

A NUMERICAL TAXONOMIC STUDY OF THE FEATHER MITE  
GENUS BREPHOSCELES (PROCTOPHYLLODIDAE: ALLOPTINAE)

by

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## ABSTRACT

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A numerical taxonomic study is presented for the genus Brephosceles. The phenetic relationships of the OTU'S from five of the six species groups of Brephosceles are examined using a number of numerical taxonomic techniques. The results of four types of clustering methods are compared using cophenetic correlation coefficients. The results of the numerical taxonomic study are used to propose a reevaluation of the genus Brephosceles.

## ACKNOWLEDGMENTS

I wish to extend special acknowledgment to Dr. Paul C. Peterson of the Department of Biology, Youngstown State University for providing encouragement and direction to my research and for providing materials for this study.

A special acknowledgement is extended to Mr. George Hall, artist, who assisted in the preparation of the figures and phenograms.

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Brephosceles. Historical Account

Caull (1927) first recognized three suprageneric subdivisions of the

## INTRODUCTION

While large numbers of publications have appeared over the last decade examining the techniques of numerical taxonomy, few attempts have been made to apply these methodologies to the solution of actual taxonomic problems. This investigation is directed toward the phenetic relationships of six species groups of the feather mite genus Brephosceles (Proctophyllodidae) using methods of numerical taxonomy.

Conventional taxonomic studies of the parasitic Acarina have stressed the use of two or three weighted characters which are believed to represent adaptations to corresponding hosts. It has been suggested that taxa produced in this fashion may represent unnatural assemblages. The purpose of the present study is to unmask these unnatural groupings using methods of numerical or phenetic methodologies in an attempt to further elaborate the association between host and parasite.

Feather mites belong to the acarine superfamily Analgoidea and are found to be obligate ectoparasites living in or on the family of birds. They are commonly found in tandem between the barbs of the wings and tail feathers and apparently exist as scavengers living on feather fragments and sloughed skin cells (Atyee and Braash, 1966). The complete life cycle develops through the following stages; egg, larva, protonymph, tritonymph, and adult. The non-feeding deutonymph is absent in the Analgoidea.

### Brephosceles, Historical Account

Gaud (1957) first recognized three suprageneric subdivisions of the



feather mite family Proctophyllodidae which include the Alloptinae, Proctophyllodinae, and Trouessartinae. Subsequently, Atyeo and Peterson (1971) raised the Alloptinae to the familial level and reassigned the Trouessartinae to the new family Alloptinae. Concomittantly, Peterson (1971a, 1971b) described two additional subfamilies in the Alloptidae; the Echinacarinae and the Oxyalinginae. Thus, the Alloptidae includes the subfamilies Alloptinae (s.s.) (12 genera), the Trouessartinae (10 genera), the Oxyalinginae (5 genera), and the Echinacarinae and Thysanocercinae (monobasic).

The Alloptinae (s.s.) as redefined contains two complexes. They include the Alloptes complex (6 genera) in which the termini of the males is entire, i.e. the terminal lobes are fused, and the Brephosceles complex (6 genera) with males bearing a marked bifurcation of the terminus. In the future, each may be afforded suprageneric status.

The genus Brephosceles was first erected by Hull (1934) for feather mites having males characterized by the development of the terminal lobes and displaying lamellae on their margins. In 1968, Peterson and Atyeo described five new genera related to Brephosceles on the basis of development of certain setae, male genital regions and the condition of epimerites I. Later, Peterson (1971) revised the genus Brephosceles erecting six species groups each of which is restricted to a single avian order. The genus is one of the largest taxa of the Alloptinae containing thirty-nine species. Table 1 is a complete listing of the species, species groups, and the order of birds to which each group is restricted as monographed by Peterson (1971).

Table 1. The Brephosceles speciesGroup I - the forficiger group

Containing only one species, this taxon is restricted to the Gaviiformes (loons).

Brephosceles forficiger  
Megnin and Trouessart (1884)

Group II - the decapus group

This group contains thirteen species of which all but three are restricted to a single host species. The entire group is restricted to the Procellariiformes (shearwaters and petrels).

Brephosceles decapus  
Gaud (1953)

Brephosceles superbus  
Dubinin (1949)

Brephosceles prolatus  
Peterson (1971)

Brephosceles pachyptilae  
Peterson (1971)

Brephosceles pelagicus  
Vitzthum (1921)

Brephosceles lunatus  
Peterson (1971)

Brephosceles pterodromae  
Peterson (1971)

Brephosceles puffini  
Peterson (1971)

Brephosceles marlae  
Peterson (1971)

Brephosceles selenopeltatus  
Peterson (1971)

Groups III - the marginiventris group

Table 1. continued

---

Of the five species in this group, two are restricted to a single host while the remainder are recorded from two or more hosts. This species group is restricted to the Procellariiformes (shearwaters, petrels, and albatrosses).

Brephosceles margineventris  
Trouessart (1889)

Brephosceles diomedei  
Atyeo and Peterson (1970)

Brephosceles disjunctus  
Peterson (1971)

Brephosceles lanceolatus  
Peterson (1971)

Brephosceles bilobatus  
Peterson (1971)

Group IV - the lambda group

This small group of four species, restricted to a single host, is restricted to the Anseriformes (ducks, geese, and swans).

Brephosceles lambda  
Trouessart (1885)

Brephosceles discidicus  
Peterson (1971)

Brephosceles anatina  
Dubinin (1951)

Brephosceles anhimae  
Peterson (1971)

Group V - the geranoxenus group

These two species of mites are ectoparasitic on two orders of birds - Gruiformes and Charadriiformes. B. geranoxenus is associated with a single host while chaubaudi is associated with three different species of birds.

Brephosceles geranoxenus  
Peterson (1968)

Brephosceles chaubaudi  
Peterson (1971)

Table 1. continued

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Brephosceles chaubaudi  
Gaud (1968)

Group VI - the charadrii group

The charadrii group is the largest species group of Brephosceles with seventeen species. Seven of these species are restricted to a single host while the remaining ten are found associated with two or more hosts. The group is parasitic on the Charadriiformes (sandpipers and plovers).

Brephosceles charadrii  
Dubinin (1951)

Brephosceles haematopi  
Peterson (1971)

Brephosceles turgidus  
Peterson (1971)

Brephosceles stephanibycis  
Peterson (1971)

Brephosceles afribycis  
Peterson (1971)

Brephosceles furcifer  
Trouessart (1885)

Brephosceles vanelli  
Gaud (1959)

Brephosceles belonopteri  
Peterson (1971)

Brephosceles tuberi  
Peterson (1971)

Brephosceles longistriatus  
Peterson (1971)

Brephosceles constrictus  
Peterson (1971)

Brephosceles hoplopteri  
Peterson (1971)

Brephosceles inornatus  
Peterson (1971)

Table 1. continued

---



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Brephosceles chilensis      *Materials Utilized*  
Peterson (1971)

Brephosceles virginensis      *Materials Utilized*  
Peterson (1971)

Brephosceles lobivanelli      *Materials Utilized*  
Peterson (1971)

Brephosceles collaricus      *Materials Utilized*  
Peterson (1971)

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All the females were measured on an American Optical Company model Fifty scope equipped with a floating stage. The males were measured with a Wild-Nearbrugg phase contrast microscope. Measurements were made with the use of a micrometer disc eyepiece and were immediately converted to microns using a table of equivalents. The measurements for each OIU along with the name of the host and the identification number of the slide were then recorded on a data sheet.

#### Characters Utilized

Character selection for the present study was based on the criteria suggested by Soma and Sneath (1963). In this sense, a character

## METHODS AND MATERIALS

### Materials Utilized

All specimens used in this study were obtained from the feather mite collection housed at Youngstown State University. Each individual specimen was considered as an OTU (operational taxonomic unit). All OTU's had been identified, mounted on a slide, and catalogued prior to use in the present study. It was the author's intention to obtain at least eight replicates of each species, especially those of the species group VI. By using many replicates, it was thought that the extent of intrataxon variation and variation due to different hosts could be detected. Since only those slides were used that were in perfect condition, it was not always possible to obtain eight replicates of every species. However, the use of such specimens made the use of the N.C. designation (no comparison) unnecessary.

All the females were measured on an American Optical Company model Fifty scope equipped with a floating stage. The males were measured with a Wild-Heerbrugg phase contrast microscope. Measurements were made with the use of a micrometer disc eyepiece and were immediately converted to microns using a table of equivalents. The measurements for each OTU along with the name of the host and the identification number of the slide were then recorded on a data sheet.

### Characters Utilized

Character selection for the present study was based on the criterion suggested by Sokal and Sneath (1963). In this sense, a character

is considered to be any attribute of a group of organisms that varies from one specimen to another and can not be logically subdivided. These characters may be either quantitative, measurements of different parts of the body, or qualitative, the presence, absence or state of a character. Of the sixty characters eventually chosen, eleven were qualitative and forty-nine quantitative.

Since feather mites display marked sexual dimorphism, only nineteen of the sixty characters were common to both sexes. Thirty-nine characters were selected for the females and forty for the males. Tables 2 and 3 list the characters indicating type and area of the body utilized for each sex. The character state values for each OTU were punched on computer cards for processing and are on file in the Biology Department, Youngstown State University.

As a result of segments being fused, lost or modified in the acari, the body has been arbitrarily divided into the following regions; the gnathosoma, (chelicerae and pedipalps) the propodosoma (region of legs I and II) and the hysterosoma (regions of legs III and IV plus terminus). The latter two regions collectively are referred to as the idiosoma. Thus the idiosoma (propodosoma and hysterosoma) is characterized as the entire body of the mite exclusive of the mouth parts. The terminal portion of idiosoma posterior to legs IV is referred to as the opisthosoma.

An effort was made to select characters in each area of the body. For both male and female OTU'S extensive use was made of idiosoma chaetotaxy. The nomenclatural system used in the present study was originally developed by Atyeo and Gaud (1966) and subsequently modified and adapted to Brephosceles by Peterson (1971).





