensis* as a full species again, on the base of its differently shaped sella and more slender skull. *Keyensis* (with its proposed subspecies *annectens*, *nanus* and *truncatus*), along with *simplex* and *robinsoni* was long considered as distinct species (e.g. Laurie and Hill 1954, Corbet and Hill 1980, Koopman 1994) but according to Corbet and Hill (1992) „there seems little to support the concept of distinct species in the Moluccas (*keyensis*) or Lesser Sunda Is (*simplex*), or the similar separation of *robinsoni* (with *thaianus* and *klossi*) in Thailand and Malaya". This opinion was anticipated by Koopman (1982) who suggested that those from the Moluccas and the Lesser Sunda Is might well be subspecies of *R. megaphyllus*. Flannery (1995b) retained *keyensis* as separate species but characterised as „appears to be a western relative of *R. megaphyllus*" and regarded its taxonomic status as uncertain. Specimens from Morobe Province (New Guinea) were mentioned by Koopman (1982) as intergrades presumably between *fallax* and the very small *vandeuseni*. The two Australian forms, the northern *ignifer* and the southern nominate subspecies were distinguished by Allen (1933) solely on the basis of colour. McKean and Price (1967) showed that this character is not valid, but distinguished the two subspecies by the average length of the forearm. Koopman (1982), however, noted that the boundary between them is uncertain, and the picture in New Guinea is even more complex.

Fig. 40.1. Lateral and frontal views of noseleaf of *R. megaphyllus* (AMNH 160289) from Australia. Scale = 3 mm.

Fig. 40.2. Lateral view of the rostral part of the skull (HNHM 70.31.1.) and occlusal view of the upper (left) and lower (right) left anterior dentition (BMNH 41.1509 – holotype) of *R. megaphyllus* both from Australia. Scale = 3 mm.

Table 40. ***R. megaphyllus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		39.5	49.5		
SL	19.05	17.00	20.42	0.84	36
CM^3L	7.28	6.64	7.87	0.33	48
ZW	9.31	8.32	10.10	0.47	32
MW	9.11	8.16	9.75	0.41	32
ML	12.71	11.37	13.58	0.54	48
CM_3L	7.74	7.02	8.47	0.33	48

***Rhinolophus nereis* Andersen, 1905**
Anamba horseshoe bat
R. nereis Andersen, 1905 (Siantan I., Anamba Is, Indonesia)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized species of its genus. The ears are medium long, as compared to the head. The horseshoe is relatively wide, almost covering the muzzle; its breadth is 9.0 mm. A secondary horseshoe is visible from above. The base of sella is separated from the internarial cup by a sudden constriction; its sides are slightly converging above the middle, widely rounded at its terminus. The lancet is relatively short, straight sided. The lower lip is with three well defined mental grooves. The tail is 17.0 mm in length. In the wings, the fifth metacarpal is slightly longer (34.0 mm) than the fourth (33.7 mm), which is only slightly longer than the shortest third metacarpal (33.2 mm). The colour is (according to Andersen 1905a) mars-brown above, base of hairs are ecru-drab; peculiar yellowish drab beneath (may be due to the formalin conservation).

Cranial and dental characters: The skull is moderately built, the zygomatic width exceeds the mastoid width. The anterior and lateral rostral swellings are medium developed, the posterior compartments are less inflated. The sagittal crest is moderate, the frontal depression is well defined, extending anteriorly to the median nasal swellings. The supraorbital crests are definite, with sharp ridges.The palatal bridge is 27% of the maxillary toothrow.
The upper canine is relatively short, the posterior upper premolar (P4) is almost reaching its heights. The first upper premolar (P^2) situated almost in the axis of the toothrow, but its cusp is almost imperceptible. The mandible is missing in the only seen individual (the holotype).

Similar species: The closest relative of the species is *R. borneensis*. Apart from its larger size, *R. nereis* is distingusihable by its different wing shape (Andersen 1905a): in

the third finger the second phalanx is lenghtened, more than 150% of the first phalanx (this value is less than 150% in the case of *R.borneensis*).

Taxonomic remarks: *R. nereis* was described as an offshoot of *R. borneensis* by Andersen (1905a) and subsequently remarked that it evidently represent the latter (Hill 1983); but its much bigger size supports the specific distinctness.

Fig. 41.1. Lateral and frontal views of noseleaf of *R. nereis* (USNM 101714 - holotype) from Siantan Island, Indonesia. Scale = 3 mm.

Fig. 41.2. Lateral view of the rostral part of the skull and occlusal view of the left upper anterior dentition of *R. nereis* (USNM 101714 - holotype) from Siantan Island, Indonesia. Scale = 3 mm.

Table 41. ***R. nereis***: External, cranial and dental measurements (mm).

		n
FA	43.5	1
SL	20.87	1
CM^3L	8.50	1
ZW	10.46	1
MW	10.05	1

***Rhinolophus stheno* Andersen, 1905**
Lesser brown horseshoe bat
R. stheno Andersen, 1905 (Selangor, Malaya)
R. s. microglobosus Csorba and Jenkins, 1998 (Na Hang Nature Reserve, Tuyen Quang Province, Vietnam, between 22º16' and 22º31'N, 105º22' and 105º29'E, 100–1082 m)

Recognised subspecies: The following subspecies are recognised - *stheno* in Java, Sumatra, Peninsular Malaysia, and Thailand south of the Isthmus of Kra; *microglobosus* in Thailand north of the Isthmus of Kra, Laos and Vietnam.

External characters: A medium sized horseshoe bat. The ears are small or medium, their length is 16.0-20.5 mm. The horseshoe is covering the majority of the muzzle, 7.2-10.4 mm in width across. A well visible supplementary noseleaf is present. The sella is almost parallel sided, only narrowing very slightly. The connecting process is rounded with scattered long hairs. The lancet is long, straight sided, its tip cuneate; the median septa is wider than the middle pockets. The lower lip has three grooves. The tail is usually short, its length is 10.9-23.0 mm. The fifth metacarpal is subequal or slightly longer (31.1-34.2 mm) than the fourth (31.0-33.8 mm), and the third is shorter than fourth (30.1-32.7 mm). The dorsal pelage light yellowish-brown at the base of hairs, reddish cinnamon-brown above; venter colour essentially the same but paler.

Cranial and dental characters: The skull is slender, the zygomatic and mastoid width are subequal. The anterior median rostral swellings are high and abruptly elevated, their

anterior wall perpendicular to the upper toothrow. The posterior swellings are reduced, the rostral profile is posteriorly strongly concave. The sagittal crest is moderately developed. The frontal depression is deeper (nominotypical form) or shallower (*microglobosus*) depending on the subspecies, the supraorbital crests are higher or lower accordingly. The interorbital region is very narrow. The palatal bridge is short, 25-27% of the upper toothrow length.
The upper canine is relatively slender, moderately long. The anterior upper premolar is developed, with a distinct cusp and included in or only very slightly extruded from the toothrow. The adjoining teeth are widely separated. The lower middle premolar is small and fully extruded from the row, the first (P_2) and third (P_4) premolars are in contact.

Similar species: Among the species of the *megaphyllus*-group, the lancet of *R. stheno* is unique bearing the median septa much wider than the middle pockets. This feature is, however, not so sharply expressed in the smaller subspecies *R. s. microglobosus*. The rounded connecting process (which is not originated at the very tip of the sella as it does in *R. arcuatus* and its allies) combined with the straight-sided lancet distinguish *R. stheno* from southeast Asian species belonging to other groups.
R. stheno is cranially characterised by the well developed, projecting anterior and reduced posterior swellings which separate the species from the other members of its group. *R. stheno* is further distinguishable from *R. malayanus* by the size of the interorbital constriction which is absolutely wider in the latter species (2.13-2.67 mm against 1.49-2.00 mm). *R. coelophyllus* and *R. shameli* have much longer frontal depression, but *R. arcuatus* is very similar in craniodental features with the exception of the vertically elevated anterior part of nasal swellings of *R. stheno*.

Taxonomic remarks: Beside its generally smaller measurements, the median anterior rostral swellings of *R. s. microglobosus* are notably smaller than those of the nominate subspecies. The separation of the two taxa was supported by statistical comparison (Csorba and Jenkins 1998).
As it was already suggested by McFarlane and Blood (1986) there are no reliable differences between *R. stheno* and *R. malayanus* in the external characters and measurements (body size, shape of lancet and relative proportions of the first and second phalanges of the third digit) reported by Lekagul and McNeely (1977). They are instead distinguishable by supraorbital and rostral characters of the cranium. McFarlane and Blood (1986) further concluded that the general similarity of the noseleaf and skull of *R. stheno* and *R. malayanus* implied a closer relationship than formerly supposed. This view was accepted by Corbet and Hill (1992), who continued to group both species in the *ferrumequinum*-group. However, Bogdanowicz (1992) in the phenetic analysis of the whole family proposed different group-level classification for the two species, but in the case of *R. stheno* with a question mark indicating uncertain affinities.
According to Robinson (1995) based on investigations carried out in western Thailand, by body measurements the two species can not tell apart with the exception of noseleaf (horseshoe) breadth, where *R. malayanus* clearly had a wider noseleaf (and lower echolocation frequency). Nevertheless, the horseshoe measurements taken by us from larger series of both species (including the larger subspecies of *R. stheno*) did not support this view.
Some characteristics of *R. stheno*, namely the wide and thickened median septa of the lancet, the more rectangular (less circular in outline) internarial cup, the very prominent anterior but reduced posterior swellings with the distinctly concave rostral profil relate

the species to the members of the *euryotis*-group, which classification was proposed by Bogdanowich (1992) on the base of phenetic analyses.

Fig. 42.1. Lateral and frontal views of noseleaf of *R. stheno* (BMNH 98.3.13.1 - holotype) from Malaya. Scale = 3 mm.

Fig. 42.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. stheno* (BMNH 98.3.13.1 - holotype) from Malaya. Scale = 3 mm.

Table 42. ***R. stheno***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		41.0	47.5		
SL	19.12	18.02	20.51	0.59	39
CM^3L	7.33	6.71	8.14	0.34	42
ZW	9.29	8.68	9.92	0.38	40
MW	9.18	8.69	9.74	0.33	41
ML	12.65	11.74	13.63	0.50	42
CM_3L	7.78	7.04	8.46	0.36	42

***Rhinolophus virgo* Andersen, 1905**
Yellow-faced horseshoe bat
R. virgo Andersen, 1905 (Pasacao, S. Camarines, Luzon, Philippines)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A small species of the horseshoe bats. The ears are small or medium, 14.7-15.3 mm in length. The horseshoe is very narrow and there is an indication of the secondary leaflet; the whole noseleaf is small. The sella is almost parallel sided or sligthly narrowed at centre; the base a little wider than the tip which boradly rounded off. The lancet is elongate, broadly triangular, its sides are only slightly concave. The lover lip is with three mental grooves. The tail is 17.9-20.2 mm in length. In the wings, the third metacarpal is the shortest (27.0-28.6 mm), the fourth and fifth are subequal (27.0-30.0 mm). The colour is distinct reddish to brownish orange above; the ventral aspect is only slightly lighter than the dorsal fur.

Cranial and dental characters: The skull is small, but strongly built; the zygomatic width usually slightly exceeds the mastoid width, they are only rarely subequal. The anterior and posterior nasal swellings are moderately developed, the rostral profil is gently sloping posteriorly. The sagittal crest is low or medium. The frontal depression is moderately deep, will defined and bordered with well visible, frequently prominent supraorbital ridges. The palatal bridge is moderately long, 30-32% of the maxillary (CM^3) toothrow length.
The upper canine is relatively short and weak, the well developed anterior upper premolar (P^2) is in the toothrow. The upper canine and the posterior upper premolar (P^4)

separated. The middle lower premolar is small or medium, and situated partly out of the row or fully external. The neighbouring anterior (P_2) and posterior (P_4) premolars are usually separated by a narrow gap, or sometimes in contact.

Similar species: *R. virgo* externally very similar to the other species of the group and can be differentiated by its measurements only. The noseleaf of this species is characteristically small, its greatest length barely exceeds 11.5 mm, its greatest breadth is about 7.0-7.5 mm. The sella is also very narrow as compared to other species. The rounded connecting process and cuneate lancet distinguish *R. virgo* from the other small-sized Rhinolophid bats.
By cranial shape and mesurements, *R. lepidus* is quite similar to *R. virgo*, but this latter species has slightly more inflated anterior nasal swellings and less developed upper canines.

Taxonomic remarks: The overall external and cranial similarities led Hill (1983) to the conclusion, that *R. virgo* is possibly conspecific with *R. celebensis*. Based on our investigation on series from different localities from the Philippines (housed in collections of USNM and FMNH) the holotype specimen described by Andersen (1905a) is the smallest known individual of the species. Although *R. virgo* smaller on average than *R. celebensis*, there is a wide overlap in all measurements. Here, following Corbet and Hill (1992) *R. virgo* is retained as distinct by virtue of its apparently small noseleaf and (in absolute value) small rostral inflations.

Fig. 43.1. Lateral and frontal views of noseleaf of *R. virgo* (USNM 573290) from the Philippines. Scale = 3 mm.

Fig. 43.2. Lateral view of the rostral part of the skull and occlusal view of the left upper (left) and right lower (right) anterior dentition of *R. virgo* (USNM 101966 - holotype) from the Philippines. Scale = 3 mm.

Table 43. ***R. virgo***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		36.5	44.0		
SL	17.11	15.82	17.95	0.44	23
CM^3L	6.44	5.80	6.76	0.21	31
ZW	8.44	7.76	8.79	0.24	28
MW	8.26	7.71	8.49	0.18	24
ML	11.35	10.40	11.91	0.28	30
CM_3L	6.90	6.30	7.30	0.23	30

***Rhinolophus pearsoni* Horsfield, 1851**
Pearson's horseshoe bat
R. pearsoni Horsfield, 1851 (Darjeeling, W. Bengal, N.E. India)
R. larvatus Milne-Edwards, 1872 (Moupin, Sichuan, China)
R. p. chinensis Andersen, 1905 (Kuatun, Fujian, SE China)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A relatively large species of the genus. The ears are large, 23.2-29.2 mm in height. The horseshoe is large completely covering the muzzle, anteriorly deeply emarginated; 9.8-12.8 mm wide. The basal third of sella widened, and after a sudden constriction the upper two thirds parallel sided with rounded apex. The connecting process is originating from the apex of sella (or very near of it) and forming a low, rounded arch. The lancet is moderately long and broadly triangular, its sides are nearly straight. The lower lip is with a single groove. The tail is 15.7-29.0 mm. The third metacarpal is by far the shortest, 32.7-38.8 mm, the fourth is slightly shorter (37.8-42.6 mm) than the fifth, which is 38.5-44.3 mm in length. The fur is dense and long, woolly in texture; the dorsal colour is mid chestnut brown, ventrally lighter.

Cranial and dental characters: The skull is strong, with short, wide braincase. The zygomata is massive, the zygomatic expansion greater than the mastoid width. The anterior median swellings are low, longer than wide; the lateral ones are well developed, the posterior compartments are small. The sagittal crest is high or very high, the supraorbital crests are moderately developed. The frontal depression is medium. The palatal bridge is relatively long, 32-37% of the maxillary toothrow length.
The upper canine is not especially strong, the posterior upper premolar is large. The anterior upper premolar is small or medium developed with small cusp and situated usually in the toothrow, sometimes very slightly extruded. The middle lower premolar is small or very small, external to a various extent, sometimes missing. The first and third lower premolars are in contact.

Bacular morphology: This species has a relatively small and extremely specialized baculum (Topál 1975). The basal cone is big, equal of width and height. The dorso-proximal margin is deeply emarginate. The ventral incision of the base has the form of an equilateral triangle with a widely rounded-off distal portion. The dorsal knob of the base is very high and well separated from other parts of the base. The ventral surface of the basal cone exhibits a wide median depression. The shaft is dorsoventrally expanded, laterally flattened blade-like structure. The tip is nearly rounded off in the dorsal view but with multiple breakings in outline in the lateral view.

Similar species: *R. yunanensis* is very similar in all details both externally and cranially, but usually larger, especially in cranial measurements. From the other species of the genus *R. pearsoni* externally is readily distinguishable by the combination of the single mental groove, the more or less rectangular constriction of the sella and the widely arched connecting process.
R. acuminatus is smaller cranially and characterised by the short frontal depression and more globular anterior median swellings. *R. affinis* has also shorter and less expressed

frontal depression, due to the better developed posterior swellings. *R. inops* and *R. subrufus* have similar external appearence, but the lower lip is with three mental grooves and the sella is not constricted below the middle; cranially, they have high and bulbous anterior median swellings.

Taxonomic remarks: Andersen (1905b) related *R. pearsoni* close to *R. macrotis*, but Tate (1943) provisionally treated *pearsoni* as a race of *R. luctus*, which latter statement is hardly understandable, knowing the enormous differences in the external appearence and cranial details of the two species.
The sympatric populations of *R. pearsoni* and *R. yunanensis* found by Yoshiyuki (1990) in North Thailand were clearly different in dimensions of external, cranial and dental measurements which evidently support the view that these taxa represent different species.
According to Andersen (1905b) *R. p. chinensis* could be distinguished from the nominate subspecies by its smaller cranial measurements, but his description was based on a single individual only. Osgood (1932) reporting specimens from Tonkin as *R. p. chinensis* on the base of their shorter tibia, but remarked, that in other characters they differ but little or not at all from typical *pearsoni*. Hill (1986) and Kock (1996) found the validity of two subspecies questionable, and our data are also support the view, that by measurements there are no subspecific differences within the species and the maintenance of *chinensis* as valid taxon is unjustified. Yoshiyuki (1990) found, that in Thailand specimens from high altitude are larger than those from low altitude, especially in forearm length.
Dobson (1876, 1878) placed *R. larvatus* in the synonymy of *R. pearsoni*, which opinion was supported by Andersen (1905b).

Fig. 44.1. Lateral and frontal views of noseleaf of *R. pearsoni* (HNHM 95.57.8.) from Nepal. Scale = 3 mm.

Fig. 44.2. Lateral view of the rostral part of the skull (HNHM 92.91.1.) and occlusal view of the upper (left) and lower (right) left anterior dentition (BMNH 79.11.21.56 – holotype) of *R. pearsoni* both from India.

Table 44. ***R. pearsoni***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		47.0	56.0		
SL	23.25	21.58	24.33	0.77	29
CM^3L	9.31	8.29	9.97	0.40	30
ZW	11.73	10.84	12.69	0.43	29
MW	10.75	10.15	11.33	0.26	29
ML	16.20	14.59	17.39	0.65	29
CM_3L	10.06	8.80	10.70	0.51	29

***Rhinolophus yunanensis* Dobson, 1872**
Dobson's horseshoe bat
R. yunanensis Dobson, 1872 (Hotha, Yunnan, China)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A large species of its genus. The ears are medium or large, 23.5-32.0 mm in height. The horseshoe is covering the whole muzzle, its breadth is 12.5-14.0 mm, and has a distinct median emargination. The sella is wide at its base, characteristically constricted near the middle and slightly tapering towards the tip above. The lancet is long, triangular and straight sided. The lower lip is with a single groove. The tail is 18.0-26.0 mm in length. In the wings, the third metacarpal is short, 37.2-41.3 mm, the fourth is 41.1-45.9 mm and the longest fifth metacarpal is 43.3-47.2 mm in length. The pelage is dense and woolly, there seem to be two rather distinct colour phases; the colour is light brown or dark greyish above, the individual hairs are unicoloured; the fur is slightly paler below.

