

**MULTIVARIATE ANALYSIS OF MORPHOLOGICAL CHARACTERS
OF *PIPISTRELLUS PIPISTRELLUS* (SCHREBER, 1774) AND
P. NATHUSII (KEYSERLING & BLASIUS, 1839) (MAMMALIA:
CHIROPTERA) FROM THE NETHERLANDS**

by

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Grol, B. P. F. E.: Multivariate analysis of morphological characters of *Pipistrellus pipistrellus* (Schreber, 1774) and *P. nathusii* (Keyserling & Blasius, 1839) (Mammalia: Chiroptera) from The Netherlands.

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Within the Vespertilionidae the genus *Pipistrellus* Kaup, 1829 is characterized by the presence of a calcar lobe (epiblema) attached to the calcar bone, the presence of two upper premolars on each side and a forearm length smaller than 38 mm. Two representatives of this genus occur in The Netherlands: *Pipistrellus pipistrellus* (Schreber, 1774) and *P. nathusii* (Keyserling & Blasius, 1839). These two species probably are closely related and are difficult to distinguish. Many authors over the years have used different morphological, dental and skull characters to differentiate these species. In this study the characters are divided into two groups: descriptive characters and biometric characters. Scanning electron photographs indicate a more pronounced dentition of the apical hair scales in the fur on the breast and back of *P. nathusii* than in that of *P. pipistrellus*. In *P. nathusii* the second upper incisor reaches beyond the caudal cusp of the first upper incisor in more than 72% of the skulls, while this feature occurs in only 8% of the skulls of *P. pipistrellus*. A gap between the second and third incisor is found in 84% of the lower jaws of *P. nathusii* and in only 21% of the lower jaws of *P. pipistrellus*. The BIOPAT computer program was used in analysing the biometric characters. A multivariate analysis including a principal component analysis of biometric characters was applied, for which purpose these characters were divided into four groups: skull, dental, external and X-ray characters. A total of 165 specimens, mainly from The Netherlands, have been examined. A discriminant analysis was used to select those characters by which these two species may best be separated. Important biometric skull characters are: condylobasal length, length of lower jaw and toothrow length ($I_1 - M_3$) and, to a lesser extent, occipital width. The most important dental character is the relative length of I_2 . However, for a better separation a discriminant function of eight dental characters is required. Essential external or X-ray characters are: length of fifth finger, third finger and forearm length. The X-ray characters show a high correlation with the external characters. The X-ray method, however, can be useful for identification of dry skins.

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CONTENTS

| | |
|--|----|
| 1. Introduction | 4 |
| 2. Material | 5 |
| 3. Methods | 6 |
| 3.1. Introduction | 6 |
| 3.2. Descriptive characters | 7 |
| 3.2.1. General remarks | 7 |
| 3.2.2. Dental characters | 8 |
| 3.3. Biometric characters | 11 |
| 3.3.1. General remarks | 11 |
| 3.3.2. Character discrimination and clustering | 18 |
| 4. Results | 23 |
| 4.1. Descriptive characters | 23 |
| 4.1.1. Hairs | 23 |
| 4.1.2. Teeth | 24 |
| 4.2. Biometric characters | 27 |
| 4.2.1. Skull characters | 27 |
| 4.2.2. Dental characters | 33 |
| 4.2.3. External characters | 36 |
| 4.2.4. X-ray characters | 42 |
| 5. Discussion | 46 |
| 5.1. Hairs | 51 |
| 5.2. Teeth | 51 |
| 5.3. Biometric characters | 53 |
| 5.4. Other characters | 58 |
| 6. Acknowledgements | 59 |
| 7. References | 59 |

1. INTRODUCTION

When in 1839 Keyserling & Blasius described *Vespertilio nathusii* as a species different from *V. pipistrellus* Schreber, 1774, the distinction was based on both external and dental characters. Since then, most authors have used only external characters to distinguish these species, while others made use of a combination of external and dental characters. In addition, in some cases skull measurements were taken. The importance of skull characters was stressed by Van de Kamp-Hilt & Van Bree (1964) and Punt et al. (1974, 1980). Stebbings (1970) and Van den Brink (1955, 1978) based the identification of the two species on the size, shape and position of the teeth in combination with the large overall size of *P. nathusii* as compared with *P. pipistrellus*. Topál (1958), Beaucournu (1963) and Claude (1977) mentioned the differences in the baculum (os penis) of both bats. Felten, Helfricht & Storch (1973) and Vierhaus (1982) examined the width of the distal epiphysis of the humerus. Hair structure was studied by Kolenati (1856) and Benedict (1957) and de-

scribed by Toschi & Lanza (1959). Méhely (1900) and Ognev (1928) also compared the ridges of the soft palate. The thumb length as compared with the wrist width, for the first time used by Miller (1912), was considered unreliable by Van de Kamp-Hilt & Van Bree (1964) and Stebbings (1968, 1970). The diagnostic value of the extension of the fur on the uropatagium as described by Keyserling & Blasius (1839), Dobson (1878) and Gaffrey (1961) was discussed by Van Eynhoven (1955). The presence of a light border at the margin of the wing membrane between the fifth digit and the foot of *P. nathusii* was first noticed by Trouessart (1884, 1910), and Rode (1947) stated: "Le long du bord inférieur du patagium entre le pied et l'extrémité du 5e doigt, on distingue une bande claire (moins blanche que chez *P. kuhli*) de 1 mm. environ de largeur". König (1959) and Bühler & König (1965), however, pointed out the limited value of this character. Saint Girons (1973) stated: "Nous avons vu que ce caractère n'est pas constant" and, according to Stebbings (1970), it cannot be considered diagnostic.

Keyserling & Blasius (1839) wrote: "Von den Schultern an zieht sich unter dem Ohr hin bis auf den Unterkiefer zu ein dunklerer, schwarzbrauner, verwischter Fleck". This supposed dark coloration of that part of the fur lived through time and has been used as a character by many authors. Description and figures of weak body parts such as size and shape of the ear and tragus appear in many identification works. Distinction of the two species on external characters only obviously is difficult and not reliable (Bels, 1938; Van Eynhoven, 1955; Van de Kamp-Hilt & Van Bree, 1964; Punt et al., 1974, 1980; Braaksma, 1970; Van Wijngaarden et al., 1971; Glas, 1975; Roer, 1976). Differences in behaviour were noted by Jäckel (1860).

With so many different and sometimes contradictory and unreliable characters, it is difficult to choose the best ones by which *P. nathusii* and *P. pipistrellus* can be separated. The purpose of this study was to find reliable morphological characters by using multivariate analysis. To this purpose the characters have been divided into four groups: skull, dental, external and X-ray characters. Clustering techniques were applied for each group and by means of discriminant analysis the characters were further selected and examined.

2. MATERIAL

In this study, 165 bats were examined, all from The Netherlands and Belgium. Thanks to the curators of the collections listed below, I had access to the specimens studied: RMNH - Rijksmuseum van Natuurlijke Historie,

Leiden; ZMA - Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam; KBIN - Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels. The RMNH collection at the time of this study consisted of 137 specimens; 64 of these were males, 50 females, 23 specimens could not be sexed; 108 were *P. pipistrellus*, 29 *P. nathusii*.

Most bats were preserved in alcohol 70%, a small number as dry skins. From all specimens the skull had been extracted and was stored dry. Some dry skins had been prepared with both wings stretched and therefore were difficult to measure. From the material of the ZMA, the 16 *P. nathusii* were examined only: nine males, three females and four unsexed specimens, all of these preserved in alcohol. In the collection of the KBIN, 12 skulls of *P. pipistrellus* were examined: three males, six females and three unsexed specimens.

3. METHODS

3.1. INTRODUCTION

For this study a number of criteria was selected from the literature, including both descriptive and biometric characters of which a precise definition could be given. Several other characters, not published before, have been considered as well, most of which are biometric and not subject to differences in interpretation. It is often very difficult to interpret characters mentioned in the literature; variations in descriptive characters are often difficult to define. In the present paper all measurements are illustrated so as to exclude any doubts that could still arise. Biometric characters are preferred here, because such characters are less arbitrary and the use of biometric data in taxonomy provides an easy way of studying intraspecific variation. Some measurements have been related to others in the form of ratios. One disadvantage of ratios is the loss of original information; in order to avoid this, in some cases the components of these ratios have been used individually as well. Another disadvantage that cannot be avoided is the possibility of a cumulative increase of errors in the ratio as a result of errors made in measuring each component. From nearly all specimens a number of descriptive and biometric characters was examined. In the case of paired structures, measurements were taken on one side of the specimen. Where both measurements were taken, the average value has been used in the data.

3.2. DESCRIPTIVE CHARACTERS

3.2.1. General remarks

The presence or absence of some descriptive dental characters is indicated by + and - (see tables 7, 8). If the rate of overlap of the lower incisors ($I_1 - I_2 - I_3$, see table 7) is distinctly present, this is indicated by +; if this character is not present, this condition is listed as -. The same applies to the presence or absence of a gap between I_2 and I_3 (see table 8).

In general, the descriptive characters used in this study are dependent of sex and age, because they are the direct result of growth. Therefore, juvenile specimens were not examined.

Pelage colour is highly variable within one species. For instance, within *P. pipistrellus* the colour of the back varies from middle dark reddish brown (Keyserling & Blasius, 1839; Jentink, 1879; Cremers, 1909) to brownish black

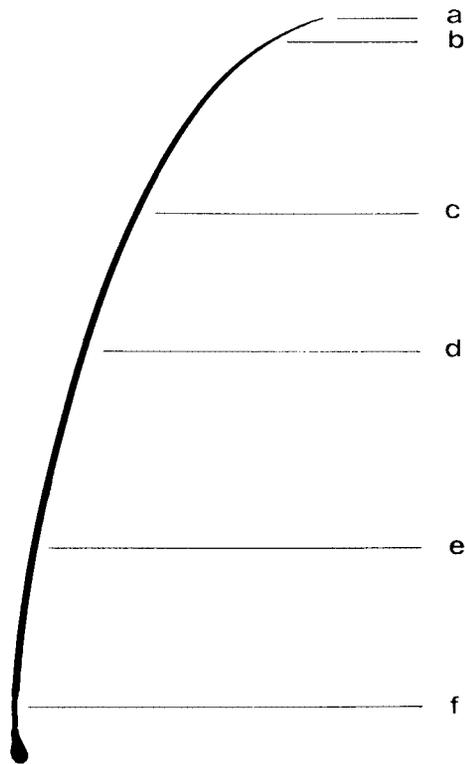


Fig. 1. Diagram of a hair of *Pipistrellus* sp.; a-f, indications of places photographed by scanning electron microscope.

(Schreber, 1774; Geoffroy Saint-Hilaire, 1809; Dobson, 1878); the same variation is found in *P. nathusii*. Individual hairs too, display a great variation in colour pattern. Generally, colour patterns in bats are not considered important taxonomic characters. Therefore, no remarks on hair and pelage colour are made in this study.

The other descriptive characters used in this study are based on the morphology of the hairs. Kolenati (1856) first described the morphology and length of the hairs of these and other bats. Great differences in hair structure exist between different species of bats, as is shown by Benedict (1957) and Toschi & Lanza (1959), who studied the apical-basal transitions in the shape of the hairs.

From the breast, head and back of several specimens of each species a hair was removed and prepared for a (Jeol 25) scanning electron microscope. A magnification of 2200 \times , in some cases up to 3300 \times , was used. Fig. 1 shows the areas of the hairs from which the photographs were taken: the top of the hair (a); sub-top (b); $\frac{1}{4}$ from top (c); the middle (d); $\frac{1}{4}$ from base (e); the base and hair follicle (f). Skull and dental characters were studied with a Wild M5 stereomicroscope, the teeth also with a Jeol 25 scanning electron microscope. The photographs of the teeth and skulls were made with a Canon AE 1 camera.

3.2.2. Dental characters

The dental characters have been divided into characters of the upper and of the lower jaw. The tooth formula in *Pipistrellus* is:

I $\frac{2-2}{3-3}$; C $\frac{1-1}{1-1}$; P $\frac{2-2}{2-2}$; M $\frac{3-3}{3-3}$, giving a total of 34 teeth. It should

be emphasized that dental characters generally are age-dependent and subject to wear. The anterior (first) incisor in the upper jaw (I^1) is bicuspid; the caudal cusp is lower than the rostral cusp (fig. 2). The length of the external (second) incisor (I_2) in comparison with the length of the caudal cusp of I^1 is used as a character by many authors, a.o. Ognev (1928), Toschi & Lanza (1959), Claude (1977) and Fairon (1978).

In the upper tooth row the anterior premolar (P^1) often is laterally visible. Fairon (1978) distinguished five classes in this character; in the present study the lateral visibility of P^1 is based on Fairon's classification and illustrated in fig. 3. The five classes used here are: I, fully visible; II, $\frac{3}{4}$ visible; III, half visible; IV, $\frac{1}{4}$ visible; V, invisible. This classification is not at all exact and transitional stages occur.

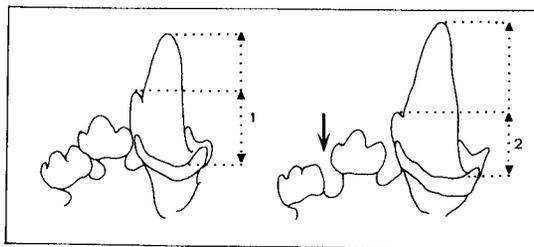
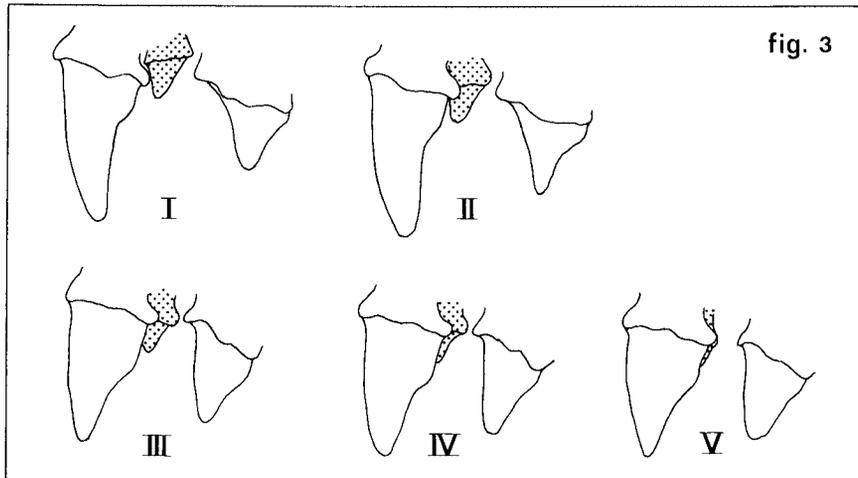


fig. 4

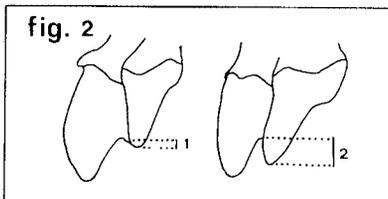


fig. 2

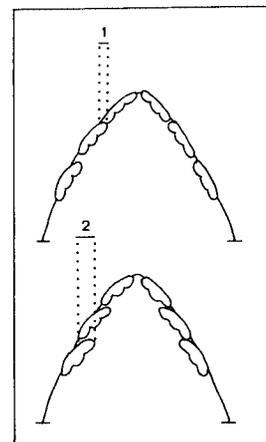


fig. 5

Fig. 2. Diagram showing the length of the second upper incisor as compared with the caudal cusp of the first incisor in *P. pipistrellus* (1) and *P. nathusii* (2). Fig. 3. Diagram showing the lateral visibility of the first upper premolar (P¹) of *Pipistrellus* sp. I, fully visible; II, $\frac{3}{4}$ visible; III, half visible; IV, $\frac{1}{4}$ visible; V, invisible. Fig. 4. Diagram showing the difference in height of the protocone of the lower canine with that of the canine itself for *P. pipistrellus* (1) and *P. nathusii* (2); the space between the second and third lower incisor as can be found in *P. nathusii*, is indicated by an arrow. Fig. 5. Diagram showing the rate of overlap of the lower incisors in *P. nathusii* (1) and *P. pipistrellus* (2).

The descriptive characters of the lower jaw are based on the lower incisors and the lower canine. A dorsal view of the lower incisors illustrates the way these teeth are arranged. This character, which shows the rate of overlap of the lower incisors, is rather difficult to define and could only be examined with the use of a stereomicroscope; it is illustrated in fig. 5. In accordance with Hanák & Gaisler (1976) and Fairon (1978), the character based on the presence or absence of a gap between the second and third lower incisor (I_2 and I_3) is also used in this study (see fig. 4).

On the lower canine the cingulum is well-developed, forming a distinct antero-basal cusp (protocone). The height of this cusp is used as a character by Miller (1912), Haltenorth (1955) and Gaffrey (1953, 1961) and is also used in this study (see fig. 4).

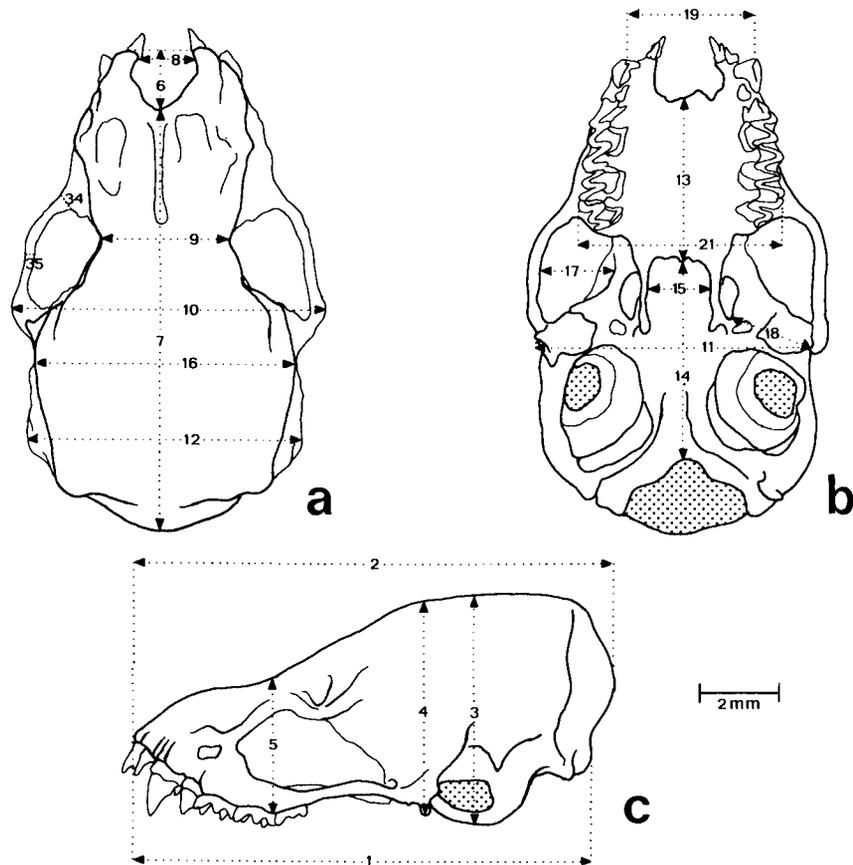


Fig. 6. Skull measurements of *Pipistrellus* sp. used in this study; for explanation, see table 1. a, dorsal view; b, ventral view; c, left lateral view.