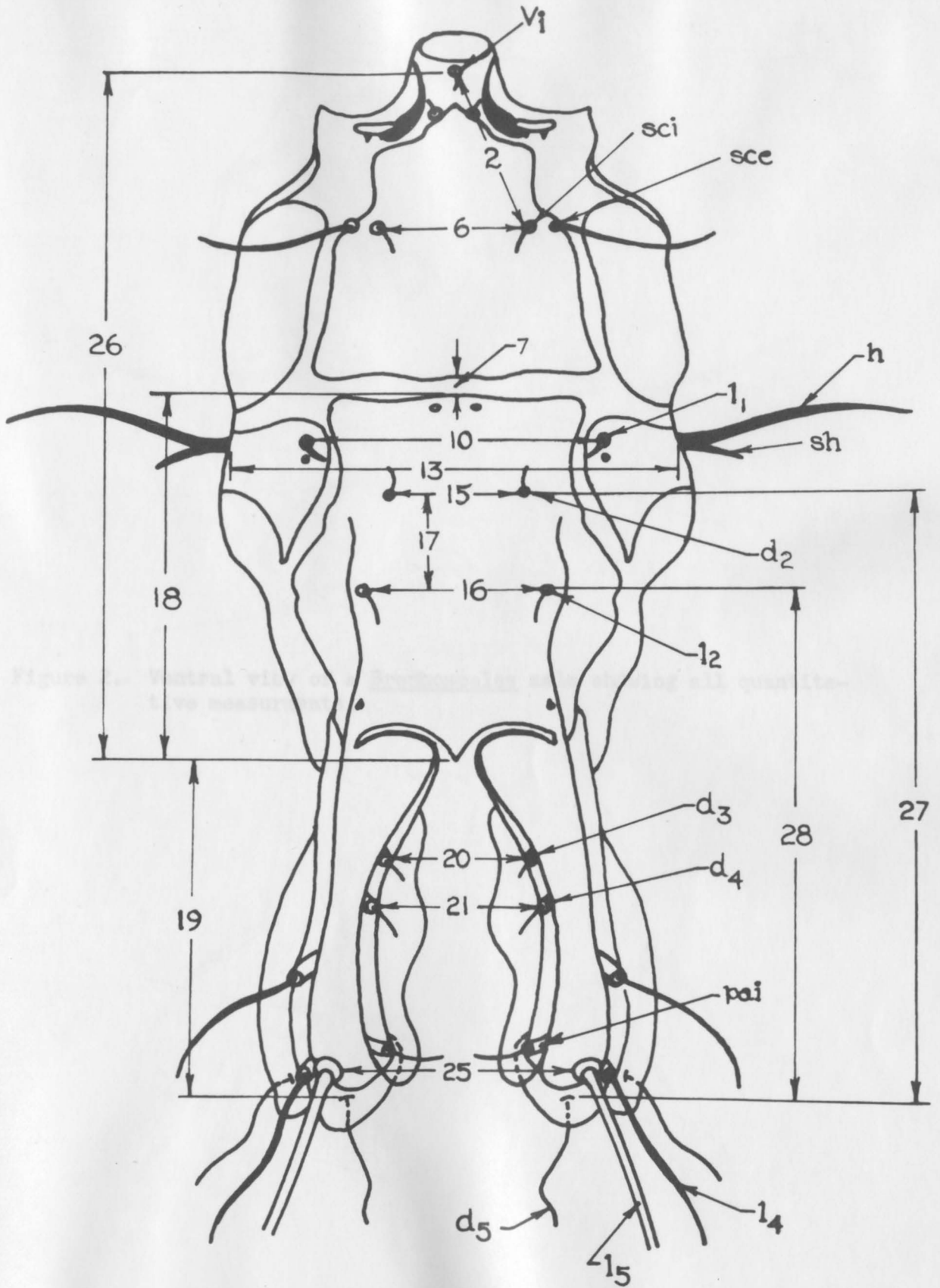
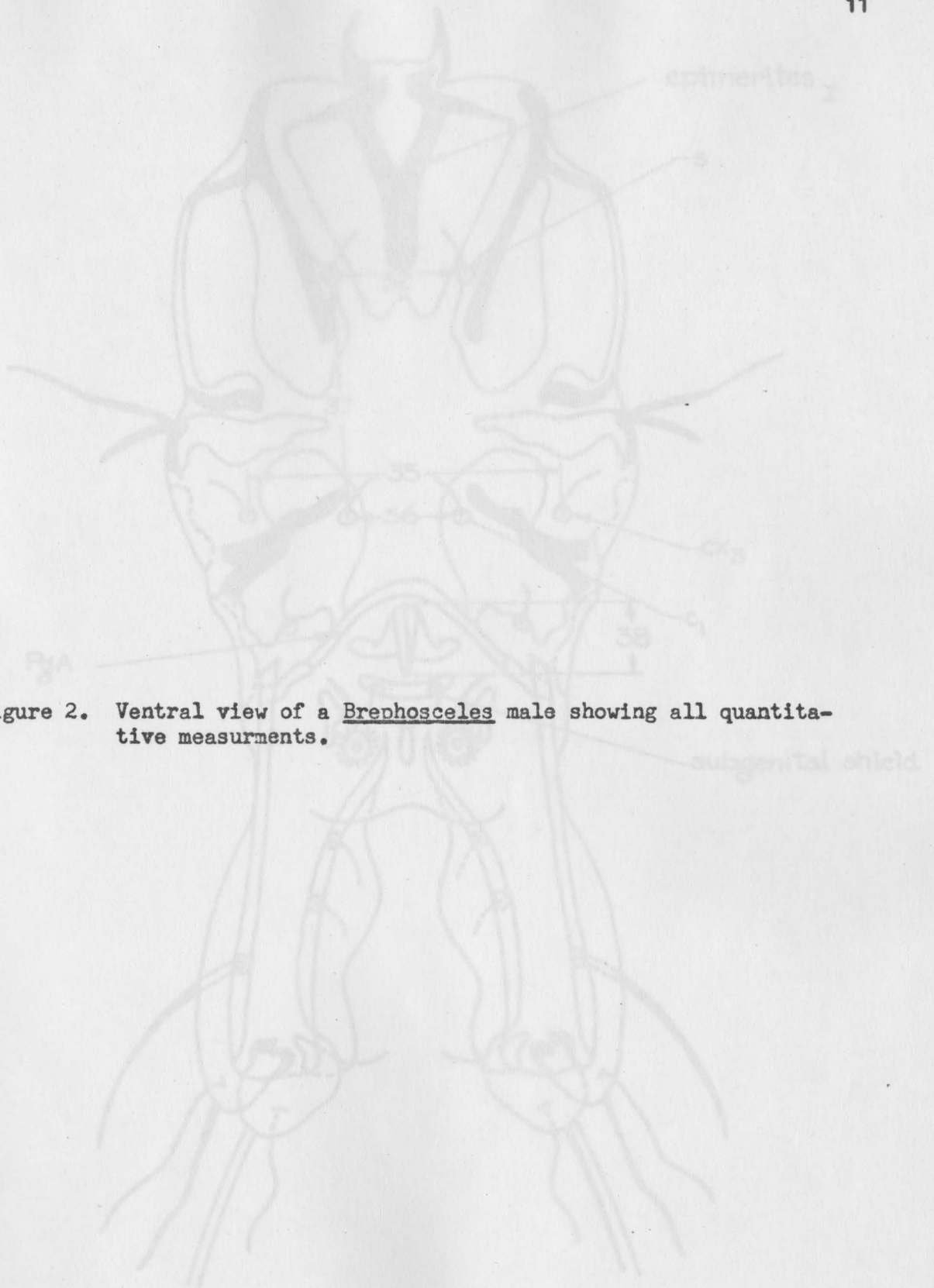
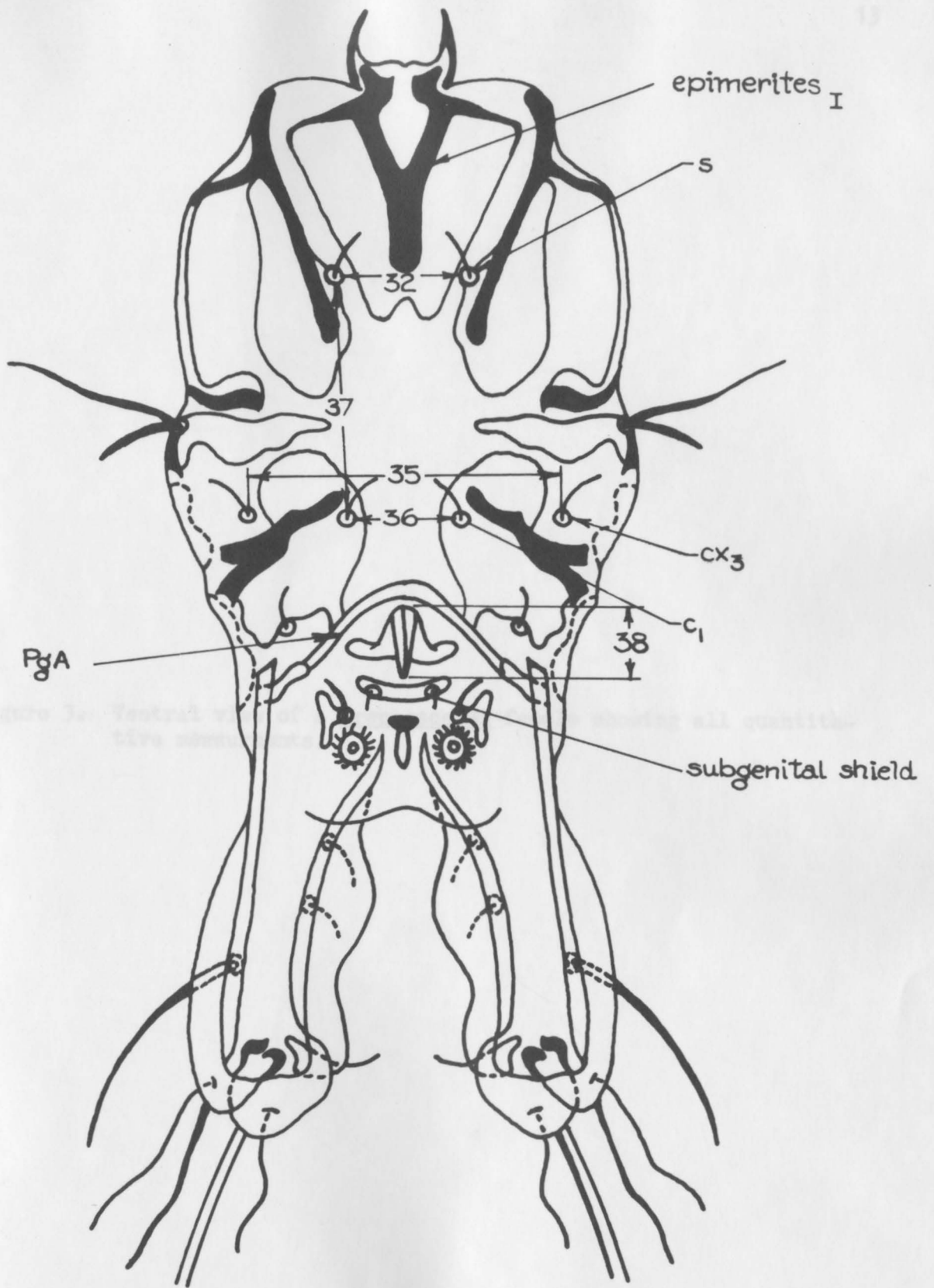


Figure 2. Ventral view of a Brephosceles male showing all quantitative measurements.





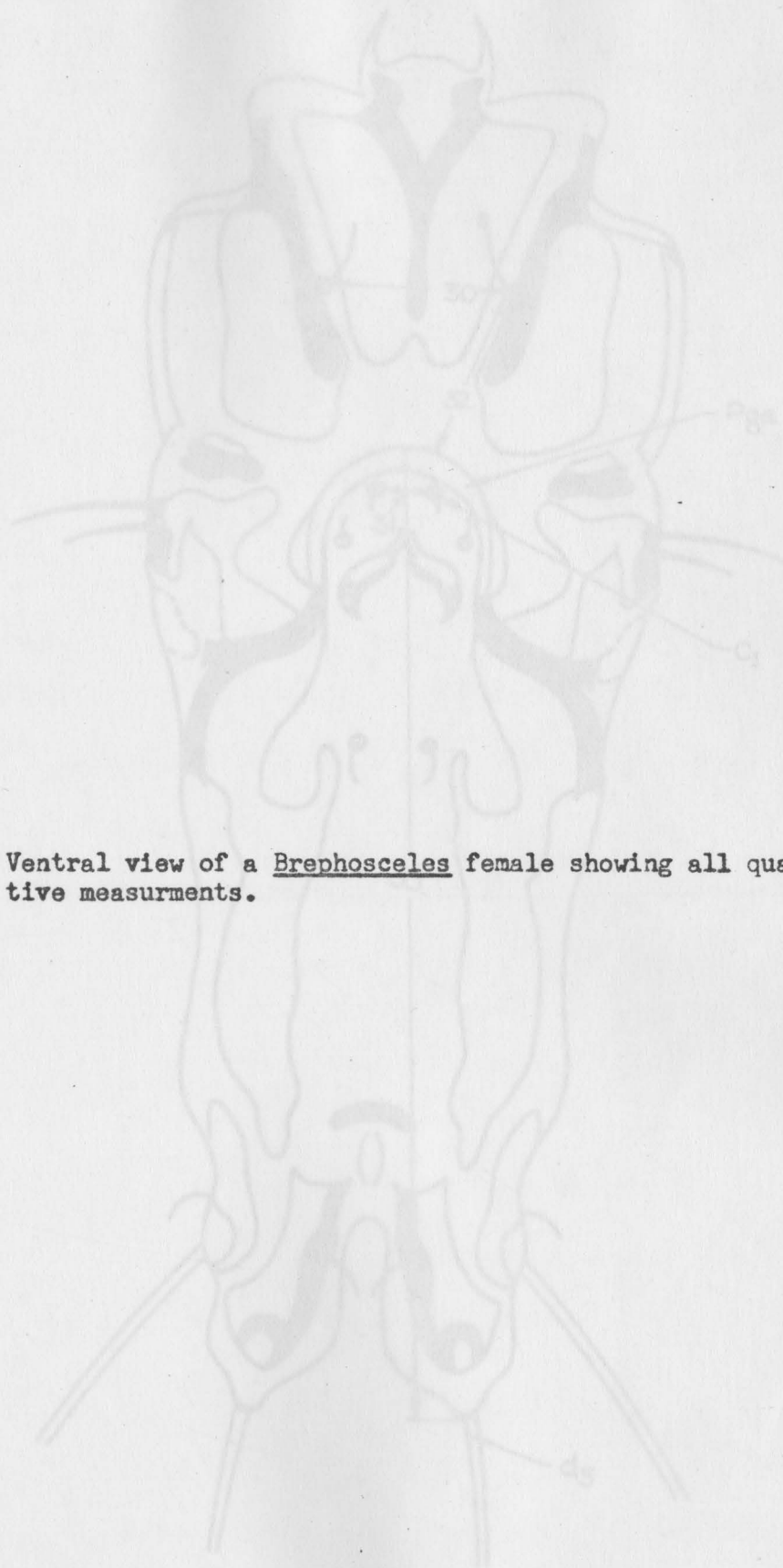


Figure 3. Ventral view of a Brephosceles female showing all quantitative measurements.

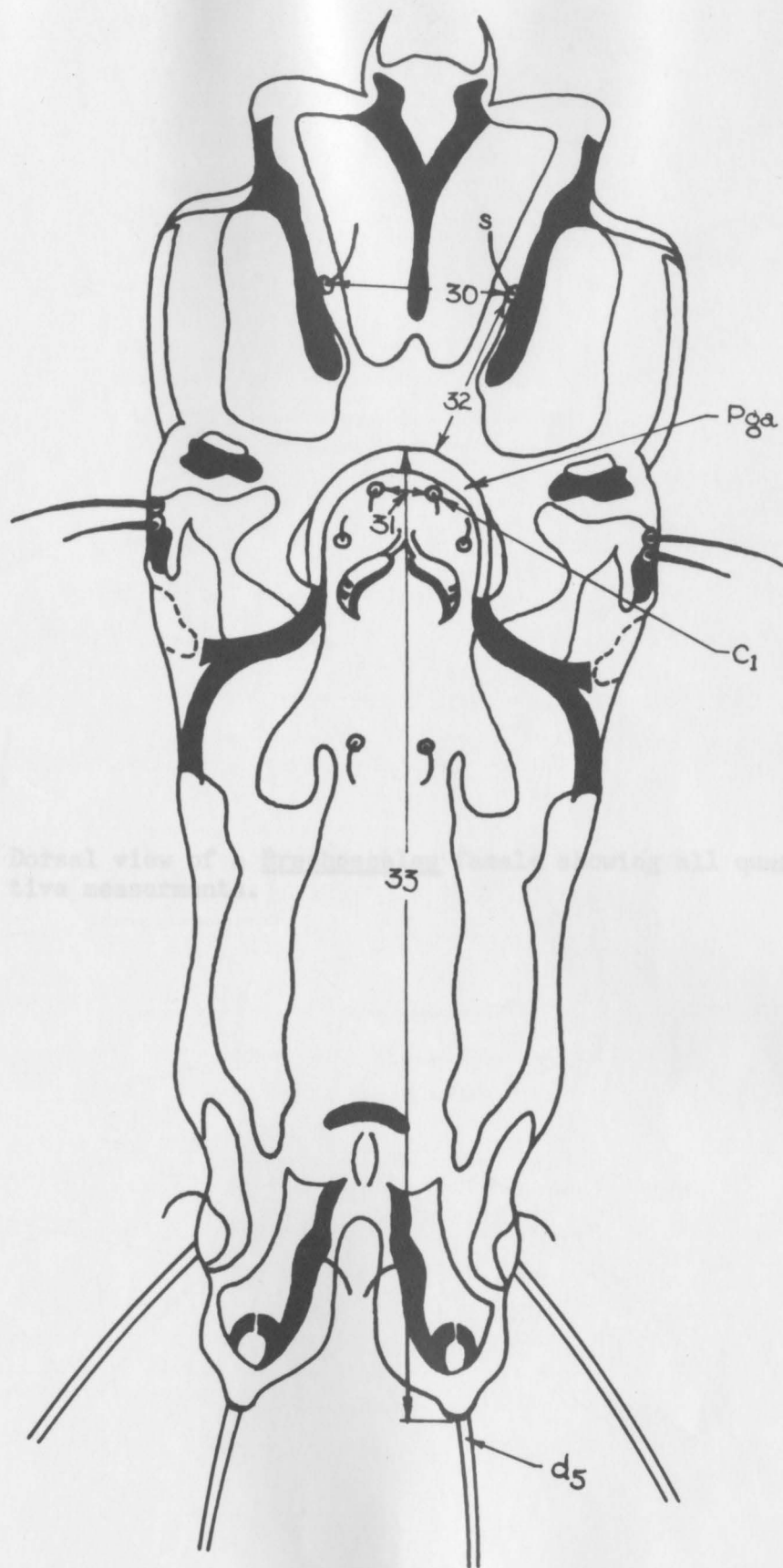


Figure 4. Dorsal view of *Exochus* sp. showing all quantitative measurements.

