Comparative Systematic Value Between Dental and External/Skeletal Features in Western European Chiroptera

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Abstract

Diagnostic characters in biosystematics have low variability and congruent distribution. In mammals they are mainly external and skeletal features. The distribution of diagnostic and non-diagnostic characters often shows a poor degree of congruence.

Dental characters of isolated teeth of 21 recent species of bats (Chiroptera) have been chosen and analyzed to compare with the distribution of external and skeletal diagnostic characters. The degree of congruence of these distributions would be a measure of the diagnostic value of dental characters.

A phenetic approach of the character analysis and clustering method (UPGMA and single linkage) and the correlation coefficient between the similarity matrices have been used for this purpose.

The classification based on dental features shows a higher power of discrimination and a lesser degree of stability than that based on the chosen external and skeletal features. Congruence between both sets of characters have been found to be one of the highest

Résumé

Les caractères diagnostiques en biosystématique sont choisis pour leur faible variabilité et leur distribution concordante. Chez les Mammifères, ils se trouvent surtout dans la morphologie externe et le squelette. D'autres caractères sont considérés non-diagnostiques en raison de leur distribution peu concordante avec les caractères diagnostiques.

Dans 21 espèces récentes de chauve-souris (Chiroptères), nous avons choisi et analysé 23 caractères des dents isolées. La distribution de ces caractères dentaires dans les espèces étudiées est comparée avec la distribution des caractères diagnostiques de la morphologie externe et du squelette, sur lesquels est fondée l'identification de ces espèces. Le degré de concordance des deux distributions serait une mesure de la valeur diagnostique des caractères dentaires, qui pourraient alors être aussi utiles dans l'identification des espèces.

Les distributions des caractères ont été analysées par la méthode phénétique UPGMA et « single linkage », puis par l'analyse de corrélations entre les matrices de similitude.

La classification basée sur les caractères dentaires montre un plus grand pouvoir de discrimination que celle fondée sur les caractères externes et squelettiques, qui ne suffit pas à distinguer les 21 espèces. Elle a par contre un degré de stabilité plus faible, car les

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(r = 0.77) and consequently, we conclude that dental characters in bats have a high diagnostic value and thus fossil and recent populations can be studied using the same criteria.

différentes méthodes arrivent à des groupements différents. La classification basée sur des caractères externes et squelettiques est plus stable, ne variant pas beaucoup quand on change la méthode de groupement.

La corrélation entre les deux matrices de similitude est l'une des plus grandes observées (0,77) ; on peut en conclure que les caractères dentaires chez les chauve-souris ont une distribution conforme avec celle des caractères diagnostiques, et donc peuvent être aussi utilisés en systématique. Par conséquent, les mêmes critères d'identification pourront être appliqués à l'étude des populations fossiles et récentes.

Introduction

Character analysis is the principal method in biosystematics, evolutionary biology, functional biology and other major branches of life sciences. The differentiation of taxa, which is the basis of all other biological and palaeontological studies, is itself based on selected diagnostic characters. A high systematic value is given to these characters because of their low variability and congruent distribution (they do not appear in every possible combination).

Biosystematics must analyze characters coming from a majority of sources: external morphology, dentition, skeletal and soft anatomy, karyological and molecular data. Congruence of character distributions obtained with diagnostic characters (mainly external and skeletal in vertebrates), and non-diagnostic features (either morphological, cytological or molecular) has been observed to be poor (Hemmer & Alcover, 1984; Luckett & Hartenberger, 1985; Sanchiz, 1985). It seems that there is no obvious overall pattern in character distribution.

In mammals, diagnostic characters of high value are mainly external and skeletal data (nose, ears, hair, tail, feet, dental formula and skull). Dental morphology of isolated teeth is rarely used as a source of diagnostic characters, and when so, at a low taxonomic level. On the contrary, dental morphology of isolated teeth is extensively used in palaeontology, and consequently, they constitute very important data for the reconstruction of evolutionary processes.

We attempt in this note to test the degree of congruence of the distribution of dental characters compared with the distribution of external and skeletal characters, using Chiroptera as a test case. The congruence among both distributions will be a measure of the diagnostic value of dental characters, as well as a test for the ability of palaeontologists to select valuable systematic characters in isolated teeth.

Material and method

We have selected twenty-one species of bats (nine genera included), which are the most common in Western Mediterranean Europe. Twenty-two external and skeletal morphological characters, and twenty-three dental ones were chosen from our observations and from the literature. For the dental characters, over fifty specimens of the most common species in Spain were studied. From other species which are more rarely found in Spain, such as *Tadarida teniotis*, *Barbastella barbastellus* and the three *Nyctalus*, only five specimens or under, were available for our study. We avoided using metric characters, commonly used in determining specimens because continuous variation does not allow objective division into discrete categories.

We do not deal in this note with phylogeny, but with character distribution. A phenetic approach would be the best procedure for studying the coherence of character distribution and the comparative congruence of classifications. The selected characters are figured (Figs. 1 and 2), and plotted in two " features × taxa " matrices (Tables I and II), one for external and skeletal features and the other for dental features. Symbols used in the character tables have no evolutionary meaning.