Cranial and dental characters: All cranial and dental characters of *R. yunanensis* are essentially the same as that of *R. pearsoni* but larger in every respects. The zygomatic width is much greater than the mastoid breadth. The anterior median swellings are longer than wide, but are much smaller than the lateral compartments. The sagittal crest is strong, especially in its anterior part. The frontal depression is relatively shallow or medium deep, the supraorbital crests are low but well defined. Tha palatal bridge is 31-34% of the upper toorow (CM^3) length.
The dentition is very heavy and massive; the upper canine and posterior premolar is strong, well developed. The anterior upper premolar is large and placed in the axis of the toothrow; the adjoining teeth are widely separated. The lower middle premolar is medium, more or less external or rarely missing.

Similar species: The very closely related *R. pearsoni* is strikingly similar in every respects, but usually smaller in forearm length and separable by craniodental measurements. The similar sized *R. subrufus* has three mental grooves on the lower lip, almost parallel sided sella and very prominent anterior nasal inflation. *R. luctus* is separable by its very elaborate noseleaf and larger cranial measurements.

Taxonomic remarks: In the description of *yunanensis*, Dobson (1872) gave no comparison with other species, but later (1876) itself synonymised it as a junior synonym of *R. pearsoni*. Andersen (1905b) considered that from published descriptions and figures of *yunanensis* and *larvatus* both were indistinguishable from typical *pearsoni* but certainly different from *R. p. chinensis*. Hinton and Lindsay (1926) when reporting a specimen from Mishmi Hills noted, "it is preferable to refer this specimen definitely to *yunanensis*, since its measurements are distinctly greater than for *pearsoni*". Although Ellerman and Morrison-Scott (1951) and Sinha (1973) treated it as synonym of *R. pearsoni*, Hill (1975, 1986) reviewed *pearsoni* and *yunanensis* in detail and recognised two distinct size categories of specific rank. All the subsequent comprehensive works (Lekagul and McNeely 1977, Corbet and Hill 1992, Koopman 1994) considered *yunanensis* to be a full species (see also comments under *R. pearsoni*).

Fig. 45.1. Lateral and frontal views of noseleaf of *R. yunanensis* (BMNH 78.976) from Thailand. Scale = 3 mm.

Fig. 45.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. yunanensis* (BMNH 9.4.4.3 - holotype) from China. Scale = 3 mm.

Table 45. ***R. yunanensis***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		51.5	64.0		
SL	26.11	24.60	27.25	0.72	22
CM^3L	10.68	10.14	11.24	0.33	23
ZW	13.10	12.16	13.95	0.57	14
MW	11.70	10.92	12.07	0.33	14
ML	18.63	17.41	19.58	0.61	22
CM_3L	11.46	10.85	12.00	0.36	23

PHILIPPINENSIS-GROUP

***Rhinolophus macrotis* Blyth, 1844**
Big-eared horseshoe bat
R. macrotis Blyth, 1844 (Nepal)
R. hirsutus Andersen, 1905 (Guimaras I., Philippines)
R. m. dohrni Andersen, 1907 (Soekaranda, Deli, NW Sumatra)
R. m. siamensis Gyldenstolpe, 1917 (Doi Par Sakang, N.W. Thailand)
R. episcopus Allen, 1923 (Wanhsien, Sichuan, China)
R. episcopus caldwelli Allen, 1923 (Yuki, Fujian, China)
R. m. topali Csorba and Bates, 1995 (Kakul Phosphate Mine, Abbotabad, Pakistan)

Recognised subspecies: The following subspecies are recognised – *macrotis* in Nepal and India; *episcopus* in Sichuan, China; *caldwelli* in south-eastern China and Vietnam; *siamensis* in Thailand, Laos and Vietnam; *dohrni* in Sumatra and Malaysia; *hirsutus* in the Philippines; *topali* in Pakistan.

External characters: A medium sized horseshoe bat. The ears are large in relation to the head, their heights between 18.5-26.0 mm. The horseshoe is 6.8-10.0 mm wide, covering the muzzle and distinctly notched at the middle. A well developed secondary noseleaf is present but usually concealed by the horseshoe. The sella is long, directed upward, broad and rounded, tonque-shaped (sometimes with covex sides), with rather long and dense hairs on its front face. The connecting process is high; its lower part almost parallel with the sella. The lancet is long with convex lateral margins and rounded (sometimes little pointed) tip. The lower lip is with three mental grooves. The tail is usually relatively long, 12.4-26.2 mm. In the wings, the third metacarpal is slightly shorter (28.5-34.5 mm), the fourth and fifth are subequal, 29.3-36.0 mm long.

The fur of upperparts is light brown (except the pale Pakistani specimens), the underparts are buffy. Colour phases are not known.

Cranial and dental characters: The skull with elongated facial part is of the general shape characteristic of the primitive species of *Rhinolophus*. The zygomata less than or rarely subequal to the mastoid width. The anterior median swellings are well inflated, long, and also expanded anteriorly. The posterior median swellings are short and small. The sagittal crest is weak; the frontal depression shallow or medium developed. The cristae supraorbitales are well visible, frequently with sharp ridges. The palatal bridge is long or very long, 39-60% of maxillary toothrow.
The upper canine is less developed, its height is only slightly exceeds the cusp of P^4. The first upper premolar (P^2) is situated in the toothrow and has a prominent cusp; C^1 and P^4 not in contact. The lower canine is slender. The size and situation of the P_3 depending on the subspecies; in the case of *R. m. topali* extremely small and extruded, in the other subspecies larger and often stands in the toothrow. Depending on the development of the middle lower premolar, P_2 and P_4 separated or in contact.

Bacular morphology: The baculum has a small basal cone slightly compressed dorsoventrally. The dorsal and ventral emarginations on the corresponding proximal margins are slight and wide. The ventral depression extend on the shaft as a ventral flat surface up to its middle length. The shaft has a thickening at the middle. It has a very slight dorsal bent near the base cone. The tip narrowly rounded off with lateral widening and a longish dorsal knob (Topál 1975).

Similar species: *R. macrotis* externally can be distinguished from the sympatric species of the *megaphyllus* and *ferrumequinum*-groups by the shape of its the connecting process, the basal part of which is running nearly parallel with the sella; the sella itself is quite long and erected upwards. Because of the long palatal bridge, weak upper canines, well developed anterior nasal swellings and the general measurements, cranially the most similar species is *R. marshalli*. The main difference between the two is the shape of the rostral part; in the case of *R. marshalli* the posterior swellings are rudimentary and the frontal depression is extending anteriorly to the posterior border of the median swellings. The skull of *R. philippinensis* is larger while *R. montanus* has semicircular median swellings.

Taxonomic remarks: Following Andersen (1905b), Wroughton (1918) kept this species very near to *R. pearsoni*, but Sinha (1973) speculated, that because of the number of the mental grooves, shape of the connecting process and base of the sella it has more affinity with *R. ferrumequinum* than with *R. pearsoni*. These views are absolutely pay no attention to the evident differences in the skull characteristics (general shape of skull and the nasal swellings, palatal bridge length etc.) by which *R. macrotis* is related to *R. philippinensis* and its allies.
Some subspecies of *R. macrotis* are readily distinguishable by the size and position of the lower middle premolar and by the width of the horseshoe (Csorba and Bates 1995). The horseshoe is very wide (over 8.5 mm) and the lower middle premolar is well developed in the case of *dohrni*; the nominate subspecies is characterised by its narrower horseshoe and smaller P_3; the noseleaf is also wide in *topali*, but the middle lower premolar is rudimentary. *R. episcopus* was characterised by Allen (1923) as a species of the *macrotis*-group but larger than *macrotis*; its subspecies *R. e. caldwelli* was

introduced in the same paper and stated being smaller than the typical form, but its relations to *R. macrotis* was not discussed.
Osgood (1932) referred specimens from northern Vietnam to *R. episcopus caldwelli* (later transferred to *R. m. caldwelli*) and *R. m. siamensis*. This claim that the two taxa (as subspecies) are sympatric in Tonkin was subsequently rejected by Corbet and Hill (1992), although specimens of the much smaller *siamensis* and the larger *caldwelli* recently collected from the same sites in Tonkin (specimens in HNHM) and Laos (Francis *et al*. 1996) verify the sympatry. Accordingly, the appropriate name for the smaller form appears to be *R. siamensis* which is genetically very similar to *R. macrotis* but differs in smaller size, slightly different noseleaf and higher echolocation calls (Francis *et al*. op. cit.).
The Philippine form *R. m. hirsutus* is characterised with very long sella (over 7 mm) and long, narrow, straigth sided lancet. Cranially is distinguishable from the other subspecies by its larger nasal swellings and shorter palatal bridge (39-40% of the CM^3 length). This taxon was first described as a distinct species but was later subsumed under *R. macrotis* (Tate 1943) and is regarded as such by the subsequent authors. However, Ingle and Heaney (1992) suspect that the Philippine population is morphologically distinct and genetically independent and will eventually be shown to be a distinct species.
As already Andersen (1907a) noted *R. macrotis* is an example of „a type of low level of evolution which has no closer relative than the primitive forms of the *Rh. philippinensis* group" and „the sella of *macrotis* might properly be described as that of a *philippinensis* deprived of its lateral expansions; the shape of the connecting process and lancet also point towards relationship with *philippinensis*". The noseleaf features of the much later described *R. montanus* (Goodwin 1979) are seemingly filling this gap (see also comments under *R. montanus*).

Fig. 46.1. Lateral and frontal views of noseleaf of *R. macrotis* (HNHM 95.56.2.) from Nepal. Scale = 3 mm.

Fig. 46.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. macrotis* (BMNH 45.1.8.416 - holotype) from Nepal. (The middle lower premolar presents only on the right side.) Scale = 3 mm.

Table 46. ***R. macrotis***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		39.0	48.0		
SL	18.10	16.96	18.83	0.44	34
CM^3L	6.55	5.66	7.12	0.26	36
ZW	8.21	7.88	8.58	0.21	34
MW	8.80	7.87	9.18	0.26	36
ML	11.49	9.94	12.25	0.45	37
CM_3L	6.78	5.89	7.31	0.25	37

***Rhinolophus marshalli* Thonglongya, 1973**
Marshall's horseshoe bat
R. marshalli Thonglongya, 1973 (foothills of Khao Soi Dao Thai, Amphoe Pong Nam Ron, Chantaburi, Thailand)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized horseshoe bat. The ears are enormous, 25.4-30.0 mm in height, reaching far beyond the muzzle when laying forward. The horseshoe is broad (7.5-9.2 mm), covering most of the upper lip even extending laterally a few millimetres beyond the muzzle; there is a narrow, deep anterior emargination. The sella is large, broad and slightly higher than wide; its upper margin semicircular. The internarial region is greatly expanded, its edges form a wing-like structure which is integral with the base of the sella. The connecting process is low, rounded and joining at the base of the lancet. The lancet is low, triangular with rounded tip. The lower lip is with three mental grooves. The tail is 16.5-25.0 mm in length. In the wings, the third metacarpal is slightly shorter (30.9-34.0 mm), the fourth is 32.1-34.6 mm and the fifth is 32.3-35.3 mm in length. The fur is moderately long, dorsally dark brown sometimes with reddish tinge and smoky grey or light yellowish-brown on the underparts. Colour phases are not known.

Cranial and dental characters: The skull is slender, with long rostral part. The zygomatic width is always less than the mastoid width. The anterior median swellings are well inflated, its anterior edge reaching beyond the front of the rostral wall, the posterior compartments are rudimentary. The sagittal crest is very low. The frontal depression is moderately deep, the cristae supraorbitales are strong but without sharp ridges. The palatal bridge is very long, 60-65% of the maxillary toothrow.
The upper canine and the posterior upper premolar are moderately developed. The first upper premolar small or medium, standing loose in the row, separate from the adjoining teeth. The middle lower premolar is small and situated in or half-displaced from the toothrow; the neighbouring premolars (P_2 and P_4) are always separated from each other.

Bacular morphology: According to Topál (1975) the bone has a pronounced upward bend and a small basal cone with deep emargination. The rather wide ventral emargination is deeper than the dorsal one. The dorsal knob is low, the ventral depression is small in extension. The tip has a narrowly rounded off point with a lateral widening and a longish dorsal knob.

Similar species: The peculiarly shaped noseleaf with low lancet and very large ears readily separate *R. marshalli* from every other species in the genus. Cranially, the only species in this size having similarly narrow skull, very long palate and bulbous anterior nasal swelling is *R. macrotis*. The main distinguishing character between the two is the shape of the rostral part of the skull; in the case of *R. macrotis* the posterior swellings are not rudimentary (although small) and the frontal depression is not extending anteriorly to the median compartments.

Taxonomic remarks: The species which was described from Thailand (Thonglongya 1973) had already been collected decades earlier in Vietnam, but the specimens (deposited in the collections of FMNH, MNHN, MNB and HNHM) were determined as

R. macrotis. The first HNHM specimen was also published under this name by Topál (1975, see also Hill and Topál 1990). Based on the structure of the internarial region and sella the systematic position of the species as a member of the *philippinensis*-group was determined by Thonglongya (op. cit.). Although clearly most closely related to *R. rex* and *R. paradoxolophus*, *R. marshalli* tends towards the other members of the group.

Fig. 47.1. Lateral and frontal views of noseleaf of *R. marshalli* (HNHM 95.60.20.) from Vietnam. Scale = 3 mm.

Fig. 47.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. marshalli* (HNHM 95.60.11.) from Vietnam. Scale = 3 mm.

Table 47. ***R. marshalli***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		41.0	48.0		
SL	18.22	17.83	18.62	0.24	14
CM^3L	6.43	6.28	6.67	0.10	14
ZW	8.29	7.95	8.48	0.16	14
MW	9.25	8.93	9.52	0.17	14
ML	11.44	11.13	11.73	0.18	13
CM_3L	6.70	6.54	6.86	0.10	14

***Rhinolophus montanus* Goodwin, 1979**
Timorese horseshoe bat
R. philippinensis montanus Goodwin, 1979 (Quoto Lou caves, near village of Lequi Mia, 5 miles S of Ermera, Timor, c. 1220 m)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized bat of the genus. The ears are enormous, 25.0-27.0 mm in length. The horseshoe is wide, covering the muzzle; the secondary leaflet is relatively well developed. The sella is very broad at base and continuous with the sides of the enlarged internarial cup; the sides of the sella is tapering gradually to a truncate tip. The connecting process is relatively high and rounded. The lancet is of the shape of a more or less equilateral triangle. The lower lip is with three mental grooves. The tail is 25.0-31.0 mm long. There is no data on the wing structure. The pelage has a somewhat woolly texture and grizzled appearence due to a scattering of pale hairs. The colour of the dorsal surface is fuscous shading to darker brown in the neck region. Most of the individual hairs are dark throughout, there is no bicolored effect. The ventral surface is paler and most of the hairs have pale tips.

Cranial and dental characters: The skull is delicately built, the zygomatic width is much smaller than the mastoid width. The anterior median swellings are well inflated, almost as wide as long when viewed from above. The lateral compartments are

moderate, the posterior ones are small. The crista sagittalis is weak; the frontal depression is shallow, bordered with ill-defined supraorbital ridges. The palatal bridge is long.
The upper canine is slender, relatively short. The first upper premolar is elongated antero-posterioly, stands loose in the toothrow but touching the cingulum of the canine; the posterior upper premolar is almost as large basally as the C^1. The lower middle premolar (P_3) crowded slightly out of line, but widely separates the adjoining premolars.

Similar species: The enormous ears and enlarged internarial cusp with the widely based sella separate the species from all its congeners except *R. philippinensis*, but this latter is greater in external and cranial measurements and has an even broader internarial cup. The shape of connecting process and lancet is similar to those of *R: macrotis*, but the sella of *R. montanus* is not parallel-sided.
Cranially the measurements, very slender skull and long palate distinguish *R. montanus* from the majority of other species; the similar *R. marshalli* has rudimentary posterior nasal inflations and anteriorly sharply demarcated frontal depression; *R. macrotis* is characterised by the shape of anterior median swellings which are longer than wide.

Taxonomic remarks: Goodwin (1979) discussed the differences between his new *montanus* and the other subspecies of *R. philippinensis* and noted its much smaller size, differently shaped sella and connecting process, more pronounced nasal swellings and the more crowded situation of the small premolars. These differences are definitely out of the intraspecific variation of *R. philippinensis* and leave no doubt that *montanus* is a full species. The external appearence of the noseleaf of *montanus* is intermediate between *R. philippinensis* and *R. macrotis* and connecting the two species.

Fig. 48.1. Lateral and frontal views of noseleaf of *R. montanus* (AMNH 237813) from Timor, Indonesia. Scale = 3 mm.

Fig. 48.2. Lateral view of the rostral part of the skull and occlusal view of the left upper (left) and right lower (right) anterior dentition of *R. montanus* (AMNH 237814 - holotype) from Timor, Indonesia. Scale = 3 mm.

Table 48. ***R. montanus***: External, cranial and dental measurements (mm).

	min	max	n
FA	43.5	46.0	
SL	18.45		1
CM^3L	6.58		1
ZW	8.05		1
MW	8.86		1
ML	11.85		1
CM_3L	6.95		1

***Rhinolophus paradoxolophus* (Bourret, 1951)**
Bourret's horseshoe bat
Rhinomegalophus paradoxolophus (Bourret, 1951) (Roche Percée Cave, near Chapa, 1700 m, Lao Key, Tonkin, Vietnam)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A fairly large species of horseshoe bats. The ears are enormous (27.0-38.8 mm in height), with greatly developed antitragus. The horseshoe is very wide (about 12.5 mm), extending laterally beyond the sides of muzzle anteriorly with a deep median emargination. There is no supplementary leaflets. The internarial lappets form a broad, cup-like structure extending beyond the base of sella. The sella is tall and wide, rounded at its apex and with a longitudinal folding extending along the middle of the front surface. The connecting process is low, rounded and joined basally by the rearward extensions of the internarial lappets and inserted on the lancet at its base. The lancet is low, rounded. The lower lip is width three mental grooves. The tail is 22.4-34.8 mm in length. In the wings, the metacarpals are almost subequal, the third is 37.4-39.0 mm, the fourth is 39.3-40.5 mm and the fifth is 38.9-39.5 mm in length. The fur is rather long, with dark brown upperparts; the individual hairs are pale at base and some tipped with rufescence. The chin and upper breast are grayish, with the remaining underparts smoky gray.

Cranial and dental characters: The skull is unusually slender, the rostrum characteristically long and there is a deep depression in front of the occipital region.. The zygomatic width is much less than the mastoid width. The anterior median swellings are very low but exceptionally elongated anteriorly as the lateral swellings do. The posterior compartments are shifted to a more lateral position, the frontal depression is deep and clearly demarcated. The sagittal crest is sharp but not high, the supraorbital crests are well defined. The palatal bridge is very long, 54-61% of the upper toothrow.
The upper canine is relatively slender but long, the posterior upper premolar is with large cusp. The moderately large anterior upper premolar is in the row and frequently separated from the neighbouring teeth by a distinct gap. The middle lower premolar from medium to very small, but stands in the axis of the toothrow or only slightly displaced.

Similar species: The species is unmistakeable by its external appearence, except *R. rex* which is very similar in every particulars but usually larger in forearm length and always greater in craniodental measurements. *R. philippinensis* is basicly similar cranially, but has differently shaped, higher but anteriorly much shorter median and lateral nasal inflations.