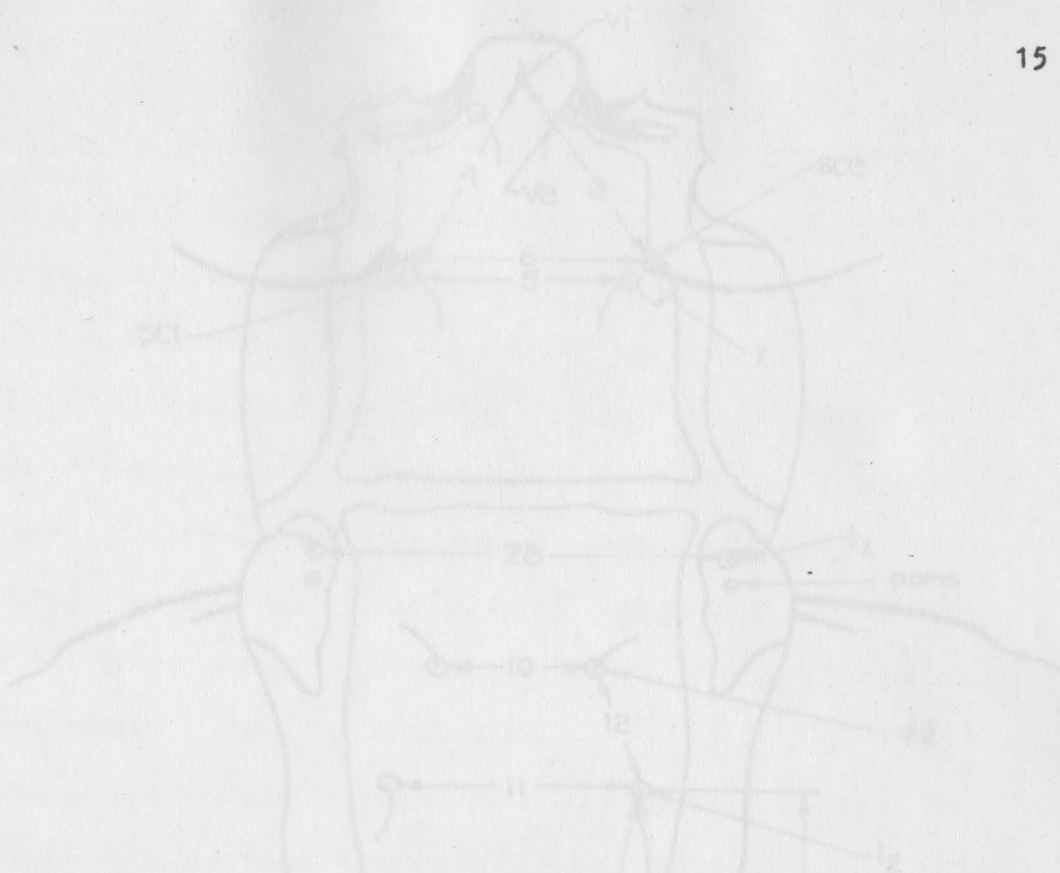
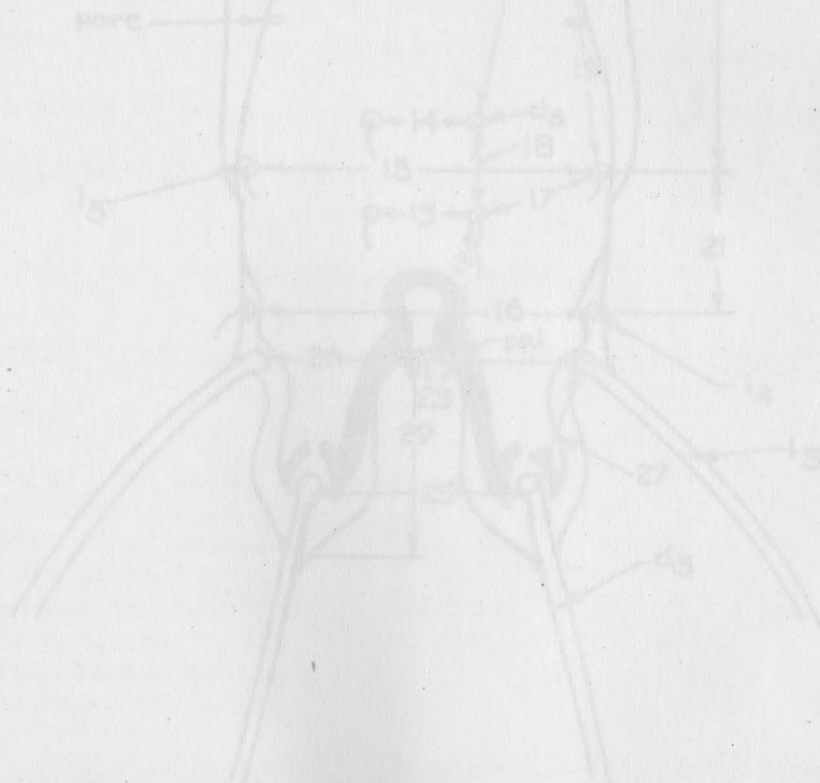
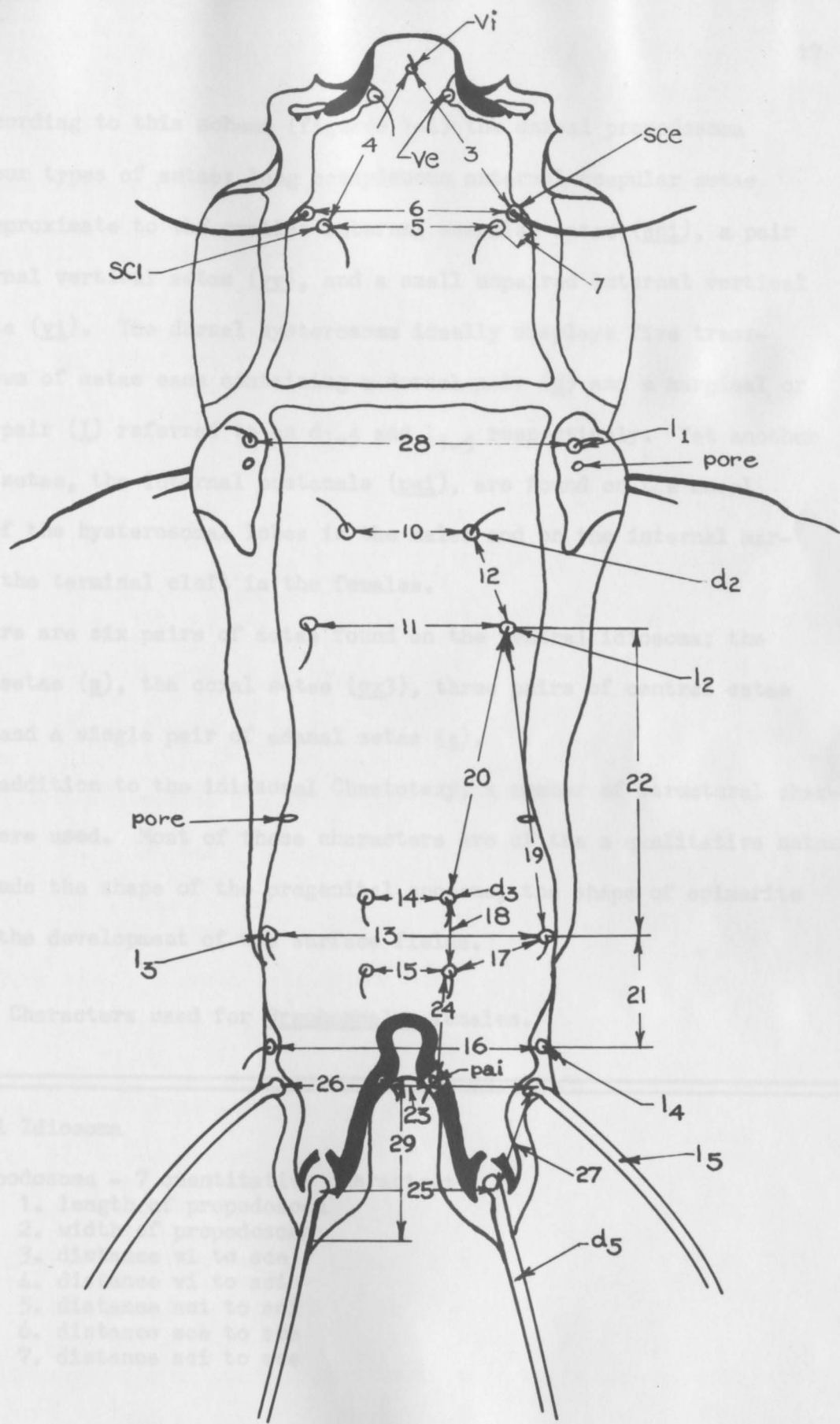


Figure 4. Dorsal view of a Brephosceles female showing all quantitative measurements.





according to this setae  
 bears four types of setae  
 (scs) approximate to the  
 of external vertex (vi).  
 setae (y). The dorsal  
 various rows of setae  
 lateral pair (l) refer  
 pair of setae, (l) and  
 margin of the terminal  
 of the terminal edge  
 There are six pairs  
 sternal setae (s), the  
 (s<sub>1-3</sub>), and a single  
 In addition to the  
 setae were used.  
 and include the shape  
 I, and the developm  
 Table 2. Characters  
 1. Dorsal Idiosoma  
 Propodeum - 7  
 1. length of propodeum  
 2. width of propodeum  
 3. distance of setae  
 4. distance of setae  
 5. distance of setae  
 6. distance of setae  
 7. distance of setae  
 Hysterosoma - 22 quantitative characters  
 8. length of hysterosoma

According to this scheme (figures 1-4) the dorsal propodosoma bears four types of setae; long conspicuous external scapular setae (sce) approximate to the smaller internal scapular setae (sci), a pair of external vertical setae (ve), and a small unpaired internal vertical microseta (vi). The dorsal hysterosoma ideally displays five transverse rows of setae each containing a dorsal pair (d) and a marginal or lateral pair (l) referred to as  $d_{1-5}$  and  $l_{1-5}$  respectively. Yet another pair of setae, the internal postanals (pai), are found on the mesal margin of the hysterosomal lobes in the males and on the internal margins of the terminal cleft in the females.

There are six pairs of setae found on the ventral idiosoma; the sternal setae (s), the coxal setae (cx3), three pairs of central setae ( $c_{1-3}$ ), and a single pair of adanal setae (a).

In addition to the idiosomal Chaetotaxy, a number of structural characters were used. Most of these characters are of the a qualitative nature and include the shape of the pregenital apodeme, the shape of epimerite I, and the development of the surface fields.

Table 2. Characters used for Brephosceles females.

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### I. Dorsal Idiosoma

#### Propodosoma - 7 quantitative characters

1. length of propodosoma
2. width of propodosoma
3. distance vi to sce
4. distance vi to sci
5. distance sci to sci (2) or about (1)
6. distance sce to sce
7. distance sci to sce

#### Hysterosoma - 22 quantitative characters

8. length of hysterosoma



Table 2. continued

- 
- 
- I. Dorsal
9. width of hysterosoma
  10. distance  $\underline{d}_2$  to  $\underline{d}_2$
  11. distance  $\underline{l}_2$  to  $\underline{l}_2$
  12. distance  $\underline{d}_2$  to  $\underline{l}_2$
  13. distance  $\underline{l}_3$  to  $\underline{l}_3$
  14. distance  $\underline{d}_3$  to  $\underline{d}_3$
  15. distance  $\underline{d}_4$  to  $\underline{d}_4$
  16. distance  $\underline{l}_4$  to  $\underline{l}_4$
  17. distance  $\underline{l}_3$  to  $\underline{d}_4$
  18. distance  $\underline{d}_3$  to  $\underline{d}_4$
  19. distance  $\underline{l}_2$  to  $\underline{l}_3$
  20. distance  $\underline{l}_2$  to  $\underline{d}_3$
  21. distance  $\underline{l}_3$  to  $\underline{l}_4$
  22. distance  $\underline{l}_4$  to  $\underline{l}_2$
  23. distance pai to pai
  24. distance pai to  $\underline{d}_4$
  25. distance  $\underline{d}_5$  to  $\underline{d}_5$
  26. distance  $\underline{l}_5$  to  $\underline{l}_5$
  27. distance  $\underline{d}_5$  to  $\underline{l}_5$
  28. distance  $\underline{l}_1$  to  $\underline{l}_1$
  29. size of cleft

II. Ventral Idiosoma - 4 quantitative characters

30. distance  $\underline{c}_1$  to  $\underline{c}_1$
31. distance  $\underline{s}$  to  $\underline{s}$
32. distance pga to  $\underline{s}$
33. distance pga to  $\underline{d}_5$

III. Body size - 2 quantitative characters

34. body length
35. body width

IV. ratios - 3 quantitative characters

36. propodosoma length to width
37. hysterosoma length to width
38. body length to width

V. Qualitative characters - 1

39. setae  $\underline{d}_3$  present (2) or absent (1)
- 
-

Table 3. Characters used for Brenhosceles males.