3.3. BIOMETRIC CHARACTERS

3.3.1. General remarks

The greater part of this study deals with the analysis of biometric characters of *P. nathusii* and *P. pipistrellus*. These characters have been divided into internal and external characters. The internal characters include skull and tooth measurements and measurements of bones made visible by means of X-ray

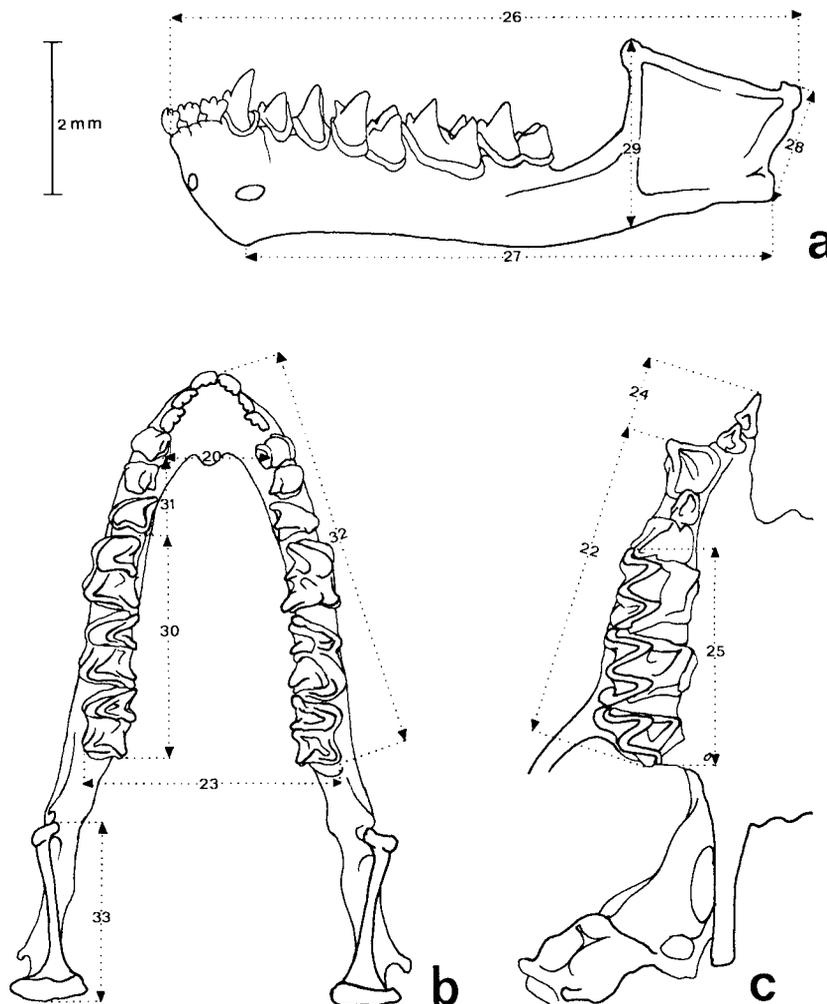


Fig. 7. Measurements of upper and lower jaw of *Pipistrellus* sp. used in this study; for explanation, see table 1. *a*, lateral view of left lower jaw; *b*, dorsal view of lower jaw; *c*, ventral view of right upper jaw.

-
1. Condylbasal length: distance from the anterior end of the premaxilla to the posterior end of the occipital condyle.
 2. Total skull length: distance from the anterior end of the premaxilla to the posterior end of the occipital.
 3. Skull height from the parietal to the most ventral point of the tympanic bulla.
 4. Skull height from the frontal part of the parietal to the post-glenoid process.
 5. Rostrum height: distance from the most ventral point of the maxilla to the top of the rostrum.
 6. Length of the nasal emargination: distance from the anterior end of the premaxilla to the nasal.
 7. Occipitonasal length: distance from the anterior end of the nasal to the posterior end of the occipital.
 8. Width of the nasal emargination: distance between the anterior ends of the premaxillae.
 9. Interorbital constriction: least width between the orbits.
 10. Zygomatic width: greatest width of the skull across the zygomatic arches.
 11. Distance between the outer margins of the glenoid fossae.
 12. Occipital width: greatest width of the skull across the occipital.
 13. Palatine length: distance from prosthion to nasion.
 14. Distance from the nasion to the edge of the foramen magnum.
 15. Width between the pterygoid processes.
 16. Parietal width: greatest width of the skull across the parietals.
 17. Orbital width: greatest width between the zygomatic arch and the skull.
 18. Distance between the mandibular foramen and the outer margin of the glenoid fossa.
 19. C - C distance, upper jaw.
 20. C - C distance, lower jaw.
 21. M³ - M³ distance.
 22. C - M³ distance.
 23. M₃ - M₃ distance.
 24. M³ - I¹ distance.
 25. M¹ - M³ distance.
 26. Dental-condyle length: length of the mandible from the anterior end of the dental to the posterior end of the condyle.
 27. Length of the lower jaw from the posterior end of the symphysis to the angular process.
 28. Distance between the condyle and the angular process of the lower jaw.
 29. Height of the mandible: distance from the ventral end to the top of the coronoid process.
 30. M₁ - M₃ distance.
 31. C - M₃ distance.
 32. I₁ - M₃ distance.
 33. Distance between the condyle and the coronoid process.
 34. Rostral width of the zygomatic arch.
 35. Median width of the zygomatic arch.
-

Table 1. Skull measurements illustrated in figs. 6 en 7.

photography of dry and alcohol specimens. All measurements are given in millimeters. Measurements of biological objects, however, give more information about the size than the shape of the object. To avoid this problem, in some cases ratios were used.

The skull measurements are illustrated in fig. 6; the numbers correspond

with the characters listed in table 1. Fig. 7 gives the measurements taken from the lower jaw and from the toothrow in the upper jaw. A total of 35 skull measurements have been taken with the aid of a Wild M5 stereomicroscope with an ocular micrometer. The measurements were taken with an accuracy of 0.05 mm. The use of a stereomicroscope and the three-dimensional properties of the material make it necessary to keep the skull always in the same position during measurement, otherwise differences of as much as 0.1-0.3 mm may arise. During this investigation the micrometer was always kept in the right ocular lens, the zero of the micrometer to the left, and the skull was positioned as in fig. 6.

The biometric tooth characters were analysed separately from the other skull measurements. Fig. 8 shows a photograph of the skull of *P. pipistrellus* in three different views. The teeth in the upper jaw are clearly visible. The skull of *P. nathusii* is shown on fig. 9. Fig. 10a is a photograph of the left upper and lower jaw of *P. pipistrellus* in labial view. The same view is shown in fig. 10b, illustrating the left upper and lower jaw of *P. nathusii*. A total of 45 biometric tooth characters have been examined. The tooth measurements from the upper jaw are shown in fig. 11. In order to express the visibility of the first premolar, three measurements were taken of the space between the canine and the second premolar as illustrated in fig. 11: characters 26, 27 and 28. Fig. 12 shows a diagram of the left lower jaw of *Pipistrellus* sp. in labial view. The numbers in this figure correspond with the characters in table 2. The height of the teeth has been measured in two ways: (a) including and (b) excluding the cingulum. The height of the teeth in the upper jaw is expressed as a percentage of the canine height. In the lower jaw only the height of the third incisor has been measured, because the first and second incisors are about equal in height. From the molars, the height of both outer buccal crown areas has been measured, i.e. the anterior and posterior border of each molar as illustrated in fig. 12.

Fig. 13 shows a simplified diagram illustrating the external measurements taken from the dorsal and ventral parts of the body. The numbers in this figure correspond with those given in table 3. Fig. 14 shows how thumb, foot and forearm have been measured. A total of 27 external measurements were taken. The measurements from alcohol specimens were taken with a pair of calipers to the nearest 0.05 mm.

Fig. 15 shows an X-ray photograph of *Pipistrellus* sp. The numbers refer to the measurements given in table 4. The X-ray method was used in dry skins, since from these no external measurements of the essential parts could be taken without damaging the specimens. The X-ray photographs were taken with the aid of a Philips PX-1000 (focus 1 m; 30 kV; 16 mA; t = 25 sec.).

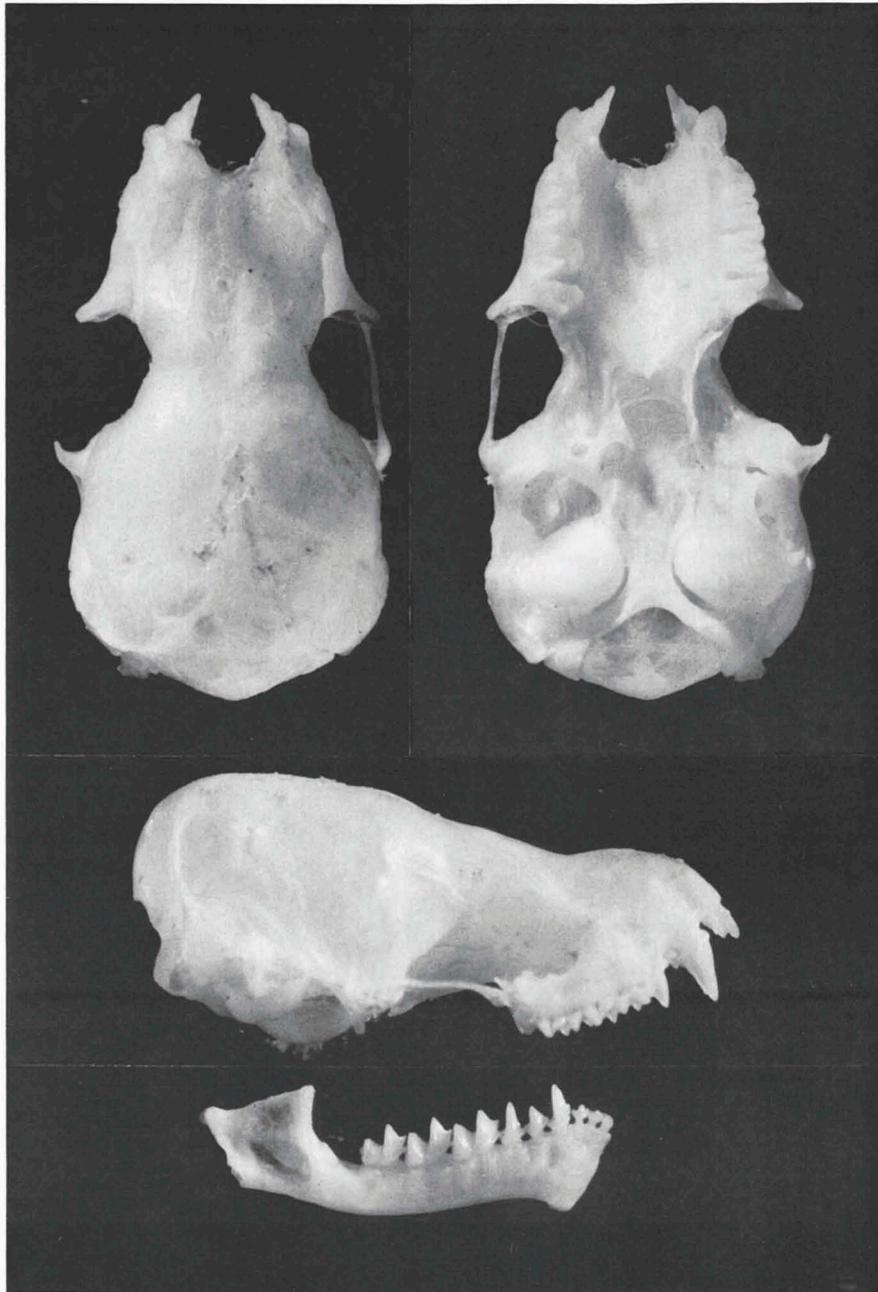


Fig. 8. Photograph of the skull of *P. pipistrellus* (RMNH 28794, ♀); a, dorsal view; b, ventral view; c, right lateral view (ca. 10×).

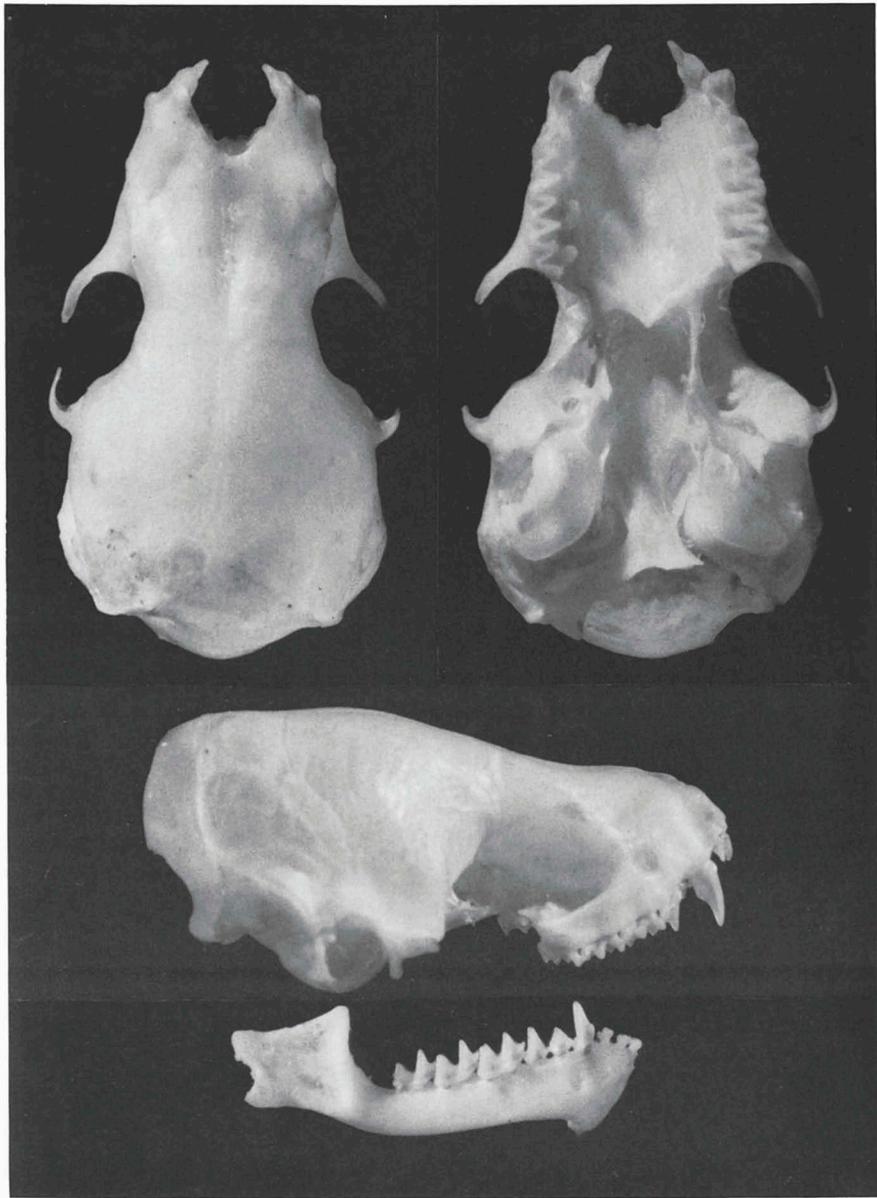


Fig. 9. Photograph of the skull of *P. nathusii* (RMNH 30734, ♂); a, dorsal view; b, ventral view, c, right lateral view (ca. 10×).

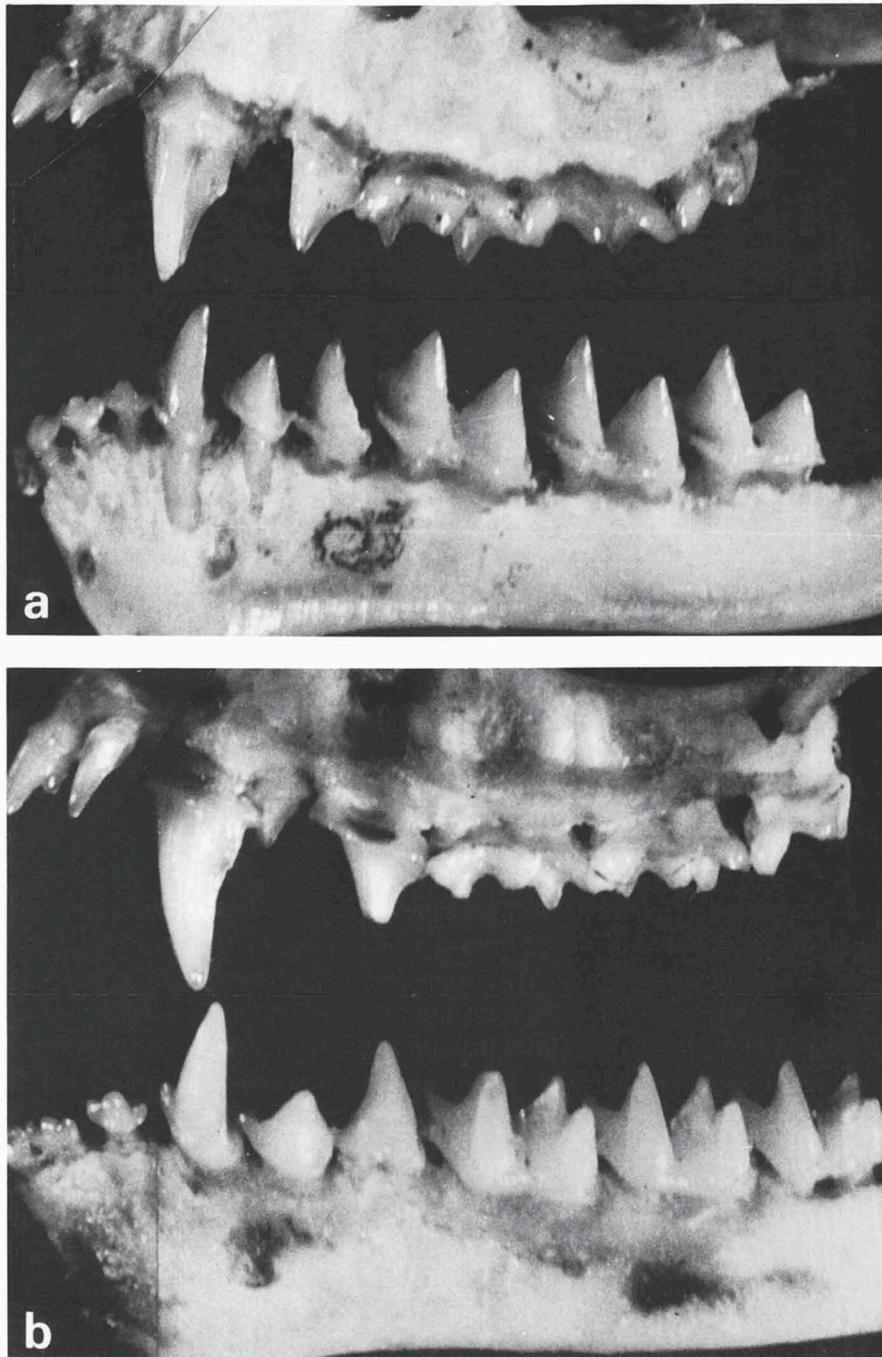


Fig. 10. Photograph of the left upper and lower jaw of *P. pipistrellus* (a) and *P. nathusii* (b) in lateral view. (ca. 40 \times).