The two similarity matrices were obtained using Jaccard index ($I = \frac{2c}{N1 + N2 - c}$). Each one has produced two phenograms by means of two different clustering methods: single linkage and UPGMA (Unweighted Pair Group Method using Arithmetic Average) (see Sneath & Sokal, 1973). Measurement of the agreement between the two similarity matrices was calculated by the product-moment correlation coefficient of Pearson, $rss = \frac{P}{\sigma_\varepsilon \sigma_D}$ (Sneath & Sokal, 1973), which varies between 0 and 1; good correlations approach value 1.

A. *External and Skeletal Features*

1. *Nose-leaf:*
   — absent (0)
   — present (1)

2. *Narine openings:*
   — opening forwards (0)
   — opening upwards (1)

3. *Tragus:*
   — absent (O)
   — long and thin (1)
   — short and thin to moderately wide (2)

4. *Ears:*
   — big, widely extending over muzzle when laid forward (0)
   — middle-sized, approximately ending at the muzzle when laid forward (1)
   — short, clearly not reaching the muzzle when laid forward (2)

5. *Ears:*
   — not joined at inner bases (0)
   — joined at inner bases (1)

6. *Antitragus:*
   — absent (0)
   — present (1)

7. *Number of mammary glands:*
   — one pair (0)
   — two pairs (1)

8. *Shape of wings:*
   — narrow (length 5th finger/length < 3rd finger 0.69) (0)
   — wide (length 5th finger/length > 3rd finger 0.70) (1)

9. *Tail:*
   — included in uropatagium, or at most, two vertebrae projecting from it (0)
   — conspicuously projecting fom uropatagium (1)

10. *Length of calcar:*
   — shorter than free border of interfemoral membrane (0)
   — approximately the same as free border of interfemoral membrane (1)
   — clearly longer than free border of interfemoral membrane (2)

11. *Epiblema:*
   — absent or rudimentary (0)
   — clearly present (1)

12. *Plagiopatagium joining the leg at:*
   — ankle (0)
   — base of outer toe (1)
   — middle of metatarsus (2)

13. *Premaxillaries:*
   — loosely joined to the skull (0)
   — fused to the skull (1)

14. *Secondary articulation of scapula:*
   — small (0)
   — middle-sized (1)
   — big (2)

15. *Distal tip of coracoid process:*
   — directed anteriorly (0)
   — directed posteriorly (1)

16. *Styloid process of humerus:*
   — long and sharp (0)
   — long and flat (1)
   — short and blunt (2)

17. *Second finger:*
   — without bony phalanx (0)
   — with one bony phalanx (1)

18. *Number of phalanges in third finger:*
   — two (0)
   — three (2)

19. *Second phalanx of third finger:*
   — twice or less than twice as long as the first one (0)
   — three times as long as the first one (1)

20. *Fibula:*
   — rudimentary (0)
   — well developed (1)

21. *Fibula articulating with:*
   — astragalus (0)
   — calcaneum (1)

22. *Feet phalanx formula:*
   — 2.2.2.2.2 (0)
   — 2.3.3.3.3 (1)