Taxonomic remarks: The genus *Rhinomegalophus* was proposed by Bourret (1951) on the base of the special structure of noseleaf and ears of its type species *paradoxolophus*. Hill (1972) pointed out, that many of the features of *paradoxolophus* (and *R. rex*) are to be found in the members of the *philippinensis* subgroup (= *philippinensis*-group) and there is little to be gained from the retention of *Rhinomegalophus* as a genus distinct from *Rhinolophus*.
R. paradoxolophus and *R. rex* are strikingly similar in every respects and as Hill (op. cit.) noted the differences deductable from the original description of the damaged type

specimen of *R. paradoxolophus* are more apparent than real. As Corbet and Hill (1992) noted, *R. paradoxolophus* may be conspecific with *R. rex* (see also comments under the latter species).

Fig. 49.1. Lateral and frontal views of noseleaf of *R. paradoxolophus* (HNHM 98.3.7.) from Vietnam. Scale = 3 mm.

Fig. 49.2. Lateral view of the rostral part of the skull (HNHM 98.3.7.) and occlusal view of the left upper (left) and right lower (right) anterior dentition (MNHN 1948.358 – holotype) both from Vietnam of *R. paradoxolophus*.

Table 49. ***R. paradoxolophus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		50.5	57.0		
SL	20.48	20.10	20.88	0.31	7
CM^3L	7.27	7.07	7.50	0.15	9
ZW	9.23	9.04	9.42	0.18	5
MW	10.24	10.08	10.40	0.14	5
ML	13.02	12.64	13.45	0.26	8
CM_3L	7.40	6.73	7.76	0.29	9

***Rhinolophus philippinensis* Waterhouse, 1843**
Philippine horseshoe bat
R. philippinensis Waterhouse, 1843 (Luzon, Philippines)
R. achilles Thomas, 1900 (Kai Is)
R. maros Tate and Archbold, 1939 (Talassa, near Maros, S Sulawesi, 300 m)
R. p. alleni Lawrence, 1939 (lower slopes of Mt. Halcon, Mindoro I., Philippines)
R. p. sanborni Chasen, 1940 (Tapadong Caves, near Lahad Data, E. coast of Sabah, Borneo)
R. maros robertsi Tate, 1952 (Phoenician Tin Mine, Mt. Amos, 18 miles S of Cooktown, northeast Queensland, 2000 ft)

Recognised subspecies: The following subspecies are recognised - *sanborni* in Borneo; *alleni* in Mindoro; *philippinensis* in the remaining Philippine islands; *maros* in Sulawesi and New Guinea; *achilles* in Keis; *robertsi* in northeastern Queensland.

External characters: A large species of the genus. The ears are enormous, 25.0-32.0 mm in height. The noseleaf and ears are brown. The horseshoe is broad (11.0-12.6 mm in width across) and especially long, concealing the muzzle. The internarial region is expanded with turned-up edges, forming a deep and very wide cup between and above the nostrils. The shape of the sella is varying, in the case of the nominate form the base of sella is narrow and widening upwards for a while, in *alleni* and *sanborni* almost parallel sided. The connecting process is very low (e.g. ssp. *alleni*) or better developed (ssp. *philippinensis*). The shape of lancet is also variable, the very tip of the long lancet is either almost parallel (Philippine forms) or distinctly triangular (ssp. *sanborni*). The

lower lip is with three mental grooves. The tail is relatively long, 25.0-35.5 mm. The proportion of metacarpals shows a relatively unspecialised condition, the third and fifth metacarpals are subequal in length (34.6-36.0 mm), the fourth is slightly longer (35.3-39.0 mm). The dorsal fur is dull brown to chestnut or brownish gray, pale gray towards the bases of the hairs; the underparts are pale brownish with sligthly darker hair bases, but the longer buffy tips make the ventral surface paler.

Cranial and dental characters: The skull is light and slender, tapering gradually from the masotid processes to the roots of canines, the mastoid width always greater than zygomatic width. The anterior median swellings are well inflated, longer than wide and protruding anteriorly a bit beyond the rostral wall. The crista sagittalis is low in front, weak or moderately developed in general. The frontal depression is medium or shallow, the bordering supreorbital crests are well defined, sometimes with sharp ridges. The palatal bridge is long, 40-47% of the maxillary toothrow length.
The upper canine and the posterior premolar (P^4) are moderately developed; the first upper premolar is invariably in the row and equally removed from the adjoining teeth by a small but distinct place. In the lower jaw, the small or medium sized P_3 is also in the row, P_2 and P_4 are widely separated.

Similar species: The species is easily separable by its external features (the peculiarly wide internarial region and horseshoe) from the other horseshoe bats. *R. creaghi* and *R. canuti* are similar cranially but their zygomatic width is greater than the mastoid width and the palatal bridge is short; *R. arcuatus* differs by its shorter rostrum, anteriorly not elongated median swellings and the more crowded situation of the anterior upper premolar (P^2). *R. paradoxolophus* and *R. rex* have lower, anteriorly even more protruding median swellings and relatively longer palatal bridge. Both *R. montanus* and *R. macrotis* look alike by cranial features but smaller.

Taxonomic remarks: *R. p. alleni* was distingushed from the typical race by its generally smaller size and differently shaped noseleaf, where the sella and narial cup narrower (Lawrence 1939). When described *R. maros*, Tate and Archbold (1939) listed the new species in the *macrotis*-group (mentioned as different from the *philippinensis*-group) and allied it close to (and only compared with) *R. rex*; probably due to the fact that that time the AMNH did not possess specimen of *R. philippinensis*. Despite the fact, that Tate (1943) itself synonymised *R. maros* with *R. philippinensis* (and even remarked that *maros* and *alleni* are virtually indistinguishable and it is possible that both represent true *R. p. philippinensis*), when described *robertsi* (Tate 1952) he used again the specific name *R. maros*. *R. m. robertsi* was also compared with *R. m. maros* only and characterised cranially as essentially the same as *maros*, but generally larger, with the teeth (and particularly P^4) distinctly larger. Subsequently, Laurie and Hill (1954) put *maros* and its subspecies into the synonymy of *R. philippinensis*. Thomas (1900) allied his new species *R. achilles* from Kei Islands to *R. mitratus* and *R. philippinensis*; but *achilles* was later synonymised as a subspecies of *R. philippinensis* by Tate (1943). In Australia, two forms of *R. philippinensis* have been observed within its range in northern Queensland. They differ in size, characteristics of the echolocation call and structure of the noseleaf. According to Pavey (1995) „one form has been variously considered to be an undescribed species, a population of a horseshoe bat from Sulawesi, or as a hybrid between the large-eared [= *R. philippinensis*] and eastern [= *R. megaphyllus*] horseshoe bats". This peculiar intermediate form is cited as „most likely to be either a hybrid

resulting from a cross between a female *R. philippinensis* and male *R. megaphyllus*, or a morphological variant of *R. philippinensis*" by Cooper *et al*. (1996). Flannery (1995a, 1995b) named these races as *maros* (the smaller form which includes *sanborni* and *alleni* as synonymies) and *achilles* (including *robertsi*); because of their sympatric occurence he also noted that they will ultimately be recognised as separate species. In the meantime, he (1995a) designated the New Guinean populations to the taxon *maros*. When investigated the cave-dwelling bats of Borneo, Chasen (1931) realised that „it is of course improbable that the Bornean race [of *R. philippinensis*] is the same as that of the Philippine islands" and subsequently described this new form as *R. p. sanborni* (Chasen 1940).
Because of its very different measurements and specifically modified noseleaf, *R. p. montanus* Goodwin, 1979 is considered here as separate species (see remarks under *R. montanus*).

Fig. 50.1. Lateral and frontal views of noseleaf of *R. philippinensis alleni* (AMNH 206736 – holotype) from the Philippines. Scale = 3 mm.

Fig. 50.3. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. philippinensis* (BMNH 55.12.26.270 - holotype) from the Philippines. Scale = 3 mm.

Table 50. ***R. philippinensis***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		47.0	57.0		
SL	21.89	20.30	23.04	0.99	18
CM^3L	8.08	7.34	8.90	0.42	21
ZW	9.84	9.04	11.06	0.60	19
MW	10.58	9.90	11.13	0.43	17
ML	14.39	13.24	15.71	0.68	21
CM_3L	8.51	7.75	9.26	0.42	20

***Rhinolophus rex* Allen, 1923**
King horseshoe bat
R. rex Allen, 1923 (Wanhsien, Szechwan, China)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A large species of its genus. The ears are enormous (29.1-35.0 mm in height); antitragus well developed, marked off by a deep notch. The horseshoe is very broad, extending far beyond the sides of the muzzle, with a deep median emargination anteriorly. There is no secondary leaflet. The internarial cup is very broad extending laterally over much of the width of the horseshoe; its lateral edges pass behind the sella and merge with the base of lancet. The sella is very large, long, tongue shaped, narrowest at its base; a longitudinal median depression is extending almost to the top of sella. The connecting process is low, with a convex outline and sloping away to join the

lancet near its base. The lancet is very short, almost concealed by the fur, its tip is broadly rounded. The lower lip is with three mental grooves. The tail is 27.5-32.0 mm in length. In the wings, the third metacarpal slightly the shortest (41.5-42.4 mm), the fourth and fifth are practically of equal length (43.0-44.8 mm). The fur is rather long; light cinnamon-buff or dark brown above; the ventral aspect is generally paler, more greyish.

Cranial and dental characters: The skull is elongated and narrow, the zygomatic width is considerably less than the mastoid width. The median nasal swellings are prominent and elliptical, protruding anteriorly well beyond the rostral wall; the lateral comparetments are also elongated. The sagittal crests is very low or low, with a deep or moderate clearly demarcated frontal depression. The supraorbital crests are medium developed. The palatal bridge is very long, 55-60% of the maxillary toothrow (CM^3).
The upper canine is with elliptical base and narrow shaft. The anterior upper premolar is small but fully in the toothrow and has a well developed cusp; usually separated form C^1 and P^4 by narrow interspaces. The lower canine less massive; the minute or small lower middle premolar also stands in the row, separating P_2 and P_4, in contact or nearly so with their cingula.

Similar species: *R. rex* and *R. paradoxolophus* can be separated by their measurements only (but see taxonomic remarks). The large size and very characteristic nasal foliation distinguish the species from other *Rhinolophus* externally. The skull of the species is easily recognisable by its measurements, low but elongated rostral part, very long palatal bridge and loosely situated upper anterior dentition; other species with similar skull characteristics are either smaller (*R. paradoxolophus*, *R. montanus*, *R. marshalli*, *R. macrotis*) or has less protruding (more circular) but more elevated median swellings and shorter palate (*R. philippinensis*).

Taxonomic remarks: As Hill (1972) summarized, *R. rex* was referred initially to the *macrotis* group of Andersen by Allen (1923) but later this author (1938) placed it in the *philippinensis* group of Andersen. Tate and Archbold (1939) referred *R. rex* to the *macrotis* group, which they thought had no close allience to the *philippinensis* group. Subsequently Tate (1943) put *R. rex* into the *philippinensis* group referring it with *R. philippinensis*, *R. macrotis* and *R. coelophyllus* to a *philippinensis* section or subgroup.
As more specimens known from the species, the differences in measurements once clearly separate *R. rex* from *R. paradoxolophus* (Hill and Topál 1990, Thonglongya 1973) become less obvious. Since there is no observable external or craniodental difference between the two species other then mensural and they occur allopatrically their specific distinctness is questionable.

Fig. 51.1. Lateral and frontal views of noseleaf of *R. rex* (AMNH 56970) from China. Scale = 3 mm.

Fig. 51.2. Lateral view of the rostral part of the skull and occlusal view of the left upper (left) and right lower (right) anterior dentition of *R. rex* (AMNH 56890 - holotype) from China. Scale = 3 mm.

Table 51. ***R. rex***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		56.5	63.0		
SL	22.00	21.95	22.05	0.05	3
CM^3L	8.11	8.02	8.26	0.10	5
ZW	9.87	9.71	9.97	0.11	4
MW	11.00	10.97	11.06	0.04	4
ML	14.18	13.93	14.39	0.17	5
CM_3L	8.28	8.21	8.45	0.10	5

PUSILLUS-GROUP

***Rhinolophus acuminatus* Peters, 1871**
Acuminate horseshoe bat
R. acuminatus Peters, 1871 (Gadok, Java)
R. sumatranus Andersen, 1905 (Lower Langkat, Sumatra)
R. a. audax Andersen, 1905 (Lombok I., Lesser Sunda Is)
R. calypso Andersen, 1905 (Kifa Juc, Bua Bua, Enggano I., off W Sumatra)
R. circe Andersen, 1906 (Nias I., off W Sumatra)

Recognised subspecies: Following Koopman (1982), the following subspecies are recognised – *acuminatus* in Java; *sumatranus* in Sumatra and Borneo; *circe* in Nias Island; *calypso* in Engano Island; *audax* in Bali and Lombok. Mainland specimens resemble those from Java or Lombok.

External characters: A medium sized species. The ears are small or medium, 16.7-21.5 mm in height. The horseshoe is 7.8-10.2 mm in breadth, does not cover the whole muzzle; its median emargination is wide. The shape of sella is varied according to the subspecies being almost parallel sided or only slightly narrowing or distinctly narrowed at centre; its tip rounded.. The connecting process is a broadly based triangle usually bluntly, sometimes sharply pointed. The lancet is with concave margins, its tip almost parallel margined. The lower lip is with three mental grooves. The tail length is 18.9-31.0 mm. In the wings, the shortest third metacarpal is 32.0-38.3 mm, the fourth (32.5-39.3 mm) and fifth (33.0-39.3 mm) metacarpals are subequal. Two colour phases are known; the fur of the dorsal surface is greyish brown, hairs are tipped ligth grey or silver or tinged with russet; ventrally greyish brown, the hairs are pale based or the fur is paler reddish brown.

Cranial and dental characters: The skull is broad, the rostral part is short. The zygomata is much broader than the mastoid width. The anterior median swellings are well inflated, the posterior ones less developed and short; the rostrum is relatively high when viewed laterally. The crista sagittalis is relatively strong, the frontal depression is shallow and very short. The crista supraorbitalis is low but with sharp ridges and combining at a point in front of the centre of orbital cavity. The palatal bridge is short, 25-28 % of the maxillary toothrow.

The upper canine is frequently narrowed after the cingulum, usually relatively slender. The P^2 is medium or well developed, usually in row or only slightly displaced. The medium sized lower middle premolar is external; the first (P_2) and third (P_4) lower premolars are frequently in contact.

Bacular morphology: Topál (1975) examined a specimen of the subspecies *calypso*. The basal cone is dorsoventrally higher than wide. Its dorsal knob is also strongly protrudes proximally. The ventral emargination on the proximal margin of the base is extremely deep, narrow and distally diverging. The shaft slightly bends dorsally, however, its ventral profile is almost straight when viewed laterally. In dorsal view, there is a slight constriction at the middle and the very tip of the bone.

Similar species: The other Asian species with triangular connecting process are much smaller. Cranially, *R. affinis* is similar, but has a lower rostral part of the skull, a less developed anterior median swellings and the upper canines are stronger and more widely based. *R. pearsoni* is usually larger cranially, and has a longer rostrum and frontal depression with supraorbital crests combining behind the centre of the orbital cavity. *R. arcuatus* is characterised by the longer rostral part of its skull and the more expressedly concave rostral profile.

Taxonomic remarks: The subspecific distinctions are slight and based mainly on minor differences in the shape of sella and the width of horseshoe; the dentition of these forms is very uniform (Andersen 1907a). There seem no consistent size differences between the subspecies (Hill 1974). Chasen (1940) mentioned a large series of this bat from Sumatra as very variable in size (forearm lengths between 47 and 52 mm) and thought possible that the series includes more than one form. He also recorded a specimen from North Borneo which is provisionally placed in *R. a. sumatranus* but remarked that it probably represent an undescribed Bornean race. Subsequently, Payne *et al*. (1985) also designated the Bornean population to *R. a. sumatranus*.
The proper taxonomic allocation of mainland and Philippine populations are uncertain (Hill and Thonglongya 1972, Koopman 1994), although specimens from Cambodia and Thailand agree very closely in colour and size with *R. a. acuminatus* from Java to which Thai specimens were referred by Shamel (1942) and Sanborn (1952).

Fig. 52.1. Lateral and frontal views of noseleaf of *R. acuminatus* (MNB 2548/1 - holotype) from Java. Scale = 3 mm.

Fig. 52.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. acuminatus* (BMNH 44.4.4.19) from Java. Scale = 3 mm.

Table 52. ***R. acuminatus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		46.0	53.0		
SL	21.20	20.08	22.21	0.62	32
CM^3L	8.36	7.70	8.98	0.33	32
ZW	11.00	10.05	11.50	0.35	32
MW	10.06	9.36	10.68	0.29	32
ML	14.67	13.76	15.64	0.51	31
CM_3L	9.10	8.56	9.85	0.36	32

***Rhinolophus cognatus* Andersen, 1906**
Andaman horseshoe bat
R. cognatus Andersen, 1906 (Port Blair, S. Andaman Is)
R. famulus Andersen, 1918 (North Central I., Andaman Is)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *famulus* in north Andaman; *cognatus* in south Andaman.

External characters: A relatively small sized species of the genus. The ears are medium, 13.5-18.3 mm in height. The horseshoe well developed, its breadth ranges 6.5-7.1 mm; a small secondary horseshoe is visible from above. The sella is relatively large, slightly narrowing from the base, its tip widely rounded. The connecting process is horn-like and slightly curved downwards. The lancet is tall, its lateral margins concave, the distal part of it is spatulate with a rounded tip. There are three mental grooves on the lower lip. The tail length is 13.0-21.0 mm. In the wings, the third metacarpal is 28-30.4 mm, the fourth is 28.5-31.2 mm and the fifth is 28.0-31.3 mm in length. There is no information on the colouration of the species.

Cranial and dental characters: The skull is of the typical shape of the group, moderately strong and the zygomatic width is greater than the mastoid width. The anterior and lateral rostral swellings are medium developed, the rostral profile is sloping backwards. The sagittal crest is moderate; the shallow frontal depression is enclosed by low but prominent supraorbital ridges. The palatal bridge is approximately 29% of the maxillary toothrow length.
The upper canine is relatively slender and long, the posterior upper premolar is well developed. The medium sized first upper premolar lies within the toothrow; the second lower premolar also stands in the row or only halfway extruded; the adjoining P_2 and P_4 are separated.

Similar species: Because of its size, spatulate lancet and curved connecting process externally the only similar species is *R. imaizumii* from which *R. cognatus* is separable on the base of cranial traits as its slightly more inflated anterior median swellings, slender upper canine and the posterior palatal emargination is wider than the anterior palatal emargination. The skull of *R. cognatus* is essentially the same as that of the other species in the group.

R. cognatus cranially differs from the small sized species of *megaphyllus*-group by its lower rostrum.

Taxonomic remarks: Andersen (1906) noted, that *R. cognatus* is allied to *R. refulgens* (= *lepidus*) and agrees in the general shape of the skull, dentition and wing structure; but differs in its larger skull, broader nasal appendages and larger ears.
Although Andersen (1918) regarded *famulus* as a distinct species of *Rhinolophus*, Ellerman and Morrison-Scott (1951) considered it as a doubtful subspecies of *R. cognatus*, while Hill (1967b) remarked that there seems little doubt that *famulus* is but subspecifically related to *cognatus*. It is quite similar in shape and size to *R. c. cognatus* except for some measurements (Sinha 1973). The skull and dentition is more robust in *cognatus* than in *famulus* (Bates & Harrison 1997).

Fig. 53.1. Lateral and frontal views of noseleaf of *R. cognatus* (BMNH 6.12.1.12 - holotype) from Andaman Islands. Scale = 3 mm.

Fig. 53.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. cognatus* (BMNH 6.12.1.12 - holotype) from Andaman Islands. Scale = 3 mm.