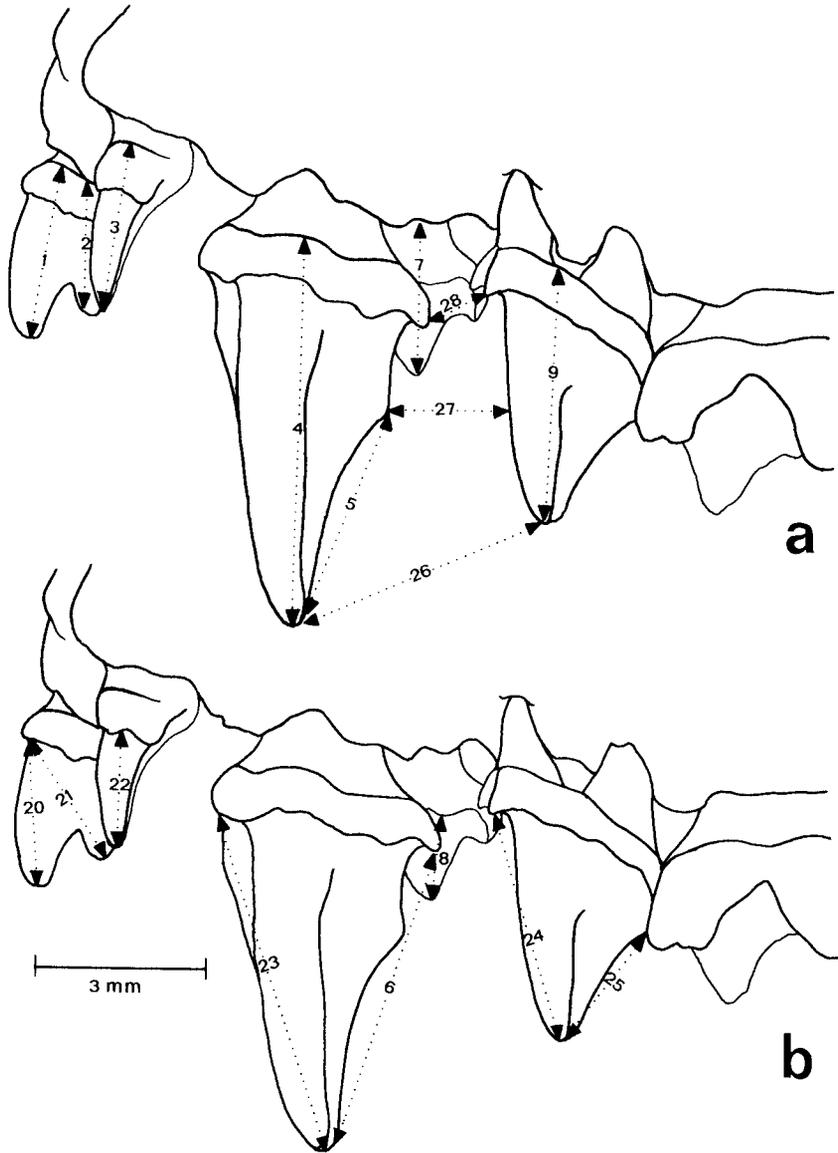


Fig. 11. Tooth measurements in the left upper jaw (in labial view) of *Pipistrellus* sp. used in this study; for explanation, see table 2.

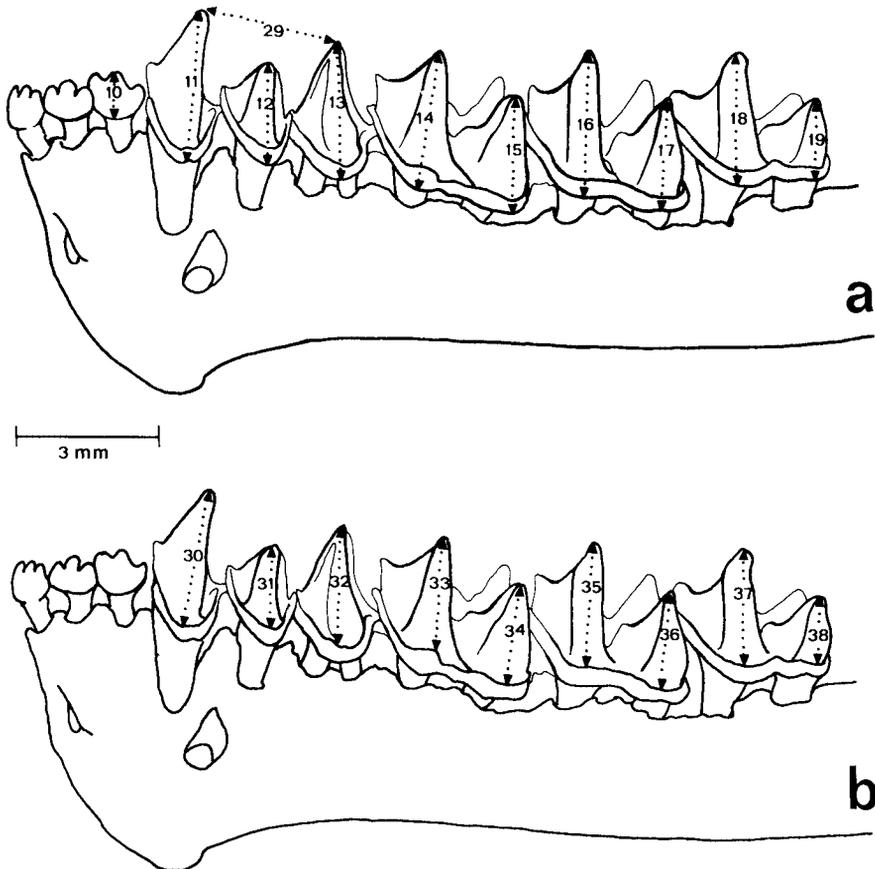


Fig. 12. Tooth measurements in the left lower jaw (in labial view) of *Pipistrellus* sp. used in this study; for explanation, see table 2.

According to Van der Straeten (1978), who compared the length of various body parts in small rodents preserved in alcohol with that of freshly killed animals, any differences between these may be neglected. However, it is known that animals which are preserved dry are subject to some shrinkage. The traditional way of bat taxidermy, by which bats were dried with wings expanded, enabled the use of the X-ray method.

3.3.2. Character discrimination and clustering

One of the aids in processing large numbers of measurements is numerical

-
1. Length of the rostral cusp of I¹ including the cingulum.
 2. Length of the caudal cusp of I¹ including the cingulum.
 3. Length of I² including the cingulum.
 4. Length of the upper canine including the cingulum.
 5. Length of the upper canine from the tip to the caudal cusp.
 6. Length of the upper canine from the tip to the posterior basicuspid of the cingulum.
 7. Length of P¹ including the cingulum.
 8. Length of P¹ excluding the cingulum.
 9. Length of P² including the cingulum.
 10. Length of I₃.
 11. Length of the lower canine including the cingulum.
 12. Length of P₁ including the cingulum.
 13. Length of P₂ including the cingulum.
 14. Length of the rostral cusp of M₁ including the cingulum.
 15. Length of the caudal cusp of M₁ including the cingulum.
 16. Length of the rostral cusp of M₂ including the cingulum.
 17. Length of the caudal cusp of M₂ including the cingulum.
 18. Length of the rostral cusp of M₃ including the cingulum.
 19. Length of the caudal cusp of M₃ including the cingulum.
 20. Length of the rostral cusp of I¹ excluding the cingulum.
 21. Length of the caudal cusp of I¹ excluding the cingulum.
 22. Length of I² excluding the cingulum.
 23. Length of the upper canine from the tip to the rostral basicuspid of the cingulum.
 24. Length of P² from the tip to the rostral basicuspid of the cingulum.
 25. Length of P² from the tip to the caudal basicuspid of the cingulum.
 26. Distance between the tip of the upper canine and the tip of P².
 27. Distance between the caudal cusp of the upper canine and P².
 28. Distance between the caudal basicuspid of the cingulum of the upper canine to the rostral basicuspid of the cingulum of P².
 29. Distance between the tip of the lower canine and the tip of P₂.
 30. Length of the lower canine excluding the cingulum.
 31. Length of P₁ excluding the cingulum.
 32. Length of P₂ excluding the cingulum.
 33. Length of the rostral cusp of M₁ excluding the cingulum.
 34. Length of the caudal cusp of M₁ excluding the cingulum.
 35. Length of the rostral cusp of M₂ excluding the cingulum.
 36. Length of the caudal cusp of M₂ excluding the cingulum.
 37. Length of the rostral cusp of M₃ excluding the cingulum.
 38. Length of the caudal cusp of M₃ excluding the cingulum.
 39. Ratio of the length of the rostral and caudal cusps of I¹ including the cingula (characters 1/2).
 40. Ratio of the length of I² and I¹ including the cingula (characters 3/1).
 41. Ratio of the length of I² and I¹ excluding the cingula (characters 22/20).
 42. Ratio of the length of I¹ and the upper canine including the cingula (characters 1/4).
 43. Ratio of the length of the rostral and caudal cusps of I¹ excluding the cingula (characters 20/21).
 44. Ratio of the length of the lower canine and P₂ including the cingula (characters 11/13).
 45. Ratio of the length of the lower canine C₁ and P₁ including the cingula (characters 11/12).
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Table 2. Dental measurements illustrated in figs. 11 and 12.

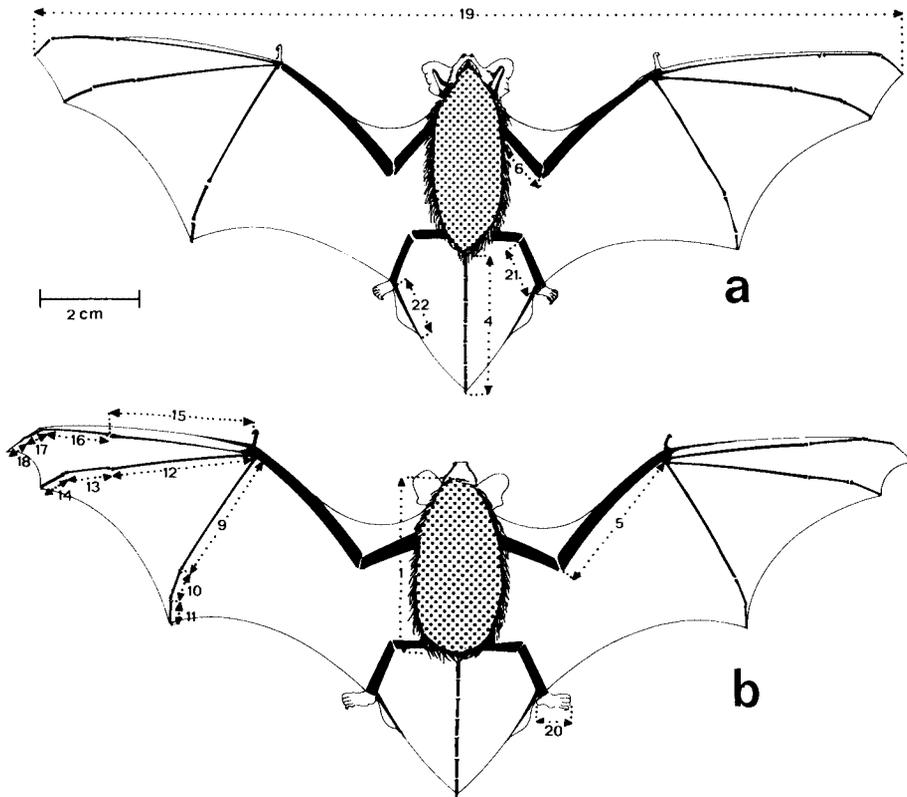


Fig. 13. External measurements of *Pipistrellus* sp. used in this study; for explanation, see table 3. a, ventral view; b, dorsal view.

taxonomy. The purpose of numerical taxonomy is to cluster the objects in "natural" taxa. The overall similarity between objects as expressed by genotypic and phenotypic characters forms the basis for taxonomic classification. Agglomerative methods in numerical taxonomy may be divided into monothetic and polythetic methods. One of the principals of monothetic clustering is the assumption that all representatives of a certain taxon share one (or more) character(s). The data of the specimens examined were also subjected to polythetic clustering, which does not start from this pre-supposition. A data set was used in which no distinct clusters were assumed (non-supervised learning). A system based on this principle may more closely approach the natural

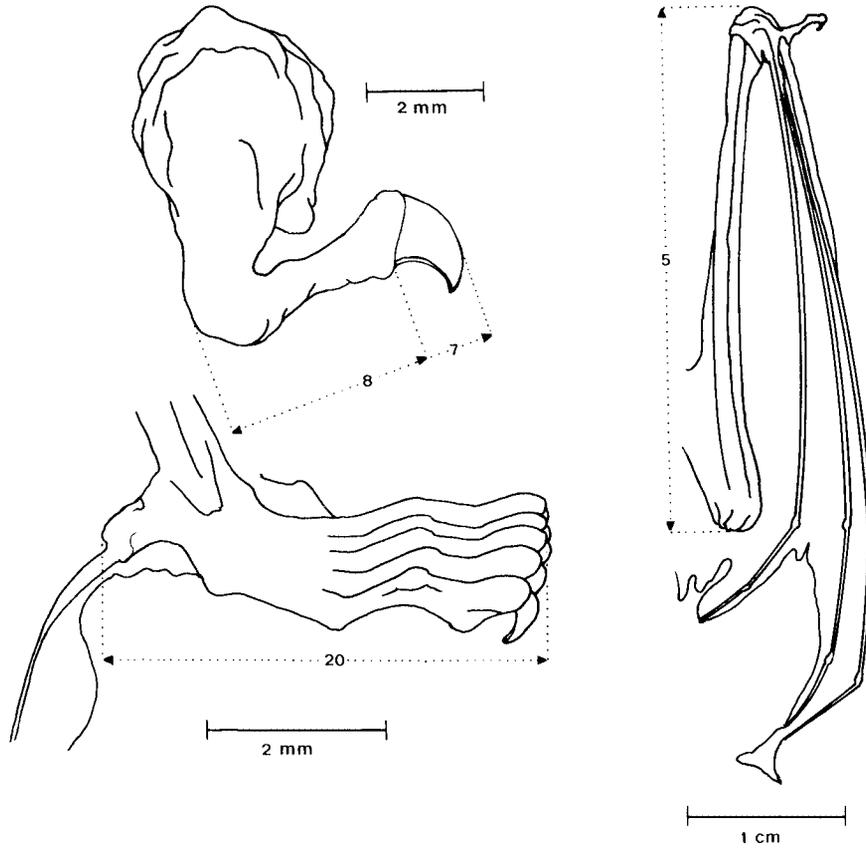


Fig. 14. External measurements used in this study; for explanation, see table 3.

relationship of specimens than a monothetic system, because it allows for the natural pluriformity in a gene pool as expressed by the often wide range of variation of the phenotype. By pattern analyses a relationship between objects may be shown at different levels. The method used here implies that those specimens which show the closest resemblance in a number of characters appear in the same cluster. To this purpose, the BIOPAT computer program (Hogeweg & Hesper, 1973) has been applied to the sets of both internal and external characters. The variables have been standardized in all multivariate analysis.

1. Body length: distance from shoulder to tail root.
2. Head length: distance from the nostrils to the back of the head (not illustrated).
3. Head and Body length: distance from the nostrils to the tail root (not illustrated).
4. Tail length: distance from the anus to the tip of the tail.
5. Forearm length.
6. Upper arm length: distance from shoulder to elbow.
7. Thumb length including the claw.
8. Thumb length excluding the claw.
9. Length of the metacarpal of the fifth finger (including the wrist).
10. Length of the first phalanx of the fifth finger.
11. Length of the second and third phalanges of the fifth finger.
12. Length of the metacarpal of the fourth finger (including the wrist).
13. Length of the first phalanx of the fourth finger.
14. Length of the second and third phalanges of the fourth finger.
15. Length of the metacarpal of the third finger (including the wrist).
16. Length of the first phalanx of the third finger.
17. Length of the second phalanx of the third finger.
18. Length of the third phalanx of the third finger.
19. Wingspan: distance between the outermost points of the third fingers with expanded wings.
20. Hindfoot length (excluding the claws).
21. Length of the tibia: distance from heel to knee.
22. Length of the calcar bone: distance from the heel to the outermost point of the calcar bone (not illustrated).
23. Total length: distance from nostril to tail tip (not illustrated).
24. Length of the fifth finger (characters 9 + 10 + 11).
25. Length of fourth finger (characters 12 + 13 + 14).
26. Length of third finger (characters 15 + 16 + 17 + 18).
27. Ratio of total length and wingspan (characters 23/19).

Table 3. External measurements from alcohol specimens, illustrated in figs. 13 and 14.

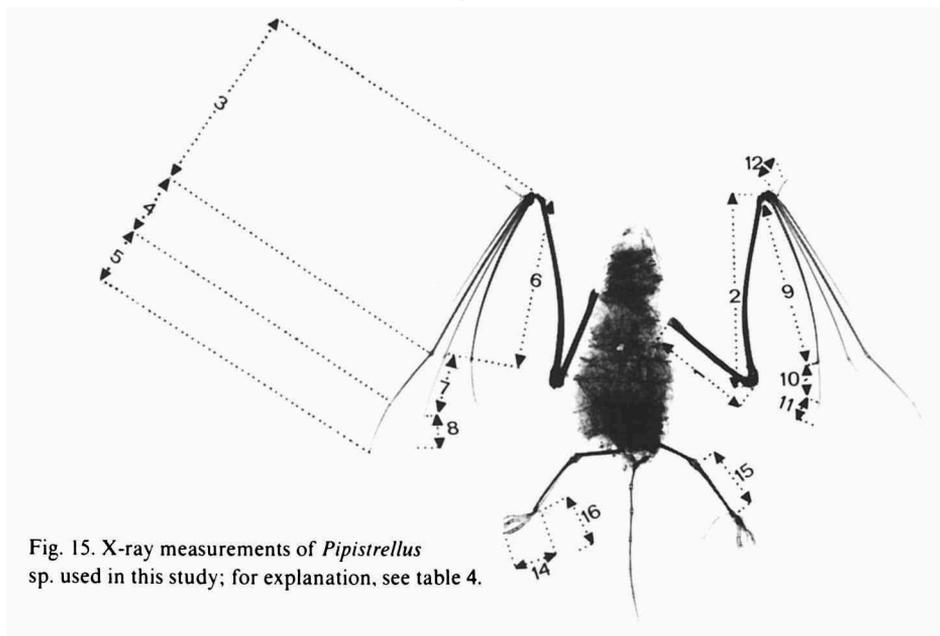


Fig. 15. X-ray measurements of *Pipistrellus* sp. used in this study; for explanation, see table 4.

-
1. Length of the upper arm.
 2. Length of the forearm.
 3. Length of the metacarpal of the third finger (including the wrist).
 4. Length of the first phalanx of the third finger.
 5. Length of the second and third phalanges of the third finger.
 6. Length of the metacarpal of the fourth finger (including the wrist).
 7. Length of the first phalanx of the fourth finger.
 8. Length of the second and third phalanges of the fourth finger.
 9. Length of the metacarpal of the fifth finger (including the wrist).
 10. Length of the first phalanx of the fifth finger.
 11. Length of the second and third phalanges of the fifth finger.
 12. Length of the thumb including the claw.
 13. Length of the thumb excluding the claw (not illustrated).
 14. Length of the hindfoot (excluding the claws).
 15. Length of the tibia.
 16. Length of the calcar bone.
 17. Length of the third finger (characters 3 + 4 + 5).
 18. Length of the fourth finger (characters 6 + 7 + 8).
 19. Length of the fifth finger (characters 9 + 10 + 11).

Note: The total length of the tail as well as the length of the femur have not been measured, since in most cases the attachment of these bones was not clearly visible on the photographs.

Table 4. X-ray measurements from dry specimens, illustrated in fig. 15.

4. RESULTS

4.1. DESCRIPTIVE CHARACTERS

4.1.1. Hairs

The pelage or fur of most mammals consists of different kinds of hairs and may be divided into underfur and overfur. In most bats there is little or no distinction between these two kinds of hairs. In fact, the pelage of most bats is rather uniform in length and overall density. In the genus *Pipistrellus* the difference between overhair and underhair is very small.

According to Benedict (1957), the length of the overhair in the genus *Pipistrellus* varies from 7-11 mm, the length of the underhair from 7-9 mm. The place of the maximum diameter in the overhair filaments (25.5μ) is situated at the distal end, in the underhair (17.0μ) in the central part of the hairs. The hairs in both *Pipistrellus* species are of the unequal hastate type with denticulate scales. Fig. 16 (above) shows a scanning electron photograph of an overhair from the back of *P. pipistrellus*. The top of the hair (a) is very thin and the hair scales show no apical dentition. The sub-top part (b) of this hair is much wider; here the V-shape of the individual hair scales is obvious, the

apex showing a clear dentition. In the $\frac{1}{4}$ from top region (c) the scales are more crowded than in the other parts. The scales in this part are also V-shaped with little dentition on the scales. The middle part of the hair (d) shows little dentition on the scales. In this region the hair is more slender and the scales are less crowded, while the V-shape of the scales is more pronounced. The base of the hair (e) shows the asymmetry of the individual hair scales. The scales are irregularly V-shaped with one side reaching higher than the other. The shaft of the hair near the follicle (f) does not show any dentition and the scales lie very tight.