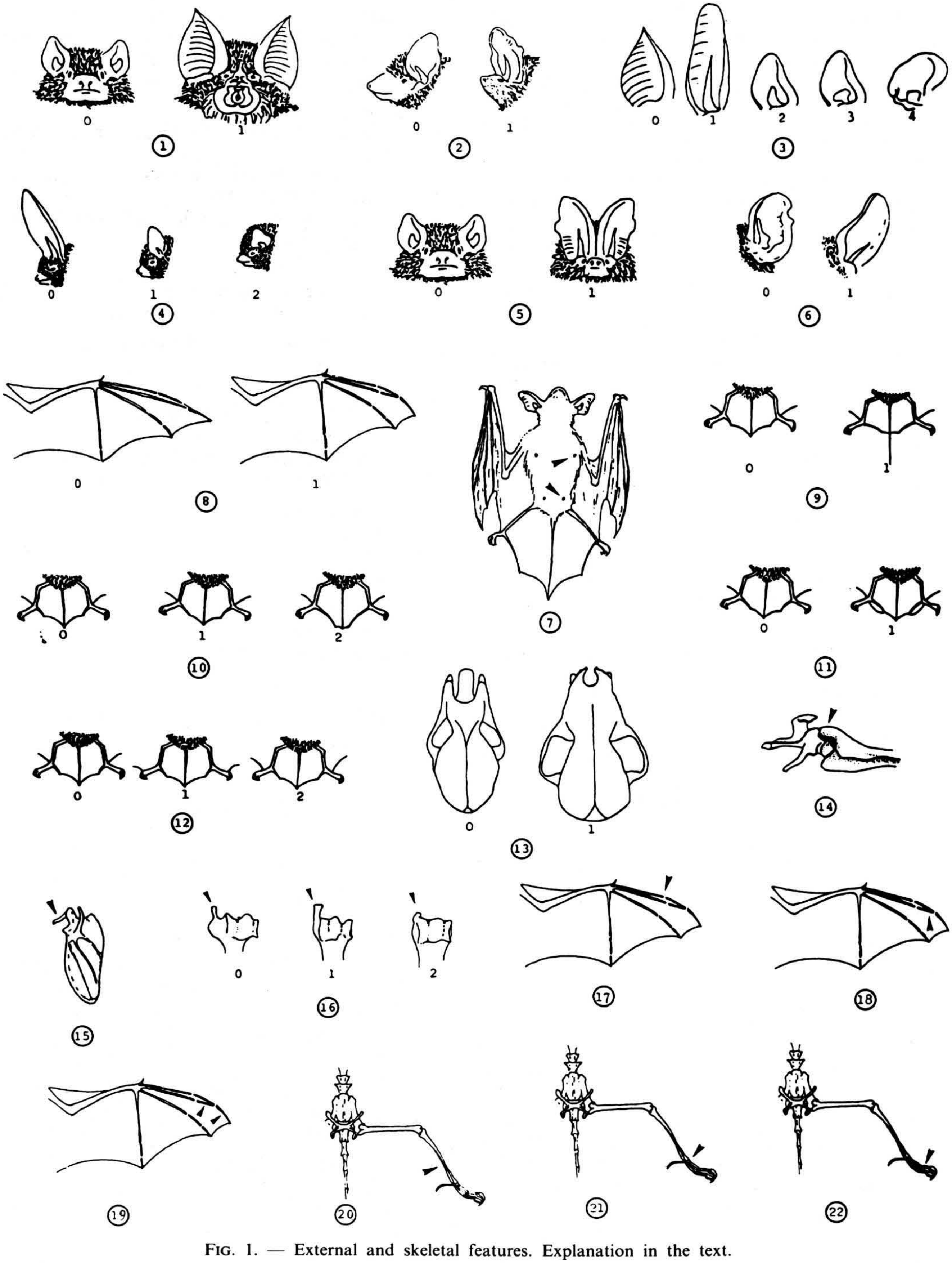

FIG. 1. — External and skeletal features. Explanation in the text.

Most of the morphological external features used for the determination of specimens were already described by Miller in 1907 and 1912. The shape of the wing has been calculated with Miller's data (1912). The presence of an extra pair of rudimentary mammary glands in *Rhinolophus* is described in Grassé (1948).

Many skeletal features also appear in Miller (1907, 1912), though some of them have been changed in our analysis according to more recent literature. This is the case, for example, of the presence of the fibula in the hind legs: according to Miller (1907) Rhinolophidae, Vespertilionidae and Molossidae present a complete fibula, whereas Dobson (1878), Flower (1885) and Flower & Lydekker (1891) describe it as incomplete in all Chiroptera except Molossidae. This fact has been recently checked by Walton & Walton (1970). These last authors are also the source of our character n. 21. On the other hand, character n. 14 has been preserved as found in Miller (1912), on the basis of personal observations. We do not agree with the data found in Walton & Walton for character n. 15, which has been included for the species of which we had material available. Character n. 15 corresponds to the three major groups in which the humera of European Chiroptera have been divided by Felten *et al.* (1973). The source of character n. 22 was Grassé (1948).

The matrix built with these characters can be observed in Table I.

B. *Dental Features*

1. *Number of cusps in* I^1:
— one, very small (0)
— one, well developed (1)
— two (2)
— three (3)

2. *Number of cusps in* I^2:
— this tooth is absent (0)
— one cusp (1)
— two cusps (2)
— three cusps (3)

3. *Number of cusps in* I_1:
— two (1)
— three (1)
— four (2)

4. *Number of cusps in* I_2:
— two (0)
— three (1)
— four (2)

5. *Number of cusps in* I_3:
— this tooth is absent (0)
— two (1)
— three (2)
— four (3)

6. *Number of grooves in upper C:*
— none (0)
— one, on the labial face (1)
— two, one on the labial face, one on the lingual face (2)
— three, one on the labial face, two on the lingual face (3)
— four, two on each face (4)

7. *Cingular cusplet at mesiolingual margin of lower C:*
— absent (0)
— present (1)

8. *Number of upper premolars:*
— one, P^4 (0)
— two, P^2 being single-rooted (1)
— three, P^2 and P^3 being single-rooted (2)
— three, P^2 is single-rooted, P^3 with three roots (3)

9. *Cingular cusplet at mesiolingual margin of* P^4:
— absent (0)
— present (1)

10. *Number of lower premolars:*
— two, P_2 is single-rooted (0)
— three, P_2 and P_3 are single-rooted (1)
— three, P_2 is single-rooted, P_3 is two-rooted (2)

11. *Cingulum of* P_4 *at labial view:*
— straight and very oblique (0)
— concave towards the roots (1)
— with two concavities, each towards a root (2)

12. *Upper molars:*
— without paraloph (0)
— with paraloph (1)

13. *Two first upper molars:*
— without heel (0)
— with heel, but without hypocone (1)
— with both heel and hypocone (2)

14. *Two first upper molars:*
— without metaloph (0)
— with metaloph (1)

15. *Two first upper molars:*
— without metaconule (0)
— with metaconule (1)

16. *Distal reduction of* M^3:
— minimal, affecting almost exclusively the postmetacrista (0)