## I. Dorsal Idiosoma

Propodosoma - 6 quantitative characters, 2 qualitative

1. vi absent (1) or present (2)
2. distance vi to sci
3. length of propodosoma
4. width of propodosoma
5. ratio of length to width
6. distance sci to sci
7. ve absent (1) or present (2)
8. distance from propodosoma to hysterosoma

Hysterosoma - 19 quantitative characters, 4 qualitative

9. shape of  $\underline{l}_1$ : spiculiform (1), setiform (2), lanceolate (3)
10. distance  $\underline{l}_1$  to  $\underline{l}_1$
11. length of  $\underline{l}_1$
12. shape of sh: spiculiform (1), setiform (2), lanceolate (3)
13. distance  $\underline{h}$  to  $\underline{h}$
14.  $\underline{d}_1$  present (2) or absent (1)
15. distance  $\underline{d}_2$  to  $\underline{d}_2$
16. distance  $\underline{l}_2$  to  $\underline{l}_2$
17. distance  $\underline{d}_2$  to  $\underline{l}_2$  at midline
18. distance hysterosoma to cleft
19. distance cleft to  $\underline{d}_5$  at midline
20. distance  $\underline{d}_3$  to  $\underline{d}_3$
21. distance  $\underline{d}_4$  to  $\underline{d}_4$
22. distance  $\underline{d}_3$  to  $\underline{d}_4$
23. distance  $\underline{d}_4$  topai
24.  $\underline{d}_4$  above (2) or below (1)  $\underline{l}_3$
25. distance  $\underline{l}_5$  to  $\underline{l}_5$
26. distance vi to cleft
27. distance  $\underline{d}_2$  to  $\underline{l}_5$  at midline
28. distance  $\underline{l}_2$  to  $\underline{l}_5$  at midline
29. width of hysterosoma at  $\underline{l}_1$
30. length of hysterosoma at midline
31. ratio of length to width of hysterosoma

## II. Ventral Idiosoma - 5 quantitative, 4 qualitative

32. distance  $\underline{s}$  to  $\underline{s}$
33. shape of epimerites I: 1, 2, or 3
34. development of surface fields:
  - well developed unfused (1)
  - well developed ventral shield (2)
  - poorly developed (3)

Table 3. continued

- 
- 
35. distance cx3 to cx3
  36. distance c<sub>1</sub> to c<sub>1</sub>
  37. distance s to c<sub>1</sub>
  38. length of genital organ
  39. subgenital shield present (2) or absent (1)
  40. shape of pregenital apodeme: 1, 2, 3, or 4
- 
- 

### Computational and Analytical Methods

The procedures and terminology used throughout this study are primarily those developed by Sokal and Sneath (1963). Most of the data processing was carried out by the Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS). The author wrote a fortran NT program using the correlation coefficient ( $r$ ) and the weighted pair group method using Spearman's sums of variables (WPGMS) as a clustering technique. Preliminary calculations were carried out using this program and the results parallel those obtained using the NT-SYS program. In addition, a program was prepared for the averaging of the basic data matrix to produce condensed or averaged OTU'S. All of the data processing was carried out at the Youngstown State University Computer Center.

Since an unusually large number of OTU'S of different sexes utilizing different characters were employed in the present study, eight basic data matrices were constructed for the data processing. They are as follows:

1. charadrii males - 92 OTU'S
2. charadrii females- 94 OTU'S
3. decapus males - 47 OTU'S

4. decapus females - 61 OTU'S
5. groups 3, 4, and 5 males - 37 OTU'S
6. groups 3, 4, and 5 females - 43 OTU'S
7. average charadrii males - 17 OTU'S
8. average charadrii females - 14 OTU'S

Two types of similarity coefficients were employed, the Pearson product-moment correlation coefficient ( $r$ ), and the average distance coefficient ( $d$ ). The former can be calculated by the computational formula

$$r_{jk} = \frac{\sum_{i=1}^n X_{ij} X_{ik} - \frac{1}{n} \left( \sum_{i=1}^n X_{ij} \right) \left( \sum_{i=1}^n X_{ik} \right)}{\left\{ \left[ \sum_{i=1}^n X_{ij}^2 - \frac{1}{n} \left( \sum_{i=1}^n X_{ij} \right)^2 \right] \left[ \sum_{i=1}^n X_{ik}^2 - \frac{1}{n} \left( \sum_{i=1}^n X_{ik} \right)^2 \right] \right\}^{1/2}}$$

While the latter calculated as follows:

$$d_{jk} = \left( \sum_{i=1}^n X_{ij}^2 + \sum_{i=1}^n X_{ik}^2 - 2 \sum_{i=1}^n X_{ij} X_{ik} \right)^{1/2}$$

In most studies requiring the use of either of the above coefficients, transformation of the basic data matrix is necessary if meaningful results are desired. Rohlf and Sokal (1965) found that the best results using the correlation coefficient were obtained when character states were standardized by conversion of the mean to zero and the standard deviation to one according to the following equation:

$$X'_{ij} = X_{ij} - X_i/S_i$$

where  $X'_{ij}$  is the standardized or transformed character state,  $X_{ij}$  is the unstandardized or raw character state,  $X_i$  is the mean of all the character values, and  $S_i$  is the standard deviation. Such standardization results in each character receiving equal weight regardless of its

relative size. The immediate effect of this procedure is a decrease in similarity between OTU'S. In the present study, no correlations less than 0.85 were found using unstandardized characters. However, when the original data was standardized, negative correlations as high as -0.20 were obtained. When data is standardized for use in calculation of the average distance coefficient there is little difference between the resulting matrix of associations and that obtained using raw character states. Moss (1968) found cophenetic correlations between standardized and unstandardized data as high as 0.927 for the distance coefficient but only 0.374 for the correlation coefficient.

When most characters are measurements of different parts of the body and the OTU'S are of different sizes, the best method of calculating coefficients of association is the correlation coefficient ( $r$ ). If the average distance coefficient ( $d$ ) is used in such cases, the character states must be converted to a percentage of the total body length or the resulting phenograms will be a measure of similarity of size rather than shape. Since the current study employs a large number of continuous quantitative variables as characters, only results obtained using the Pearson product-moment correlation coefficient are reported.

Once data has been standardized and a matrix of associations calculated, some type of clustering technique must be used to summarize graphically the phenetic relationships between OTU'S. These techniques are referred to as hierarchical clustering schemes and a wide variety have appeared in the literature. Of the numerous types used in the present study, it was found that the unweighted pair group method using arithmetic averaging (UPGMA) and the weighted pair group method using arithmetic averaging (WPGMA) gave the highest cophenetic correlations

between the original matrix of correlations and the resulting phenogram. According to Rohlf (1970), of all the hierarchical clustering schemes which make use of two dimensional displays and which place similar OTUS together, the UPGMA gives the best results.

The precision with which a given clustering technique translates a matrix of correlations into a phenogram is measured by the cophenetic correlation coefficient. A high correlation shows a minimum distortion of the original matrix of correlations and indicates a high degree of confidence that the resulting phenogram is an accurate representation of actual phenetic relationships. Low values indicate a large amount of distortion and a low level of confidence in the phenogram produced. While no acceptable levels of correlation have been established for use in numerical taxonomic studies, values much less than 0.80 are generally considered to be questionable. In the present study, only phenograms having cophenetic correlations of 0.79 or higher have been used.

A total of eight phenograms were produced each one corresponding to one of the basic matrices. The clustering technique used in each case was the UPGMA. Owing to the difference between the phenons produced in the charadrii group and the existing species, the phenons were averaged and run with species groups three, four and five to determine their relationship to these groups and to one another.

only phenograms obtained using the UPGMA method will be reported here.

#### The charadrii group

Figures 5 and 6 are the phenograms produced from the basic data matrices of the males and females of group six, the charadrii group. Both phenograms show some disparity between the established tax and

## RESULTS OF NUMERICAL TAXONOMIC ANALYSIS

Calculation of Pearson's product-moment correlation coefficient ( $r$ ) from the standardized basic data matrix produced eight similarity matrices. Each matrix was clustered using a variety of clustering techniques which produced a total of twenty phenograms. Because a phenogram is a one-dimensional representation of a multi-dimensional association, the results obtained for a given clustering method must be interpreted in terms of the similarity matrix from which it was generated. The best method of judging such a relationship is the cophenetic correlation coefficient. This coefficient is a measure of the amount of information transferred from the similarity matrix to the phenogram by any given clustering method. Table 4 provides a comparison of the different types of clustering techniques used with each of the eight basic data matrices.

The data from table 4 clearly shows the large range of correlations obtained using the many types of clustering methods in general use. It can also be seen that in the present study the unweighted pair group method using arithmetic averaging (UPGMA) consistently gave higher cophenetic values than any of the other methods tested. For this reason, only phenograms obtained using the UPGMA method will be reported here.

### The charadrii group

Figures 5 and 6 are the phenograms produced from the basic data matrices of the males and females of group six, the charadrii group. Both phenograms show some disparity between the established taxa and

the groups produced by the clustering routine. For this reason, it was decided to draw phenon lines in an attempt to determine the number of

Table 4. Comparison of cophenetic correlation coefficients of several types of clustering methods.

Data matrix	No. of OTU'S	Correlation			
		UPGMA	WPGMA	COMPLETE	SINGLE
Male: <u>charadrii</u>	92	.79	.71	.75	.42
Female: <u>charadrii</u>	94	.85	.81	.83	---
Male: <u>decapus</u>	47	.88	.86	---	---
Female: <u>decapus</u>	61	.85	.84	---	---
Groups 3, 4, and 5 males	37	.93	.87	---	---
Groups 3, 4, and 5 females	43	.86	.85	---	---
Average <u>charadrii</u> males with 3, 4, and 5	54	.88	---	---	---
Average <u>charadrii</u> females with 3, 4, and 5	57	.84	---	---	---

phenons present. It was not possible to draw such a line at any given level of correlation and still produce reasonable groups leading to taxonomic stability. Therefore, a variable line was drawn around the 0.50 level of correlation for the females and 0.65 for the males. This



procedure produced a total of fifteen phenons for the females and seventeen for the males.

With the exception of phenon 1 (four species and twenty-eight OTU'S) and some minor splitting (one OTU) of afribycis, longistriatus, and hoplopteri, the phenetic groups of the female charadrii are strikingly similar to those produced by traditional methods. Phenon 1 appears to represent a large homogeneous complex made up of charadrii, virginensis, inornatus, and collaricus. On the basis of the characters used in the present study, these four species are indistinguishable. They form a single large phenon similar in structure to most of the others produced in the study.

Generally, the males of the charadrii group show less affinity with established taxa than the females. This is not surprising in view of the fact that all the males of this species group are indistinguishable (Peterson, 1971). This is also reflected by the low cophenetic correlation obtained during clustering (0.79). Phenon 2 a complex made up of three species (longistriatus, charadrii, and virginensis) is very similar to that found in the female group. One further point concerns the splitting of the species virginensis. The eight OTU'S of this species are found associated with three widely separated phenons. The remainder of the phenons show a close relationship to established taxa.

Even though the male charadrii group is represented by a different group of characters (males and females have 19 characters in common) the resemblance to the female study is obvious. For example, phenon 2 of the males with its close association to phenon 3 (inornatus) and 4 (collaricus) shows a strong resemblance to phenon 2 of the females.

Figure 5. Phenogram produced from the correlation matrix of 92 charadrii males.  $r = 0.79$ .

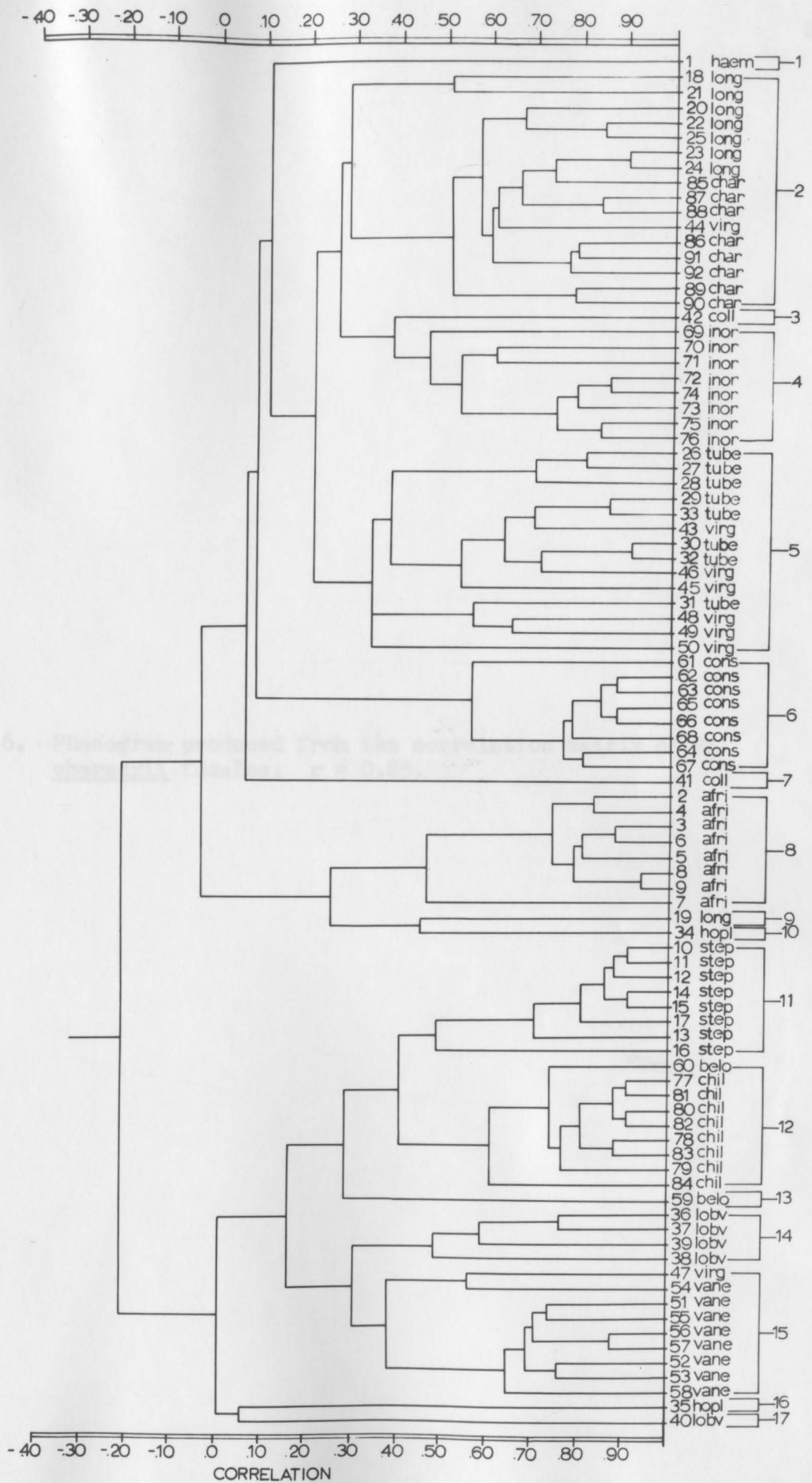


Figure 6. Phenogram produced from the correlation matrix of 94 charadrii females.  $r = 0.85$ .