Table 53. ***R. cognatus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		37.5	41.0		
SL	16.91	16.19	18.01	0.97	3
CM^3L	6.50	6.13	6.88	0.38	3
ZW	8.60	8.47	8.75	0.14	3
MW	8.09	7.87	8.37	0.26	3
ML	11.37	10.78	11.92	0.57	3
CM_3L	6.97	6.58	7.35	0.39	3

***Rhinolophus convexus* Csorba, 1997**
Round-leaf horseshoe bat
Rhinolophus convexus Csorba, 1997 (Gunung Jasar, Tanah Rata, Cameron Highlands, 4°28'N, 101°22'E, 1600 m, Pahang, Malaysia).

Recognised subspecies: All specimens referred to the nominate form.

External characters: A small sized horseshoe bat. The ears are small, 15.2-15.7 mm in height. The horseshoe does not cover the muzzle, its width is about 7.5 mm; a secondery leaflet is present. The sella gradually narrows towards the tip and curves downward at its terminus. The connecting process is long and slender; in lateral view the anterior margin is concave and continuously sloping toward the base of sella. The lancet is more or less an equilateral triangle, its tip broadly rounded with convex lateral margins. The lower lip has three grooves. The tail is 18.2-21.6 mm long. In the wings, the third metacarpal is the shortest (29.9-31.2 mm), the fourth (31.5-32.8 mm) and the fifth (31.0-32.5 mm)

metacarpals are subequal. The fur is rich russet brown above, the individual hairs are unicoloured. Hairs of the venter are paler and shorter.

Cranial and dental characters: The skull is moderately built, the zygomatic width is slightly exceeds the mastoid width. The anterior median swellings are low, slightly shorter than wide, the posterior swellings are medium developed. The sagittal crest is low but distinct, the frontal depression is shallow, flanked by sharp supraorbital ridges. The palatal bridge is short, about 26% of the maxillary toothrow.
The upper canine is relatively slender, the posterior upper premolar is well developed, almost reaching the height of the canine. The anterior upper premolar is medium and aligned in the toothrow. The middle lower premolar is small and extruded from the row, but the adjoining teeth (P_2 and P_4) are separated by a distinct gap.

Similar species: The unique combination of the widely rounded lancet and long, pointed connecting process tell apart *R. convexus* externally from all its congeners. By cranial characters, the species is practically indistinguishable from *R. lepidus* but larger than *R. pusillus*, *R. monoceros*, *R. cornutus* and *R. subbadius*. *R. imaizumii* and *R. shortridgei* have the same skull proportions but with much heavier dentition.
The similar sized species of the *megaphyllus*-group (*R. malayanus*, *R. celebensis*, *R. virgo*) all have more prominent anterior median swellings and higher rostrum.

Taxonomic remarks: The species was said as most closely related to *R. subbadius* on the base of the shape of lancet (Csorba 1997); but further examination revealed that the lancet of *R. subbadius* is rather hastate and not straight sided (see comments under this latter species). The DNA sequences suggest a close relationship with *R. pusillus* (A. Guillen, *pers. comm* 2000).

Fig. 54.1. Lateral and frontal views of noseleaf of *R. convexus* (HNHM 95.55.14. - holotype) from Malaya. Scale = 3 mm.

Fig. 54.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. convexus* (HNHM 95.55.14. - holotype). Scale = 3 mm.

Table 54. ***R. convexus***: External, cranial and dental measurements (mm).

	min	max	n
FA	42.0	43.0	
SL	16.90	17.43	2
CM^3L	6.40	6.61	2
ZW	8.55	8.91	2
MW	8.27	8.42	2
ML	11.35	11.90	2
CM_3L	7.02	7.17	2

***Rhinolophus cornutus* Temminck, 1834**
Little Japanese horseshoe bat
R. cornutus Temminck, 1834 (Japan)
R. c. pumilus Andersen, 1905 (Okinawa I., Ryukyu Is)
R. perditus Andersen, 1918 (Ishigaki I., S. Ryukyu Is)
R. c. orii Kuroda, 1924 (San-Mura, Tokunishima, N. Ryukyu Is., 300 feet)
R. miyakonis Kuroda, 1924 (Nishisato, Miyakojima I., Ryukyu Is)

Recognised subspecies: Following Hill & Yoshiyuki (1980) the following subspecies are recognised - *cornutus* in the main islands of Japan; *pumilus* in Okinawa; *perditus* in Ishigaki-jima; *miyakonis* in Miyako-jima; *orii* in Amami-oshima and Tokunoshima.

External characters: A small species of the genus. The ears are medium, 16.0-19.0 mm in height. The horseshoe is 6.2-6.7 mm in breadth. The sella is pandurate, constricted above middle; broadly rounded at tip. The connecting process is varying from subtriangular to more horn-like and curved. The lancet is hastate, its sides are clearly concave. The lower lip is with three grooves. The tail is 17.0-27.0 mm long. In the wings, the shortest third metacarpal is 27.7-31.1 mm, the fourth (27.7-32.7 mm) and the fifth (27.7-32.5 mm) are subequal in length. The fur is woolly, glossy; the general colour of the back is grey-brown, the base of individual hairs are light beige. The underside is similar in colour but paler.

Cranial and dental characters: The general outline of skull is relatively long and narrow, the zygomatic width less than or subequal to the mastoid width. The anterior median swellings are small, subcircular, the posterior compartments are moderate. The rostral profile is gently sloping posteriorly or rarely almost straight. The sagittal crest is weak or moderate, the frontal depression is medium or quite deep; the supraorbital crests are well visible but usually not sharp. The palatal bridge is short or medium, 29-33% of the CM^3 length.
The upper canine is moderately long or even short, the posterior upper premolar nearly or fully reaches its height. The P^2 is well developed and situated either in the row or displaced to a various extent. P_2 is moderate or small and lying almost in the toothrow or external; the adjoining premolar are in contact or separated accordingly.

Bacular morphology: The dorsal emargination of the basal cone is very deep, the ventral incision is much shorter. The shaft is nearly cylindrical, its distal half is distinctly bent (figures are provided by Yoshiyuki 1989). The average length of the bone is given as 4.23-4.80 mm, depending on the subspecies (Yoshiyuki 1989).

Similar species: Because of the high external and cranial morphological similarity, *R. cornutus* from Japan is separable from the Taiwanese *R. monoceros* and the widely distributed *R. pusillus* and *R. lepidus* only on geographical ground. *R. imaizumii* (beside its heavier dentition) seems to be larger, as the few known specimens of *R. convexus* which is further distinguishable by its differently shaped lancet. *R. shortridgei* has greater skull measurements and much longer upper canines, *R. osgoodi* is characterised by its longer forearm.
The species of the *megaphyllus*-group are recognisable by their higher rostrum and more inflated median swellings.

Taxonomic remarks: There are three syntype specimens of the species in the RMNH, Leiden collection. The skull of a mounted specimen (RMNH 35188) has been removed recently which is designated as lectotype herein. The paralectotype specimens are RMNH 35187 a mounted individual with its skull intact and RMNH 35191 a single skull.

According to Hill and Yoshiyuki (1980) *R. cornutus* differs from *R. pusillus* by its narrower and more horn-like connecting process but the authors also stated that *R. cornutus* and *R. pusillus* seems highly probable conspecific. The species is reported outside of Japan from Guanxi, China (Wang *et al*. 1962) but there is no clear proof of this determination. Other specimens from China once reported as *R. pumilus* (= *R. cornutus*) were consequently referred to *R. pusillus* (Corbet and Hill 1992).

Yoshiyuki (1989) provided detailed description of the species and introduced a different taxonomy (see also Yoshiyuki *et al* 1989). She considered *pumilus* (with *miyakonis* as its subspecies) and *perditus* specifically distinct from *cornutus* on account of slightly different colouration and different external and craniodental measurements. This specific arrangement was followed by Maeda (1996), although this latter author also included *R. imaizumii* as a synonym of *R. perditus*. The evaluation of this taxonomic opinion is, however, difficult since Yoshiyuki (op. cit.) did not provide minimum and maximum measurements and only the mean values are published in the determination key and in the tables. Yoshiyuki also characterised *R. c. cornutus* with the P_3 situated in the toothrow, but the lectotype specimen (available only recently, see above) is showing this particular tooth fully external. Also, the separation of *pumilus* and *perditus* is partly based on the situation of the first upper premolar given as external in the case of *pumilus*; nevertheless, the holotype of this taxon has this tooth lying almost in the axis of the toothrow. This means, that the situation of the small premolars among these taxa is at least a questionable taxonomic character and conclusions based on this feature are dubious. As already Andersen (1905a) remarked, the position of P_3 is of no importance for the identification and the position of this tooth is "vacillating" in the whole *lepidus* (= *pusillus*) section. Yoshiyuki *et al*. (1989) provided mean values for the crown measurements of the small upper premolars of *cornutus*, *orii* and *pumilus* and considered the differences alone support the specific distinctness of *pumilus*.

Yoshiyuki *et al*. (op. cit.) clarified that in the group of *R. cornutus* clinal variation is apparent, that is, the body size is evidently larger in the populations of the northern region or mountain areas than in those of the southern region or lowland areas.

Fig. 55.1. Lateral and frontal views of noseleaf of *R. cornutus* (MNHN 1983.1948) from Japan. Scale = 3 mm.

Fig. 55.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. cornutus* (RMNH 35188 - lectotype) from Japan. Scale = 3 mm.

Table 55. ***R. cornutus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		38.0	41.0		
SL	16.13	15.14	16.67	0.53	7
CM^3L	5.79	5.60	5.97	0.13	10
ZW	7.75	7.52	8.19	0.20	9
MW	7.89	7.51	8.17	0.21	8
ML	10.31	9.99	10.80	0.31	8
CM_3L	6.15	5.96	6.66	0.20	11

***Rhinolophus imaizumii* Hill and Yoshiyuki, 1980**
Imaizumi's horseshoe bat
R. imaizumii Hill and Yoshiyuki, 1980 (Otomi-do Cave, Iriomote I., Yayeyama Is., Ryukyu Is., Japan)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A relatively small species of horseshoe bats. The ears are medium, about 20 mm in height. The horseshoe is relatively broad, covering the muzle, about 7.3 mm in width accross. The sella is broad basally, at its centre is almost as wide as at the basal part; narrowing a little above central region to a rounded, anteriorly deflected tip. The connecting process is a narrow, slender, anteriorly projecting horn. The lancet is with slightly concave lateral margins and narrow, more or less spatulate terminal part with rounded tip. The lower lip is with three grooves. The tail is about 20 mm in length. In the wings, the third metacarpal is 30.9-32.5 mm, the fourth is 31.1-33.1 mm and the fifth is 31.0-32.6 mm in length. The colour of the dorsal surface is bright brown, the hairs are pale brown at the base and for much of their length, tipped with darker brown. The ventral surface is lighter, the hairs are similarly creamy for much or all of their length.

Cranial and dental characters: The skull is strong, the zygomatic width slightly exceeds the mastoid width. The anterior median swellings are expressedly small, more or less circular in outline; the posterior compartments are better developed, but the rostral profil is sloping posteriorly. The sagittal crest is low or moderate, rarely quite strong. The weak supraorbital ridges are enclosing a shallow frontal depression. The palatal bridge is short, 30-31% of the maxillary toothrow.
The upper canine is short, relatively strong and massive. The anterior upper premolar is moderate, with a small but definite cusp, and lying in the toothrow. The upper canine and posterior premolar (P^4) are separated. The lower canine is more slender. The middle lower premolar is small or medium, extruded from the toothrow; the neighbouring premolars (P_2 and P_4) are separated by a very narrow gap or their cingula are in contact.

Bacular morphology: The basal part of the baculum is with shallow ventral and deeper dorsal emargination; the depth is nearly one-fourth of the basal cone length. The shaft is

continously curving upwards. The average length of the baculum is given as 4.43 mm (Yoshiyuki 1989, figures are provided).

Similar species: *R. imaizumii* is similar in most respect (both externally and cranially) to *R. cognatus* but differs from it by its smaller narial swellings and generally heavier dentition. The strong upper canine and wider molars also separate the species from its other close relatives (*R. cornutus*, *R. pusillus*, *R. lepidus*) in the group; *R. shortridgei* has a similarly wide based upper canine, but this tooth is much longer this latter taxon. The small species of the *megaphyllus*-group have generally higher rostrum and more prominent anterior swellings.

Taxonomic remarks: When discussed the relationship of their newly described species Hill and Yoshiyuki (1980) noted, that there is little doubt that *R. subbadius*, *R. monoceros*, *R. cognatus* and *R. imaizumii* scarcely justify recognition as a distinct section or subgroup of the *pusillus*-group as was done by Andersen (1905a, 1918) and Tate and Archbold (1939). This distinction rests only on the horn-like appearence of the connecting process, a condition foreshadowed in both *R. cornutus* and *R. pusillus*. Bogdanowicz (1992) grouped together all of these species in his *pusillus*-subgroup (according to him a subgroup of the *megaphyllus*-group).
R. imaizumii was mentioned as synonymy of *R. perditus* by Maeda (1996), which latter taxon was listed by him as full species.

Fig. 56.1. Lateral and frontal views of noseleaf of *R. imaizumii* (BMNH 80.465 - paratype) from Japan. Scale = 3 mm.

Fig. 56.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. imaizumii* (BMNH 80.465 - paratype) from Japan.

Table 56. ***R. imaizumii***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		40.0	43.0		
SL	18.01	17.66	18.40	0.34	5
CM^3L	6.77	6.66	6.80	0.06	5
ZW	8.57	8.47	8.78	0.13	5
MW	8.32	8.20	8.47	0.10	5
ML	11.63	11.23	11.80	0.23	5
CM_3L	7.16	6.84	7.30	0.20	5

***Rhinolophus lepidus* Blyth, 1844**
Blyth's horseshoe bat
R. lepidus Blyth, 1844 (Calcutta, India?)
R. monticola Andersen, 1905 (Masuri, Kumaon, NW India)
R. refulgens Andersen, 1905 (Gunong Igar, Perak, Malaya, 2000 ft)
R. feae Andersen, 1907 (Biapo, Karin Hills, SE Burma)
R. refulgens cuneatus Andersen, 1918 (Sukaranda, Deli, NE Sumatra)

Recognised subspecies: The following subspecies are recognised - *monticola* in Afghanistan and northwestern India; *lepidus* in central and northeastern India; *feae* in northern Burma and northern Thailand; *refulgens* in Malay Peninsula; *cuneatus* in Sumatra.

External characters: A small sized horseshoe bat. The ears are small or medium, their length is 13.0-20.6 mm. The horseshoe is 6.0-8.0 mm in breadth, not covering the whole muzzle. The sella is narrow, and according to Andersen (1907b) parallel margined from base to summit in the case of *feae* or distinctly expanded below the middle and considerably narrower at summit than at base (*refulgens*). The tip of the triangular shaped connecting process is generally broadly rounded off. The lancet is well developed; the tip is variable in shape, in some specimens it is broadly rounded off and in others more pointed. The sides of the lancet are typically strongly concave, in others almost straight. The lower lip is with three grooves. The tail is 12.2-28.0 mm. In the wings, the third metacarpal is 27.2-33.3 mm, the fourth is 28.6-33.8 mm and the fifth is 27.8-33.4 mm in length. The general colour above is between wood-brown and cinnamom, the base of hairs is light drab. The pelage of *refulgens* is distinctive; the fur is commonly very dark brown, occasionally bright foxy orange. The tips of the hairs in both phases of the pelage are paler, giving the effect of a silvery gloss (Medway 1965). The underside is wood-brown or drab.

Cranial and dental characters: The skull is small, but strongly built, the zygomatic width is slightly greater or usually subequal to the mastoid width. The anterior median swellings are small, subsircular in outline; the posterior ones are relatively well inflated, the rostral profil is slightly sloping backwards or sometimes nearly straight. The sagittal crest is medium or moderately strong but flattened posteriorly. The frontal depression is shallow or very shallow and bordered with low supraorbital ridges. The palatal bridge is 25-30% of the upper toothrow length.
The upper canine is well developed, usually greatly exceeds the height of the second upper premolar (P4). The first premolar (P^2) is with a distinct, frequently well developed cusp and situated in the toothrow. The position of P_2 is very variable, within or external to the toothrow; when external P_2 and P_4 are in contact.

Bacular morphology: Based on specimens from the Indian Peninsula (Topál 1975) the baculum has an elongated S-shape with a dorsal bend near the basal cone and a ventral turn near the tip. The dorsal edge of the basal cone is shorter than the ventral one and with a proximally bulging dorsal knob, otherwise with a wide emargination, just as in the ventral margin. The ventral surface of the base shows a depression. The shaft is nearly cylindrical in cross section and tapering towards the tip. The latter is broadly rounded off and generally wide from the dorsal view.

Similar species: There is some overlap in all the external and cranial measurements between *R. lepidus* and *R. pusillus* and a minority of specimens from Himalayan region are difficult to assign with confidence to one or other species (Bates and Harrison 1997). The same situation occurs in the Malay Peninsula, as well. As compared with other species within the group, *R. osgoodi* has a relatively smaller skull but absolutely longer palatal bridge (over 2.5 mm); *R. imaizumii* is characterised by its larger cranial measurements and short, strong upper canine; *R. shortridgei* is usually also greater cranially and has a very long C^1 and strong sagittal crest.
R. borneensis is almost always larger in cranial and dental measurements and the nasal swellings (especially the anterior median ones) are more prominent. *R. celebensis* is similar by size and shape but has a higher rostrum, more globular anterior median swellings and relatively smaller upper canine.
Although *R. mehelyi* is overlapping with *R. lepidus* in the upper toothrow length, its skull is always larger and has a relatively low, anteriorly protruding anterior median swellings.

Taxonomic remarks: The taxa *monticola* and *feae* were proposed as separate species by Andersen (1905a, 1907b). Aellen (1959b) determined specimens from Afghanistan as *R. l. monticola* and remarked that since the published measurements of *monticola* are entirely fall within the size variation of *lepidus*, *monticola* is only a subspecies of the latter or even simply the synonym of it. Sinha (1973) although listed both *monticola* and *feae* as separate species, found no other differences between the above taxa and *R. lepidus* than the relative length of metacarpals; the subsequent comprehensive works of Corbet and Hill (1992) and Koopman (1994) recognised them as subspecies of *R. lepidus*. Similarly, according to Hill and Yoshiyuki (1980) there seems no reason to retain *refulgens* as a species distinct from *lepidus* which it resembles in every essential particular. Following Hill and Yoshiyuki (1980) specimens from the Himalayan region are provisionally referred to *R. l. monticola*. In general, these northern montane individuals are characterised by their smaller size (Bates & Harrison 1997). The holotype of *monticola* is an unusually small individual; externally (forearm 37.0 mm) it is within the range of *R. pusillus* although its cranial measurements are consistent with those of *R. lepidus*. A juvenil topotype of *monticola* is typical *R. lepidus* in all respects (forearm 39.6 mm). In the case of the holotype the possibility of a mis-matched skull has to be considered (Bates and Harrison 1997).
The large, cranially heavily built *R. shortridgei* and the large-bodied but cranially small *R. osgoodi* are mentioned as subspecies of *R. lepidus* by Corbet and Hill (1992) but they are recognised here as separate species.

Fig. 57.1. Lateral and frontal views of noseleaf of *R. lepidus* (HNHM 93.16.4.) from India. Scale = 3 mm.

Fig. 57.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. lepidus* (HNHM 92.83.1.) from India. Scale = 3 mm.