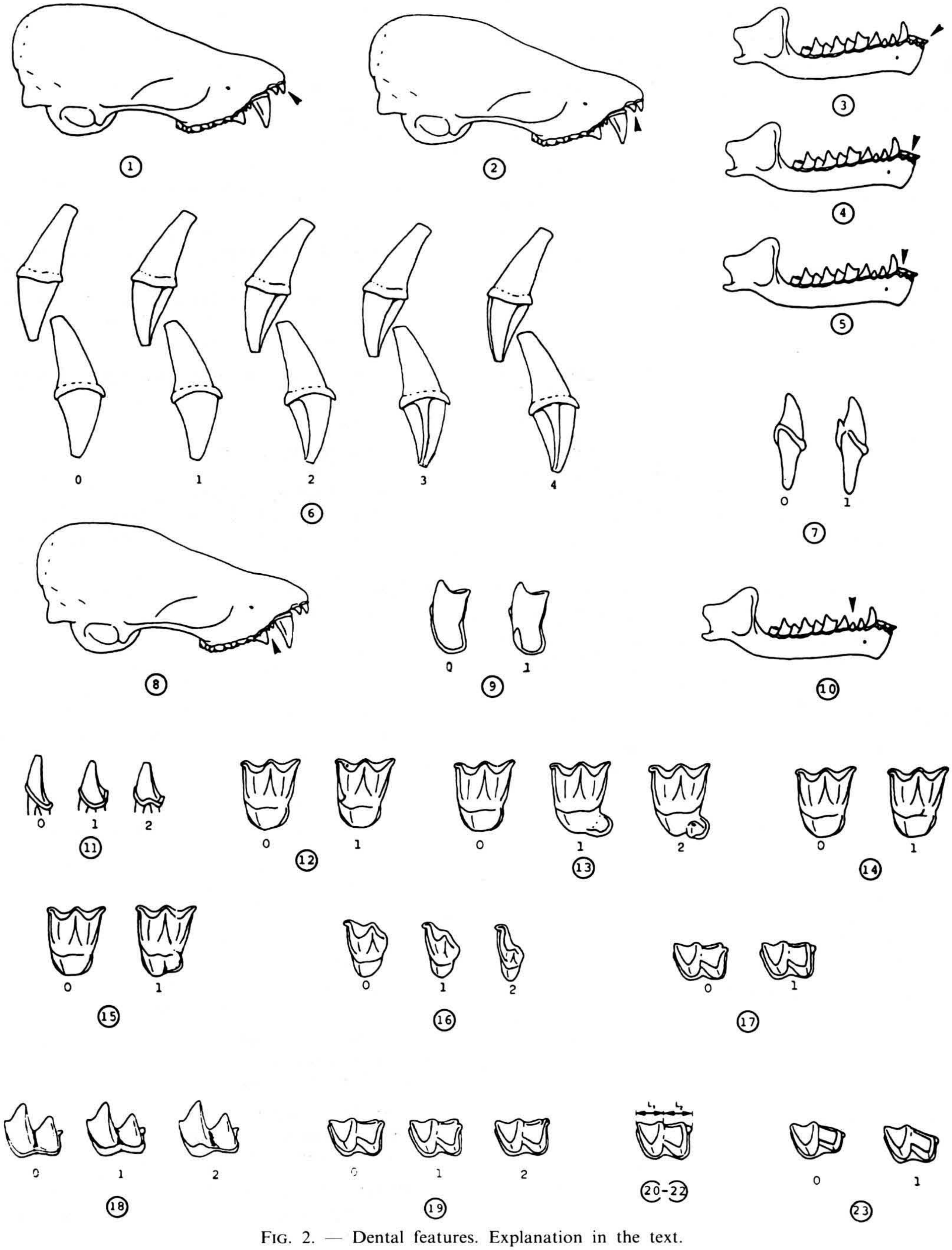

FIG. 2. — Dental features. Explanation in the text.

— intermediate, postparacrista and premetacrista somewhat reduced (1)
— very strong, postparacrista and premetacrista strongly reduced (2)

17. *Pattern of lower molars:*
— nyctalodont (0)
— myotodont (1)

18. *Thickness of labial cingulum in lower molars:*
— thin (max. height cingulum/length tooth < 0.09) (0)
— thick (max. height cingulum/length tooth > 0.12) (1)
— thick at trigonid, thin at the talonid (2)

19. *Base of hypoconulid in* M_1 *and* M_2*:*
— in line with the entoconid (0)
— more labial than the entoconid (1)
— more lingual than the entoconid (2)

20. *Trigonid of* M_1*:*
— open (length trigonid > length talonid (0)
— regular (length trigonid $\simeq$ length talonid) (1)
— closed (length trigonid < length talonid) (2)

21. *Trigonid of* M_2*:*
(as n. 20)

22. *Trigonid of* M_3*:*
(as n. 20)

23. *Relative location of hypoconid in* M_3*:*
— clearly more labial than in M_2 (O)
— about the same as in M_2 (1)

The terminology used for the dental characters is after Van Valen (1966) and posterior modifications found in de Bruijn & Rümke (1974). In the systematics of recent bats, only dental formulae have been taken into account. In Miller (1907, 1912) some characters of the tooth morphology in bats are described, such as the presence of a heel in the upper molars, the presence of a hypocone (n. 13), and the metaconule, which he refers to as a hypocone (n. 15); the " secondary commissures ", which are the paraloph (n. 12) and the metaloph (n. 14).