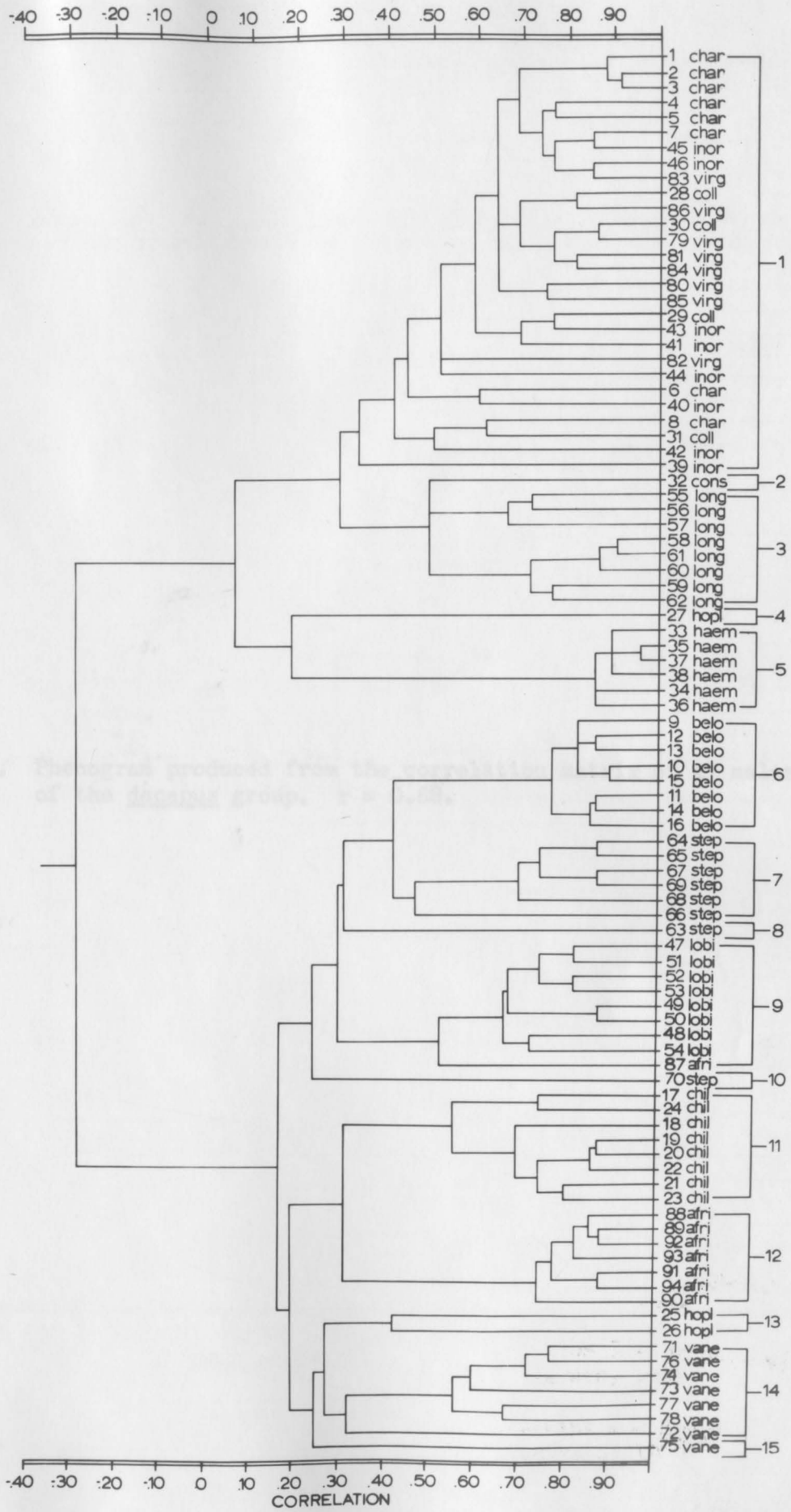
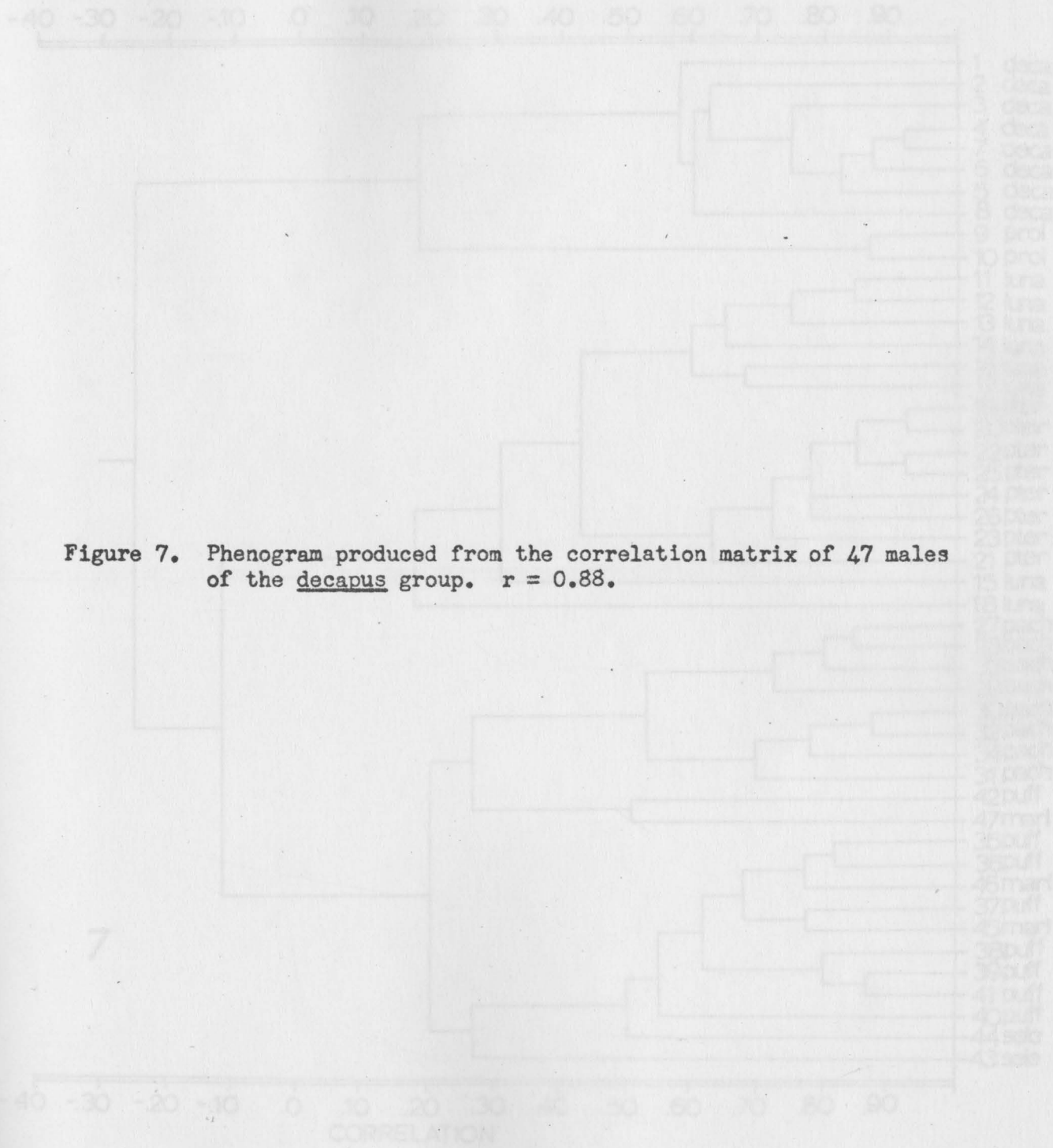
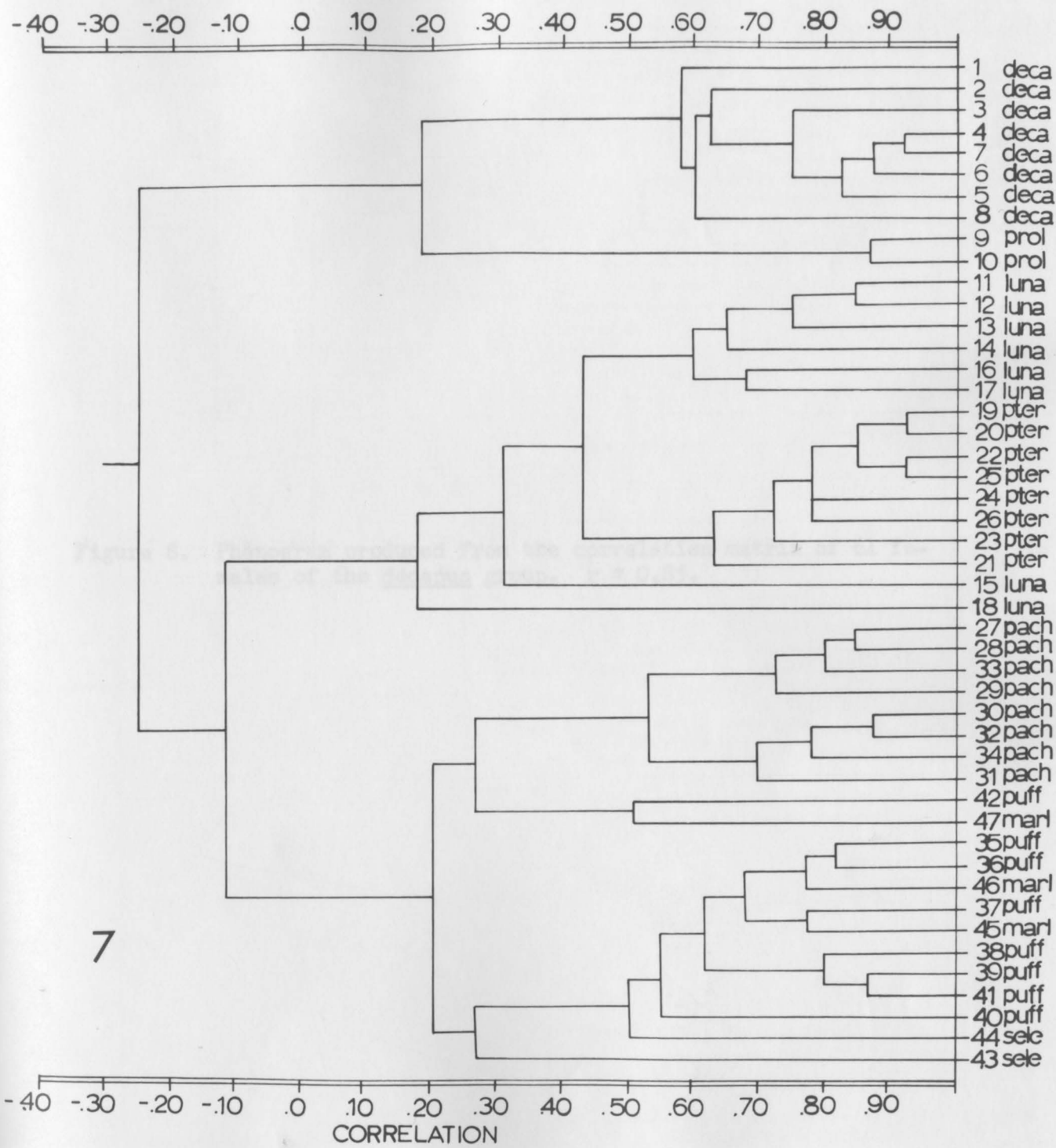


Figure 7: Dendrogram produced from the correlation matrix of the *disparis* group.  $r = .90$ .