Table 57. ***R. lepidus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		37.0	43.0		
SL	16.66	15.77	17.35	0.38	49
CM^3L	6.23	5.66	6.75	0.20	51
ZW	8.19	7.71	8.66	0.22	49
MW	8.09	7.65	8.34	0.15	48
ML	10.88	10.20	11.63	0.31	52
CM_3L	6.63	5.96	7.21	0.25	51

***Rhinolophus monoceros* Andersen, 1905**
Formosan lesser horseshoe bat
R. monoceros Andersen, 1905 (Baksa, Taiwan)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A small sized horseshoe bat. The ears are medium in relation to the head, 15.9-17.2 mm in height. The horseshoe is relatively wide, almost covering the muzzle, 5.6-6.7 mm in width accross. The sella is wide at its base and after the middle continuously converging toward the broadly rounded tip. The connecting process is slightly variable in shape, being a pointed triangle or a slightly curved horn. The lancet is definitely hastate, the sides are concave and the terminus is more or less spatulate. The lower lip is with three mental grooves. The tail length is 15.2-16.6 mm. In the wings, the third metacarpal is the shortest (25.0-29.6 mm), the fourth and the fifth are subequal, 26.0-30.2 mm in length. The pelage is wood-brown with a reddish tint; the underside is similar in colour but lighter.

Cranial and dental characters: The skull is small and moderately built. The ratio of the zygomatic and mastoid breadth is variable; in most cases they are subequal but the zygomatic width is sometimes smaller or rarely even slightly larger than the mastoid width. The anterior median swellings are very small, the posterior compartments are better developed; the rostral profile is nearly straight or slightly sloping posteriorly. The sagittal crest is weak or rarely medium developed. The frontal depression is shallow and flanked with low but demarcated supraorbital ridges. The palatal bridge is relatively short, 26-29% of the upper toothrow.
The upper canine is short, moderately weak, the posterior upper premolar is well developed. The anterior upper premolar (P^2) is medium sized, always situated in the axis of the toothrow. In the lower jaw, the middle premolar small or medium, more or less extruded but separating the adjoining premolars.

Similar species: The species is not separable from *R. pusillus* and *R. cornutus* neither by external nor by craniodental characters. *R. lepidus* is characterised by a usually shorter, wide-based triangular connecting process and almost always greater cranial and dental measurements. The other species in the group are all greater cranially and have larger and/or stronger upper canine.

The small sized species of the *megaphyllus*-group are separable on the base of their higher rostrum and well inflated nasal swellings.

Taxonomic remarks: The type of *R. monoceros*, a subadult specimen, has been described as having a broad and short lancet (Andersen 1905a). However, the examination of large series of the species showed much variation in shape of the lancet, even within the same population. This variation largely bridges the differences thought to be diagnostic between *R. monoceros* and *R. cornutus-R. pusillus* (Csorba 1997). This finding may supports the view of Koopman (1994) that *R. monoceros* is probably a subspecies of *R. cornutus*, but because of the genetic isolation of the Taiwanese population the retention of the specific status is suggested.

Fig. 58.1. Lateral and frontal views of noseleaf of *R. monoceros* (HNHM 98.20.11.) from Taiwan. Scale = 3 mm.

Fig. 58.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. monoceros* (HNHM 2000.9.5.) from Taiwan. Scale = 3 mm.

Table 58. ***R. monoceros***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		34.0	40.0		
SL	15.26	14.71	15.79	0.26	23
CM^3L	5.57	5.32	5.78	0.11	23
ZW	7.31	6.94	7.56	0.17	23
MW	7.41	7.19	7.75	0.14	24
ML	9.73	9.17	10.12	0.23	25
CM_3L	5.84	5.57	6.03	0.12	23

***Rhinolophus osgoodi* Sanborn, 1939**
Osgood's horseshoe bat
R. osgoodi Sanborn, 1939 (Nguluko, N of Likiang, Yunnan, China)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized species of the genus. The ears are medium or large in relation to the head, 15.3-17.4 mm in height. The horseshoe is wide, almost covering the whole muzzle, about 6.4 mm in width accross. The sella is relatively broad, parallel sided and widely rounded at its terminus. The connecting process is variable in shape, being either a pointed or a more or less bluntly rounded triangle. The lancet is with almost straight sides. The tail is 15.0-15.3 mm in length. In the wings, the metacarpals are gradually lengthened but the differences are small. The third metacarpal is 32.7-32.9 mm, the fourth is 33.1-34.0 and the fifth is 33.4-33.8 mm in length. The pelage is warm russet-brown above, slightly lighter and more greyish in the ventral aspect.

Cranial and dental characters: The skull is moderately strong, of the few specimens known the zygomatic width is less than the mastoid breadth. The anterior median swellings are medium developed as the posterior compartments does; the rostral profile is sloping backwards. The sagittal crest is weak, the frontal depression is shallow and bordered by well defined, more or less sharp ridges. The palatal bridge is long, 43-48% of the upper toothrow (CM^3) length.
The upper canine is very short, usually shorter than the exceedingly wide-based posterior upper premolar and only rarely exceeds its heights. The anterior upper premolar is medium sized, situated in the main axis of the row; in the lower jaw the middle premolar (P_3) is small and fully or partly extruded. The anterior and posterior lower premolars are very close to each other, their cingula sometimes touching each other.

Similar species: By external characters - due to its large forearm measurements - among the members of its group only *R. lepidus*, *R. cognatus* and *R. convexus* are similar. The latter species has much narrower, horn-like connecting process; *R. cognatus* and *R. lepidus* are recognisable by their differently shaped, more concave-sided lancet. Cranially, the short upper canine and long palatal bridge separate the species from its group-members. Similarly long palate occur only among the species of the *philippinensis*-group, but they have larger skull, longer rostrum, elongated anterior and reduced posterior swellings.

Taxonomic remarks: The first (and apparently the only known) specimens of this species were reported by Osgood (1932) as „*Rhinolophus lepidus* subsp.?". Osgood mentioned that the specimens do not seem referable to any species previously recorded from China, but they are closely related to *lepidus*, *monticola*, *refulgens* and *shortridgei* and as judged from descriptions, the individuals did not agree exactly with any of these already known forms. The specimens were later on introduced as new species by Sanborn (1939) on the base of their unusually long forearm but small cranial measurements. The specific distinctness of *R. osgoodi* was not generally accepted; although Koopman (1994) listed it as separate species, Corbet and Hill (1992) put it under the synonymy of *R. lepidus* with a question mark.
Based on cranial and external characters, by phenetic analyses Bogdanowicz (1992) grouped *R. osgoodi* together with *R. pusillus* and its allies in his *pusillus*-subgroups but indicated its uncertain position as a member of this subgroup. Although by the shape of the nasal foliation *R. osgoodi* seems related to these species, some cranial features as the higher anterior swellings and mainly the peculiarly long palatal bridge suggest a different taxonomic position but its relationships remained unresolved.

Fig. 59.1. Lateral and frontal views of noseleaf of *R. osgoodi* (FMNH 33690) from China. Scale = 3 mm.

Fig. 59.2. Lateral view of the rostral part of the skull and occlusal view of the left upper (left) and right lower (right) anterior dentition of *R. osgoodi* (FMNH 33296 - holotype) from China. Scale = 3 mm.

Table 59. ***R. osgoodi***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		41.0	46.0		
SL	16.35	16.29	16.45	0.09	3
CM^3L	5.84	5.76	5.89	0.06	4
ZW	7.68	7.54	7.82	0.14	3
MW	8.04	7.94	8.17	0.12	3
ML	10.41	10.25	10.52	0.14	3
CM_3L	6.11	6.04	6.15	0.06	3

***Rhinolophus pusillus* Temminck, 1834**
Least horseshoe bat
R. minor Horsfield, 1823 (Java) (preoccupied by *Vespertilio ferrum-equinum minor* Kerr, 1792)
R. pusillus Temminck, 1834 (Java)
R. minutus Miller, 1900 (Siantan I., Anamba Is) (preoccupied by *Vespertilio minutus* Montagu, 1808).
R. gracilis Andersen, 1905 (Malabar Coast, India)
R. minutillus Miller, 1906 (replacement name for *R. minutus* Miller, 1900)
R. blythi Andersen, 1918 (Almora, Kumaon, India, 5500 ft)
R. blythi szechuanus Andersen, 1918 (Chunking, Sichuan, China)
R. blythi calidus Allen, 1923 (Yenping, Fujian, SE China)
R. blythi parcus Allen, 1928 (Nodoa, Hainan I., China)
R. pagi Tate and Archbold, 1939 (N. Pagi I., Mentawai Is)
R. p. lakkhanae Yoshiyuki, 1990 (Tham Song Phi Nong, Chom Thong, Chiang Mai, Thailand, 18º35'N, 98º29'E)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *blythi* in northwestern India; *gracilis* in southern India; *szechuanus* in northeastern India, Myanmar, southwestern China and Thailand; *calidus* in eastern China; *parcus* in Hainan; *minutillus* in Malay Peninsula and Anambas; *pagi* in Mentawai; *pusillus* in Java and Borneo.

External characters: A very small species of the horseshoe bats. The ears are medium, 13.0-20.1 mm in height. The horseshoe is relatively wide (6.0-8.0 mm), with small anterior median emargination. The sella is slightly constricted in the middle and gradually narrowing to a widely rounded trip. In lateral view, the connecting process is usually triangular in shape comparable to but usually more acute than that of *R. lepidus*; in some specimens more horn-like. The lancet is typically distinctly hastate but its shape and size varies from a short equilateral triangle to a more elongate structure. The lower lip is with three mental grooves. The tail is 12.9-26.0 mm long. In the wings, the third metacarpal is slightly shorter (24.2-29.5 mm) than the fourth (24.8-30.4 mm) and the fifth metacarpal (25.1-30.2 mm) which are subequal in length. The pelage is very fine and soft; the dorsal fur is from dark brown to smoky-grey or cinnamon-red brown, the individual hairs with paler base; on the belly the colour is greyish white or reddish.

Cranial and dental characters: The skull is moderately built, the zygomatic width is either slightly wider or narrower than the mastoid width, or very frequently they are subequal. The anterior median swellings are very small, but the posterior ones are more or less well inflated. The rostral profil is nearly straight or gently sloping posteriorly according to the developement of the posterior compartments. The sagittal crest is weak or moderate, the frontal depression is shallow or almost invisible. The supraorbital crests are ill defined, the ridges are low. The palatal bridge is moderately short or medium, 28-34% of the upper toothrow length.
The upper canine is moderately long. The upper anterior premolar is well developed and in the toothrow, the canine and the posterior upper premolar are always widely separated. The lower second premolar is minute or medium, usually out of row to a different extent; the first (P_2) and third (P_4) lower premolars are separated or in contact.

Bacular morphology: The baculum of this species is relatively very large among the bacula of the other horseshoe bats. It has a distinct but not very strong dorsal bend. The Vietnamese and Indian specimens investigated by Topál (1975) show a certain kind of difference, especially in the morphology of the basal cone. The dorso-proximal edge of the base is shorter than the ventral margin, with a wide and deep emargination in the Vietnamese specimen. The shaft is roughly cylindrical with a slight thickening in the middle when viewed from above. The tip is a laterally widened knob.

Similar species: Unlike *R. hipposideros* the third metacarpal is about equal to or exceeds the combined length of its respective phalanges. The third upper premolar of *R. pusillus* is without a distinct fourth commissure and metastyle (Bates and Harrison 1997). The two species are further distinguishable by the shape of the zygomata which is weak in *R. hipposideros* but expressedly strong in *R. pusillus*.
Since the shape of rostral profil seems variable character of both *R. pusillus* and *R. lepidus* only the average size differences are separating them; the largest specimens of *R. pusillus* tentatively determined as belong to this species are virtually indistinguishable from small *R. lepidus*. *R. monoceros* and *R. cornutus* are also separable on geographic ground only. *R. osgoodi* is larger by forearm measurements and has short upper canines and relatively smaller skull; *R. imaizumii* and *R. convexus* are larger (the former is also characterised by its strong, widely based upper canine); *R. cognatus* has a longer lancet with spatulate tip and slightly more inflated nasal swellings.

Taxonomic remarks: The types of *R. pusillus* in the RMNH, Leiden caused a lot of mental labour. Dobson (1878) investigated the types and concluded they are "undoubtedly specimens of *R. hipposiderus*" which led to the statement that *R. hipposideros* should occur in Java. Andersen (1905a) later speculated that "an interchange of labels has taken place in that Museum" and stated that „the bat figured and described by Temminck as pusillus was certainly no *hipposiderus*". Since at the beginning in the Leiden Museum the small specimens were always kept in glass vials, with a little round label glued on the cork cover (C. Smeenk *pers. comm)*. Needless to say, these labels may have come off, so there was always the danger of specimens becoming mislabelled or interchanged. In fact, the type series in Leiden consists of five syntypes (RMNH 35177-35181), of which three are indeed, represent *R. hipposideros* (RMNH 35178 and 35179 mounted specimens, skulls intact; RMNH 35181 separate skull). One of the remaining two specimens (RMNH 35177) consists of a skull of *R.*

pusillus and a mounted skin of *R. hipposideros*; the another one (RMNH 35180 mounted with skull intact) is with no doubt, *R. pusillus*. These facts explain, why Dobson (1878) and Jentink (1887) referred *R. pusillus* to the synonymy of *R. hipposideros* and clarify that Andersen (1905a) was right when accepted Temminck's statement that the types of *R. pusillus* were brought from Java. From the syntypes representing genuine *R. pusillus*, the RMNH 35177 specimen (the cleaned skull) is designated herein as lectotype.

From India, Sinha (1973) assigned all specimens currently referred to *R. pusillus* to *R. cornutus*. Hill and Yoshiyuki (1980) noted that it was highy probable that these two taxa are conspecific but Corbet and Hill (1992) and Koopman (1994) maintained them as discrete species. Because of the geographic and probably genetic isolation of the Japanese population this separation seems to be reasonable.

The shape of the rostral profile of *R. pusillus* was desribed by Corbet & Hill (1992) as being nearly straight, almost horizontal (contrary to the upward-curwing rostral profile of *R. lepidus*). Knowing the lectotype specimen of the former and the variablity of both species, this character is not typical or uniform and can not be used to tell apart the two species. The development of the posterior median swellings (which is influencing the shape of the rostral profil) is either a variable feature within both species in question or it has a taxonomic significance not fully understand yet.

Andersen (1918) separated *szechuanus* from the nominotypical race of *blythi* on account of its paler colour. According to Sinha (1973) the colour varies much in both subspecies and, therefore can not be treated as a differentiating character; as such, *szechuanus* was considered as a synonym of *blythi*. The taxon *calidus* was also separated from *R. blythi szechuanus* by its bright cinnamon colouration by Allen (1923) but was retained as valid subspecies of *R. pusillus* (Koopman 1994). Osgood (1932) referred a specimen from Tonkin as *R. blythi calidus*, but remarked that the distinction of the named forms within the „*pusillus*-series" are not very clear and it might be preferable to regard all the forms as races of *R. pusillus*. *R. p. gracilis* (known from a single specimen from Malabar) is provisionally considered as a discrete taxon. *R. minutillus* was also mentioned as perhaps subspecifically allied to *pusillus* (Chasen 1940). Sinha (1973) listed *gracilis* as near to *blythi*; examination of the holotype of *gracilis* confirms that it is very similar to *blythi* and *szechuanus* (Corbet and Hill 1992). The type series of *R. pagi* is heterogeneous regarding the shape of the connecting process (see comments under *R. subbadius*); the taxon was first considered to belong to *R. pusillus* by Hill and Yoshiyuki (1980). Lekagul and McNeely (1977) regarded the Thai population as *R. p. szechuanus*, but based on 31 specimens from that region Yoshiyuki (1990) described a new subspecies *lakkhanae* characterised by the average shorter tail and shorter skull as compared with the Chinese and more northern subspecies. According to our measurements this taxon is fully overlap with those of the known southern subspecies and even with several Chinese specimens; therefore the geographic limits and the taxonomic validity of this subspecies is highly questionable. Kock (1996) also remarked, that the separation of *blythi*, *gracilis*, *szechuanus* and *lakkhanae* is problematic and these taxa are not clearly defined.

Specimens tentatively referred to this species from Laos appear to represent at least two and probably three species, based on genetic, morphological and echolocation call differences (Francis *et al*. 1999), but further study is required to determine their identities.

Fig. 58.1. Lateral and frontal views of noseleaf of *R. pusillus* (HNHM 95.60.27.) from Vietnam. Scale = 3 mm.

Fig. 58.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. pusillus* (RMNH 35177 - lectotype) from Java.

Table 58. ***R. pusillus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		33.5	40.0		
SL	15.66	14.84	16.51	0.43	44
CM^3L	5.79	5.41	6.26	0.20	50
ZW	7.65	6.98	8.27	0.33	42
MW	7.70	7.25	8.26	0.24	41
ML	10.16	9.48	10.93	0.34	49
CM_3L	6.13	5.64	6.65	0.23	49

***Rhinolophus shortridgei* Andersen, 1918**
Shortridge's horseshoe bat
R. lepidus shortridgei Andersen, 1918 (Pagan, Irrawaddy R., Burma)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A small-medium sized species of the genus. Since only dry study skins are known of the species, the external characters are uncertain and incomplete. The horseshoe does not cever the muzzle, a small secondary leaflet is present. The ears are medium, 16.0-19.0 mm in height. The sella is more or less parallel sided, widely rounded above, the connecting process is a pointed triangle. The lancet is with concave sides. The lower lip is with three prominent mental grooves. The tail is 20.5-25.0 mm. In the wings, the third metacarpal 30.9-31.7 mm, the fourth (31.6-33.0 mm) and the fifth (31.3-33.0) mm subequal in length. The upper sides are light brown, the individual hairs are bicoloured, greyish at their base, brown above; the ventral aspect is much lighter, dirty white or grey, the hairs are unicoloured.

Cranial and dental characters: The skull is strongly built, the zygomatic width exceeds the mastoid breadth. The anterior median swellings are low and very small, the posterior compartments are relatively large; the rostral profile is slightly curving upwards near the tip. The sagittal crest is strong or very strong in its full length, extending rearwards almost to the lambda. The frontal depression is shallow, the supraorbital crests are clearly defined. The palatal bridge is 27-31% of the maxillary toothrow length.
The upper canine is especially large, almost twice as long as the posterior premolar (P^4) and its basal area equal to even larger than that of P^4. The anterior upper premolar is medium and situated in the row. In the lower jaw, the canine is also long; the middle

premolar (P_3) is small or moderate, half-way or fully extruded from the main axis of the toothrow. The adjoining premolars are usually separated from each other.

Similar species: *R. shortridgei* is not separable from *R. lepidus* and its closest relatives on the base of external characters, but its triangle-shaped (not horn-like) connecting process tell apart it from *R. imaizumii*, *R. cognatus* and *R. convexus*. Cranially, the very long and heavily based canines and strong sagittal crest help the identification within the *pusillus*-group.
The similar sized species of the megaphyllus-group are all characterised by their higher rostral part of skull and more inflated nasal swellings.

Taxonomic remarks: According to Sinha (1973) the taxon *shortridgei* differs from *R. l. lepidus* in having a longer hind foot (55-63%, against 45.8-47.5% of the tibia) and longer mandible. The description of this taxon as a subspecies of *R. lepidus* was published by Oldfield Thomas on behalf of Andersen (1918), based on the short notes of the latter. The diagnostic characters of *shortridgei* ("skull and teeth averaging larger") appeared only in the key given for the species and subspecies of the *pusillus*-group but without comparisons even of the measurements with the other named forms.
A specimen of *R. shortridgei* (USNM 577473) caught some 140 km NE of the type locality (Pagan, Myanmar) was collected together with an individual of *R. lepidus* which is clearly differs in measurements (SL 17.68 vs. 16.73, CM^3 6.61 vs. 6.37) and having much smaller upper and lower canines. The actual sympatry of these two forms supports the specific distinctness of *R. shortridgei*.