Palaeontologists have occasionally mentioned other characters (ns. 6, 19, 20, 21, 22, 23) in the description of fossil material, though no formal definition of features is found in the literature. For example, the openness of the trigonid in lower molars is sometimes mentioned, but no criterium to define " open " or " closed " is given.

We have added three new characters (ns. 11, 16, 18), as we consider them of systematic importance.

Results

The similarity matrices obtained with the Jaccard index are shown in Table III ; the left half belongs to the external and skeletal features and the right half of the table belongs to the dental features. From each matrix we have obtained two different phenograms shown in Figs. 3 and 4, using single and average linkage. The four classifications are not identical, and we shall compare the congruence between them, and with the actual systematic arrangement.

Classifications based on external and skeletal features show a more constant pattern, with three main groups: Rhinolophidae, Molossidae and Vespertilionidae, with the first one quite distant from the two others. According to these arrangements, there is no reason for a Miniopteridae family group, as has been proposed by Mein & Tupinier (1977). The character pattern distribution is very coherent, and many diagnostic characters (ns. 1, 3, 10, 12, 13, 14, 16, 17, 18, 21, 22) can be retained. However, the level of specific differentiation is very poor, most of the species being morphologically identical. Absolute metric data are necessary to distinguish them.

Classifications based on dental features show a higher power of discrimination. Most of the species can be separated with a single morphologic dental character without using absolute metric data. The two families Rhinolophidae and Vespertilionidae appear clearly in both clusters, very far from one another. The Molossidae are also well characterized by dental features, but its position changes in both clusters. Miniopteridae appear as an independent taxon at the same level of differentiation as Molossidae. This taxon has been proposed on the basis of a heterogeneous set of characters (number of upper premolars, type of flight, reproductory physiology); the morphology of isolated teeth confirms its differences from the Vespertilionidae. The pattern of distribution of dental characters is less coherent than in the other case and consequently, the two classifications vary in a higher degree. However, diagnostic characters with high systematic value can be retained from our study (ns. 1, 5, 13, 16, 18).

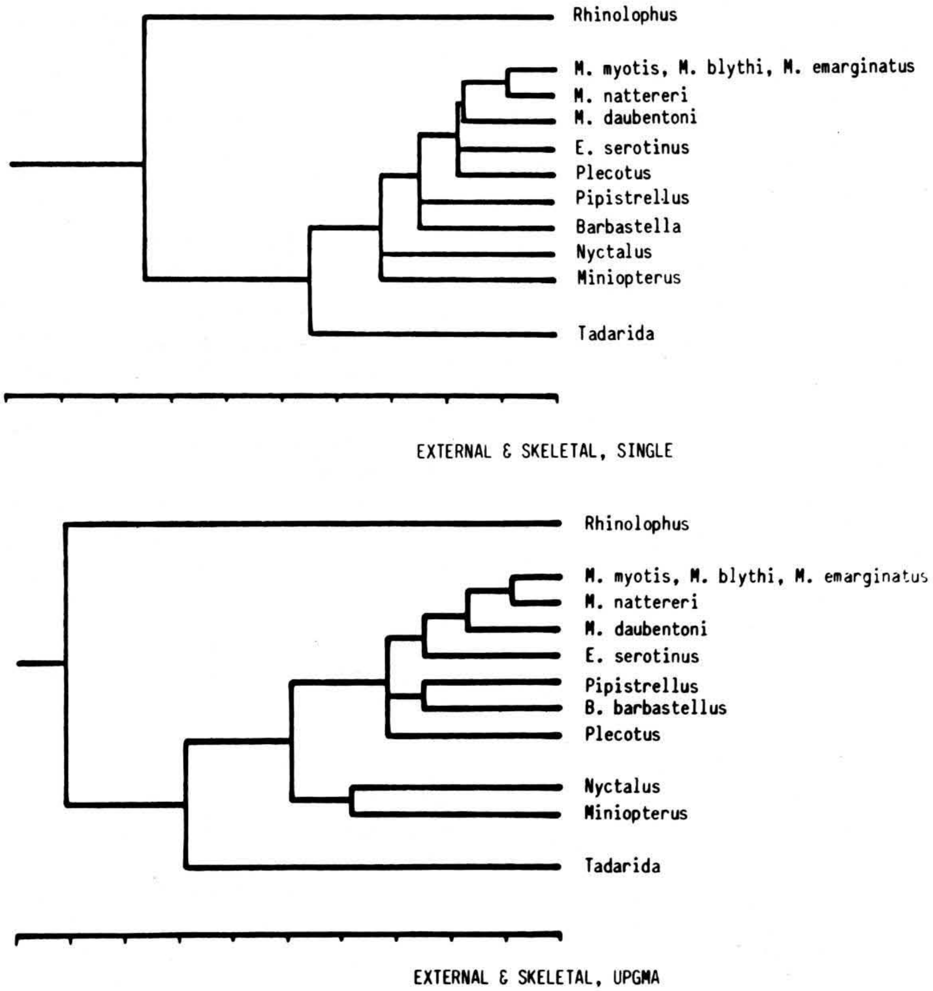

FIG. 3. — Single linkage and UPGMA clusters obtained with the external and skeletal features.

Congruence between classifications based on different sets of characters can be measured by correlating the two similarity matrices. The Pearson coefficient of correlation, r, is a good estimate of the degree of correspondence between the character distributions. In our case, r reaches a value of 0.77, which can be considered as a good agreement between both distributions. In Table IV, several correlations of two sets of characters in different groups can be compared with our results.