7

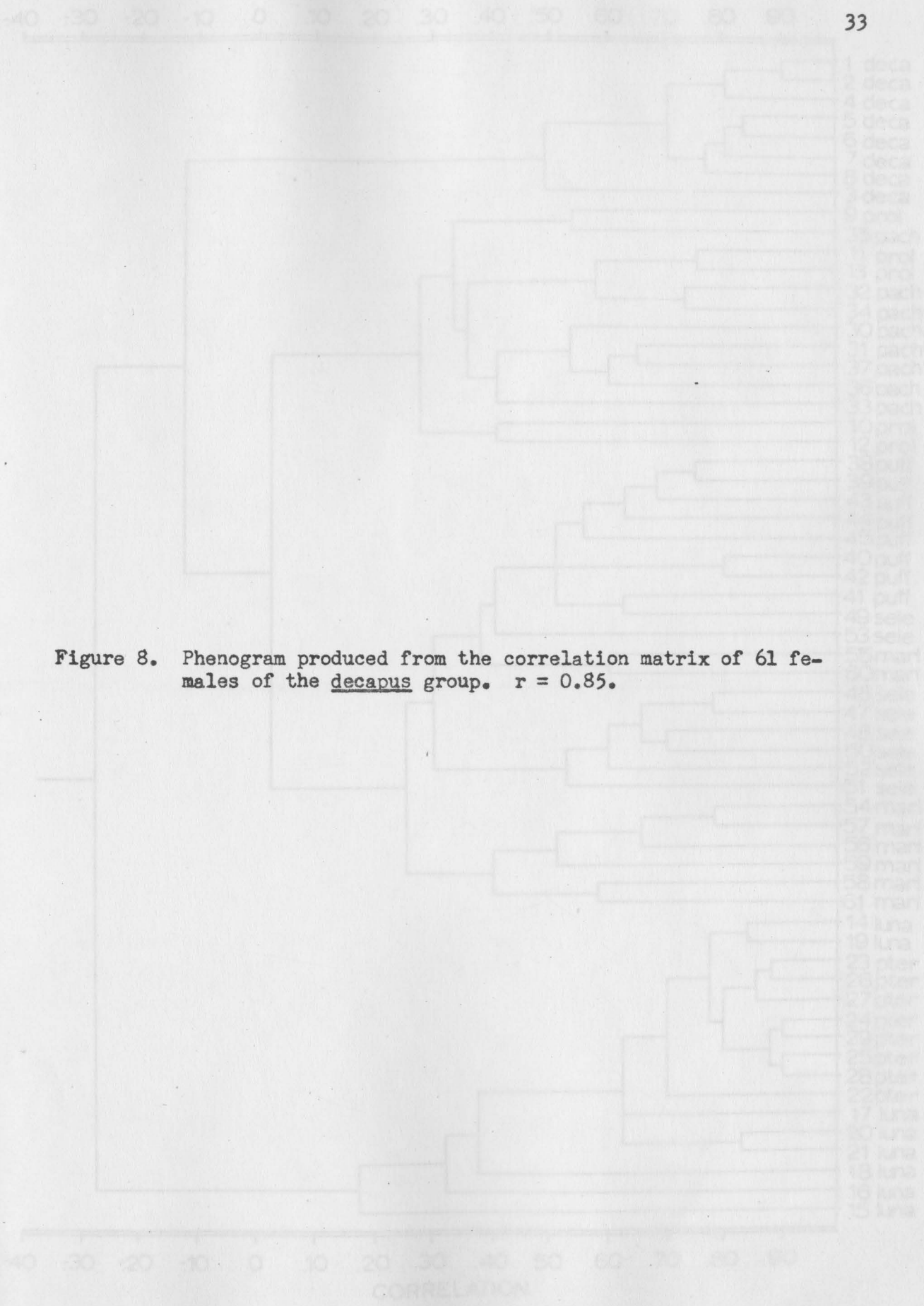


Figure 8. Phenogram produced from the correlation matrix of 61 females of the decapus group.  $r = 0.85$ .



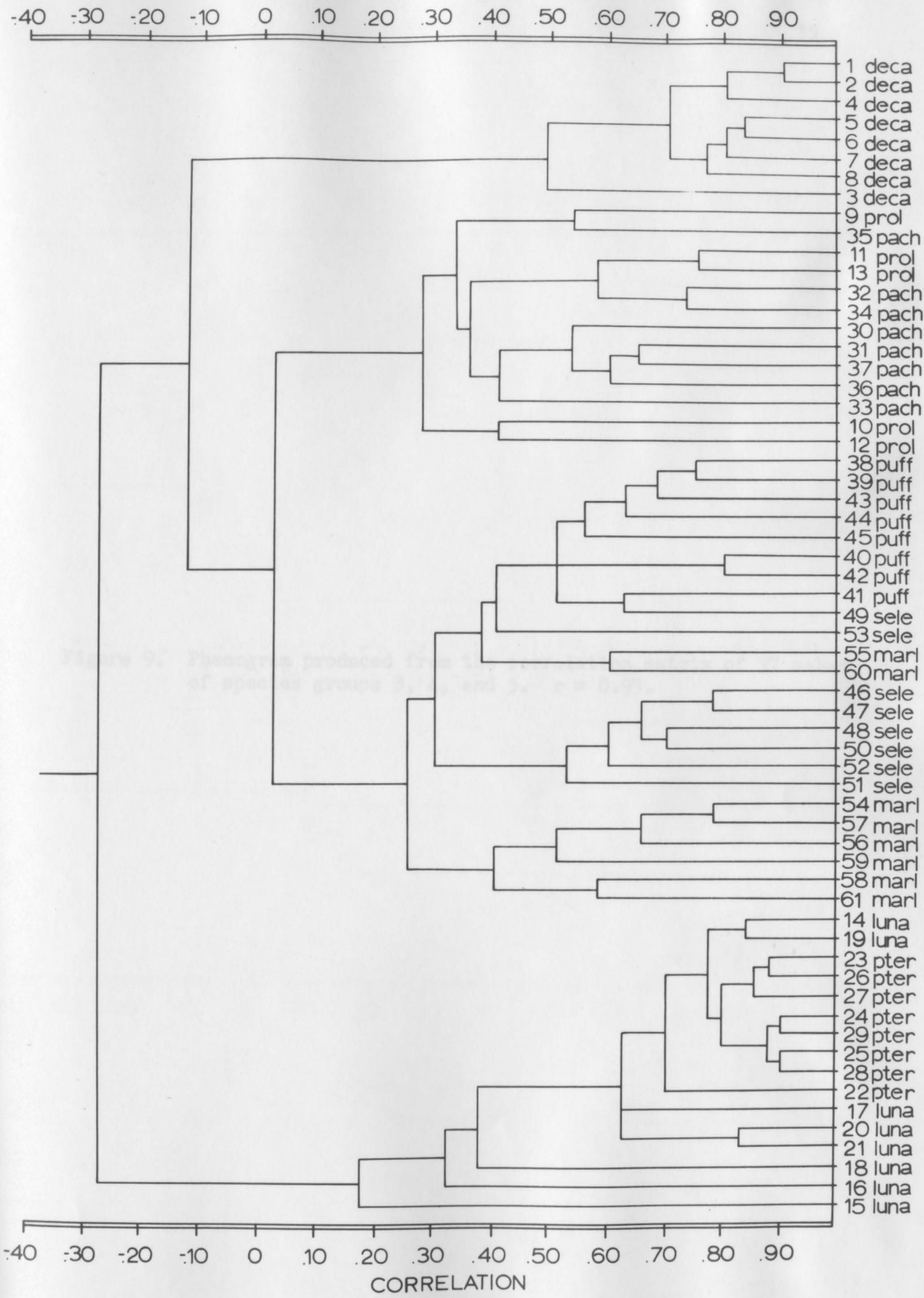
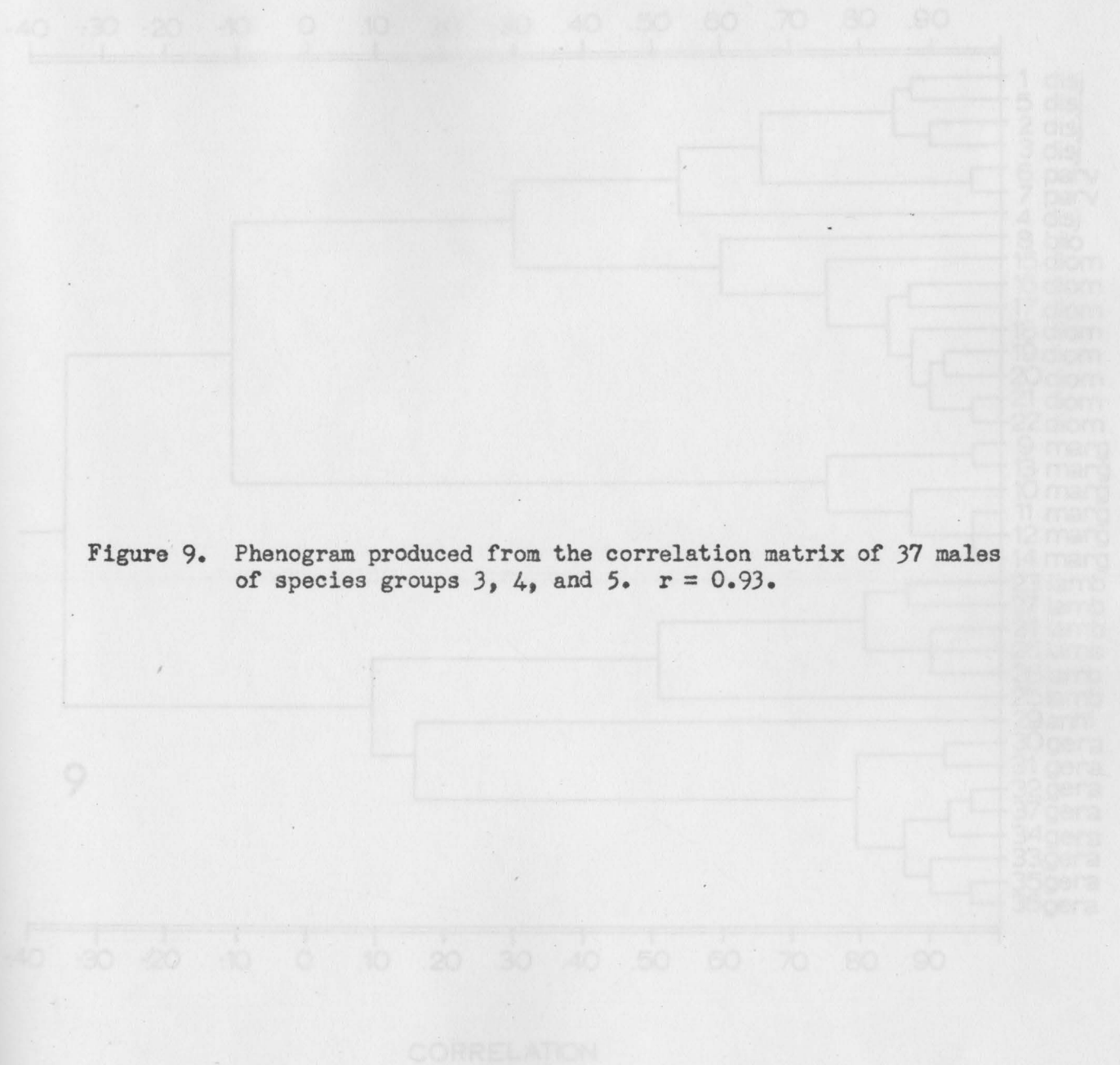


Figure 9. Dendrogram produced from the analysis of species groups 1 and 2.  $r = 0.75$