Fig. 61.1. Lateral view of the rostral part of the skull (BMNH 18.8.3.1 – holotype) from Myanmar, and occlusal view of the upper (left) and lower (right) left anterior dentition (HNHM 93.15.1.) from India of *R. shortridgei*.

Table 61. ***R. shortridgei***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		39.0	42.0		
SL	17.72	17.24	17.97	0.26	6
CM^3L	6.77	6.53	7.17	0.22	7
ZW	8.71	8.56	8.87	0.12	5
MW	8.48	8.29	8.71	0.14	6
ML	11.98	11.73	12.78	0.37	7
CM_3L	7.26	7.00	7.73	0.24	7

***Rhinolophus subbadius* Blyth, 1844**
Little Nepalese horseshoe bat
R. subbadius Hodgson, 1841 (nomen nudum).
R. subbadius Blyth, 1844 (Nepal)
R. garoensis Dobson, 1872 (Garo Hills, Meghalaya, India)

Recognised subspecies: All specimens referred to the nominate form.

External characters: The smallest Rhinolophid bats of the world. The ears are small or medium, 14.1-18.0 mm in height. There is no information on the shape and size of the horseshoe; the sella is broader at base, constricted in the middle. The connecting process is extending forwards into a slender, sharply pointed horn. The lancet is more or less hastate. The lower lip is with three grooves. The tail is 16.0-19.0 mm. In the wings, the third metacarpal is 24.3-25.7 mm, the fourth is 25.0-26.7 mm, the fifth is 25.0-26.8 mm in length. The colour is dorsally cinnamon brown, the pelage is with greyish white bases and brownish tips. In general the shoulders are a little paler; the underparts are slightly paler than the back.

Cranial and dental characters: The skull is very small but moderately built. The zygomatic and mastoid width was measurable only on two individuals; in one case the zygomatic breadth exceeds the mastoid breadth, on the other the zygomatic width was smaller. The anterior median swellings are small and short, the posterior swellings are better developed. The sagittal crest is moderate, the frontal depression is shallow. The supreorbital ridges are ill-defined. The palatal bridge is 29-31% of the maxillary toothrow.
The upper canine is slender, moderately long. The P^2 is small or medium but with a distinct cusp and situated in the axis of the toothrow. P_3 is minute or absent, when present is usually external but rarely in the row. The first (P_2) and third (P_4) premolars are in contact.

Similar species: Due to the variations of the noseleaf shape among other small species in the *pusillus*-group, beside the forearm differences there is no reliable external character by which *R. subbadius* is separable from *R. pusillus* and its allies. Cranially, however, the very narrow rostrum (C^1-C^1 width 2.7-3.2 mm, M^3-M^3 width less than 5 mm) distinguish *R. subbadius* from all the other horseshoe bats.

Taxonomic remarks: The holotype of *R. subbadius* can not be traced There is a need to determine if *garoensis* (holotype in the Zoological Survey Collection, Calcutta) is a discrete taxon, or a synonym of *R. subbadius* - as Andersen (1905a) noted, „evidently the same species" - or a synonym of *R. pusillus* (Bates and Harrison 1997). In the original description of *R. garoensis* Dobson (1872) allied it to *R. cornutus* from which it differs mainly in smaller size but also noted its broadly triangular lancet. The horn-like appearence of the connecting process and the lancet being more or less equilateral triangle of *R. subbadius* and *R. monoceros* was frequently used as the main distinguishing character from other members of the *pusillus*-group in the groupings of the genus (Andersen 1905a, 1918, Tate and Archbold 1939) or in determination keys (Corbet and Hill 1992). But the shape of the connecting process is highly variable in both *R. cornutus* (Yoshiyuki 1989) and *R. pusillus* (Bates and Harrison 1997) being short triangle or more slender and curved. Tate and Archbold (1939) also remarked the differences within the type series of *R. pagi* (in two paratypes the connecting process is curved forwards, but in the holotype and three others it is erect); therefore this character has limited taxonomic value. The careful examination of the series of dry skins from Myanmar referred to by Hill (1962) as *R. subbadius* showed a distinctly hastate lancet with concave margins. The deformed and dried noseleaf of the specimens may resulted the overlooking of this feature. Already Andersen (1905a) pointed out, that he doubt that the lancet shape in a large series will prove to be quite safe for the discrimination.

However, due to the generally very small measurements and narrowed rostrum (Bates and Harrison 1997) the specific distinctness of this form is acceptable.
The detailed descriptions of the species (Hill 1962, Bates and Harrison 1997) are based on a series derived from northern Myanmar and housed in the BM(NH). The record of Dobson (1876) from Mussoorie (also cited by Wroughton 1918) is an erroneous data which was drawn from specimens shown by Andersen (1905a) to be *R. monticola* (= *R. lepidus monticola*). The measurements given for the species by Hill and Yoshiyuki (1980) include a specimen which is in fact referable to *R. pusillus* (Bates and Harrison 1997). There is also highly probable, that the young-subadult specimens from Tonkin reported by Osgood (1932) on which the North Vietnamese distribution of the species is based (investigated by the senior author in the FMNH) are also belong to *R. pusillus*.

Fig. 62.1. Lateral view of head and frontal view of noseleaf of *R. subbadius* (after Dobson 1876, drawings of *R. garoensis*)

Fig. 62.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) anterior dentition of *R. subbadius* (BMNH 50.406) from Myanmar. Scale = 3 mm.

Table 62. ***R. subbadius***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		33.5	38.0		
SL	14.81	14.45	15.01	0.21	5
CM^3L	5.38	5.19	5.61	0.12	12
ZW	7.10	6.87	7.43	0.29	3
MW	7.22	7.10	7.37	0.12	7
ML	9.43	9.14	9.82	0.23	12
CM_3L	5.73	5.48	5.98	0.16	12

ROUXII-GROUP

***Rhinolophus rouxii* Temminck, 1835**
Rufous horseshoe bat
R. rouxii Temminck, 1835 (Pondicherry and Calcutta, India)
R. rubidus Kelaart, 1850 (Kaduganava, Sri Lanka)
R. fulvidus Blyth, 1851 (error for *R. rubidus* Kelaart, 1850)
R. cinerascens Kelaart, 1852 (Fort Frederick, Sri Lanka)
R. rammanika Kelaart, 1852 (Anamapoora Hill, Kaduganava, Sri Lanka)
R. petersi Dobson, 1872 (type locality unknown)

Recognised subspecies: After Thomas (1997) the following subspecies are recognised - *rouxii* in peninsular India and southern Myanmar; *rubidus* in Sri Lanka.

External characters: A medium sized horseshoe bat which is very variable in size throughout its distribution area. The ears are small, 14.5-22.0 mm in heights. The

horseshoe is narrow related to the muzzle, its breadth is 7.0-9.2 mm. A small secondary leaflet is frequently present. The sella is practically parallel sided (sometimes with a slight constriction at the middle) from base to summit which broadly rounded off. The connecting process is rounded. The lancet is of variable height, hastate, abruptly narrowed in the middle; the tip is well developed and slender. The lower lip is with three grooves. The tail is 20.5-33.0 mm long. In the wings, the third metacarpal is the shortest (34.0-39.6 mm); the fourth is 34.5-41.0 mm, the fifth is 35.3-41.2 mm in length and they are subequal in length or the fifth is slightly longer. The pelage is soft and silky. Two colour phases and intermediate stage are known. The upperside of dark phase is brown, base of hairs drab; the underside is wood brown or light drab. The red phase is both above and below orange-rufous. Empirical evidence suggests a seasonal bias in colour such that the orange and rufous tints predominate from October to April and the paler phases are more comon in specimens collected from May to September (Sinha 1973).

Cranial and dental characters: The skull is heavily built, the zygomatic breadth is always well exceeds the mastoid breadth. The anterior median swellings are small and low, the posterior compartments are wide. The sagittal crest is strong or moderately developed. The frontal depression is shallow, the cristae supraorbitales are well visible but not especially sharp. The palatal bridge is 27-31% of the maxillary toothrow.
The upper canine is long and massive, and not in contact with the second upper premolar. The anterior upper premolar is medium sized and situated in the toothrow or sometimes half external. The lower canine is more slender than the upper tooth. The small middle lower premolar (P_3) partly or fully external, rarely missing; the first (P_2) and third (P_4) lower premolars are sometimes in contact.

Bacular morphology: The heavily built bone has a simple curvature that is ventrally bent in the last third to fourth length. The basal portion is slightly pressed dorsoventrally. The simple ventral emargination is wide and deeper than the dorsal one.The shaft is somewhat higher than wide, that is, laterally compressed. The tip has a lateral widening, rather flat dorsoventraly (Topál 1975).

Similar species: The second phalanx of third metacarpal is usually less than 66% of the length of the metacarpal; in *R. affinis* it is usually about 73% (Bates and Harrison 1997). The two species are further distinguishable by the shape of lancet, which is clearly hastate in *R. rouxi* but straight sided in *R. affinis*; cranially they are uniform, although *R. affinis* in most cases has a relatively shorter palatal bridge. *R. ferrumequinum* differs by its higher connecting process and larger forearm; cranially by the reduced, fully extruded anterior upper premolar.
The most closely related *R. sinicus* is separable solely on the bases of the average size differences (being smaller cranially and dentally) and distribution patterns. *R. thomasi* is indistinguishable externally but almost always smaller by craniodental measurements and has a weak upper canine.

Taxonomic remarks: The type series of *R. rouxi* stored in RMNH, Leiden consists of five mounted specimens all derived from Calcutta. Although, Temminck (1835) in his description of the species had given Pondicherry and Calcutta as type localities, no type specimen obtained from Pondicherry had been located. From the syntypes, the skull of an adult male mounted specimen (RMNH 35221) with relatively well preserved noseleaf was extracted recently and this specimen is designated herein as lectotype. The

paralectotypes are: RMNH 35222, adult male (?), mounted, skull inside; RMNH 35223, adult male (?), mounted, skull lost; RMNH 35224, subadult female, mounted, skull inside; and RMNH 35225, adult female, mounted, skull inside.
On the base of colour differences Andersen (1905a) speculated that the "southern form would have to stand as *Rh. rouxi rubidus* Kelaart, the Himalayan as *Rh. rouxi typicus*". However, according to Thomas (1997) the specimens from the Himalayas are referable to *R. sinicus* (see comments there), while specimens from the rest of India (including those from Calcutta, the type locality of *R. rouxi*) belong to *R. rouxi*.
Based on two specimens from unknown locality, Dobson (1872) described the species *R. petersi* and allied it to the *acuminatus*-section (group). Andersen (1905a) stated that this description was meagre and vague, based on an individual peculiartity and referred the name as a synonym of *R. rouxi*. Tate and Archbold (1939) listed *petersi* again as a distinct species, but offered no explanation for their decision. This view was followed by Ellerman and Morrison-Scott (1951), but subsequently, Sinha (1973) re-examined the type of *petersi* and revealed that it is nothing but an example of *R. rouxi rouxi*.
The taxonomy of the species in the Indian Subcontinent is insufficiently known. The differences in the noseleaf structure, measurements and DNA sequences both in Sri Lanka and in India may indicate the presence of more than one species (Bates, *pers. comm*. 1999, Thomas 1997).

Fig. 63.1. Lateral and frontal views of noseleaf of *R. rouxii* (HNHM 92.138.1.) from India. Scale = 3 mm.

Fig. 63.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. rouxii* (RMNH 35221 - lectotype) from India. Scale = 3 mm.

Table 63. ***R. rouxii***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		44.0	52.5		
SL	21.46	19.97	22.82	0.67	48
CM^3L	8.66	7.88	9.24	0.33	49
ZW	11.01	10.16	11.94	0.40	47
MW	10.13	9.49	10.51	0.23	47
ML	14.77	10.64	15.75	0.82	49
CM_3L	9.33	8.45	9.95	0.37	49

***Rhinolophus sinicus* Andersen, 1905**
Chinese rufous horseshoe bat
R. rouxi sinicus Andersen, 1905 (Chinteh, Anhui, China)
R. thomasi septentrionalis Sanborn, 1939 (Nguluko, N of Likiang, Yunnan, China, 27º05'N, 100º15'E)

Recognised subspecies: The following subspecies are recognised - *sinicus* in the Himalayas, northern Vietnam, southeastern China and Sichuan; *septentrionalis* in Yunnan.

External characters: A medium or moderately large species of the genus. The ears are small, their length is 15.8-21.0 mm. The horseshoe is relatively wide but not covering the whole muzzle, 8.1-8.2 mm wide; the usually well developed secondary leaflet is well visible from above. The sella is practically parallel sided, widely rounded off at its terminus. The connecting process is rounded. The lancet is definitely hastate but its tip is variable in length, sometimes expressedly short, in other cases long. There are three mental grooves on the lower lip. The tail is 19.5-30.0 mm in length. In the wings, the third metacarpal is the shortest (33.0-36.8 mm), and the fourth (34.2-37.4 mm) is shorter than or sometimes subequal to the fifth (35.4-39.2 mm). The general colour is about the dark phase of *R. rouxi*; colour phases not known. The upperside is wood brown sometimes with reddish tints, the ventral aspect is only slightly lighter.

Cranial and dental characters: The skull is massive, the zygomatic width is always remarkably greater than the mastoid breadth. The anterior median swellings are relatively small, the posterior ones moderately developed; the rostral profile is definitely concave. The sagittal crest is medium or high, the frontal depression is shallow and bordered with visible but low spraorbital ridges. The palatal bridge is 26-30% of the maxillary toothrow (CM^3) length.
The upper canine is well developed, much longer than the posterior upper premolar (P^4). The anterior upper premolar is medium, lying in the toothrow or slightly extruded but the adjoining teeth are widely separated. In the lower jaw, the middle premolar medium sized or small and partly or fully extruded from the row; the cingula of P_2 and P_4 in contact or nearly so.

Similar species: *R. sinicus* is characterised by its relatively large wings; the second phalanx of the third metacarpal is very long, 23.1-25.9 mm (65.0-75.3% of its respective metacarpal length). In *R. rouxi* the second phalanx of this digit is 19.2-26.0 mm (52.8-67.5% of the metacarpal) (Bates and Harrison 1997). *R. sinicus* is averaging smaller in skull measurements than *R. rouxi* but the overlap between the measurements is significant but the two species are separable on geographical ground. The separation of *R. sinicus* from *R. thomasi* is again very problematic and beside the usually smaller size of the latter, only the relative size of the upper canine (slightly exceeding the height of the posterior premolar in *R. thomasi*) is known as distinguishing character by which the two species could be tell apart.
R. affinis is similar in the proportions of the skull, but larger in measurements.

Taxonomic remarks: The taxon *sinicus* was described as a subspecies of *R. rouxi* (Andersen 1905a) who separated it on the base of its smaller skull and toothrow measurements. As Andersen remarked, the general size of *sinicus* as is the smallest example of the typical form of *R. rouxi*. This suggested taxonomic position of *sinicus* was generally accepted, but Thomas (1997) in her detailed work, evidenced that based on phenetic analysis and DNA techniques *sinicus* represents a distinct species. According to Thomas (op. cit.) the fourth and fifth metacarpals of *R. rouxi* are approximately 2% different in length, whilst in *R. sinicus* these metacarpals are consistently the same length.

Nevertheless, the relation and the specific boundary between *R. sinicus* and *R. thomasi* is not clear. The very hastate, excessively shortened lancet thought to be diagnostic for *R. thomasi* (Andersen 1905a, Corbet and Hill 1992, Koopman 1994) is not clearly expressed in all specimens of that species, while a similar shortening of lancet can be found in several *R. sinicus*. The types of both species are unusually small specimens of their own taxa and almost all the subsequently collected individuals are larger. It means, that although the type of *R. sinicus* is much larger than the type of *R. thomasi* (therefore justify the specific distinctness), overlaps in size with the majority of the known *R. thomasi* specimens (determined on the base of the short upper and lower canine only). On average, *R. sinicus* is much bigger than *R: thomasi*, but specimens obtained from Fukien and Sichuan (China) and housed in the collections of USNM and FMNH are intermediate in size (FA 44.7-48.9, SL 18.43-20.09, CM^3 7.04-7.66 mm) and difficult to assign to either of the species; provisionally, they are included here in the table given for *R. sinicus*.

The taxon *septentrionalis* once was described and later widely accepted as a subspecies of *thomasi*, differing from the nominotypical race by its larger size and slightly extruded anterior upper premolars (Sanborn 1939). The type of *septentrionalis* and other specimens from Yunnan stored in the FMNH and USNM agreeing in every respect with each other and are, however, much bigger in external measurements than *thomasi* and *latifolius* (FA 51.1-55.5 vs. 40.5-48.0; SL 19.79-20.98 vs. 17.87-19.98; and CM^3 7.65-8.40 vs. 6.82-7.67 mm), and have strong, widely based, long canines. These differences support the view, that *septentrionalis* differs from *R. thomasi* at specific level and referable to *R. sinicus*. The large external measurements (the forearm length is over 50 mm) validate the subspecific separation of *septentrionalis* within *R. sinicus*.

Fig. 64.1. Lateral and frontal views of noseleaf of *R. sinicus* (HZM 23.28155) from India. Scale = 3 mm.

Fig. 64.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. sinicus* (BMNH 99.3.1.6 - holotype) from China. Scale = 3 mm.

Table 64. ***R. sinicus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		43,5	55,5		
SL	19,93	18,43	20,98	0,56	54
CM^3L	7,65	7,04	8,40	0,34	62
ZW	10,33	9,44	10,99	0,33	56
MW	9,52	8,87	10,17	0,25	57
ML	13,40	12,26	14,46	0,58	63
CM_3L	8,19	7,50	8,85	0,38	62

***Rhinolophus thomasi* Andersen, 1905**
Thomas's horseshoe bat
R. thomasi Andersen, 1905 (Karin Hilla, SE Burma)
R. t. latifolius Sanborn, 1939 (Muong Moun, Tonkin, Vietnam)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized species of its genus. The ears are small in relation to the head, 16.0-21.5 mm in height. The horseshoe moderately wide but does not cover the whole muzzle, its breadth is 7.2-8.9 mm. A well developed secondary leaflet is frequently present. The sella is practically parallel sided, broadly rounded off at its terminus. The connecting process is rounded. The lancet is short, its tip is sometimes almost rudimentary, in other cases better developed. The lower lip with three well defined mental grooves. The tail length is 18.3-27.5 mm. In the wings, the metacarpals are gradually shortened, the third is 30.4-34.0 mm, the fourth is 31.3-35.5 mm and the fifth is 32.3-36.5 mm in length. The colour of the upper parts is rich brown with russet tint; the individual hairs are light yellow at the base and medium brown at the tip; the colour of the belly is lighter.

Cranial and dental characters: The skull is relatively strong, the zygomatic width is significantly greater than the mastoid breadth. The anterior median swellings are small, the posterior compartments are better dveloped. The rostral profil is clearly sloping rearwards. The sagittal crest is moderately high, the frontal depression is shallow or medium. The supraorbital crests are obliterated or well demarcated. The palatal bridge is 30-31% of the upper toothrow length.
The upper canine is only slightly exceeds the height of the posterior upper premolar, its basal area is usually small. The first upper premolar is small, lying almost in the axis of the row or fully external The upper canine and P^4 are in contact or separated according to the position of P^2. The lower middle premolar is small and external, the neighbouring teeth are touching each other or very nearly so.

Bacular morphology: According to Topál (1975) the bone is a rather lightly built structure with a double curvature. The dorsoventrally flattened basal cone is evidently smaller than in R. rouxi, still the emarginations on the proximal edge are the same. The shaft is laterally compressed its proximal ventral constriction is immediately at the basal cone. The bone shows an elongated S-shape from lateral view.