CONCLUSION

The comparative study of character distributions of external and skeletal vs. dental morphology in Chiroptera shows a good correlation between both classifications. Dental features are better for the identification of species than external and skeletal features. Half of the external characters and one quarter of the dental ones show a high systematic value, appearing as diagnostic characters in the main clusters. The good agreement between both kinds of characters allows one to compare the results of studies of fossil and recent species of Chiroptera, and is a proof of the ability of the palaeontologists in selecting valid systematic characters in isolated teeth.

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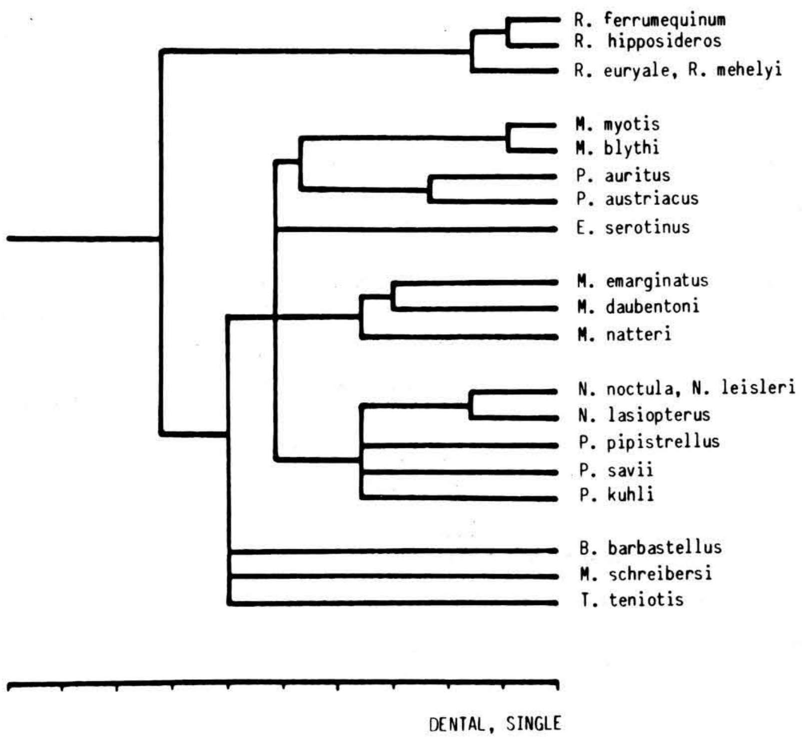

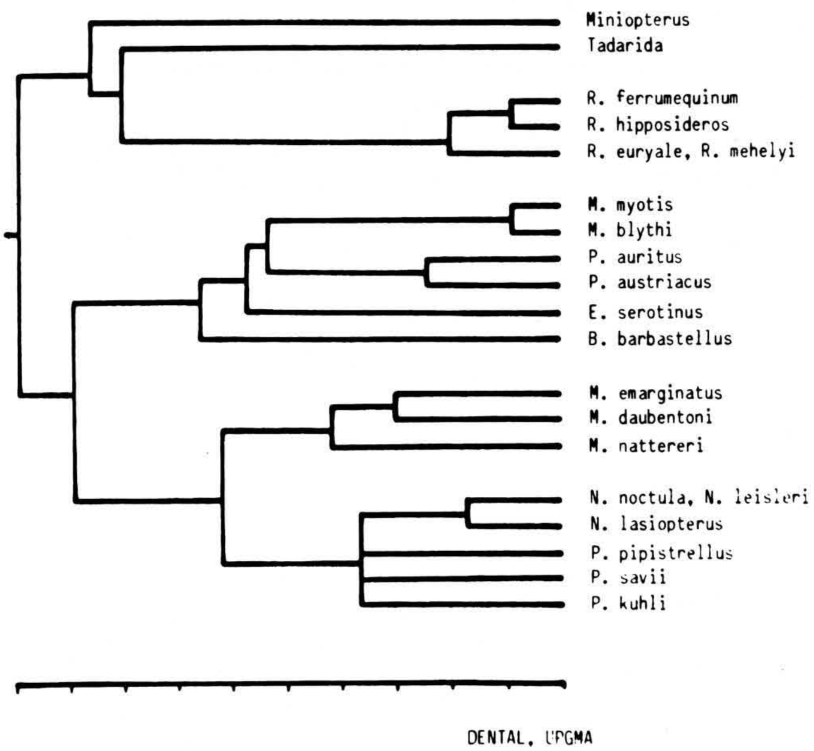

FIG. 4. — Single linkage and UPGMA clusters obtained with the dental features.

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TABLE I. Distribution in the different species of the external and skeletal features.