Fig. 16 shows the same areas of a hair from the back of *P. nathusii*. The top of the hair (a) does not differ from that of *P. pipistrellus*. The scales of the sub-top (b), however, show an appreciable difference in that the dentition is more pronounced than in *P. pipistrellus*. The $\frac{1}{4}$ from top region of the hair (c) corresponds with that in *P. pipistrellus* and shows the characteristic V-shaped scales with dented apex. The middle part of the hair (d) shows the same condition as in *P. pipistrellus* with only slightly more dented apices. The basal part of the hair (d-f) shows no marked differences in structure as compared to *P. pipistrellus*. The hairs from the breast and head of the same specimens are not markedly different from those from the back. In some cases the scales in the sub-top and middle parts of the hairs in *P. nathusii* and *P. pipistrellus* show V-shaped scales with ribbed apex only, probably a result of wear, so there may be a marked difference in hair structure between worn and unworn hairs. The more pronounced dentition of the hair scales of *P. nathusii* is expressed in the Dutch and German names: in Dutch this species has been called "ruige dwergvleermuis", in German "Rauhhaufledermaus", indicating the roughness of the fur. I was unable, however, to feel any difference in this respect between living or dead specimens of both species.

4.1.2. Teeth

In both species the first and second incisors in the upper jaw are clearly visible in labial view (figs. 8, 9). The length of the second upper incisor is compared with the length of the caudal cusp of the first incisor as drawn in fig. 11. In *P. pipistrellus* I^2 has been described as being of about the same length as the caudal cusp of I^1 ; in *P. nathusii* the length of I^2 is said to be greater than that of the caudal cusp of I^1 . The difference in the relative length of I^2 is visible on the photographs of the upper jaw of *P. pipistrellus* and *P. nathusii* (fig. 10). This character has been examined in 133 specimens: 33 *P. nathusii* and 100 *P. pipistrellus*. The results are listed in table 5. In 72.7% of the skulls of *P.*

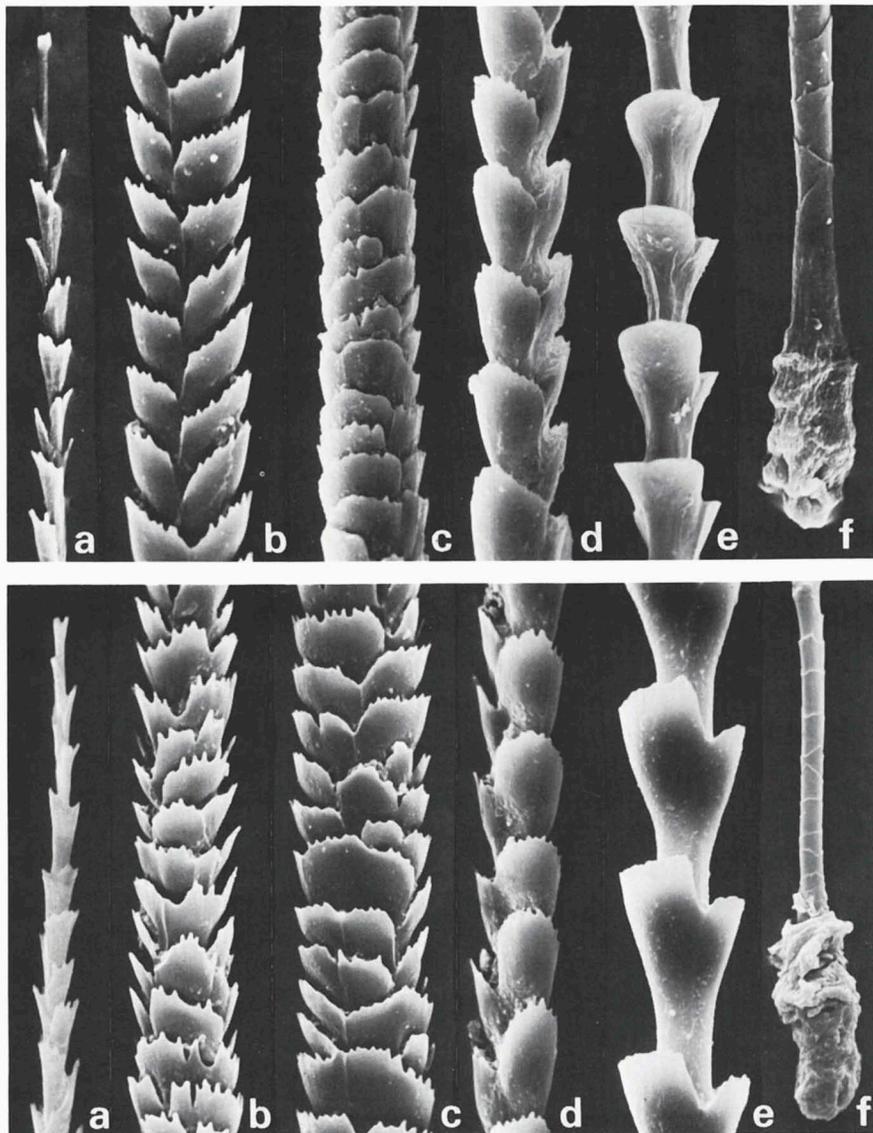


Fig. 16. Scanning electron photograph of a hair from the back of *P. pipistrellus* (above) and *P. nathusii* (below). a-f, according to fig. 1 (ca. 2100 \times). The dentition of the scales of *P. nathusii* is more distinct than that of *P. pipistrellus*.

nathusii I² reaches beyond the caudal cusp of I¹; in 27.3% I² is as long as or shorter than the caudal cusp of I¹. As for *P. pipistrellus*, in 8.0% of the skulls I² reaches beyond I¹; in 92.0% I² is as long as or shorter than I¹.

| species | total number | $I^2 > I^1$ | | $I^2 = I^1$ | | $I^2 < I^1$ | |
|------------------------|-----------------|-------------|------|-------------|------|-------------|------|
| | | number | % | number | % | number | % |
| <i>P. nathusii</i> | 33 | 24 | 72.7 | 4 | 12.1 | 5 | 15.2 |
| <i>P. pipistrellus</i> | 100 | 8 | 8.0 | 16 | 16.0 | 76 | 76.0 |

Table 5. Length of I^2 compared with the length of the caudal cusp of I^1 .

| species | total number | CLASS I | | CLASS II | | CLASS III | | CLASS IV | | CLASS V | |
|------------------------|-----------------|---------|------|----------|------|-----------|------|----------|------|---------|-----|
| | | number | % | number | % | number | % | number | % | number | % |
| <i>P. nathusii</i> | 33 | 12 | 36.4 | 12 | 36.4 | 7 | 21.2 | 1 | 3.0 | 1 | 3.0 |
| <i>P. pipistrellus</i> | 103 | 8 | 7.8 | 26 | 25.2 | 36 | 35.0 | 23 | 22.3 | 10 | 9.7 |

Table 6. Visibility of the upper premolar (P^1) in labial view.

For both species, the visibility of P^1 as expressed by the classes indicated in fig. 3 is given in table 6. In *P. pipistrellus* P^1 has been described as very small and partly hidden by the canine in lateral view (Stebbing, 1970). Miller (1912: 204) noted: "large upper premolar separated from canine by distinct space in which the small premolar is clearly visible from outer side". Rode (1947) wrote: "La première prémolaire est petite et rejetée sur la face interne du maxillaire". In *P. nathusii* P^1 is said to be better developed than in *P. pipistrellus*, placed clearly within the toothrow (Keyserling & Blasius, 1839; Miller, 1912; Saint Girons, 1973) and thus well visible in labial view; this lateral visibility has been noticed by many other authors. According to Rosevear (1965), this character depends partly upon the size of P^1 , partly upon the length of the gap between the canine and the posterior premolar (P^2). In 72.8% of our material of *P. nathusii* P^1 is fully or $\frac{3}{4}$ visible in labial view; in 27.2% of the cases P^1 is half or fully hidden behind the canine. As for *P. pipistrellus*, in 33.0% P^1 is fully or $\frac{3}{4}$ visible, while in 67.0% P^1 is half or fully hidden from labial view.

Miller (1912) found that the lower incisors in *P. pipistrellus* are more crowded than in *P. nathusii*. In *P. pipistrellus* the three lower incisors overlap, in *P. nathusii* they are linked but do not overlap according to Rode (1947) and Baumann (1949). Table 7 gives the situation in the 147 specimens examined. In 59.6% of the skulls of *P. pipistrellus* this overlap occurs; in 40.4% the overlap is absent or indistinct. The lower incisors overlap in 21.1% of the skulls of *P. nathusii*; in 78.9% of the specimens this feature is absent or not clear.

The presence or absence of a gap between the second and third lower incisor (I_2 en I_3) has been examined in 133 specimens (table 8). In 83.8% of the skulls of *P. nathusii* a gap between these incisors is clearly visible in labial view. Of *P. pipistrellus*, 20.8% has this gap; in 79.2% of the skulls this feature is absent or not clear.

| species | total number | OVERLAP + | | OVERLAP - | | OVERLAP intermediate | |
|------------------------|--------------|-----------|------|-----------|------|----------------------|------|
| | | number | % | number | % | number | % |
| <i>P. nathusii</i> | 38 | 8 | 21.1 | 22 | 57.8 | 8 | 21.1 |
| <i>P. pipistrellus</i> | 109 | 65 | 59.6 | 25 | 22.9 | 19 | 17.5 |

Table 7. Rate of overlap in the lower incisors ($I_1 - I_2 - I_3$).

| species | total number | GAP + | | GAP - | |
|------------------------|--------------|--------|------|--------|------|
| | | number | % | number | % |
| <i>P. nathusii</i> | 37 | 31 | 83.8 | 6 | 16.2 |
| <i>P. pipistrellus</i> | 96 | 20 | 20.8 | 76 | 79.2 |

Table 8. Presence and/or absence of a gap between I_2 and I_3 .

According to Miller (1912), in *P. pipistrellus* the apex of the cingulum on the lower canine rises to the level of the middle of the posterior border of the canine; in *P. nathusii* the apex of this anterior protocone does not rise above the level of the basal third of the canine. Haltenorth (1955) states: "Innerer Kronrandabsatz der unteren Eckzähne nur ein Drittel eckzahnhoch" in *P. nathusii*; "nur ½ eckzahnhoch" in *P. pipistrellus*. Fig. 4 illustrates the height of the protocone of the lower canine in comparison with the total height of the canine. Table 9 shows the situation in the 122 specimens examined for this character. In *P. nathusii* 53.3% of the specimens have a protocone ½ as high as or lower than the canine; in 46.7% this height is more than ½ the canine height. In *P. pipistrellus* 30.4% of the specimens show a protocone of at most ½ the canine height, in 69.6% of the cases this protocone is higher.

| species | total number | PC > 1/3 C | | PC ≤ 1/3 C | |
|------------------------|--------------|------------|------|------------|------|
| | | number | % | number | % |
| <i>P. nathusii</i> | 30 | 14 | 46.7 | 16 | 53.3 |
| <i>P. pipistrellus</i> | 92 | 64 | 69.6 | 28 | 30.4 |

Table 9. Height of the protocone of the lower canine (PC) compared with the height of the canine itself (C).

4.2. BIOMETRIC CHARACTERS

4.2.1. Skull characters

The data input consisted of 35 skull measurements from 126 suitable adult specimens (see table 1). The specimens have been divided into the following

groups: (1) *P. nathusii* (17 males, 11 females and 8 of unknown sex); (2) *P. pipistrellus* (45 males, 26 females and 19 of unknown sex). A principal component analysis was carried out of these two groups, giving a two-dimensional projection of the objects according to their co-ordinates. It should be noted that in the principal component analysis the variables were first standardized; the mean square distance has been used as the similarity coefficient. The principal component analysis gives a high Eigen value for the first principal component axis (PCA): 68.67, while the second and third PCA's have Eigen values of 2.99 and 2.42, respectively. The first PCA thus accounts for 69% of the total variance. The Eigen values express the distribution of the specimens over each axis and result in a cluster which is elongated in the direction of the first axis, a consequence of the great variation in these characters, so that separation is possible by using the first three PCA's only. Using these three PCA's, about 74% of the information stored is available for clustering. The result of the principal component analysis is shown in fig. 17a, b. Here the first PCA is plotted on the X-axis against the second PCA on the Y-axis in fig. 17a, against the third PCA in fig. 17b. The distinction between the two species clusters is very clear.

According to a similarity matrix based on the mean square distances of the objects in the multi-dimensional space, a dendrogram was made using Ward's averaging method; this is given in fig. 18. This two-dimensional representation of the dendrogram shows the phenetic relationship of each specimen. There is a high dissimilarity between the two clusters (*P. nathusii* and *P. pipistrellus*); within each cluster there is a high similarity as indicated on the X-axis. Only five specimens of *P. nathusii* are placed in the wrong cluster.

A linear discriminant analysis was carried out with all 35 characters. The three best discriminating characters (according to table 1) were: 1, 26 and 32: the condylobasal length, the length of the lower jaw (from dental to condyle) and the length of the toothrow in the lower jaw. With these three characters an estimated probability of relocation shows that 86% of the *P. nathusii* specimens belong to the *P. nathusii* cluster, whereas 14% are placed within the *P. pipistrellus* cluster. As for *P. pipistrellus*, 98% of the specimens are placed within the *P. pipistrellus* cluster, 2% in the *P. nathusii* cluster.

The discriminant analysis resulted in the following discriminant functions:

$$X_{sk.} = 0.54 X_1 + 1.48 X_{26} + 2.64 X_{32} - 2.93 \text{ for } P. nathusii;$$

$$X_{sk.} = -0.22X_1 - 0.59 X_{26} - 1.06 X_{32} - 0.47 \text{ for } P. pipistrellus.$$

For the *P. nathusii* cluster the mean value of the discriminant function is: $\bar{X}_{sk.} = 368.52$, with $346.90 < X_{sk.} < 382.79$ and $S = 8.45$; for the *P. pipistrel-*

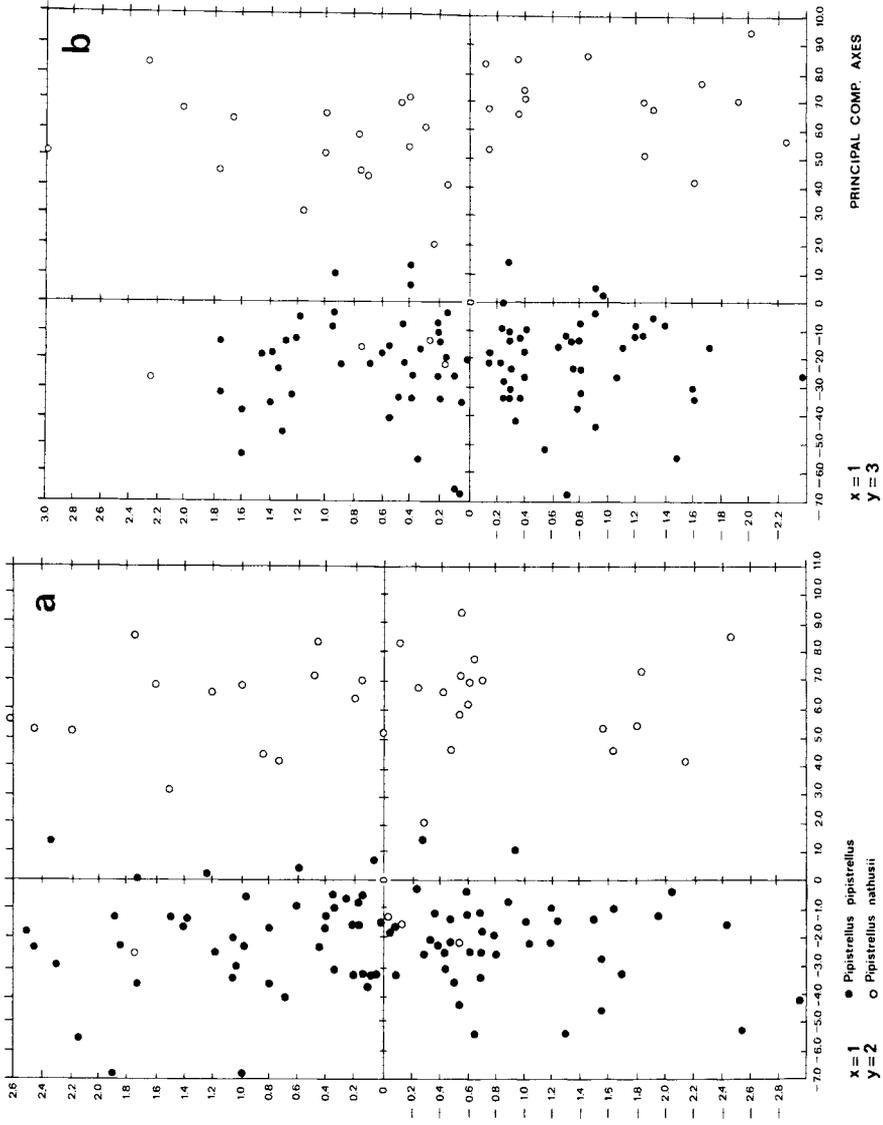


Fig. 17. Plot resulting from a principal component analysis of normalized biometric skull data. *a*, first and second principal axes; *b*, first and third principal axes.

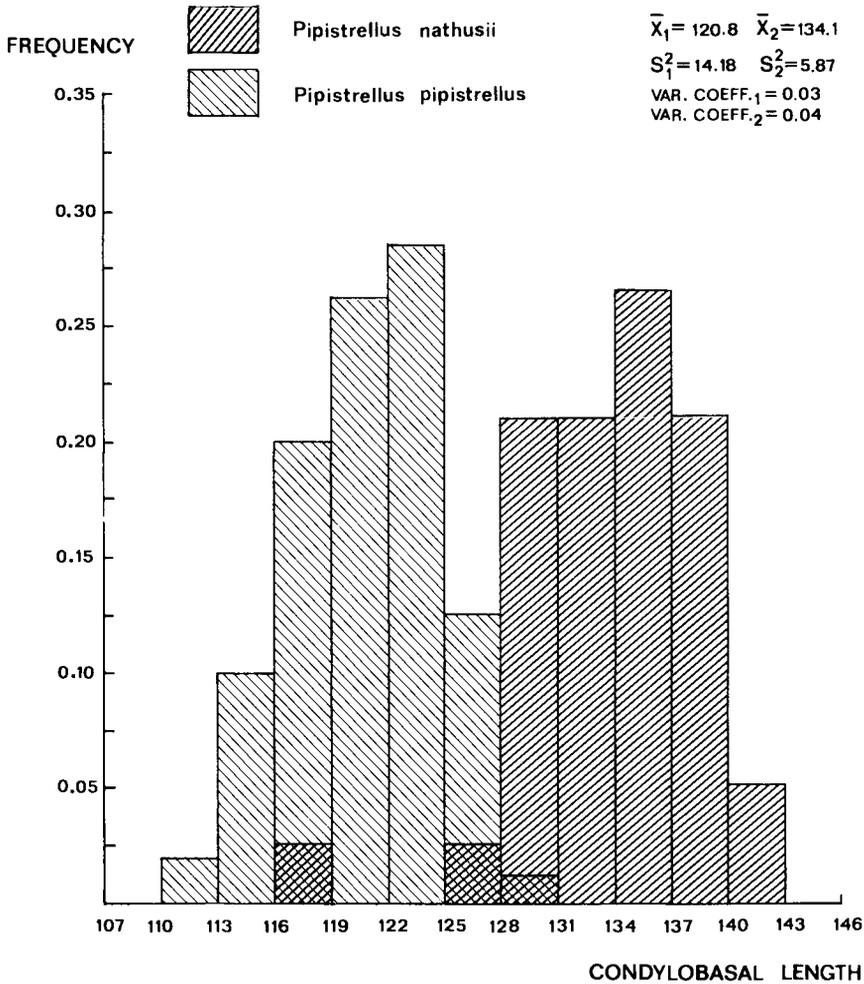


Fig. 19. Frequency distribution of the condylobasal length in both *Pipistrellus* species.

lus cluster this value is: $\bar{X}_{sk} = -134.69$, with $-142.01 < X_{sk} < -122.87$ and $S = 19.14$.