Similar species: The closest relative of *R. thomasi* is *R. sinicus* which is very similar in most respects, but larger on average and differs above all having a long, wide-based upper canine. *R. rouxi*, the third species in the group is also alike externally but larger in cranial and dental measurements.
The largest specimens of *R. shortridgei* and *R. imaizumii* are slightly overlapping in cranial measurements with *R. thomasi* but these species have stronger canines and less sharply curved rostral profile. *R. borneensis* also falls to the size-class of *R. thomasi*, but characterised by its straight sided lancet and more prominent anterior nasal swellings.

Taxonomic remarks: The species was first mentioned by Thomas (1892) who pointed out that it could scarcely be identified with any hitherto known form, but refrained from describing it as new. In the description of *R. thomasi* Andersen (1905a) noted its small

size as compared to *R. rouxi* (including the form *sinicus*) excessively shortened lancet and P^2 external to the toothrow. In fact, the type of *R. thomasi* is one of the smallest specimen of the species ever collected, the development of the terminal part of lancet is variable (as in specimens of *R. sinicus*) and the situation of the small upper premolar is variable - extruded in the holotype and one more individual seen by Andersen and stored in BMNH but almost exactly in the row in other specimens collected together with the type (USNM 142553-4). In the case of the type of *latifolius* (FMNH 32230) the P^2 is also in the row (see Fig. 62.3). Probably this is the reason why Koopman (1994) characterised the species as having an anterior upper premolar greatly reduced though in toothrow.
The minute differences of the shape of sella and size of ear and tail between the forms *thomasi* and *latifolius* (Sanborn 1939) do not support the subspecific separation; therefore the taxon *latifolius* is regarded here as the synonym of *thomasi*.
The small forearm measurements of specimens netted in north-east Thailand and in central Laos (40.8-43.9 mm and 42.2-44.7 mm, respectively) published by Robinson and Smith (1997) and Robinson and Webber (1998) supported the field identification.

Fig. 65.1. Lateral and frontal views of noseleaf of *R. thomasi* (BMNH 90.4.7.10 - holotype) from Myanmar. Scale = 3 mm.

Fig. 65.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. thomasi* (BMNH 90.4.7.9) from Myanmar. Scale = 3 mm.

Table 65. ***R. thomasi***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		40.5	48.0		
SL	18.95	17.87	19.98	0.66	20
CM^3L	7.22	6.82	7.67	0.27	21
ZW	9.70	9.22	10.12	0.30	17
MW	9.06	8.75	9.43	0.24	17
ML	12.73	11.79	13.33	0.47	19
CM_3L	7.72	7.32	8.10	0.29	19

TRIFOLIATUS-GROUP

***Rhinolophus beddomei* Andersen, 1905**
Lesser woolly horseshoe bat
R. beddomei Andersen, 1905 (Wynaad, Madras, India)
R. b. sobrinus Andersen, 1918 (Kala Oya, North Central Province, Sri Lanka)

Recognised subspecies: Following Bates and Harrison (1997) the following subspecies are recognised - *beddomei* in southern India; *sobrinus* in Sri Lanka.

External characters: A fairly large horseshoe bat. The ears are blackish, medium long, 21.0-34.0 mm in height. The characteristics of the noseleaf is perfectly the same as in *R. luctus*. The horseshoe is very wide, covering the whole of the muzzle with a distinct, wide median emargination. The base of sella is with pronounced lateral lappets on both sides; the sella is broad, widely rounded off. The connecting process is relatively low, broadly rounded. The lancet is long and pointed or rounded. The lower lip is with one groove. The tail is 35.0-48.0 mm. In the wings, the third metacarpal is 33.4-43.6 mm, the fourth is 39.4-51.2 mm and the fifth is 40.5-53.2 mm in length. The pelage is essentially the same as in *R. luctus*; long, woolly, uniformly dark brown or black on both the upper and underparts, the individual hairs are with paler tips.

Cranial and dental characters: The skull is robust, with the zygomatic width exceeds the mastoid width. The anterior median swellings are elongated, but not extending anteriorly to the upper edge of the nasal orifice which is formed by a protruding bony rim. The posterior swellings are situated more laterally, in connection with the long and deep frontal depression. The crista sagittalis is very well developed, suddenly elevating after the junction of the strong and sharp supraorbital crests and extending backward to the lambda. The palatal bridge is approximately one-third of the CM^3 length.
The canines are strong but relatively short in relation to the height of the posterior premolars (P^4 and P_4). The first upper premolar medium and lies within the toothrow or only slightly displaced; it is not usually in contact with the upper canine, of which only rarely have the concavity on its extero-posterior base. The second lower premolar is small or medium and is extruded from toothrow to a variable extent. The first (P_2) and third (P_4) lower premolars are almost in contact.

Similar species: Within the *trifoliatus*-group the species can be separated mainly by measurements. *R. beddomei* further distinguishable from *R. trifoliatus* by its larger and approximated upper incisors (see drawings in *R. luctus*). The characteristically formed noseleaf is separating *R. beddomei* from other species outside the *trifoliatus*-group.
Cranially, *R. beddomei* is separable from the similar sized species (*R. pearsoni*, *R. yunanensis*, *R. subrufus*) by its deep and long frontal depression, high supraorbital crests and the suddenly elevated anterior sagittal crest.

Taxonomic remarks: Based on size differences (supported by statistical analysis) and the shape of upper canine, Topál and Csorba (1992) separated *R. beddomei* (usually regarded as only subspecies) from *R luctus* at specific level. This view was later accepted by Bates and Harrison (1997). Specimens from Sri Lanka are significantly smaller than those from peninsular India and have been referred to *R. b. sobrinus*.

Fig. 66.1. Lateral and frontal views of noseleaf of *R. beddomei* (BMNH 82.3.3.1 - holotype) from India. Scale = 3 mm.

Fig. 66.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. beddomei* (BMNH 82.3.3.1 - holotype) from India. Scale = 3 mm.

Table 66. ***R. beddomei***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		54.5	64.5		
SL	26.66	25.05	27.80	1.17	4
CM^3L	9.92	9.21	10.49	0.55	5
ZW	13.66	12.35	14.39	0.81	6
MW	12.02	11.31	12.47	0.51	4
ML	18.25	17.64	18.86	0.53	5
CM_3L	10.68	10.09	11.07	0.44	5

***Rhinolophus formosae* Sanborn, 1939**
Formosan woolly horseshoe bat
R. formosae Sanborn, 1939 (Taiwan)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A large species of the genus. The ears are medium, 27.8-33.0 mm in height; their colour is blackish. The noseleaf is also jet black in colour. The horseshoe is wide, covering the muzzle and with a deep notch at the middle of the lower margin; its width is 12.3-13.7 mm. The base of sella is with a pair of circular basal lappets. The connecting process is moderately low, running almost parallel with the sella. The lancet is long or very long, its terminal part is narrow and bordered with straight sides. The lower lip is with one mental groove. The tail is 27.9-39.0 mm in length. In the wings the fifth metacarpal is the longest (44.0-48.4 mm) and beside the medium long fourth metacarpal (42.0-47.4 mm) the third is by far the shortest (36.0-40.5 mm). The fur is silky and glossy, particularly on neck and shoulder, its colour is uniform dull black both on the dorsal and ventral sides.

Cranial and dental characters: The skull is strong and heavily built. The zygomatic breadth is much greater than the mastoid breadth. The anterior median nasal swellings are moderately developed, slightly elongated but their anterior border do not reach the upper part of nasal orifice. The lateral swellings are well developed, the posterior ones are small. The frontal depression is very deep, narrow and long, its sides form strong and sharp supraorbital ridges converging towards a moderately developed sagittal crest. The palatal bridge is consistently 41-42% of the maxillary toothrow.
The upper canine is strong and massive but short, only slightly exceeds the height of the posterior premolar. The anterior upper premolar is medium or quite large, lying in the toothrow or partly extruded; its crown area is larger than that of the upper incisor. The large upper premolar (P^4) is well developed and not in touch with the canine. In the lower jaw, the middle lower premolar is small or rarely missing at all, external to the row; P_2 is less than half as high as P_4 and they are almost always in contact.

Similar species: The distinctive colouration, specially formed sella, very deep and narrow frontal depression combined with the shape of the median nasal swellings separate *R. formosae* from the other species except the members of its group. Within group, the similar-sized species are *R. beddomei* (occuring only in south India and Sri Lanka and not distinguishable by external or craniodental features) and *R. trifoliatus*.

This latter species is, however, usually smaller, different in the colour of the nasal appendages and has smaller, widely separated upper incisors and higher sagittal crest.

Taxonomic remarks: Although the taxon *formosae* was described as a separate species, the subsequent comprehensive works (Corbet and Hill 1992, Koopman 1994) considered it only as a subspecies of *R. luctus*. However, Ando *et al*. (1980) reported a diploid number of *formosae* very different from that of other subspecies of *luctus*. As Hood *et al*. (1988) discussing these caryotypes pointed out, such differences between subspecifically differentiated populations of *R. luctus* are striking and cited that most examples of chromosomal polymorphism in bats have been associated with the hybridization of chromosomal races or involve cases of cryptic species (Baker *et al*. 1985). Yoshiyuki and Harada (1995) based on the different karyotypes and the evident size differences between the forms, considered *formosae* specifically distinct. This separation is fully acceptable (and was followed by Lin *et al*. 1997), but one of the remarks of the authors „[*R. formosae*] cannot be regarded as belonging to the *luctus* group, but to another group of species" is hardly understandable. *R. formosae* and *R. luctus* are definitely very closely related, as it is supported by their general (external and craniodental) similarity.

Fig. 67.1. Lateral and frontal views of noseleaf of *R. formosae* (HNHM 98.20.1.) from Taiwan. Scale = 3 mm.

Fig. 67.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. formosae* (HNHM 98.20.1.) from Taiwan. Scale = 3 mm.

Table 67. ***R. formosae***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		57.0	61.0		
SL	25.46	24.02	26.53	0.82	7
CM^3L	9.99	9.27	10.61	0.54	7
ZW	12.75	11.83	13.60	0.70	7
MW	11.53	10.90	12.21	0.48	7
ML	17.81	16.91	18.33	0.51	7
CM_3L	10.60	9.93	11.01	0.38	7

***Rhinolophus luctus* Temminck, 1834**
Woolly horseshoe bat
R. luctus Temminck, 1834 (Tapos, Java)
R. morio Gray, 1842 (Singapore)
R. perniger Hodgson, 1843 (Nepal)
R. lanosus Andersen, 1905 (Kuatun, N.W. Fujian, China)
R. geminus Andersen, 1905 (Kediri, E. Java, 2000–3000 ft)
R. morio foetidus Andersen, 1918 (Baram, Sarawak, Borneo)
R. lanosus spurcus Allen, 1928 (Nodoa, Hainan I., China)

Recognised subspecies: The following subspecies are recognised - *perniger* in northern India, Myanmar, Vietnam, Laos, northern Thailand; *lanosus* in southeastern China; *spurcus* in Hainan; *morio* in Malay Peninsula, northern Sumatra; *luctus* in southern Sumatra, Java, Bali; *foetidus* in Borneo.

External characters: The largest species of horseshoe bats. The ears are medium, 27.9-44.0 mm in height. The noseleaf and ears are dull black or dark grey-brown. The horseshoe is wide, projecting in front and on either side beyond the upper lip, 12.2-18.5 mm in breadth. It has a distinct median emargination which cleraly divides it into two halves. The internarial cup is with upturned edges. The base of the sella has a flange on each side that forms pronounced circular basal lappets; the tip of the parallel-sided sella deflected downwards and forwards. The connecting process broadly rounded off and very reduced. The lancet is well developed, subacutely pointed and the tip is rounded off. The lower lip is with a single mental groove. The tail is 35.9-61.0 mm. In the wings, the third metacarpal is characteristically short (40.2-53.7 mm) averaging only 83.8-87.9% of the length of the fourth metacarpal which is 46.8-61.5 mm; the fifth metacarpal is 48.2-63.6 mm in length. The fur is long and fluffy, on the upperparts dark gray-brown or black with pale tips to many of the hairs producing a frosted effect; the underparts is a more pronounced grey.

Cranial and dental characters: The skull is very large and robust; the zygomatic breadth is much greater than the mastoid breadth. The anterior median swellings are relatively low or medium developed, antero-posteriorly elongated and do not reach anteriorly the upper border of the nasal orifice. The posterior compartments are reduced and shifted laterally; their place is mainly occupied by the very deep and elongated frontal depression. The sagittal crest is exceptionally high and suddenly elevated after the junction of the prominent blade-like supraorbital crests. The palatal bridge is long, 37-39% of the upper toothow length.
The upper canine is very strong, massive and short, its height only slightly exceeds the cusp of the well developed posterior upper premolar. The first upper premolar is a large or medium sized functional tooth, situated in the toothrow or at most partly extruded; its anterior border fits into a concavity in the posterior base of the upper canine. The situation of the middle lower premolar is very variable even within the given subspecies; the adjoining P_2 and P_4 are separated or touching each other accordingly.

Similar species: The very large size alone separates *R. luctus* from the majority of the species. The similar sized *R. rufus* distinguishable externally by its differently shaped noseleaf and three mental grooves; cranially by the shorter frontal depression, minute upper incisors and larger anterior swellings. *R. yunanensis* also has one mental groove but has very different nasal foliation, smaller skull and shallower frontal depression.
Within the group, the larger specimens of *R. beddomei* overlap in forearm length with *R. luctus* but they are smaller in skull and teeth measurements and the two species are separated geographically. The same is true for *R. formosae*, as well. *R. trifoliatus* is separable by its smaller size, different colouration and cranially by the shape and size of the upper incisors which in *R. luctus* are relatively large, situated close to each other and their tips are convergent.

Taxonomic remarks: When re-described *perniger* in detail, Andersen (1905c) remarked that the taxon „has hitherto wrongly been confounded with *Rh. luctus*", and

separated the former as distinct species on the base of its larger ear, tibia and cranial measurements. Subsequently, based on more material Sinha (1973) stated that difficult to distinguish between these two taxa. Andersen (op. cit.) also separated *lanosus* as specifically distinct, based on its smaller size and less developed sagittal crest and smaller teeth as compared to *R. perniger*. Because of the above craniodental characters, Andersen related *lanosus* to *sedulus* and placed it in the *sedulus* section of his *philippinensis*-group. Describing *R. geminus* from Java, Andersen (1905c) separated his new species from *perniger* by its shorter ears and tail, but based on only a single immature specimen. He stated, „as might be expected, from the general character of the mammalian fauna of Java, this species is much more closely related to the Himalayan form (*perniger*) than to *Rh. luctus* from Borneo and the Malay Peninsula" - Andersen seemingly did not taken into consideration, that the type specimen of *luctus* is also derived from Java. These two forms are, however, con-subspecific. Several forms (*geminus*, *foetidus*, *morio*, *lanosus*) now accepted as subspecies of *R. luctus* but described under other species names were synonymised at first by Chasen (1940) and followed by Tate (1943). Quite surprisingly, along these forms Tate (op. cit.) listed *pearsoni* and *chinensis* (= *R. p. pearsoni*) as provisional races of *R. luctus*, as well. Since both *chinensis* and *lanosus* were collected from Kuatun, Fukien, Tate remarked that „two subspecies of a species cannot occur in the same locality...these two *Rhinolophus* must be either full species or synonyms".

Fig. 68.1. Lateral and frontal views of noseleaf of *R. luctus* (BMNH 79.11.15.10 – holotype of *R. l. geminus*) from Java. Scale = 3 mm.

Fig. 68.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. luctus* (RMNH 35175 - holotype) from Java. Scale = 3 mm.

Table 68. ***R. luctus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		58.0	80.5		
SL	30.28	27.83	32.55	1.18	59
CM^3L	11.71	10.50	12.90	0.50	67
ZW	15.28	14.20	16.45	0.54	59
MW	13.43	12.37	14.37	0.43	58
ML	21.51	19.68	23.28	0.84	65
CM_3L	12.56	11.03	14.08	0.53	67

***Rhinolophus sedulus* Andersen, 1905**
Lesser woolly horseshoe bat
R. sedulus Andersen, 1905 (Sarawak, Malaysia)

Recognised subspecies: All specimens referred to the nominate form.

External characters: A medium sized species of the genus. The ears are medium in relation to the head, 22.0-23.0 mm in length. The noseleaf and the ears are dark brown or black. The breadth of horseshoe is approximately 10.3 mm, the median emargination is relatively small. There are circular lateral lappets at the base of sella which is nearly parallel sided above and deflected downwards at the tip. The connecting process is moderately low. The lancet is nearly straight sided in its full length. The lower lip is with one mental groove. The tail is 20.0-31.0 mm in length. In the wings, the third metacarpal is considerably shortened, its length is 27.0-30.5 mm, the fourth is 31.7-34.5 mm and the fifth is 32.3-35.8 mm in length. The fur of the upperside is a shade of dark brown or black, with greyish tips to the hairs; the underside is generally the same in colour but without greyish reflection.

Cranial and dental characters: The skull is small but heavily built. The zygomatic breadth is always exceeds the mastoid breadth, but the difference is sometimes quite small. The anterior median swellings are medium, do not reach anteriorly the border of the rostrum; the posterior compartments are less inflated. The crista sagittalis is less developed than in the related species, but the frontal depression is deeply hollowed and the bordering supraorbital crests are prominent with sharp ridges. The palatal bridge is moderately long. 31-34% of the upper toothrow (CM^3) length.
The upper canine is short but not especially strong, the tip of the posterior premolar (P^4) is almost reaching the height of C^1. The first upper premolar (P^2) is medium or quite large but its cusp is minute; the tooth is situated in the row. The middle lower premolar is external to a different extent, the first (P_2) and third (P_4) premolars are in contact or nearly so.

Similar species: The characteristically trilobated sella, dark colouration and small size make the species unmistakable at first sight. *R. sedulus* is much smaller than its relatives in the *trifoliatus*-group, both externally and cranially. The character combination of the relatively large and approximated upper incisors, deep and long frontal depression and the bony rim which separates the anterior upper border of rostrum from the median swellings distinguishes the species from all other similar sized horseshoe bats.

Taxonomic remarks: According to Andersen (1905c) the skull of *R. sedulus* is very much nearer to *R. philippinensis* than to *R. trifoliatus*. However, beside the obvious similarity in the nasal foliation, the characteristically deep frontal depression and the shape of the anterior nasal swellings are evidently connected the species to the *trifoliatus*-group. According to Tate and Archbold (1939) specimens from Borneo appear to be closely related to *R. trifoliatus* from Java.

Fig. 69.1. Lateral and frontal views of noseleaf of *R. sedulus* (BMNH 65.334) from Malaya. Scale = 3 mm.

Fig. 69.2. Lateral view of the rostral part of the skull and occlusal view of the upper (left) and lower (right) left anterior dentition of *R. sedulus* (BMNH 7.1.1.292 - holotype) from Borneo. Scale = 3 mm.

Table 69. ***R. sedulus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		38.0	44.0		
SL	19.74	18.90	20.80	0.68	9
CM^3L	7.28	6.77	8.22	0.45	10
ZW	9.91	9.41	10.35	0.33	8
MW	9.40	9.00	9.77	0.33	8
ML	13.08	12.24	14.35	0.68	9
CM_3L	7.69	7.15	8.74	0.49	10

***Rhinolophus trifoliatus* Temminck, 1834**
Trefoil horseshoe bat
R. trifoliatus Temminck, 1834 (Bantam, W Java)
R. solitarius Andersen, 1905 (Tanjong Pamuja, Bangka I)
R. t. niasensis Andersen, 1906 (Nias I)
R. edax Andersen, 1918 (Singapore I)

Recognised subspecies: Following Koopman (1994) the following subspecies are recognised - *edax* from northeastern India, Thailand through the Malay Peninsula; *trifoliatus* in Sumatra, Java and Borneo; *niasensis* in Nias; *solitarius* in Bangka.