EXTERNAL AND SKELETAL FEATURES

	Nose		Ears				M.g.	Patagium					S.	Scap.		Arm				H. limbs		
SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Rhinolophus ferrumequinum	1	—	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	—	0	1	0
Rhinolophus mehelyi	1	—	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	—	0	1	0
Rhinolophus euryale	1	—	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	—	0	1	0
Rhinolophus hipposideros	1	—	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	—	0	1	0
Myotis myotis	0	0	1	1	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	1
Myotis blythi	0	0	1	1	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	1
Myotis emarginatus	0	0	1	1	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	1
Myotis nattereri	0	0	1	0	0	1	0	1	0	1	0	1	1	1	1	2	1	1	0	0	0	1
Myotis daubentoni	0	0	1	1	0	1	0	1	0	2	0	2	1	1	1	2	1	1	0	0	0	1
Pipistrellus pipistrellus	0	0	2	1	0	1	0	1	0	2	1	1	1	1	0	2	1	1	0	0	0	1
Pipistrellus kuhli	0	0	2	1	0	1	0	1	0	2	1	1	1	1	0	2	1	1	0	0	0	1
Pipistrellus savii	0	0	2	1	0	1	0	1	0	2	1	1	1	1	0	2	1	1	0	0	0	1
Eptesicus serotinus	0	0	2	2	0	1	0	1	0	1	0	1	1	1	—	2	1	1	0	0	0	1
Nyctalus noctula	0	0	3	2	0	1	0	0	0	1	1	0	1	1	—	2	1	1	0	0	0	1
Nyctalus lasiopterus	0	0	3	2	0	1	0	0	0	1	1	0	1	1	—	2	1	1	0	0	0	1
Nyctalus leisleri	0	0	3	2	0	1	0	0	0	1	1	0	1	1	—	2	1	1	0	0	0	1
Barbastella barbastellus	0	1	1	1	1	0	0	1	0	1	1	1	1	1	—	2	1	1	0	0	0	1
Plecotus auritus	0	1	1	0	1	1	0	1	0	1	0	1	1	1	—	2	1	1	0	0	0	1
Plecotus austriacus	0	1	1	0	1	1	0	1	0	1	0	1	1	1	—	2	1	1	0	0	0	1
Miniopterus schreibersi	0	0	2	2	0	1	0	0	0	1	0	0	1	1	0	2	1	1	1	0	0	1
Tadarida teniotis	0	0	4	0	1	1	0	1	0	1	0	0	1	2	0	1	1	1	—	1	0	1

TABLE II. Distribution in the different species of the dental characters.

DENTAL FEATURES

	Incisors					C		Premolars				Upper molars								Lower molars			
SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Rhinolophus ferrumequinum	0	0	1	1	0	1	0	1	0	1	2	0	1	0	0	0	0	0	1	0	0	0	1
Rhinolophus mehelyi	0	0	1	1	0	0	0	1	1	1	2	0	1	0	0	0	0	0	1	0	0	0	1
Rhinolophus euryale	0	0	1	1	0	0	0	1	1	1	2	0	1	0	0	0	0	0	1	0	0	0	1
Rhinolophus hipposideros	0	0	1	1	0	1	0	1	0	1	2	0	1	0	0	0	0	0	1	0	0	1	1
Myotis myotis	3	3	2	2	3	2	0	2	0	1	2	0	0	0	0	2	1	2	0	1	1	0	0
Myotis blythi	3	3	2	2	3	2	0	2	0	1	2	0	0	0	0	2	1	2	0	1	1	1	0
Myotis emarginatus	3	3	2	2	3	2	1	2	0	1	2	1	0	1	1	1	1	2	0	2	2	2	0
Myotis nattereri	3	3	2	2	3	1	1	2	0	1	1	0	0	0	1	1	1	2	1	1	2	2	0
Myotis daubentoni	3	3	2	2	3	3	1	2	1	1	1	1	0	1	1	1	1	2	1	2	2	2	0
Pipistrellus pipistrellus	2	3	2	1	3	1	1	1	1	0	1	1	0	0	1	1	0	2	2	2	2	2	1
Pipistrellus kuhli	2	3	2	1	3	1	1	1	0	0	0	1	0	1	1	2	0	2	2	2	2	2	0
Pipistrellus savii	2	3	2	1	3	1	1	1	1	0	0	0	0	0	1	1	1	2	0	2	2	2	0
Eptesicus serotinus	2	2	2	2	3	3	1	0	1	0	2	0	0	0	1	2	1	2	0	0	1	0	0
Nyctalus noctula	2	2	2	2	3	0	1	1	1	0	0	1	0	1	1	1	0	2	0	2	2	2	1
Nyctalus lasiopterus	2	2	2	2	3	1	1	1	1	0	0	1	0	1	1	1	0	2	1	2	2	2	1
Nyctalus leisleri	2	2	2	2	3	0	1	1	1	0	0	1	0	1	1	1	0	2	0	2	2	2	1
Barbastella barbastellus	2	3	2	2	3	2	1	1	0	0	1	0	0	0	0	1	0	1	2	0	0	0	0
Plecotus auritus	2	2	1	2	3	2	1	1	0	1	2	0	0	0	0	2	1	2	2	1	2	2	0
Plecotus austriacus	2	2	1	2	3	2	1	1	0	1	2	0	0	0	0	2	1	2	0	0	2	1	0
Miniopterus schreibersi	2	1	1	2	2	4	1	3	1	2	0	1	1	1	1	1	0	1	1	0	2	1	1
Tadarida teniotis	*1*	*0*	*0*	*0*	*1*	*0*	*0*	*1*	*1*	*0*	*1*	*1*	*2*	*0*	*0*	*1*	*0*	*2*	*1*	*2*	*2*	*2*	*1*

TABLE III. Similarity matrices. Upper right, dental characters; lower left, external and skeletal.