Fig. 19 is a frequency diagram based on the distribution of character 1 (condylobasal length) over the objects. Some overlap appears, but the tops of the graph are well separated. Separation occurs at a condylobasal length of about 12.8 mm. As for character 26 (dental-condyle length), little overlap exists (fig 20); separation occurs at a value of about 9.1 mm. The occipital width does not show sufficient differentiation for separation of both species; this character, however, has been used by many authors. Fig. 21 shows the distribution of the objects in a diagram plotting character 1 (condylobasal

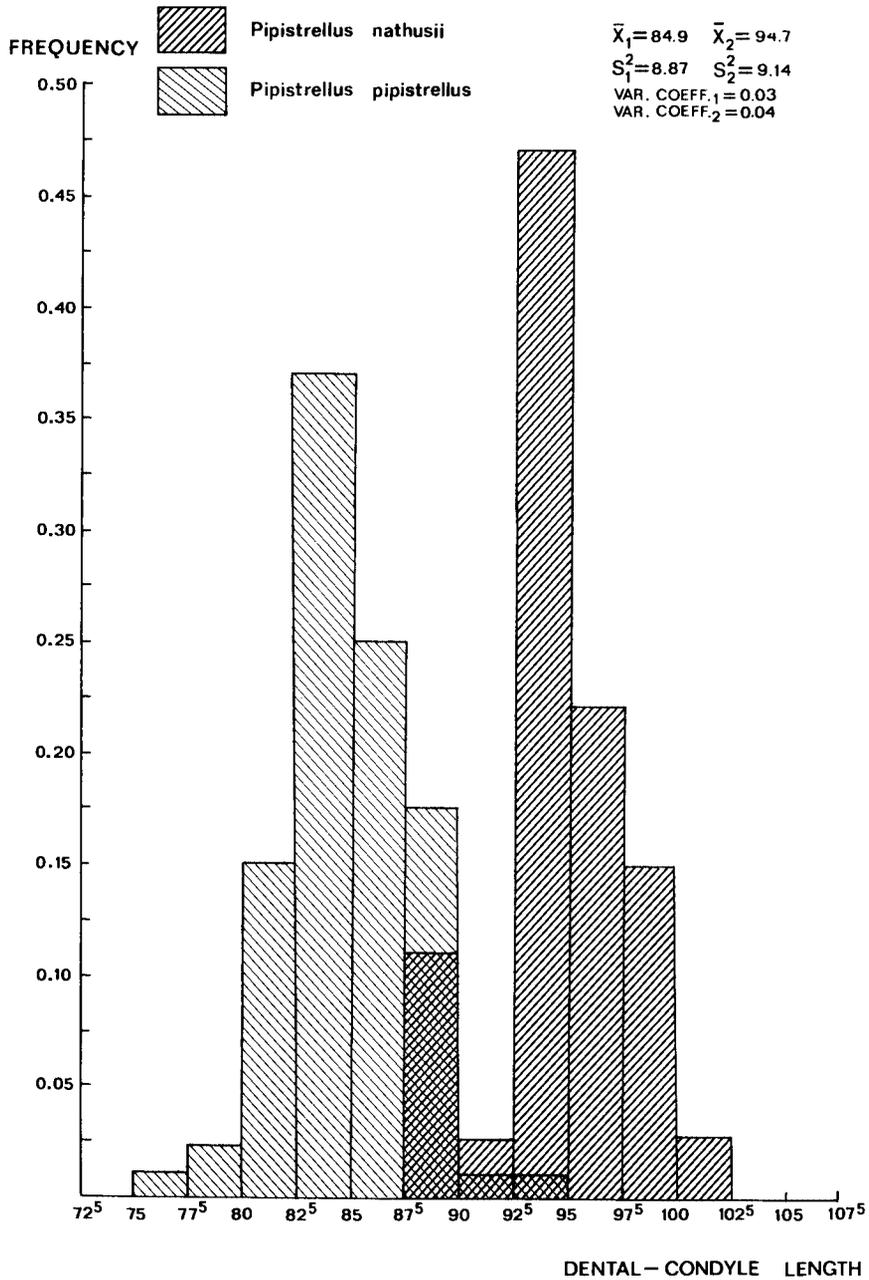


Fig. 20. Frequency distribution of the dental-condyle length in the lower jaw of both *Pipistrellus* species.

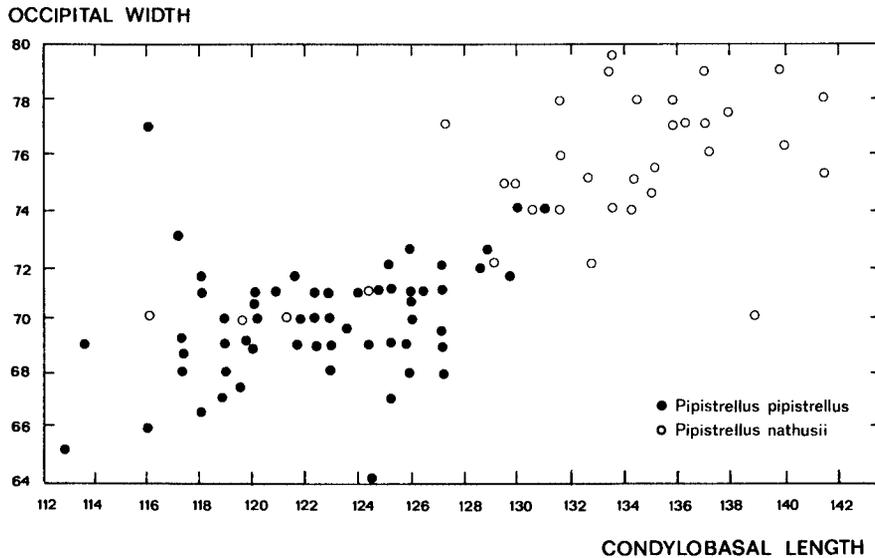


Fig. 21. Plot showing the relationship between the condylobasal length and the occipital width of the skull in both *Pipistrellus* species.

length) against character 12 (occipital width). The two species are now widely spread within two distinct clusters. Other frequently used skull characters are not considered diagnostic and cannot be used for identification of *P. pipistrellus* and *P. nathusii*.

4.2.2. Dental characters

In addition to skull characters, the program was applied to 45 dental characters of 124 specimens (see table 2). The data matrix consisted of: (1) *P. nathusii* (16 males, 18 females); (2) *P. pipistrellus* (45 males, 45 females). The principal component analysis of this data matrix resulted in an Eigen value of 43.05 for the first principal component axis, 14.19 for the second and 6.31 for the third PCA. The first PCA thus accounts for 43% of the total variance. The three principal component axes explain 66% of the variation. The result of the principal component analysis is shown in the plots illustrating the distribution of the specimens along the three principal component axes (fig. 22a, b). In fig 22a the first PCA is plotted on the X-axis against the second PCA on the Y-axis; in fig. 22b the first PCA is plotted against the third PCA. The objects are separated into two distinct clusters; only few specimens are placed in the wrong cluster.

A two-dimensional dendrogram using Ward's averaging (fig. 23) shows a

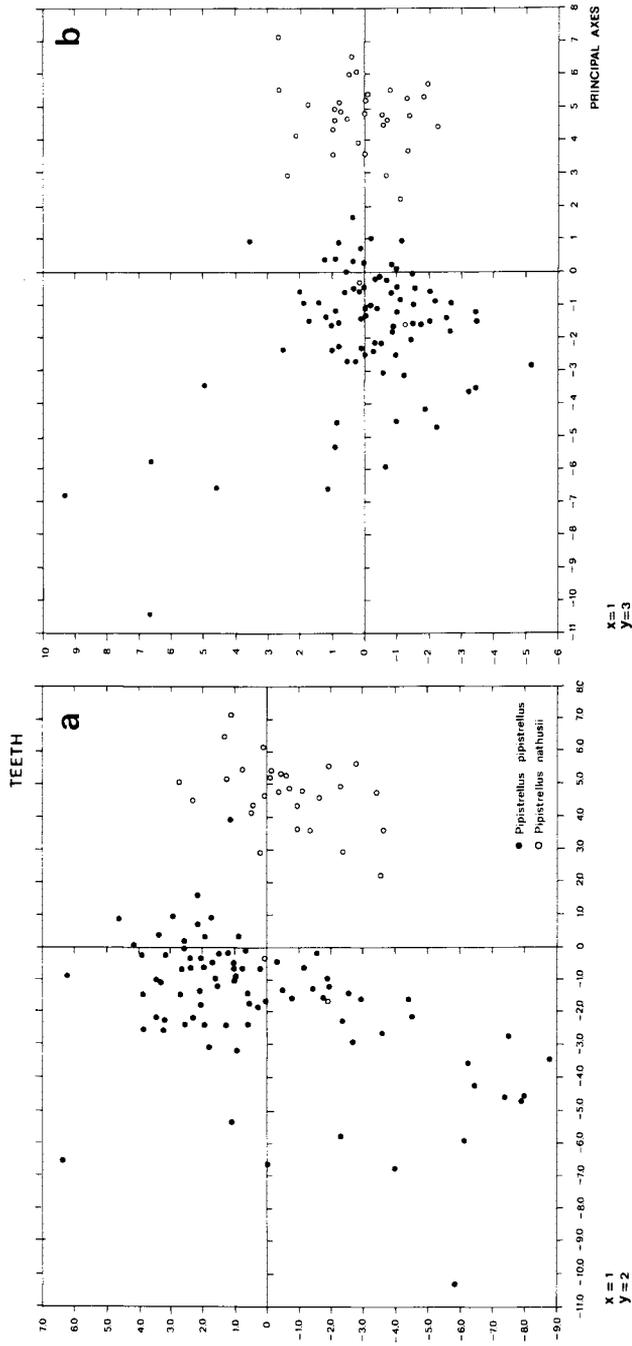


Fig. 22. Plot resulting from a principal component analysis of normalized biometric tooth data; a, first and second principal axes; b, first and third principal axes.

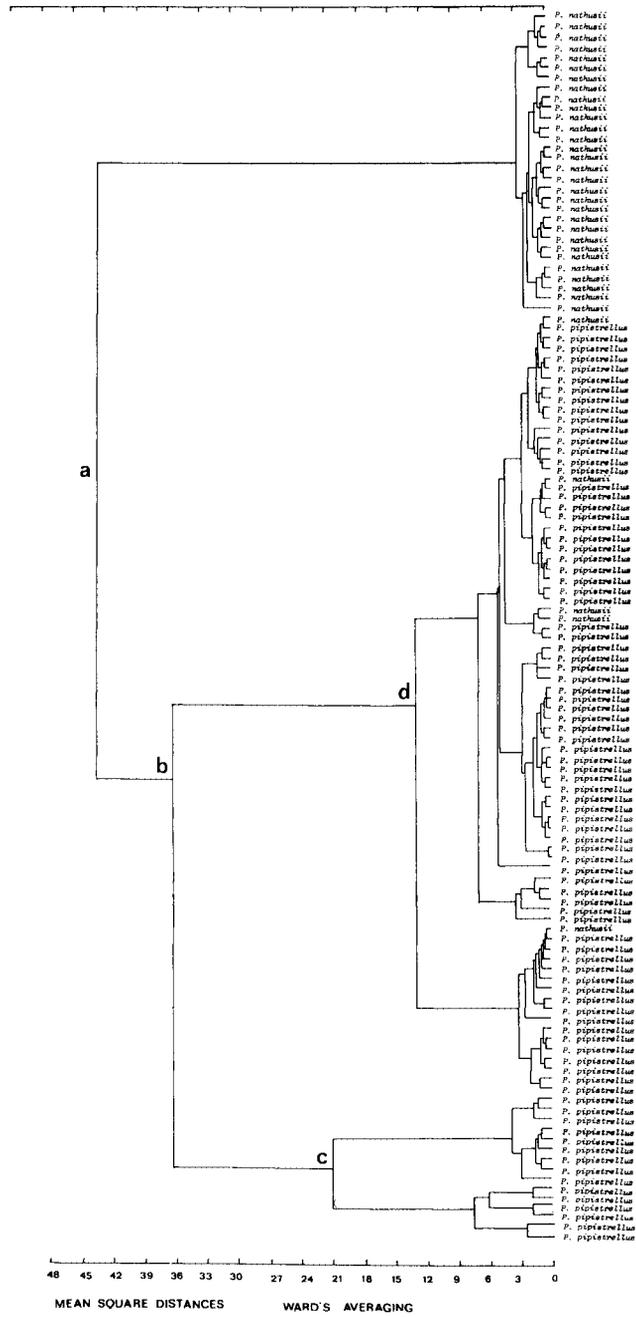


Fig. 23. Dendrogram resulting from Ward's averaging in Q-mode from standardized biometric tooth data.

separation of the objects into two well-marked clusters. In the *P. pipistrellus* group the mutual relationship among the objects is quite obvious. Two major subdivisions appear within this species group, probably caused by differences in tooth length due to dental wear. The division is indicated (b) in fig. 23. At this level with a mean square distance of 36, the 15 specimens belonging to group c had very worn teeth. Only five *P. nathusii* specimens are placed in the wrong cluster. Not all of these five specimens, however, are the same as are placed in the wrong cluster in fig 18, using skull characters.

With the 45 dental characters a discriminant analysis was carried out. After selection eight characters remained. With these characters an estimated probability of relocation shows that 88% of the *P. nathusii* specimens belong to the *P. nathusii* cluster; 97% of the *P. pipistrellus* specimens belong to the *P. pipistrellus* cluster. The characters are: canine length (character 4); I¹ length excluding the cingulum (character 20); I² length excluding the cingulum (character 22); C - P² distance (character 26); C - P₂ distance (character 29); length of the rostral cusp of M₂ excluding the cingulum (character 35); the ratio I²/I¹ (character 40) and the ratio I¹/C including the cingulum (character 42).

These eight characters resulted in the following discriminant functions:

$$X_{\text{dent.}} = 1.43 X_4 - 2.18 X_{20} + 7.74 X_{22} + 1.15 X_{26} + 1.37 X_{29} - 1.36 X_{35} + 1.60 X_{40} - 3.85 X_{42} - 4.44 \text{ for } P. \textit{nathusii};$$

$$X_{\text{dent.}} = -0.55 X_4 + 0.83 X_{20} - 2.96 X_{22} - 0.44 X_{26} - 0.52 X_{29} + 0.52 X_{35} - 0.61 X_{40} + 1.47 X_{42} - 0.65 \text{ for } P. \textit{pipistrellus}.$$

For the *P. nathusii* cluster the mean value of the discriminant function is: $\bar{X}_{\text{dent.}} = 279.26$, with $214.94 < X_{\text{dent.}} < 318.82$ and $S = 23.62$; for the *P. pipistrellus* cluster this value is; $\bar{X}_{\text{dent.}} = -77.49$, with $-111.17 < X < -51.81$ and $S = 10.43$.

The best single character of these is character 22 (length of I²). This length as compared with that of the canine gives a frequency diagram with considerable overlap (fig. 24); therefore, this character alone cannot be used to separate both species. Fig. 25 shows the relationship between the length of the two upper incisors. When only lower jaws are available (as for instance can be found in owl pellets), cluster separation is possible by plotting the M₃ - canine distance against the M₃ - I₁ distance as shown in fig. 26. Little overlap occurs in this case.

4.2.3. External characters

From 55 specimens, 27 external measurements were taken (see table 3) and

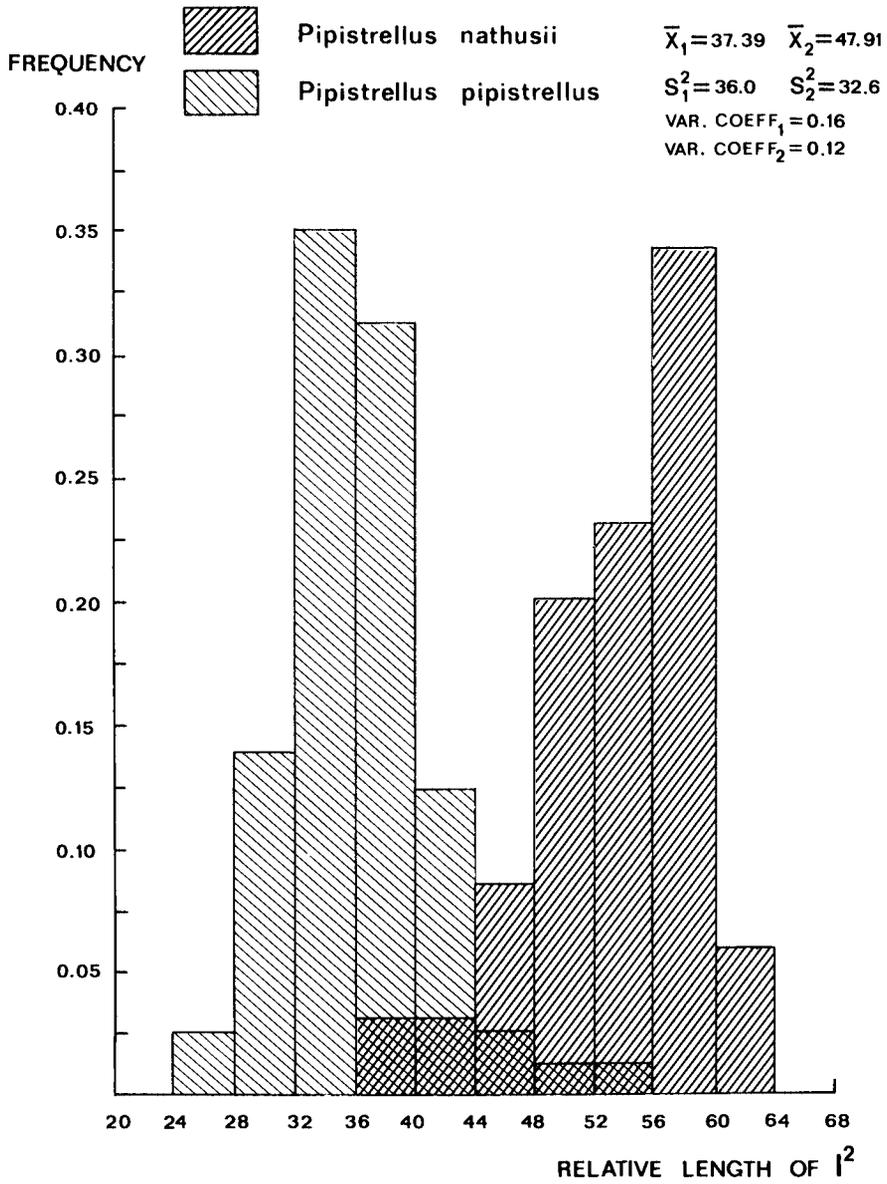


Fig. 24. Frequency distribution of the length of the second upper incisor in both *Pipistrellus* species.

used as computer input data, independently of skull, dental and X-ray characters. The specimens consisted of: (1) *P. nathusii* (9 males, 7 females); (2) *P.*