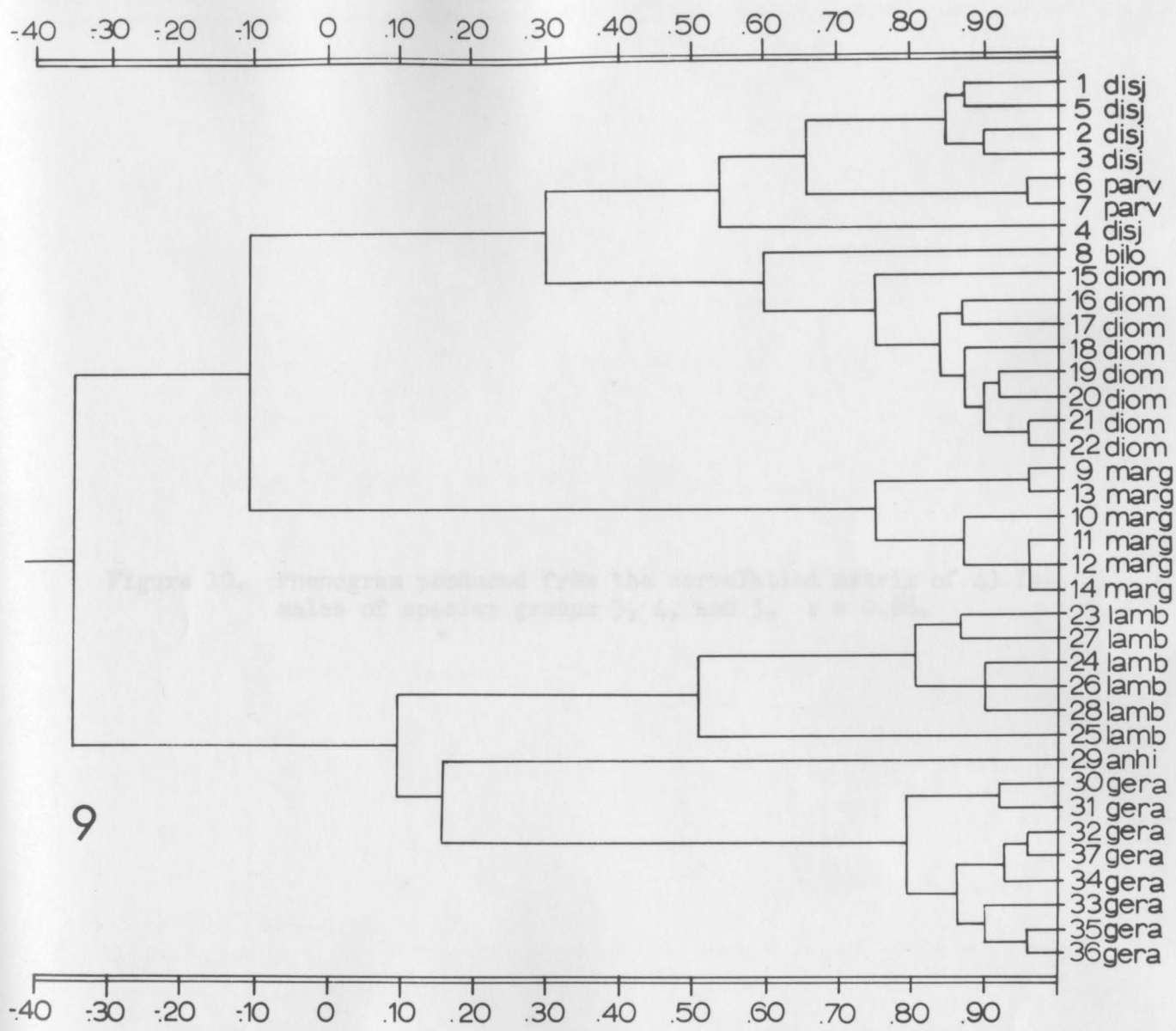
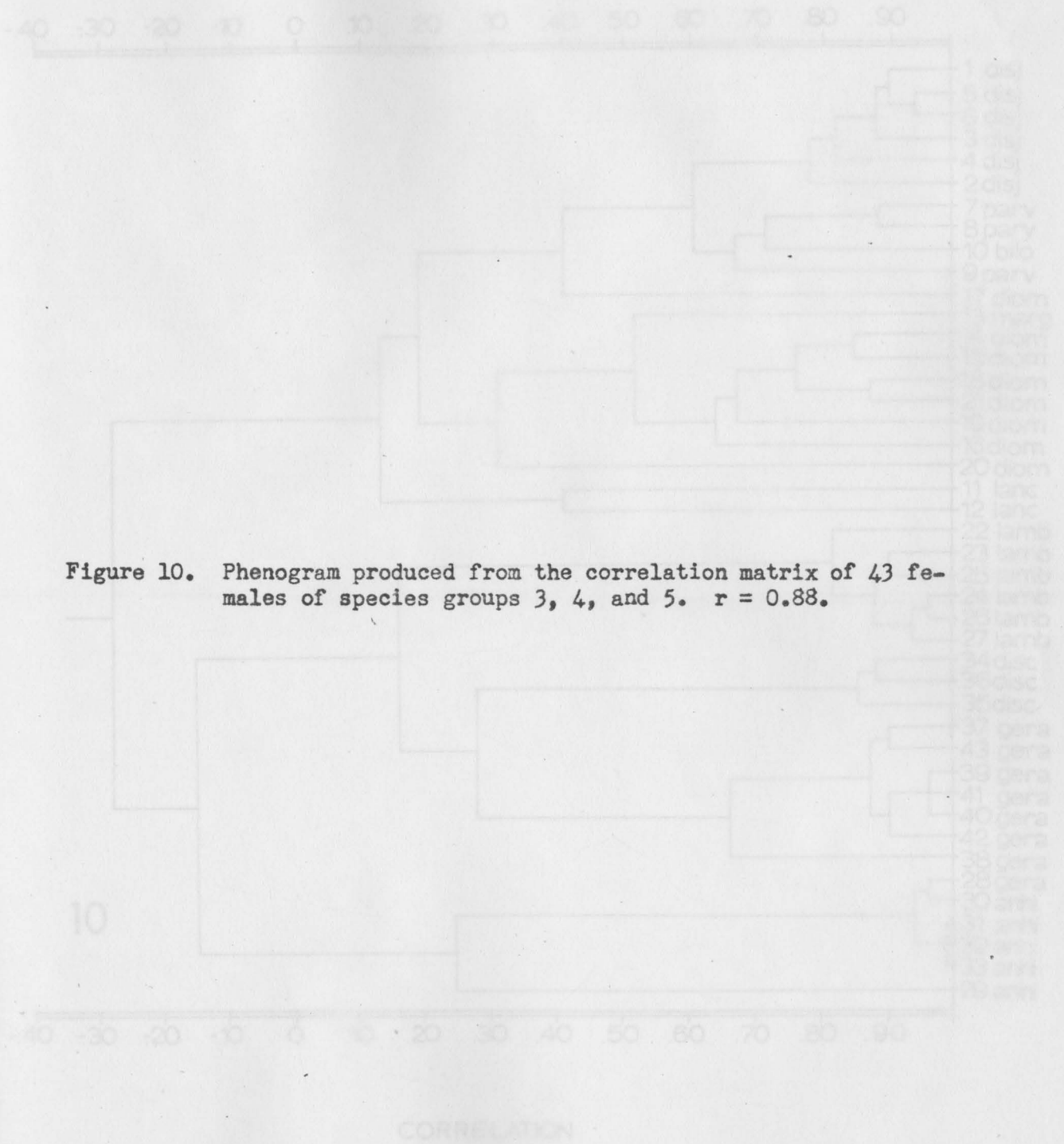
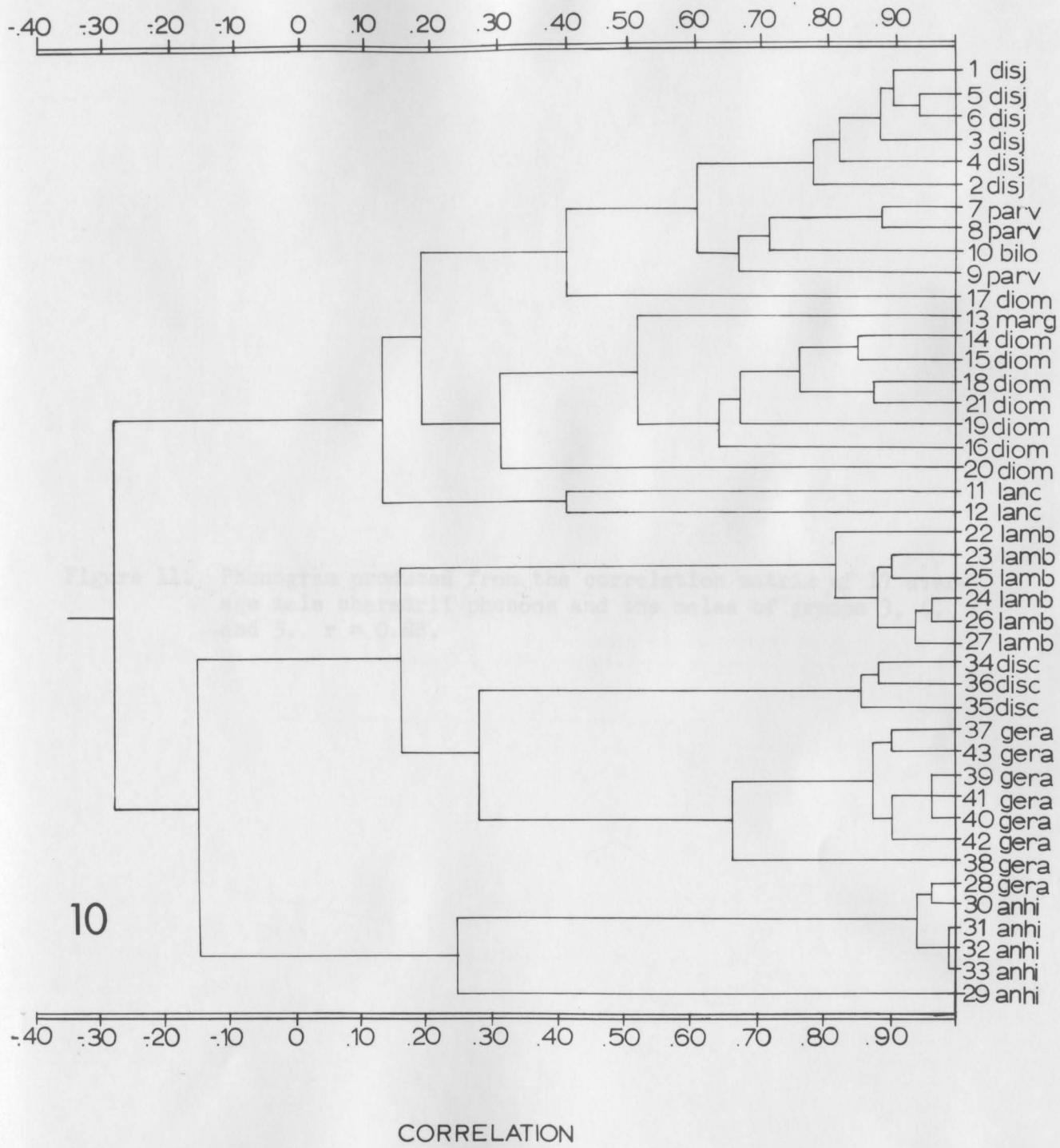


Figure 10. Dendrogram prepared from the correlation matrix of 36 species groups by 4, and 5.  $r = 0.85$

CORRELATION





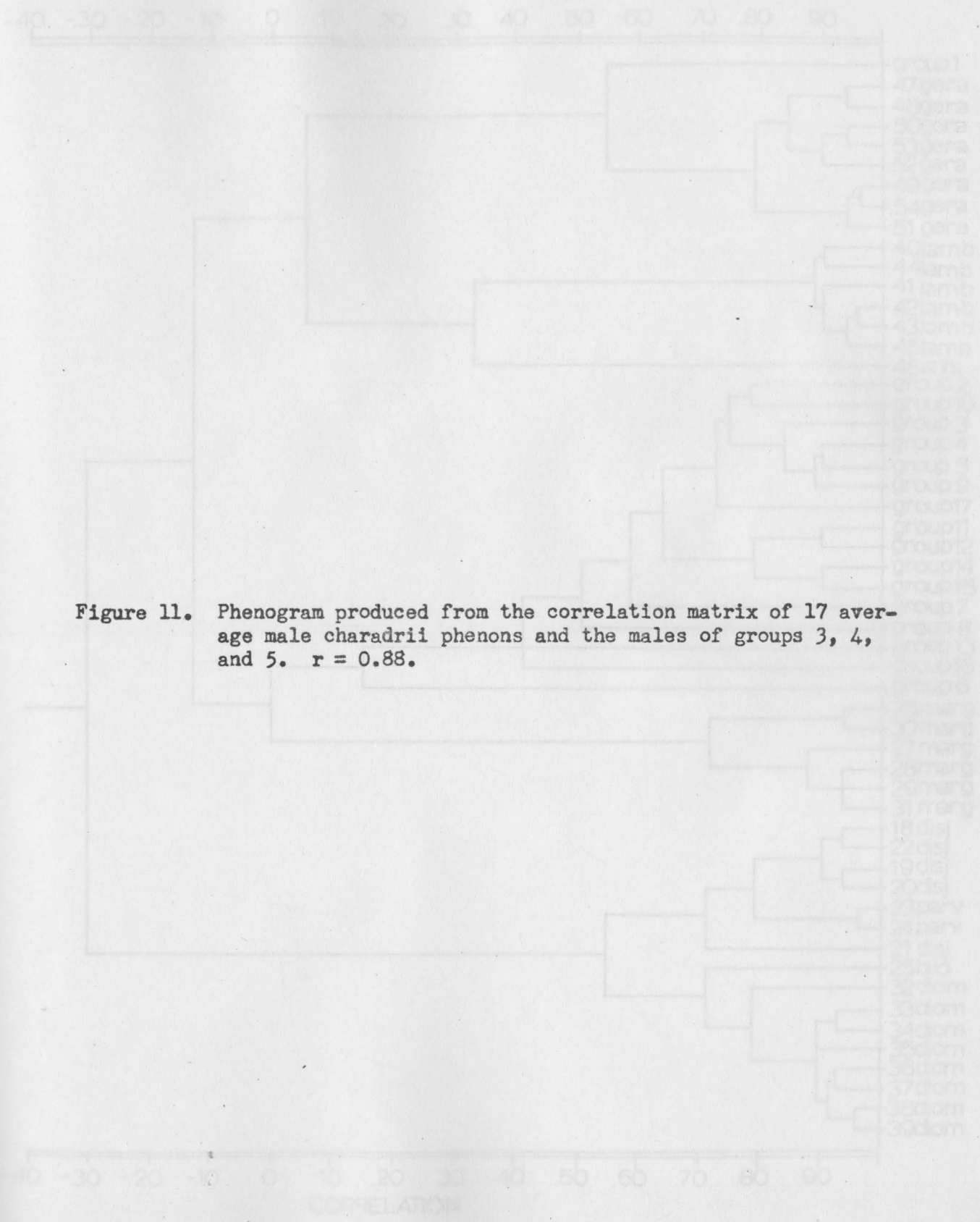
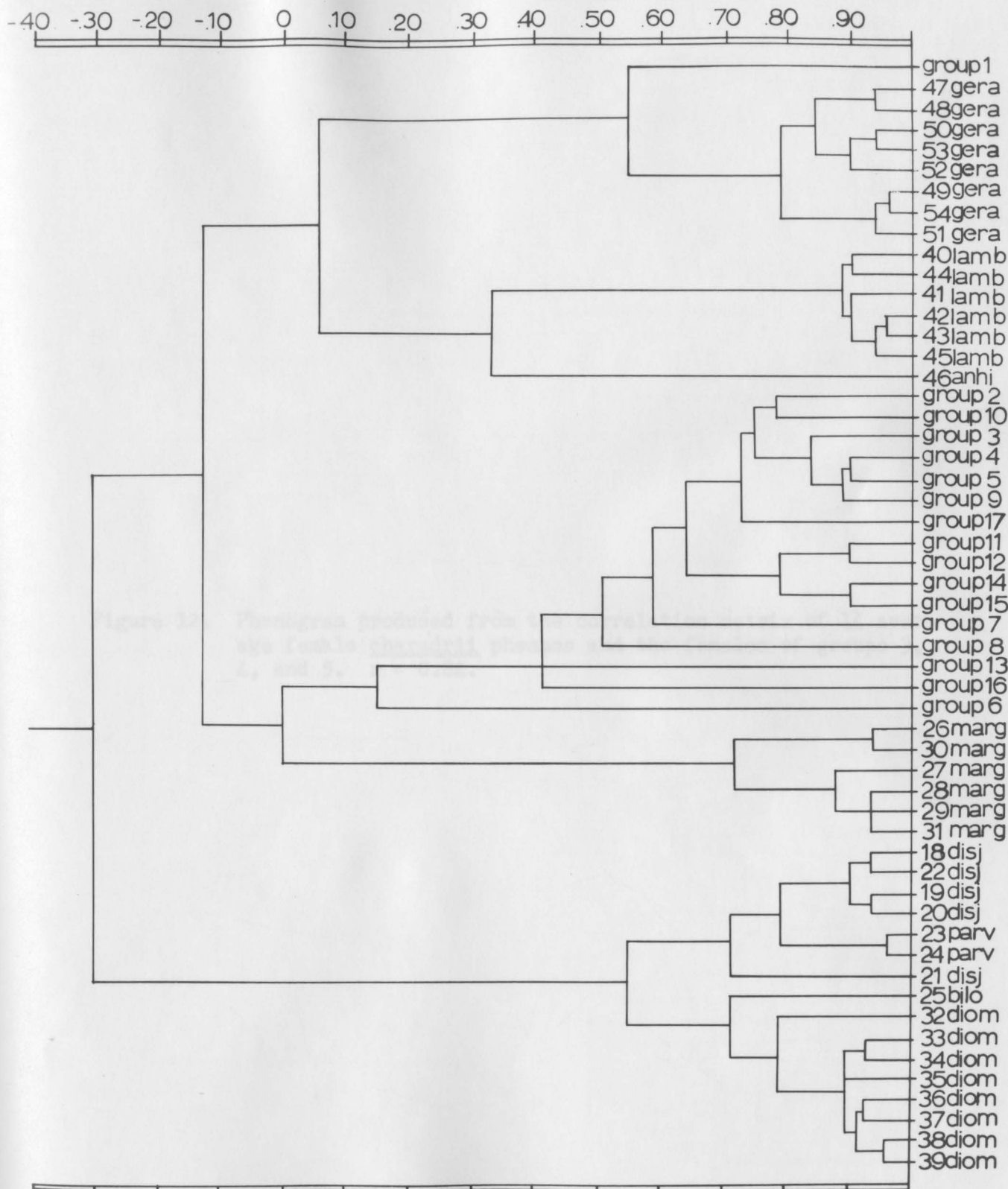


Figure 11. Phenogram produced from the correlation matrix of 17 average male charadrii phenons and the males of groups 3, 4, and 5.  $r = 0.88$ .