External characters: A medium sized or relatively large species of *Rhinolophus*. The noseleaf and the bases of ears are yellow or yellowish-brown; the ears are medium long and 22.0-27.0 mm in height. The breadth of the relatively wide horseshoe is 10.5-12.4 mm. The sella is narrow, about 1.4 mm in breadth at its apex; there are circular lateral lappets at the base. The connecting process is low. The lancet is quite long, slightly emarginated below its tip. The lower lip is with a single mental groove. The tail is 25.7-38.0 mm in length. In the wings, the third metacarpal is quite shortened, 29.8-37.0 mm, the fourth is 33.5-42.0 mm, and the fifth is the longest, 35.8-43.8 mm in length. The fur is long and woolly, light coloured, pale buffy brown to brownish grey above and below. One rather large specimen from Borneo had dark membranes and dark brown fur.

Cranial and dental characters: The skull is heavy and robust, the zygomatic width is greatly exceeds the mastoid breadth. The anterior median swellings are relatively well inflated but not reaching anteriorly the border of the nasal orifice. The posterior compartments are reduced, in connection with the deep or very deep and narrow frontal depression. The cristae supraorbitales are high with sharp ridges. The sagittal crest is very high anteriorly but flattened rearwards. The palatal bridge is 34-39% of the upper toothrow length.
The upper canine is massive and short only barely exceeds the height of the posterior upper premolar. The first upper premolar (P^2) is small or medium and lying in the

toothrow or sometimes extruded from the axis; the upper canine and the second premolar are separated. The situation of the small or minute second lower premolar is variable being extruded to different degrees from the toothrow or fully missing. Corresponding to this, P_2 and P_4 are also well separated or quite in contact.

Similar species: The yellowish colour of the noseleaf, the external and craniodental measurements distinguish the species from the other members of the *trifoliatus*-group. Unlike *R. luctus* and *R. formosae* the upper incisors are minute and widely separated from each other. The combination of the very deep and long frontal depression, the anterior median swellings which are not reaching the upper rim of the nasal orifice and the well defined sagittal crest of *R. trifoliatus* sharply distinguish the species from all other similar sized horseshoe bats.

Taxonomic remarks: In their notes on the *philippinensis*-group, Tate and Archbold (1939) found that it is difficult to separate Andersen's subgroups of *trifoliatus* and *philippinensis*, and linked *R. trifoliatus* to *R. philippinensis* (although with a question mark) but with no explanations. Later on, Tate (1943) listed *R. trifoliatus* as the only species of its own section and separated it from his *luctus*-section on the bases of the weakly pigmented facial membranes, the high, tapered sella and widely separated upper incisors.
R. edax was described from Singapore as a separate species but later on listed by Chasen (1940) as a subspecies of *R. sedulus*. Nevertheless, based on its larger size and more robust dentition, Tate (1943) considered *edax* conspecific with *trifoliatus*, which view was accepted by Corbet and Hill (1992). Koopman (1994) applied *edax* as valid subspecies name for all the mainland Asian population of the species. Despite the view of Koopman, according to Sinha (1973) specimens from India (and also from the Asian mainland and the Great Sunda Islands) are all referred to *R. t. trifoliatus*. The taxon *solitarius* was distinguished by its shorter tail and tibia (Andersen 1905c) and according to Andersen (1905d) „closely allied to, but specifically distinc from, *Rh. trifoliatus*" but agrees with *R. trifoliatus* in every important characters. Chasen (1940) mentioned *solitarius* as a subspecies of *R. trifoliatus*. *R. t. niasensis* was considered by Andersen (1906) „so exceedingly like the typical *trifoliatus* that, for the present at least, I do not think advisable to separate it as a distinc species".

Fig. 70.1. Lateral and frontal views of noseleaf of *R. trifoliatus* (BMNH 82.159) from Borneo. Scale = 3 mm.

Fig. 70.2. Lateral view of the rostral part of the skull (BMNH 65.337) from Malaya and occlusal view of the upper (left) and lower (right) left anterior dentition (RMNH 35194 – holotype) from Java of *R. trifoliatus.* Scale = 3 mm.

Table 70. ***R. trifoliatus***: External, cranial and dental measurements (mm).

	mean	min	max	s	n
FA		48.0	58.0		
SL	22.79	21.80	24.68	0.64	33
CM^3L	8.76	8.14	9.55	0.37	38
ZW	11.94	11.07	12.93	0.44	28
MW	10.68	10.10	11.17	0.27	24
ML	15.93	14.87	17.41	0.66	36
CM_3L	9.34	8.68	10.29	0.39	35

INCERTAE SEDIS

***Rhinolophus mitratus* Blyth, 1844**
Mitred horseshoe bat
R. mitratus Blyth, 1844 (Chaibassa, Orissa, India)

Recognised subspecies: Only one specimen known.

External characters: According to Sinha (1973) „the ears large, horseshoe broad; internarial lobes abnormally expanded upwards forming a deep cavity; vertical part of sella short and rounded its base not expanded as in *R. trifoliatus*. Lower lip with single mental groove. Fur brown dorsally and light brown ventrally." The tail is 30 mm in length. In the wings, the metacarpals are distinctly increasing in length, the third is the shortest (37.5 mm), the fourth is 40.0 mm, the longest fifth metacarpal is 41.5 mm in length.

Cranial and dental characters: The skull of the holotype is damaged and according to Sinha (op. cit.) no measurements can be taken.

Taxonomic remarks: According to Dobson (1878) *R. mitratus* resembles very closely in form of the central noseleaf to *R. philippinensis*. Andersen (1905c) also linked this species to his *philippinensis*-group, because of the cup-like expansion of the base of sella and internasal lobes and the shape of the ears. Tate and Archbold (1939), Tate (1943) and Ellerman and Morrison-Scott (1951) considered it nearer to *R. trifoliatus*. Based on the description of Sinha (1973) the specific distinctness of *mitratus* can not be evidenced; the taxon is probably close to *R. pearsoni*.

Fig. 71. Frontal and lateral views of head of *R. mitratus* (after Dobson 1876).

Table 71. ***R. mitratus***: External, cranial and dental measurements (mm).

		n
FA	57.1	1

5. ÖSSZEFOGLALÓ

A diplomamunka tárgyául választott család, a patkósdenevérek (Rhinolophidae), a denevérek rendjének jól körülhatárolható csoportja, melyen belül azonban a nagyfokú küllemi és csonttani hasonlóságnak köszönhetően, mindig is problémás volt az egyes fajok elválasztása. Az első átfogó, határozókulcsokat is tartalmazó cikkek ANDERSEN (1905a, 1905b, 1905c, 1905d, 1905e, 1905f, 1918) nevéhez kötődnek, ám azóta egyetlen ilyen munka sem jelent meg. Mivel a család 71 (egyetlen genusba tartozó) faja még a denevérek között is különösen egyveretűnek számít, a fontos határozóbélyegeket hordozó összetett orrfüggelék a száraz bőrökön nagymértékben torzul, és a koponya illetve fogazati jellegzetességek változatossága, használhatósága nem volt ismeretes, elhatároztam, hogy a fellelhető típuspéldányok vizsgálatával, valamint a világ nagy múzeumai gyűjteményeinek átvizsgálásával magam próbálok meg egy határozót összeállítani.

Az anyaggyűjtés során az alábbi múzeumok anyagait vizsgáltam át:

- American Museum of Natural History, New York
- Field Museum of Natural History, Chicago
- Forschunginstitut Senckenberg, Frankfurt
- Harrison Institute, Sevenoaks
- Institute of Ecological and Biological Resources, Hanoi
- Magyar Természettudományi Múzeum, Budapest
- Museum d'Historie Naturelle, Genf
- Museum für Naturkunde, Berlin
- Museum National d'Histoire Naturelle, Párizs
- National Museum of Natural History, Leiden
- National Museum of Natural Science, Taichung
- Natural History Museum, London
- Naturhistorisches Museum, Bécs
- Staatliches Museum für Naturkunde, Stuttgart
- Thailand Institute of Scientific and Technological Research, Bangkok
- United States National Museum of Natural History, Washington
- Zoological Museum of Moscow State University, Moszkva

A fenti múzeumok gyűjteményeiben mintegy 4000 példányt (bőröket, koponyákat, alkoholos preparátumokat) vizsgáltam és határoztam meg illetve ellenőriztem faji hovatartozásukat, közülük 2000-ről vettem fel alapvető méreteket (alkarhossz, hatféle koponya,- és fogazati méret), és mintegy 400 vonalas rajz készült orrfüggelékekről, koponyákról és fogazatokról. Mindössze néhány kivétellel alkalmam volt a jelenleg elfogadott fajok típussorozatainak példányait megtekinteni; ahol erre nem volt mód, illetve azok állapota nem volt megfelelő, a típuslelőhelyről vagy annak közeléből származó példányokról készültek rajzok. A rajzok jelentős részét Ujhelyi Péter készítette, és mindegyik végső kidolgozása az ő nevéhez fűződik. Munkámat elősegítendő, részben saját gyűjtőutaimon, részben kiterjedt cserékkel igyekeztem minél több fajból példányokat szerezni a Magyar Természettudományi Múzeum Emlősgyűjteményébe, ahol az évek során ily módon a világ 10 legjobb gyűjteménye közé sorolható összehasonlító anyag gyűlt össze.

Egységes rendszerbe foglaltam és ábrán bemutattam a patkósdenevérek speciális morfológiai jellegzetességeinek nevezéktanát és rögzítettem a méretfelvételek módszerét. Kritikusan értékeltem a család szisztematikai feldolgozásakor használható rendszertani bélyegeket. A világon a Rhinolophidae családdal kapcsolatban 1903-2002 között publikált összes irodalom rendszertani vonatkozását feldolgoztam, és minden faj esetében értékeltem a különböző szerzők taxonómiai-szisztematikai véleményét.

Az anyaggyűjtéssel párhuzamosan feldolgoztam az egyes gyűjtemények meghatározatlan anyagait és természetesen a saját gyűjtéseimből származó állatokat is. Ennek során az alábbi új taxonok kerültek leírásra:

Rhinolophus macrotis topáli Csorba és Bates, 1995 (Pakisztán)
Rhinolophus convexus Csorba, 1997 (Malájzia)
Rhinolophus stheno microglobosus Csorba és Jenkins, 1998 (Vietnám)
Rhinolophus maendeleo Kock, Csorba és Howell, 2000 (Tanzánia)

Az új fajok és alfajok leírása mellett több esetben revideáltam az eddigi taxonómiai álláspontot, az alábbi eredményekkel:

R. anderseni Cabrera, 1909 – **új szinoníma** (= *R. arcuatus* Peters, 1871)
R. beddomei Andersen, 1905 – **revideált státusz**
R. euryale barbarus Andersen and Matschie, 1904 **új szinoníma** (= *R. euryale euryale* Blasius, 1853)
R. euryale meridionalis Andersen and Matschie, 1904 **új szinoníma** (= *R. euryale euryale* Blasius, 1853)
R. formosae Sanborn, 1939 **revideált státusz**
R. hipposideros vespa Laurent, 1937 **új szinoníma** (= *R. hipposideros escalerae* Andersen, 1918)
R. megaphyllus klossi Andersen, 1918 **új szinoníma** (= *R. megaphyllus robinsoni* Andersen, 1918)
R. montanus Goodwin, 1979 **új státusz**
R. pearsoni chinensis Andersen, 1905 **új szinoníma** (= *R. pearsoni pearsoni* Horsfield, 1851)
R. ruwenzorii Hill, 1942 **revideált státusz**
R. ruwenzorii hilli Aellen, 1973 **új státusz**
R. shortridgei Andersen, 1918 **új státusz**
R. sinicus Andersen, 1905 **új státusz**
R. sinicus septentrionalis Sanborn, 1939 **új kombináció**
R. thomasi latifolius Sanborn, 1939 **új szinoníma** (= *R. thomasi thomasi* Andersen, 1905)

Az összegyűlt ismeretek birtokában elkészült egy olyan, ábrákkal, mérettáblázatokkal kiegészített határozókulcs, melynek segítségével összes eddig ismert faj meghatározható. Ez számos esetben kézben tartott élő példányok esetében is alkalmazható, máshol (a fajok nagyfokú hasonlósága és a bélyegek jellege miatt) preparátum készítése szükséges. Emellett elkészült minden faj részletes szöveges jellemzése, egységesen az alábbi szerkezeti felépítést követve: **Nevezéktan** (az adott fajhoz tartozó összes leírt forma felsorolása szerzővel, pontos citációval); **Alfajok** (a jelenleg elfogadott illetve általam érvényesnek tartott alfajok felsorolása); **Külső jellegzetességek** (az orrfüggelék, fül, színezet, egyéb taxonómiai szempontból fontos tulajdonságok ismertetése); **Koponya,- és fogazati jellegzetességek**; **Hasonló fajok** (a

határozóban nem szereplő, de a határozást megerősítő bélyegek felsorolása); **Taxonómiai megjegyzések** (a fajjal kapcsolatos különböző taxonómiai álláspontok, megjegyzések történeti áttekintése és kritikai értékelése). A szöveget és az ábrákat **mérettáblázatok** egészítik ki, melyek minden faj esetében egységesen (egyetlen kutató által) mért adatokat tartalmaznak a faj teljes elterjedési területéről, így biztos támpontot adnak eddig ismeretlen taxonok felismeréséhez.

1. APPENDIX

ACKNOWLEDGEMENTS

At first I would like to express my deepest thanks for my tutor György Topál who established a valuable collection, built up the scientific background and provided continuous moral support on which base I could start and finally, finish this work. I am also indebted to my other colleagues: Dávid Csanádi for his technical support and for caring so many specimens and Istvánné Vörös and Éva Lengyel in the Library of HNHM for helping me during my frantic search for old and hardly available literatures. My special thanks are due to Péter Ujhelyi who was my keen-eyed company during several museum visits, produced many of the line drawings and gave the finishing touches for all figures.

I am most grateful to Paula Jenkins, Daphne Hills, Mary Sheridan, Richard Sabin, Richard Harbord and Andrew Cabrinovic for their kind help in the unparalleled collection of The Natural History Museum, London. Many thanks are due to the following curators and other staff members for their help while studying specimens under their care: Nancy Simmons and Fiona Brady of American Museum of Natural History, New York; Lawrence Heaney and William Stanley of Field Museum of Natural History, Chicago; Cao Van Sung and Pham Duc Tien of Institute of Ecology and Biological Resourches, Hanoi; Renata Angermann of Museum für Naturkunde, Berlin; Jacques Cuisin of Musem National d'Histoire Naturelle, Paris; Yen-Jean Chen of National Museum of Natural Science, Taichung; Friederika Spitzenberger of Naturhistorisches Museum, Vienna; Chris Smeenk of National Museum of Natural History, Leiden; Dieter Kock of Forschungsinstitut Senckenberg, Frankfurt; Fritz Dieterlen and Carsten Leidenroth of Staatliches Museum für Naturkunde, Stuttgart; Sunee Kruthanut, Lakkana Pakarnseree and Jarujin Nabhitabhata of Thailand Institute of Scientific and Technological Research, Bangkok; Michael Carleton and Sharon Jones of United States National Museum of Natural History, Washington; Alex Borissenko and Sergey Kruskop of Zoological Museum of Moscow State University, Moscow. Josephina Barreiro of Museo Nacional de Ciencias Naturales, Madrid kindly managed a detailed drawings of *R. anderseni* and Francois Baud (Museum d'Historie Naturelle, Geneve) loaned valuable specimens.

My work was supported by the Hungarian National Scientific Research Fund (OTKA), by The Royal Society (two occasions), Smithsonian Institution (Short-Term Visitor Award), Field Museum of Natural History (Visiting Scientist Scholarship) and by the American Museum of Natural History (Collection Study Grant).

2. APPENDIX
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3. APPENDIX
FIGURES

All figures listed in the text can be found in the attached CD in electronic format (jpg files).

4. APPENDIX

SCIENTIFIC PUBLICATIONS ON THE SUBJECT OF THE DISSERTATION

Selected publications can be found in the attached CD in electronic format (pdf files).

Papers / Tudományos közlemények

CSORBA, G. & DEMETER, A. 1990. Zoological collectings by the HNHM in Korea. 90. A report on the collecting of the Tenth Expedition. - *Miscnea. zool. hung.* **5**: 95-97.

TOPÁL, GY. & **CSORBA, G**. 1992. The subspecific division of *Rhinolophus luctus* Temminck, 1835, and the taxonomic status of *R. beddomei* Andersen, 1905 (Mammalia, Chiroptera). - *Miscnea. zool. hung*. **7**: 101-116.

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CSORBA, G. & BATES, P. J. J. 1995. A new subspecies of the horseshoe bat *Rhinolophus macrotis* from Pakistan (Chiroptera, Rhinolophidae). - *Acta zool. hung*. **41(3):** 285-293.

CSORBA, G., FUISZ, T. & KELEN, B. 1997. New birds and bats from Pulau Tioman, Pahang, Malaysia. - *Malay. Nat. J*. **50**: 197-200.

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KOCK, D., **CSORBA, G**. & HOWELL, K. M. 2000. *Rhinolophus maendeleo* n. sp. from Tanzania, a horseshoe bat noteworthy for its systematics and biogeography (Mammalia: Chiroptera: Rhinolophidae) - *Senckenbergiana Biol*. 80: 233-239.

CSORBA, G. 2002. Remarks on some types of the genus *Rhinolophus*. - *Annls hist.-nat. Mus. natn. hung.* 94: 217-226.

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CSORBA, G. & UJHELYI, P. 2005. A patkósdenevérek (Rhinolophidae) rendszertani felosztása. (The classification of the genus *Rhinolophus*.) - In: Molnár, V., Orbán, É. & Molnár, Z. (eds): *Proceedings of the II., III. and IV. Conference on the Bat Conservation in Hungary*. Hungarian Bat Research Society, Budapest, pp. 59-62.

NGUYEN TRUONG SON & **CSORBA, G.** 2008. Preliminary results on bat surveys in Bac Huong Hoa protected area and Da Krong Nature Reserve, Quang Tri Province. - In: *Proceedings of the 2nd National Scientific Conference on Ecology and Biological Resources*. IEBR, Hanoi, pp. 532-536.

Book / Könyv

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CSORBA, G. 2007. Rejtett diverzitás ázsiai erdőlakó denevéreknél. Cryptic diversity of Asian forest-interior bats. *VI. Magyar Denevérvédelmi Konferencia*. Mártély.

A PATKÓSDENEVÉREK RENDSZERTANA. TAXONOMY OF THE HORSESHOE BATS OF THE WORLD (CHIROPTERA: RHINOLOPHIDAE)

Értekezés a doktori (Ph.D.) fokozat megszerzése érdekében
a ..... tudományágban

Írta: ..... okleveles .....

Készült a Debreceni Egyetem ..... doktori iskolája
(..... programja) keretében

Témavezető: Dr. . . . . .

A doktori szigorlati bizottság:
elnök: Dr. ……
tagok: Dr. ……
Dr. ……

A doktori szigorlat időpontja: 200… . …… … .

Az értekezés bírálói:
Dr. .....
Dr. ……
Dr. .....

A bírálóbizottság:
elnök: Dr. .....
tagok: Dr. ……..
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Dr. ……..
Dr. ……..

Az értekezés védésének időpontja: 200… . …… … .