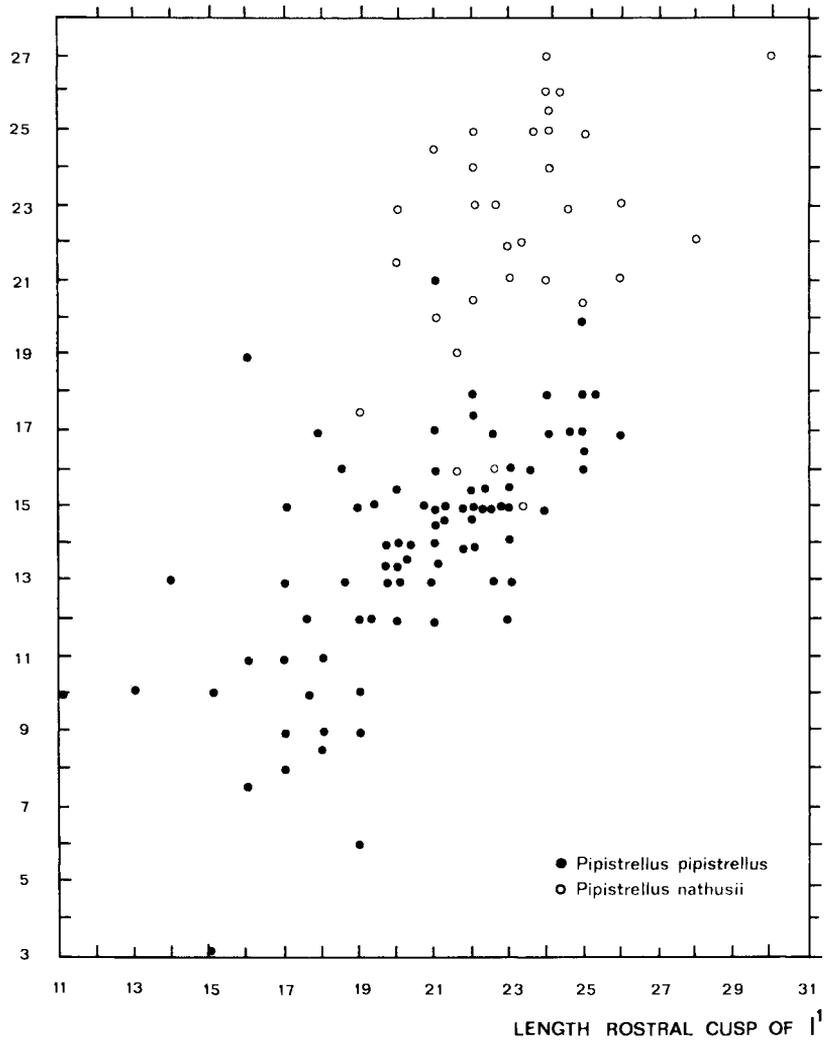
I^2 LENGTH

Fig. 25. Plot showing the relationship between the length of the rostral cusp of the first and the length of the second upper incisor in both *Pipistrellus* species.

pipistrellus (22 males, 17 females). All bats were preserved in alcohol. A principal component analysis was carried out of these two groups. This resulted in an Eigen value of 67.43 for the first principal component axis, 6.04 for the second and 4.99 for the third PCA. These three principal components thus

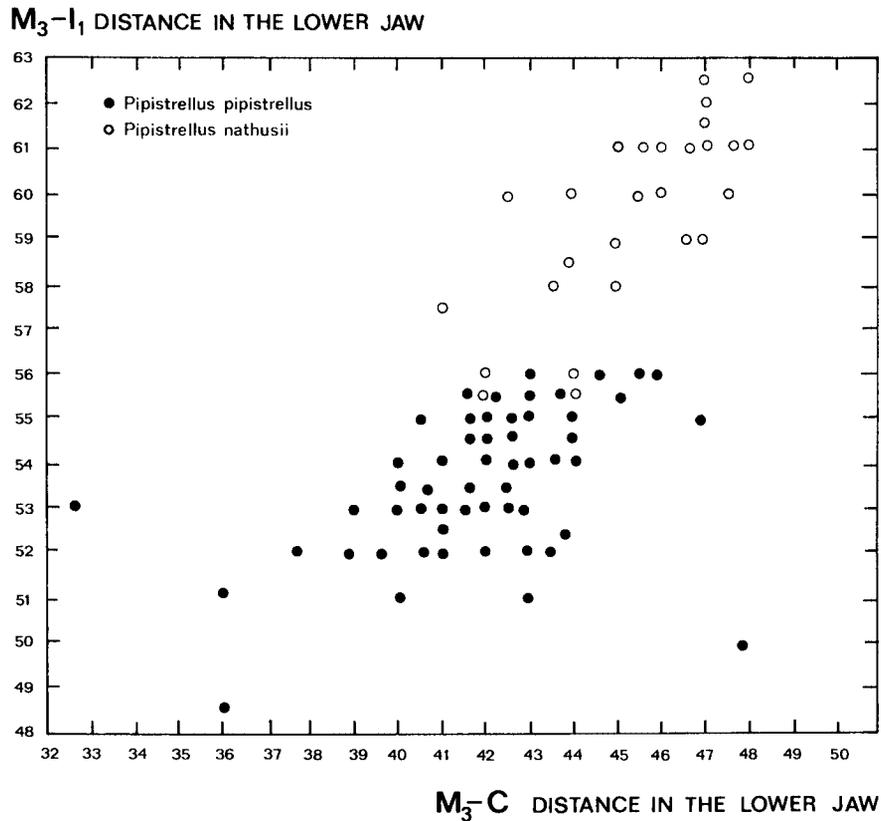


Fig. 26. Plot showing the relationship of the M_3-C distance and the M_3-I_1 distance in both *Pipistrellus* species.

account for 78% of the total variance. A two-dimensional projection of the objects according to their co-ordinates on the three principal component axes is presented in fig. 27a, b. In fig. 27a the first PCA is plotted against the second PCA, in fig. 27b against the third PCA. A clear separation into two clusters appears.

A dendrogram using Ward's averaging method is given in fig. 28. Again, a distinct primary separation into two species groups is visible; only three specimens of *P. nathusii* are placed within the *P. pipistrellus* cluster.

A discriminant analysis was carried out to select the best discriminating characters. Characters 24 (fifth finger length) and 26 (third finger length) have the highest value for each cluster and, to a lesser extent, characters 5 (forearm length) and 23 (total length). The highest estimated probability of relocation is obtained by using character 24. This character is easily measured and there-

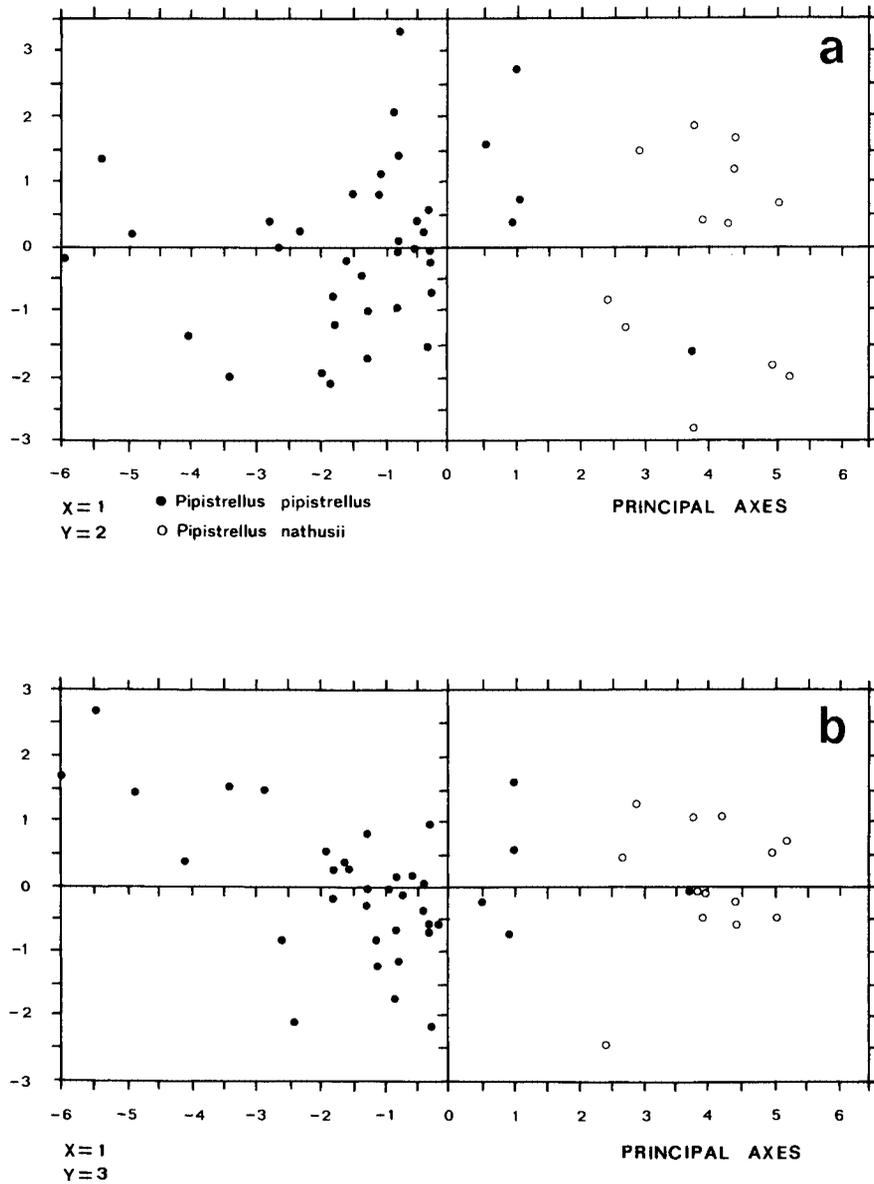


Fig. 27. Plot resulting from a principal component analysis of normalized biometric external data; a, first and second principal axes; b, first and third principal axes.

fore very reliable; the same applies to character 26 and, to a lesser extent, to character 5.

EXTERNAL MEASUREMENTS

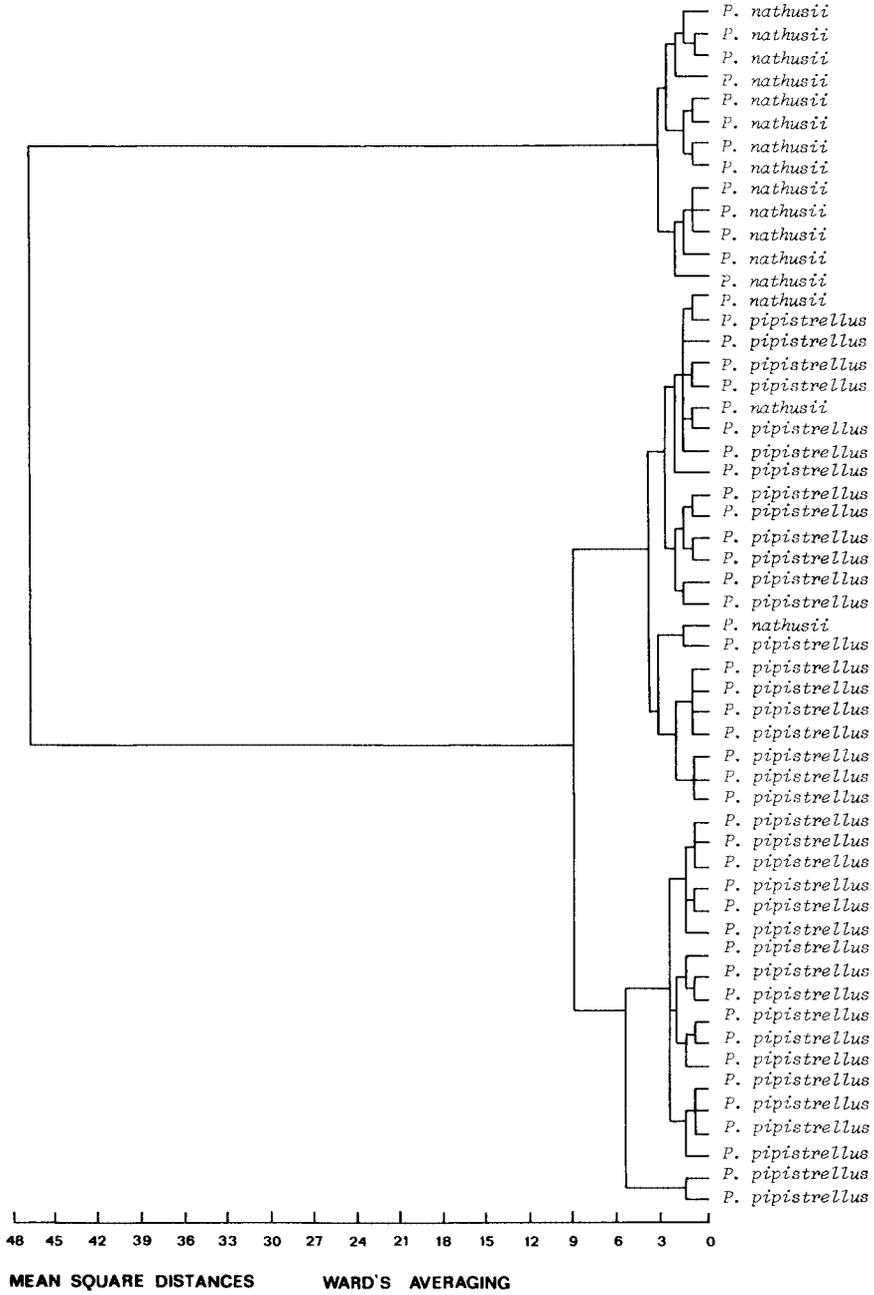


Fig. 28. Dendrogram resulting from Ward's averaging in Q-mode from standardized biometric external data.

The discriminant analysis resulted in the following discriminant functions:

$$\begin{aligned} X_{\text{ext.}} &= 3.26 X_{24} - 1.53 X_{26} + 0.66 X_5 - 2.40 \text{ for } P. \textit{nathusii}; \\ X_{\text{ext.}} &= -1.34 X_{24} + 0.63 X_{26} - 0.27 X_5 - 0.40 \text{ for } P. \textit{pipistrellus}. \end{aligned}$$

The mean value of the *P. nathusii* cluster is: $\bar{X}_{\text{ext.}} = -162.41$, with $-174.71 < X < -134.15$ and $S = 4.69$. For the *P. pipistrellus* cluster the mean value is: $\bar{X}_{\text{ext.}} = -27.53$, with $-30.86 < X_{\text{ext.}} < -21.48$ and $S = 2.11$. The mean value of the *P. nathusii* cluster using these three characters is based on 94 specimens. In addition to the museum specimens, data of 78 living animals measured over the last three years are included, resulting in the above-mentioned discriminant values. The mean value of the *P. pipistrellus* cluster is based on data of 78 specimens; in this case the values of 39 living specimens collected over the last three years have been added.

When using only character 24 (fifth finger length), the discriminant function results in an estimated probability of relocation for 88% of the *P. nathusii* and 100% of the *P. pipistrellus* specimens. When using only character 5 (forearm length), the probability of relocation is 81% of the *P. nathusii* and 87% of the *P. pipistrellus* specimens. The discriminant function depending on character 26 (third finger length) is of the same order as those for the two characters mentioned before. For this character the probability of relocation for *P. nathusii* is 81%, for *P. pipistrellus* 95%.

The frequency diagrams of these three characters are given in figs. 29-31. In all three figures overlap is small. Separation of the two clusters occurs at a fifth finger length of about 42 mm. Separation into two clusters is obvious when plotting forearm length against fifth finger length as shown in fig. 32. The same applies when plotting forearm length against third finger length (fig. 33); again, the centres of the two clusters are wide apart. An even more reliable separation is obtained when plotting fifth finger length against third finger length as shown in fig. 34.

4.2.4. X-ray characters

The BIOPAT program has been applied to 19 X-ray characters of 49 specimens (see table 4). These specimens consisted of: (1) *P. nathusii* (6 males, 6 females); (2) *P. pipistrellus* (22 males, 15 females). The measurements were taken from dry skins. The principal component analysis of the two groups shows the same tendency as the analysis of external characters. The Eigen values of 32.34 for the first axis, 3.90 for the second and 2.28 for the third axis again result in an elongated cluster with its greatest variation around the first principal component axis. In these three PCA's a total variance of 83% is stored.

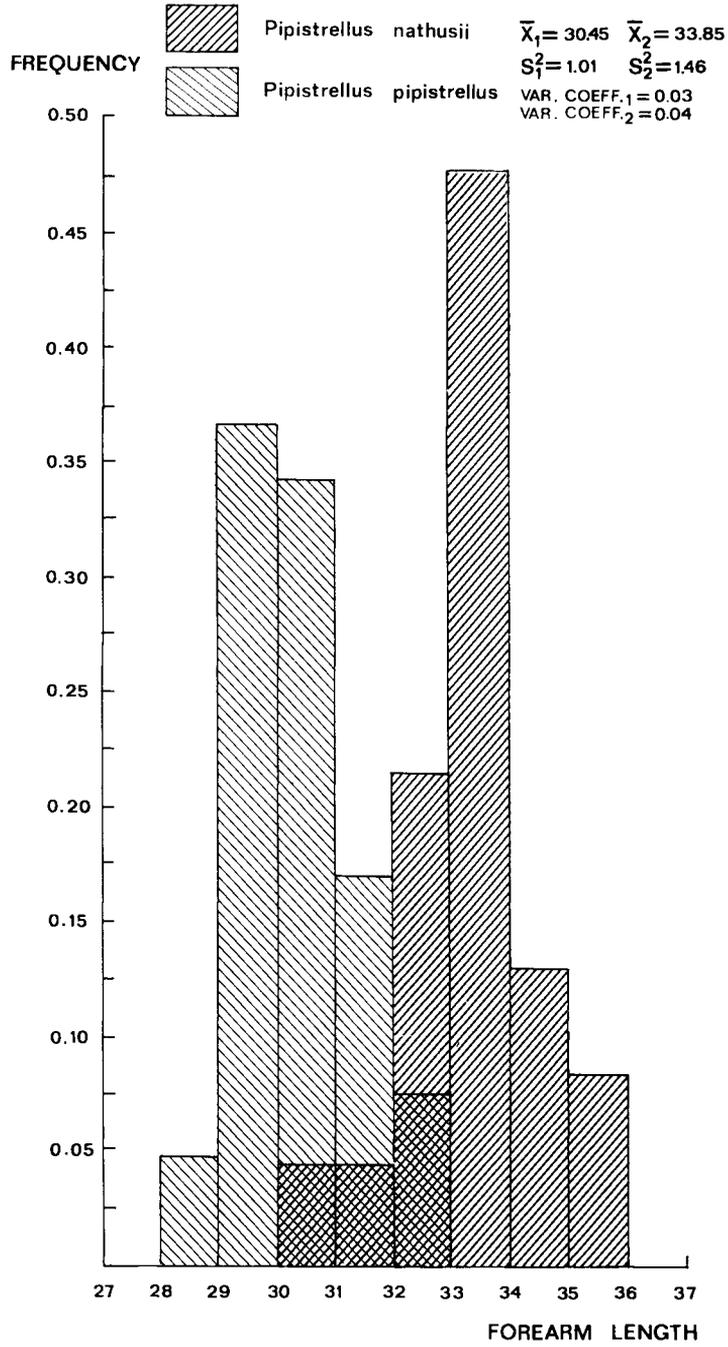


Fig. 29. Frequency distribution of the forearm length in both *Pipistrellus* species.