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*
1	—	84.0	84.0	91.7	21.1	17.9	7.0	15.0	4.5	15.0	12.2	12.2	12.2	7.0	12.2	7.0	24.3	21.1	24.3	15.0	21.1
2	100	—	100	76.9	17.9	15.0	4.5	9.5	7.0	15.0	7.0	12.2	15.0	12.2	12.2	12.2	21.1	17.9	21.1	17.9	27.8
3	100	100	—	76.9	17.9	15.0	4.5	9.5	7.0	15.0	7.0	12.2	15.0	12.2	12.2	12.2	21.1	17.9	21.1	17.9	27.8
4	100	100	100	—	17.9	21.1	7.0	15.0	4.5	15.0	12.2	12.2	9.5	7.0	12.2	7.0	21.1	21.1	27.8	17.9	21.1
5	25.0	25.0	25.0	25.0	—	91.7	48.4	48.4	31.4	15.0	21.1	27.8	43.8	15.0	12.2	15.0	35.3	48.4	48.4	2.2	9.5
6	25.0	25.0	25.0	25.0	100	—	48.4	48.4	31.4	15.0	21.1	27.8	39.4	15.0	12.2	15.0	31.4	48.4	53.3	4.5	9.5
7	25.0	25.0	25.0	25.0	100	100	—	58.6	70.4	35.3	43.8	43.8	31.4	43.8	39.4	43.8	27.8	39.4	39.4	17.9	15.0
8	21.2	21.2	21.2	21.2	91.3	91.3	91.3	—	64.3	39.4	35.3	48.4	31.4	27.8	35.3	27.8	35.3	43.8	35.3	15.0	17.9
9	25.0	25.0	25.0	25.0	83.3	83.3	83.3	76.0	—	43.8	39.4	43.8	31.4	43.8	48.4	43.8	24.3	27.8	24.3	24.3	24.3
10	17.6	17.6	17.6	17.6	69.2	69.2	69.2	63.0	69.2	—	64.3	64.3	27.8	58.6	64.3	58.6	39.4	27.8	21.1	24.3	39.4
11	17.9	17.9	17.9	17.9	69.2	69.2	69.2	63.0	69.2	100	—	58.6	27.8	53.3	58.6	53.3	35.3	35.3	27.8	21.1	21.1
12	17.6	17.6	17.6	17.6	69.2	69.2	69.2	63.0	69.2	100	100	—	43.8	53.3	53.3	53.3	35.3	35.3	35.3	17.9	24.3
13	18.8	18.8	18.8	18.8	82.6	82.6	82.6	82.6	68.0	75.0	75.0	75.0	—	35.3	31.4	35.3	35.3	39.4	48.4	15.0	9.5
14	15.2	15.2	15.2	15.2	61.5	61.5	61.5	61.5	55.6	61.5	61.5	61.5	68.0	—	84.0	100	27.8	27.8	27.8	35.3	35.3
15	15.2	15.2	15.2	15.2	61.5	61.5	61.5	61.5	55.6	61.5	61.5	61.5	68.0	100	—	84.0	27.8	27.8	24.3	39.4	35.3
16	15.2	15.2	15.2	15.2	61.5	61.5	61.5	61.5	55.6	61.5	61.5	61.5	68.0	100	100	—	27.8	27.8	27.8	35.3	35.3
17	11.8	11.8	11.8	11.8	68.0	68.0	68.0	61.5	55.6	61.5	61.5	61.5	55.6	50.0	50.0	50.0	—	39.4	39.4	17.9	17.9
18	15.2	15.2	15.2	15.2	75.0	75.0	75.0	82.6	61.5	55.6	55.6	55.6	68.0	50.0	50.0	50.0	75.0	—	76.9	12.2	15.0
19	15.2	15.2	15.2	15.2	75.0	75.0	75.0	82.6	61.5	55.6	55.6	55.6	68.0	50.0	50.0	50.0	75.0	100	—	17.9	12.2
20	17.6	17.6	17.6	17.6	51.7	51.7	51.7	51.7	46.7	51.7	51.7	51.7	68.0	68.0	68.0	68.0	35.5	44.8	44.8	—	17.9
21	8.1	8.1	8.1	8.1	35.5	35.5	35.5	40.0	31.3	31.3	31.3	31.3	37.9	42.9	42.9	42.9	29.0	42.9	42.9	55.6	—

TABLE IV. Comparative results of studies on congruence of characters between different sets of characters (Sneath & Sokal, 1973). The high value of correlation obtained between the two sets of characters in Chiroptera means that the grouping obtained with the external and skeletal features used in the current systematics is highly similar to that obtained with the chosen dental characters. The use of these for the identification of dental remains is, thus, highly justified.

Group of organisms	Sets of characters	N of charac-ters	Value of r
Angiosperm	Floral/Vegetative	61/32	0.17
Bees	Head/the rest	60/62	0.61
Butterflies	External/Internal	100/96	0.69
Birds	Wing/Leg External/Skeletal	82/93 72/51	0.62 0.73
Chiroptera	Extern. & Skelet. Dental	22/23	0.77