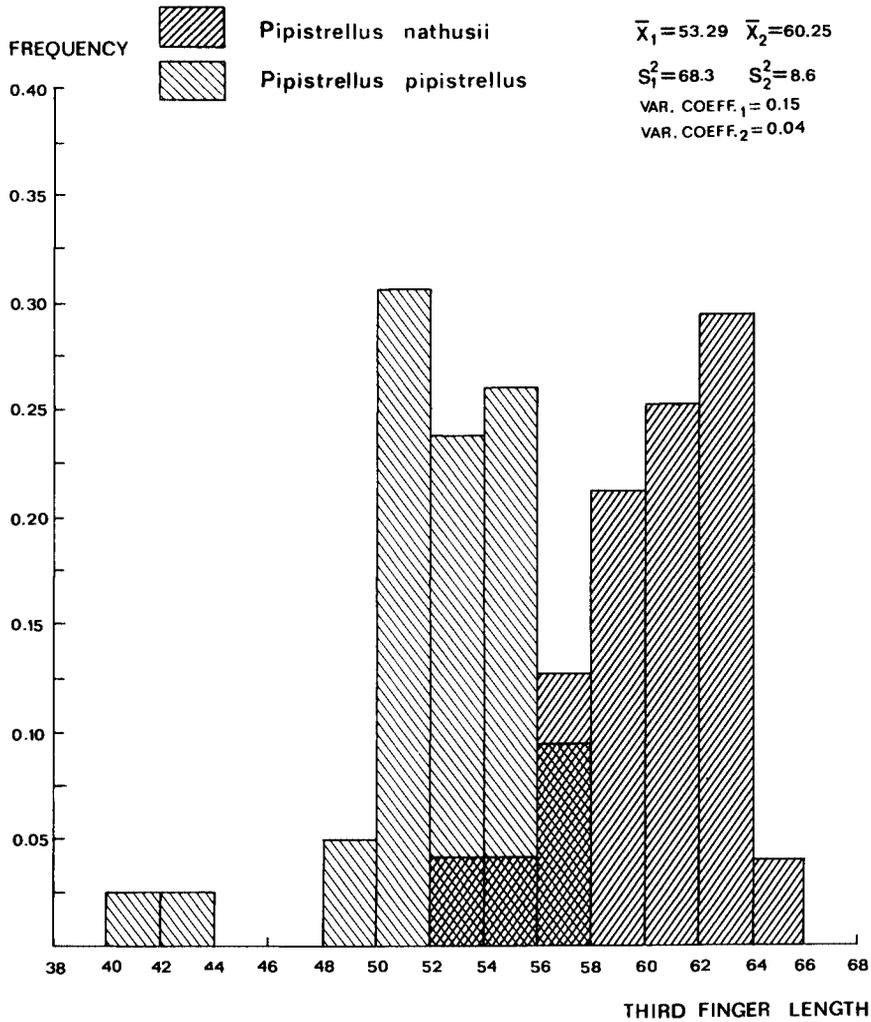


Fig. 30. Frequency distribution of the third finger length in both *Pipistrellus* species.

The result of this analysis is presented in fig. 35a, b. Fig. 35a illustrates the plotting of the first PCA (on the X-axis) against the second PCA (on the Y-axis). In fig. 35b the first PCA is plotted against the third PCA. The objects are separated into two distinct clusters.

A dendrogram according to Ward's averaging is shown in fig. 36. Only one specimen of *P. pipistrellus* is placed in the wrong cluster. The similarity of this dendrogram with that based on the external characters again is very obvious.

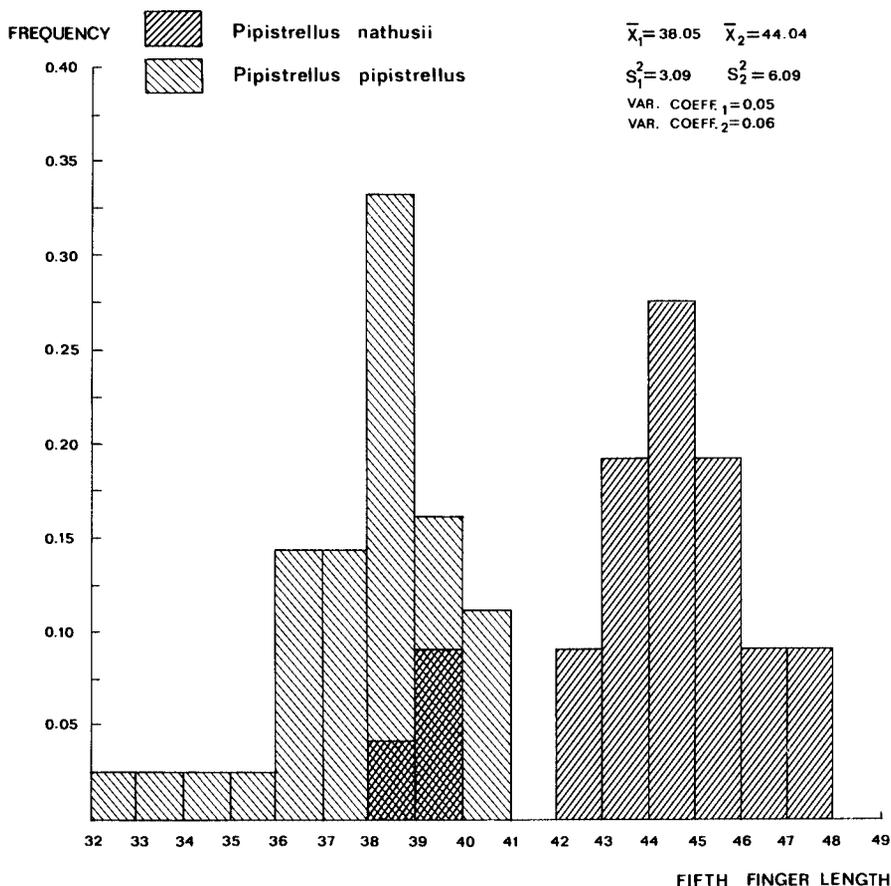


Fig. 31. Frequency distribution of the fifth finger length in both *Pipistrellus* species.

A discriminant analysis resulted in a discriminant function with three major characters: 19 (fifth finger length), 17 (third finger length) and 2 (forearm length). Using these three characters, the following discriminant functions were obtained:

$$X_{x\text{-ray}} = 4.37 X_{19} - 0.29 X_{17} + 0.66 X_2 - 3.14 \text{ for } P. \textit{nathusii};$$

$$X_{x\text{-ray}} = -1.42 X_{19} + 0.09 X_{17} - 0.21 X_2 - 0.33 \text{ for } P. \textit{pipistrellus}.$$

For the *P. nathusii* cluster the mean value is: $\bar{X}_{x\text{-ray}} = 193.11$, with $187.31 < X_{x\text{-ray}} < 203.20$ and $S = 5.49$; for *P. pipistrellus* the mean value is: $\bar{X}_{x\text{-ray}} = -55.11$ with $-65.20 < X_{x\text{-ray}} < -45.39$ and $S = 3.15$. The results are comparable with those of the analysis of external characters because of the high cor-

THIRD FINGER LENGTH

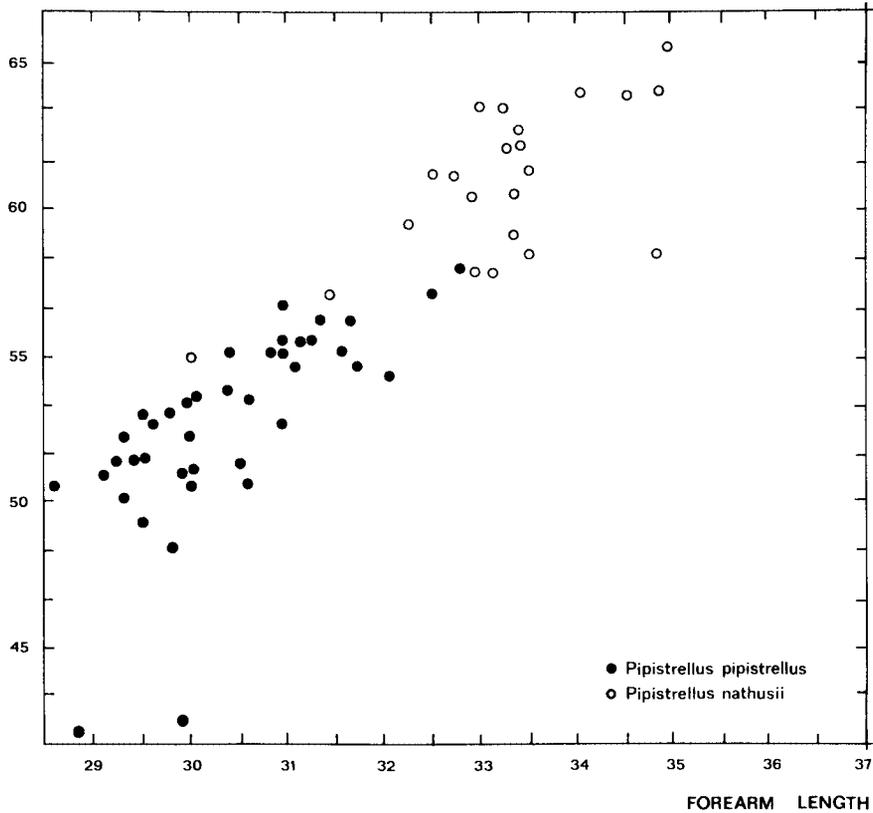


Fig. 32. Plot showing the relationship between the forearm length and the length of the fifth finger in both *Pipistrellus* species.

relation between external and X-ray characters. The advantage of using X-ray measurements is that in this way dry skins can be identified as well.

Since in X-ray photographs all three characters are equally well visible, we have refrained from calculating the discriminant functions for each separate character here.

5. DISCUSSION

In our material the number of *P. nathusii* specimens is smaller than that of *P. pipistrellus*, but may be regarded as representative. It is not clear whether the various characters are subject to clinal variation.

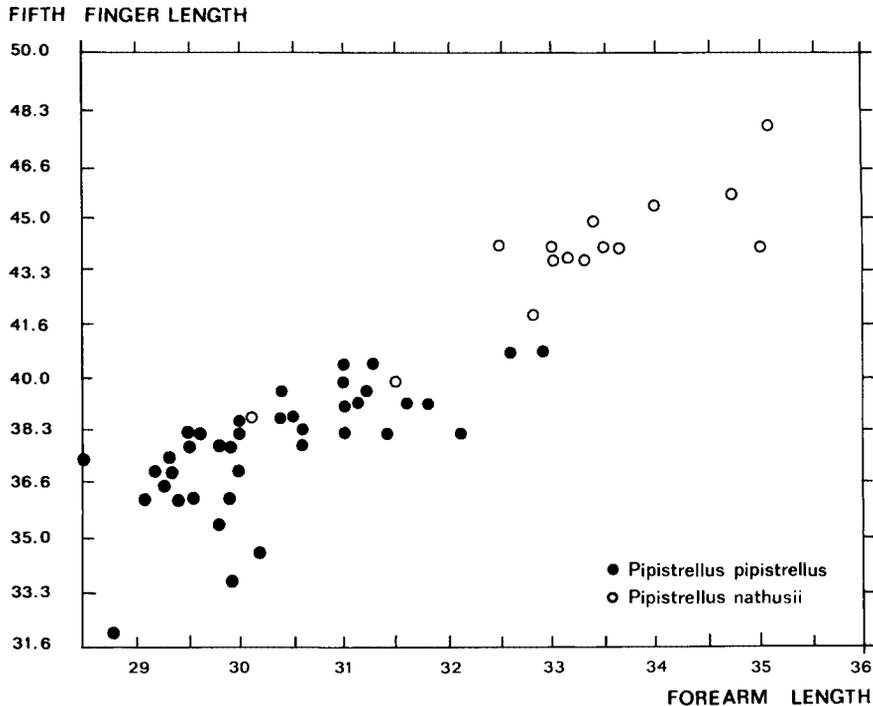


Fig. 33. Plot showing the relationship between the forearm length and the length of the third finger in both *Pipistrellus* species.

In dried and/or half-decayed specimens a number of external characters such as shape of the ear and colour of the pelage are no longer clearly visible and identification often is difficult. On the other hand, identification of living specimens is hampered by the fact that most of the characters of skull and teeth present difficulties whereas the other characters are subjective, e.g. the colour of hairs and wing and the shape of the ear (Heise, 1979).

At birth the milk-teeth of bats are fully developed and have the shape of sharp, curved hooks (Eisentraut, 1937). A new-born *Pipistrellus* begins life with all 22 milk-teeth present; eruption of the permanent dentition may begin in the second week after birth and end somewhere during the weaning period. After three weeks the permanent dentition is already visible, but is not yet full-grown. In this study the presence of permanent dentition has been used as the criterium for classifying a specimen as adult. In addition to this, young bats are easily distinguished from adults by the thickened metacarpal and interphalangeal joints. By their first winter they differ from adults only in the

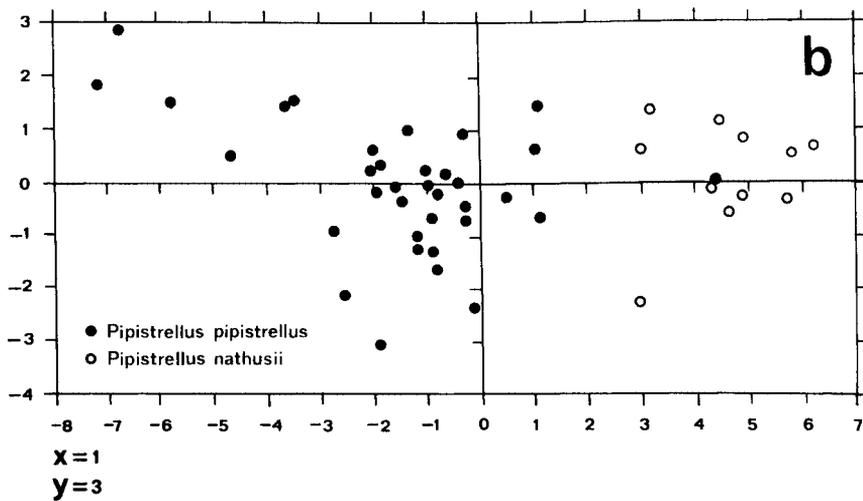
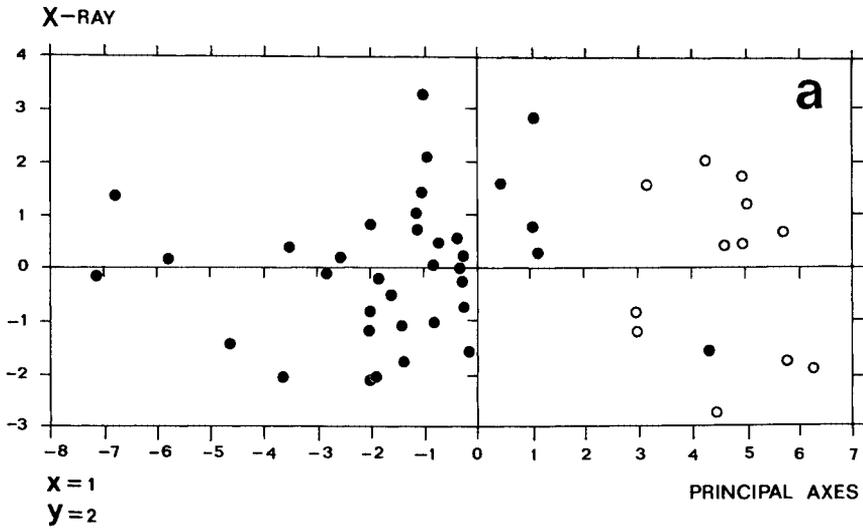


Fig. 35. Plot resulting from a principal component analysis of normalized biometric X-ray data: a, first and second principal axes; b, first and third principal axes.

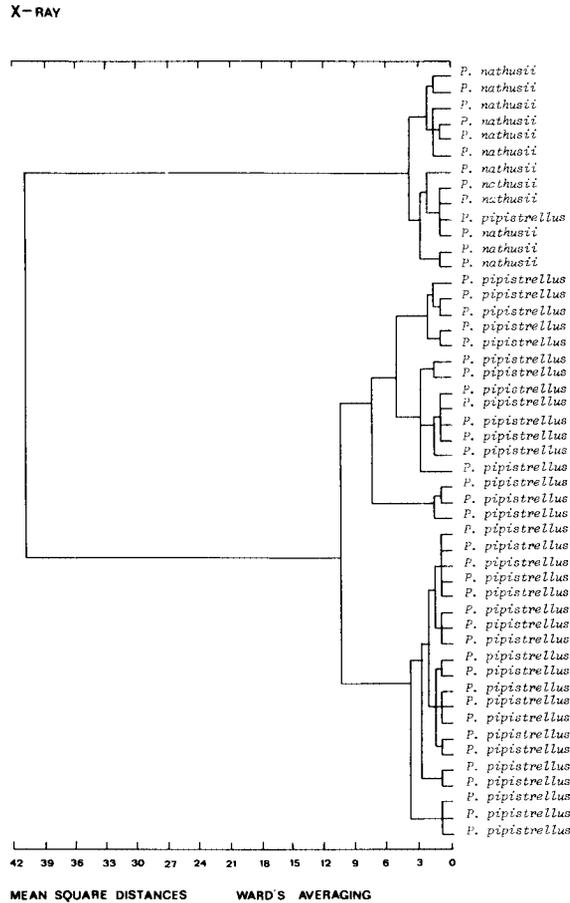


Fig. 36. Dendrogram resulting from Ward's averaging in Q-mode from standardized biometric X-ray data.

colour of their fur and slightly lesser weight (Eisentraut, 1937; Kowalski, 1955).

Initially, the sexes were treated separately, but since males and females did not appear in different clusters, they subsequently have been treated as one group. According to Schmidt (1978), the length of the forearm and fifth finger differs significantly between males and females of *P. nathusii*. In this study, however, any such difference is not apparent (t-test; $p = 0.01$).

5.1. HAIRS

Benedict (1957) has already pointed out that there is no consistent correlation between habitat and hair structure in bats. He refers to the uniformity of hair structure in the cosmopolitan genus *Myotis* from such different environments as rain forest, desert and taiga. He also states that closely allied groups often have similar hair characters. However, variation occurs within families, so that hair structure may serve as a good character at the generic level. Interspecific variation, however, is small and usually limited to differences in size and pigmentation. In *Pipistrellus* pigmentation varies individually. The differences in micro-structure of individual hair scales should also be taken into account.

In this study no remarks have been made upon hair colour, because descriptions of hair colour are often subjective and tend to vary widely within each species. According to Stebbings (1977), the colour of the fur in *P. pipistrellus* is quite variable and evidently shows local differences.

Koch (1862-1863), Schäff (1911) and Stehli & Brohmer (1961) a.o., following Keyserling & Blasius (1839), mention the dark coloration of the fur behind the ears in *P. nathusii*. In our specimens this dark spot has not been found. The extension of the fur on the uropatagium as a character is mentioned by e.g. Eykman (1937), IJsseling & Scheygrond (1950), Van Eyndhoven (1955) and Gaffrey (1961). We agree with Heise (1979) that this character is not reliable.

5.2. TEETH

Dental wear in bats is difficult to define and hard to measure. The effect of parodontal disease, which was found by Vierhaus (1981) in 43% of mostly adult specimens of central European *P. pipistrellus* ($n = 23$) and in two out of nine *P. nathusii*, has not been investigated because parodontitis can hardly have affected the dental and jaw length values chosen in this study. Claude (1977) states: "Die Höhe des zweiten, oberen Schneidezahns ist als Bestimmungsmerkmal nicht immer eindeutig". Fairon (1978) found that in 82% of the Belgian *P. pipistrellus* I^2 is smaller than I^1 . In this study this feature has been found in 76% of the *P. pipistrellus* and in 15.2% of the *P. nathusii* specimens. This character therefore can be useful for identification, but is not as reliable as is often assumed.

Stebbing (1970) and Fairon (1978) have already pointed out the doubtful value of the lateral visibility of P^1 . The visibility class percentages as found in

this study (see table 6) correspond with the data presented by Fairon, if our classes III and IV are combined. According to Baumann (1949), P¹ is laterally visible for the greater part in both *P. pipistrellus* and *P. nathusii*. In our opinion this character is of doubtful value because of the great intra-specific variation in this respect.

Miller (1912) states that the lower incisors of *P. pipistrellus* are more crowded than in *P. nathusii*; in the latter species they are linked but do not overlap. This feature was poorly illustrated by Miller for both species (labial view). This difference was emphasized and illustrated (dorsal view) by Didier & Rode (1935) and Saint Girons (1973). The overlap is distinct in less than 60% of the Dutch *P. pipistrellus* specimens. In less than 80% of the Dutch *P. nathusii* specimens the lower incisors are linked and do not overlap (see table 7). Besides, the rate of overlap is not always well-defined and transitional stages occur. An additional disadvantage is the difficulty of examining this character in living specimens, since the lower incisors are placed deeply in the gums. In our opinion the diagnostic value of this character is very doubtful.

Hanák & Gaisler (1976) found a gap between I₂ and I₃ in 3% of their *P. pipistrellus* specimens; this gap is present in 11.25% of the Belgian material of *P. pipistrellus* examined by Fairon (1978); the percentage in our material is much greater (see table 8). Saint Girons (1973) does not mention a gap between I₂ and I₃. Beaucournu (1963) illustrates several projections of the lower incisors in a number of *Pipistrellus* species; he notes a gap between two incisors of one *P. nathusii* male, but from his illustration it is not clear whether this gap is situated between I₁ and I₂ or between I₂ and I₃. He states that the position of the incisors in the lower jaw, which has been used as a specific character by Miller (1912), Cabrera (1914) and Aellen (1961), is not different in both species and probably subject to individual variation. However, in 83.8% of the Dutch *P. nathusii* specimens the gap between the second and third lower incisor is distinctly present; in 79.2% of the Dutch *P. pipistrellus* specimens this gap is absent. In our opinion this character can be useful for identification, but does not completely separate the two species.

The length of the protocone on the lower canine, used as a character by a.o. Schäff (1911), Haltenorth (1955) and Gaffrey (1961), is said by Vierhaus (1982) to be reliable. In our opinion, however, this character is subject to considerable individual variation and cannot be considered diagnostic (see table 9).

5.3. BIOMETRIC CHARACTERS

Some skull measurements are difficult to define exactly, such as for instance the height of the skull, since there is no well-marked reference point on the frontal or parietal. In general it is difficult to compare data given by different authors and based on different numbers of bats. Every author has his own particular way of taking measurements. According to Rosevear (1965), the length of the metacarpal, being that of single bone, can be measured precisely; however, though the distal joint is quite clear, it is not always easy to determine the exact point of origin at the wrist. In this study the metacarpal and external finger and forearm length have been measured including the wrist to the extreme tip, whereas Van der Straeten et al. (1981) measured these excluding the wrist; Schmidt (1978) and Heise (1979) used a pair of callipers for measuring the forearm length (including the wrist) and a steel ruler for measuring the fifth finger (excluding the wrist). Therefore, the data presented in tables 10-14 show some variation.

The values of the two most important skull characters (condylobasal length and mandible length) measured by different authors are presented in table 10. In *P. pipistrellus* the condylobasal length varies from 10 mm (Tupinier, 1975) to 13.1 mm (this study). The average length recorded in this study (12.25 mm) does not differ significantly (t-test, $p = 0.05$) from the average value found by Miller (1912) (11.41 mm); Miller, however, recorded a smaller range. The range of the condylobasal length in this species mentioned by other authors is below the average value found in this study. In *P. nathusii* the condylobasal length as found in this study ranges from 11.6 to 14.3 mm, with an average of 13.35 mm. This does not differ significantly (t-test, $p = 0.05$) from the average length mentioned by Miller (1912) (12.83 mm). The overlap in condylobasal length between *P. pipistrellus* and *P. nathusii* as found in this study does not appear from the values given by others as shown in this table.

The average values of the mandible length in *P. pipistrellus* measured by Fairon (1978) and Miller (1912) (8.33 and 8.23 mm, resp.) do not differ significantly (t-test, $p = 0.05$) from the results of this study (8.49 mm). The average mandible length in *P. nathusii* found by Miller (9.18 mm) agrees well with the results of this study (9.47 mm) and is not significantly different (t-test, $p = 0.05$). The mandible length found by Rode & Didier (1946) and Cabrera (1914), however, are much lower.

The forearm lengths in both *Pipistrellus* species measured by different authors are presented in table 11. The average value in *P. pipistrellus* varies from 29.9 mm (Ognev, 1928) to 32.88 mm (Stebbing, 1973). This considerable range reflects the great individual variation in *Pipistrellus*. The average value

| | CONDYLOBASAL LENGTH | | MANDIBLE LENGTH | |
|-----------------------------------|------------------------|-----------------------------------|--------------------------|-----------------------------------|
| | <i>P. pipistrellus</i> | <i>P. nathusii</i> | <i>P. pipistrellus</i> | <i>P. nathusii</i> |
| Baumann (1949) | 11 - 11.8 | | | |
| Beaucournu (1963) ♂ | | 12.8 (n=1) | | 9.4 (n=1) |
| Cabrera (1914) | 11.2 | | 8.2 | 8.5 |
| Dinale (1958) | | 13.0 (n=1) | | 9.2 (n=1) |
| Dumitresco & Orghidan (1963) | 11 - 11.5 | | | |
| Eykman (1937) | 11 - 11.8 | (n=5) 12.4 - 13.4 | 8 - 9 | 8.8 - 9.6 |
| Fairon (1978) | 10.8 - 11.45 | (n=7) (11.25) | 7.45 - 8.7 | (8.33) (n=25) |
| Gaffrey (1961) | 11.0 - 12.0 | 12.4 - 13.4 | | |
| Hanák & Gaisler (1976) | | 12.0 - 13.4 | | |
| Müller (1912) | 11.0 - 11.8 | (n=38) 12.4 - 13.4 (12.83) | 8.0 - 8.8 (8.23) | 8.8 - 9.6 (9.18) |
| Ognev (1928) | 11.2 - 11.8 | (n=7) 12.2 - 13.9 (13.3) | (n=12) | (n=13) |
| Rode & Didier (1946) | 11 - 12 | 12 - 13 | 8 - 8.5 | 8 - 8.8 |
| Stebbing (1977) | 11 - 12 | | | |
| Van der Straeten et al. (1981) ♀♀ | | | | 9.70 (n=1) |
| Tupinier (1975) | 10 - 11.1 | | | |
| Vierhaus & Bülow (1978) | | 12.4 (n=1) | | 9.5 (n=1) |
| <i>Grol (this study)</i> | 11.0 - 13.1 | (12.25)(n=90) 11.6 - 14.3 (13.35) | (n=36) 7.5 - 9.25 (8.49) | (n=90) 8.75 - 10.25 (9.47) (n=34) |

Table 10. Minimum-maximum values, mean values, and number of measurements (n) of the condylobasal length and mandible length in both *Pipistrellus* species, according to literature data and the present study.

| | | FOREARM LENGTH | | | |
|--------------------------------|-----|------------------------|---------------------|--------------------|------------------|
| | | <i>P. pipistrellus</i> | | <i>P. nathusii</i> | |
| Aellen (1961) | ♂ ♂ | | | 32 - 33 | (33) |
| Barbu (1968) | ♂ ♂ | | | 33.0 - 35.1 | (33.6) |
| Barrett-Hamilton (1910-1911) | | 27.5 - 31.2 | | | |
| Bauer (1956) | | 28.2 - 31.1 | | | |
| Baumann (1949) | | 27 - 32 | | 32 - 35 | |
| Beaucournu (1963) | ♂ | | | 33.1 | (n = 1) |
| Bels (1938) | | 31 | | 33 | |
| Van den Brink (1955, 1978) | | 27 - 34 | | 31 - 37 | |
| Bühler & König (1965) | | 28 - 33 | | | |
| Cabrera (1914) | | 29 - 32 | | 31 - 35 | |
| Claude (1977) | | 28.5 - 32.9 | (30.6) | 30.0 - 35.65 | (33.7) |
| Dinale (1958) | | 30 | | 33.0 - 34.7 | |
| Dumitresco & Orghidan (1963) | | 28.5 - 32.5 | | | |
| Eisentraut (1957) | | 30 - 34 | | | |
| Eykman (1937) | | 28 - 32 | | 32 - 35 | |
| Fairon (1978) | | 29.1 - 33.55 | (31.06) (n = 77) | | |
| Gaffrey (1961) | | 27 - 34 | | 32 - 35 | |
| Hanák & Gaisler (1976) | | 28.8 - 33.0 | | 31.3 - 36.5 | |
| Heise (1979) | ♀ ♀ | 28.5 - 34.1 | (31.6) (n = 91) | 31.5 - 37 | (34.4) (n = 80) |
| Heise (1979) | ♂ ♂ | 29 - 32.3 | (31.2) (n = 17) | 32.3 - 34.7 | (33.4) (n = 33) |
| Hürka (1966) | | 28 - 34.1 | | | |
| Jentink (1879) | | 32 | | | |
| Koch (1862-1863) | | 30.0 | | 34.5 | |
| Kowalski (1955) | | 28 - 33 | | 32 - 36.5 | |
| Landsman (1933) | | 31 | | 33 | |
| Méhely (1900) | | 30 - 32.5 | | 33 - 35 | |
| Miller (1912) | | 27.6 - 32 | (n = 27) | 32.4 - 35 | (33.2) (n = 9) |
| Ognev (1928) | | 28.2 - 31.5 | (29.9) (n = 8) | 33.0 - 36.0 | (34.2) (n = 13) |
| Punt et al. (1974) | | 28 - 35 | | 31 - 37 | |
| Rode (1947) | | 30 - 32 | | 32 - 35 | |
| Saint Girons (1973) | | 27 - 33 | | 31 - 36.5 | (34.11) |
| Schmidt (1978) | ♀ ♀ | | | 32 - 37 | (34.6) (n = 87) |
| Schmidt (1978) | ♂ ♂ | | | 32 - 36 | (33.8) (n = 42) |
| Stebbings (1970) | ♂ ♂ | 28.7 - 32.9 | (30.89) (n = 204) | 33.0 | (n = 1) |
| Stebbings (1973)* | | 28.9 - 35.0 | (31.00 - (n = 1930) | | |
| | | | | 32.88) | |
| Van der Straeten et al. (1981) | ♀ ♀ | 30.0 - 33.9 | (32.2) (n = 4) | 35.0 | (n = 1) |
| Tupinier (1975) | | 30.2 - 31.0 | (n = 3) | | |
| Vierhaus & Bülow (1978) | | | | 32 - 35 | (33.56) (n = 16) |
| IJsseling & Scheygrond (1950) | | 27 - 32 | | 32 - 35 | |
| Grol (<i>this study</i>) | | 28.5 - 32.95 | (30.65) (n = 45) | 30.0 - 35.65 | (33.70) (n = 28) |

* Average values for colonies of ♀ ♀ *P. pipistrellus*.

Table 11. As in table 10, forearm length.

of the forearm length in *P. pipistrellus* found in this study (30.65 mm) does not differ significantly from the results found by other authors (t-test, $p = 0.05$). In *P. nathusii* the average value of the forearm length varies from 33 mm (Allen, 1961; Stebbings, 1977) to 34.2 mm (Ognev, 1928). The average value found in this study (33.70 mm) is not significantly different from the average values found by others (t-test, $p = 0.05$). The high average values found by Schmidt (1978) and Heise (1979) are based on female bats only. The overlap in forearm length between these two species as found in this study shows that this character does not completely separate both species. The individual variation of the forearm length in both species is considerable.

| | THIRD FINGER LENGTH | | | |
|-----------------------------------|------------------------|--------|---------------------|----------------------|
| | <i>P. pipistrellus</i> | | <i>P. nathusii</i> | |
| Beaucournu (1963) ♂ | | | | 60.3 |
| Cabrera (1914) | 52.7 - 53.8 | | | |
| Eykman (1937) | 52 - 56 | | | 58 - 65 |
| Van Eyndhoven (1955) | ± 55 | | | |
| Koch (1862-1863) | 55.0 | | | 65.9 |
| Méhely (1900) | 47 - 55 | | | 58 - 62 |
| Miller (1912) | 49 - 58 | (n=27) | | 58 - 65 (62.0) (n=9) |
| Punt et al. (1974) | 49 - 53 | | | 58 - 65 |
| Van der Straeten et al. (1981) ♀♀ | 52.0 - 56.0 (54.4) | (n=4) | | 59.3 (n=1) |
| Tupinier (1975) | 52.7 - 53.8 | | | |
| <i>Grol (this study)</i> | 42.35 - 57.80 (53.41) | (n=45) | 56.9 - 66.3 (61.87) | (n=28) |

Table 12. As in table 10, third finger length.

The third finger lengths measured by different authors are presented in table 12. The average value for the third finger length in *P. pipistrellus* as found in this study (53.41 mm) corresponds with the data found by other authors and is not significantly different from the average value found by Van der Straeten et al. (1981) (t-test, $p = 0.05$). The same applies to the third finger length in *P. nathusii*. The average value found in this study (61.87 mm) does not differ significantly from that found by Miller (1912). The differences in third finger length between both species are great.

The fifth finger lengths in both *Pipistrellus* species measured over the years are presented in table 13. In *P. pipistrellus* the average value found in this study (39.05 mm) does differ significantly from the average values found by Stebbings (1970) and Fairon (1978) (t-test, $p = 0.05$). This difference may be due to the fact that Fairon included juvenile specimens in his measurements. The average value of the fifth finger length in *P. pipistrellus* measured by Stebbings is based on male specimens only. The average fifth finger length in

| | | FIFTH FINGER LENGTH | | | |
|-----------------------------------|---------------|------------------------|----------|--------------------|------------------|
| | | <i>P. pipistrellus</i> | | <i>P. nathusii</i> | |
| Barbu (1968) ♂♂ | | | | 42.5 - 46.0 | (43.1) |
| Bauer (1956) | 37 - 39 | | | 42.5 - 46 | |
| Baumann (1949) | ± 40 | | | ± 46 | |
| Beaucournu (1963) ♂ | | | | 44.5 | (n = 1) |
| Van den Brink (1955, 1978) | ± 37 | | | ± 45 | |
| Cabrera (1914) | 35 | | | 38 | |
| Claude (1977) | 38 - 40 | (n = 6) | | 42.5 - 48 | (45.0) (n = 16) |
| Eykman (1937) | 37 - 41 | | | 41 - 47 | |
| Van Eyndhoven (1955) | ± 40 | | | ± 46 | (n = 1) |
| Fairon (1978) | 29.4 - 41.25 | (37.80) | (n = 66) | | |
| Gaffrey (1961) | | | | 44 - 47 | |
| Heise (1979) ♀♀ | 36 - 42 | (39.2) | (n = 91) | 43 - 47.5 | (45.2) (n = 80) |
| Heise (1979) ♂♂ | 36 - 41 | (39.1) | (n = 17) | 42 - 46 | (44.1) (n = 33) |
| Jentink (1879) | 39 | | | | |
| Klawitter (1974) | | | | 42.5 - 47 | (n = 133) |
| Koch (1862-1863) | 39.4 | | | 43.3 | |
| König (1959) | 43 | | | 44 - 47 | |
| Kowalski (1955) | 40 | | | 46 | |
| Landsman (1933) | 40 | | | 46 | |
| Méhely (1900) | 34 - 41 | | | 43.5 - 47 | |
| Miller (1912) | 34.6 - 42 | (n = 27) | | 41 - 47 | (45.3) (n = 9) |
| Punt et al. (1974) | 34 - 42 | | | 41 - 47 | |
| Saint Girons (1973) | 38 - 42 | | | ± 46 | |
| Schmidt (1978) ♀♀ | | | | 42 - 48 | (44.99) (n = 87) |
| Schmidt (1978) ♂♂ | | | | 42 - 46.5 | (44.1) (n = 42) |
| Stebbins (1970) | 34.5 - 38.5 | (39.91) | (n = 10) | 43.5 | (n = 1) |
| Van der Straeten et al. (1981) ♀♀ | 38.0 - 40.0 | (38.8) | (n = 4) | 44.2 | |
| Tupinier (1975) | 37.6 - 39.3 | | | | |
| Vierhaus & Bülow (1978)* | | | | 42 - 46 | (44.05) (n = 16) |
| IJsseling & Scheygrond (1950) | ± 40 | | | ± 46 | |
| Grol (this study) | 38.80 - 43.50 | (39.05) | (n = 45) | 39.45 - 49.80 | (45.76) (n = 28) |

* Average value for both ♂♂ and ♀♀.

Table 13. As in table 10, fifth finger length.

P. nathusii found in this study (45.76 mm) differs significantly from the average values found by Barbu (1968), Vierhaus & Bülow (1978), Schmidt (1978), and Heise (1979) (t-test, $p = 0.05$). This can partly be explained by the fact that the measurements taken by Vierhaus & Bülow were taken in a different manner, excluding the wrist, and also by the fact that the values given by Schmidt (1978) and Heise (1979) are based on male specimens only. A second explanation can be found in the fact that the variance in fifth finger length in both species is very low ($S_1^2 = 3.09$; $S_2^2 = 6.09$ for *P. pipistrellus* and *P. nathusii*, respectively).

The clustering methods used here give good results, but this does not imply

that no other clustering methods are possible. In many cases certain characters could not be measured because the parts in question were damaged or missing. In these specimens, the average value of that particular character for the species has been used.

5.4. OTHER CHARACTERS

In this paper descriptive characters such as the differences in the shape of ear and tragus etc., have not been discussed. In many identification works the tail, body, head and ear length as well as the wingspan are used. In our opinion, however, it is impossible to give exact values for these measurements. Baumann (1949) found that the ears in *P. pipistrellus* are more pointed than those of other *Pipistrellus* species. Didier & Rode (1935: 152) following Trouessart (1910) write of *P. nathusii*: "Les oreilles sont moins échancrées sur leur bord externe qui est presque droit, le tragus est un peu plus court, le bord interne plus concave". The ear length, the curvature of the tragus and the wingspan are essential differences between the two species according to Rode (1947). In our opinion, however, these characters are not diagnostic.

Along the border of the patagium between the fifth finger and the hindfoot some *P. nathusii* specimens show a pale white border, which is smaller and less white than in *P. kuhlii* (Kuhl, 1817). The diagnostic value of this character has never been examined, although Baumann (1949), Bühler & König (1965), Stebbings (1970) and Saint Girons (1973) discuss this feature.

The thumb length as compared to the wrist width has often been mentioned as a useful character (a.o. Miller, 1912; Ognev, 1928; Van den Brink, 1955, 1978; Toschi & Lanza, 1959; Bühler & König, 1965), but its value is doubted by Van de Kamp-Hilt & Van Bree (1964), Stebbings (1970) and Van der Straeten et al. (1981). The discriminant analysis of external and X-ray characters carried out in this study resulted in a low discriminant value of the thumb length; in our opinion this character cannot be considered diagnostic.

According to Topál (1958), the length and shape of the baculum are important taxonomical characters in bats. The differences in this respect between both *Pipistrellus* species are given by Toschi & Lanza (1959) and Claude (1977). The baculum in both species is minute and cannot be prepared without damaging the specimen. However, in most cases it is not necessary to examine the baculum when other useful discriminating characters are available.

Vierhaus (1982) has been searching for other distinguishing characters between *P. pipistrellus* and *P. nathusii*. He found clear morphological differences in the angular process of the mandible, the dimension of the lower premo-

lars and the shape of the male pelvic bone. He stresses the differences in the distal epiphysis of the humerus as already pointed out by Felten et al. (1973). He also states that the differences in the angular process do not completely separate the species. It is not clear, however, whether the differences in shape of the pelvic bone, the angular process and the distal epiphysis of the humerus may be the result of individual variation. These characters have not been examined in this study.

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