CORRELATION

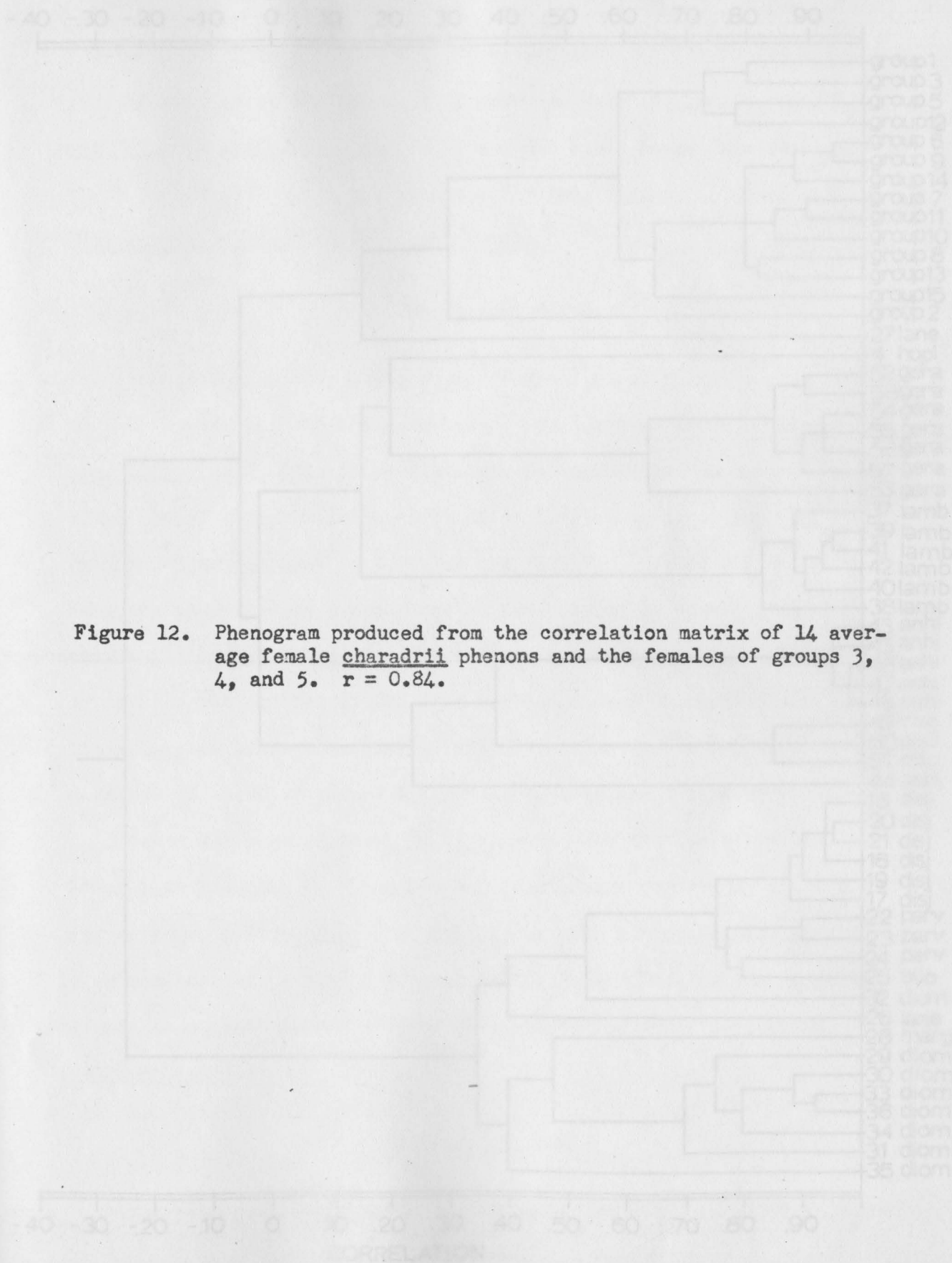
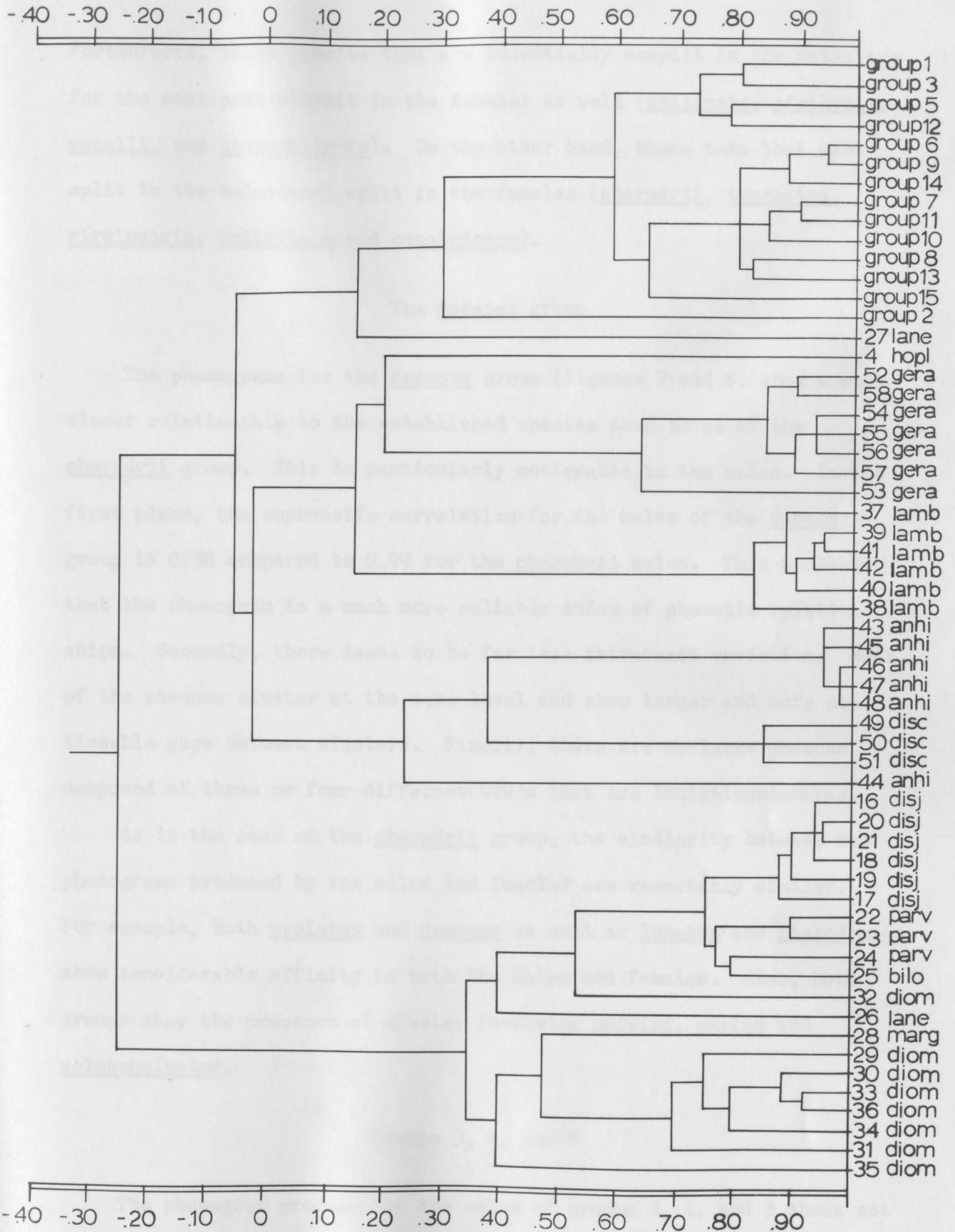


Figure 12. Phenogram produced from the correlation matrix of 14 average female charadrii phenons and the females of groups 3, 4, and 5.  $r = 0.84$ .





CORRELATION

Furthermore, those species that are essentially unsplit in the males are for the most part unsplit in the females as well (chilensis, afribycis, vanelli, and stephanibycis). On the other hand, those taxa that were split in the males were split in the females (charadrii, inornatus, virginensis, collaricus and constrictus).

#### The decapus group

The phenograms for the decapus group (figures 7 and 8) show a much closer relationship to the established species than those of the charadrii group. This is particularly noticeable in the males. In the first place, the cophenetic correlation for the males of the decapus group is 0.88 compared to 0.79 for the charadrii males. This indicates that the phenogram is a much more reliable index of phenetic relationships. Secondly, there seems to be far less intrataxon variation. Most of the phenons cluster at the same level and show larger and more noticeable gaps between clusters. Finally, there are no large phenons composed of three or four different OTU's that are indistinguishable.

As in the case of the charadrii group, the similarity between the phenograms produced by the males and females are remarkably similar. For example, both prolatus and decapus as well as lunatus and pterodromae show considerable affinity in both the males and females. Also, both groups show the presence of cluster involving puffini, marlae and selenopeltatus.

#### Groups 3, 4, and 5

The phenogram produced by the males of groups 3, 4, and 5 shows not

only a high degree of affinity with existing taxa, but also gave the highest cophenetic correlation obtained during the entire study (0.93). Without exception, each phenon corresponds to an existing species. It can also be seen that not only are the gaps separating the taxa quite large, but the intrataxon variation is small with all phenons being related at the 0.75 level or higher.

Since there are OTU's present from three different species groups in the basic data matrix, it would be expected that three clusters would form at a level of correlation somewhat less than that usually associated with the species level (for this particular study the species level has not been found to be lower than 0.50). This is exactly the case. If one were to draw a line across figure 9 at the 0.30 level, exactly three phenons would be produced each one corresponding to a single species group.

While the females of groups 3, 4, and 5 (figure 10) show a high correlation with established taxa, there are some deviations. For example, species group 4 is split by the eight OTU's of groups 5. While this is more apparent in the females, it also shows up in the males as well. Figure 9 shows that anhimae of groups 4 clusters with geranoxenus of groups 5 before it does with lambda of group 4. In addition, some of the species of the group 3 females show signs of forming a rather heterogenous cluster in the middle of group 3. One wonders if this might not be more pronounced if more OTU's were included in the present study.

Averaged charadrii phenons as OTU's

The charadrii phenons from figures 5 and 6 were averaged and run

as individual OTU's with groups 3, 4, and 5. The resulting phenograms (figures 11 and 12) show that these OTU's form a well defined cluster with both males and females. These phenograms show a consistent association between the charadrii phenons and groups 4 and 5. In both cases, the charadrii phenons are more closely related to these two groups than they are to group 3.

Another interesting effect produced by the inclusion of the average charadrii phenons in this group is the reduction of group splitting. This is particularly noticeable in the females. It will be remembered that group 4 was split by group 5. When these OTU's were run with the averaged charadrii phenons, the split did not occur.

Another problem encountered during the interpretation of the numerical data concerns the use of different characters for the males and females of each species group. This practice made it necessary to calculate separate matrices of correlation for each group. In such cases, the phenogram that most closely conformed to existing groups was used. As it turned out, the phenogram that gave the best fit of established groups also had the highest cophenetic correlation. In the following discussion, a proposed classification based on numerical data will be presented and compared to that established by Peterson (1971).

#### The charadrii group

Since the males of the charadrii group are known to be morphologically indistinguishable and also produced a low cophenetic correlation (0.79), the females have been used exclusively for the classification of this group. A total of fifteen phenons were produced by draw-

## DISCUSSION

In this study, the recognition and definition of subgroups and taxospecies is based on the interpretation of phenograms. Since it was not possible to define taxa by simply drawing a phenon line at some level of similarity, a certain amount of subjectivity entered into the final selection of taxa. This problem has been encountered by other workers (Herrin, 1969 and Manischewitz, 1971) and clearly points out the inability of even the most sophisticated numerical methods to completely eliminate the subjectivity from the process of classification.

Another problem encountered during the interpretation of the numerical data concerns the use of different characters for the males and females of each species group. This practice made it necessary to calculate separate matrices of correlation for each group. In such cases, the phenogram that most closely conformed to existing groups was used. As it turned out, the phenogram that gave the best fit of established groups also had the highest cophenetic correlation. In the following discussion, a proposed classification based on numerical data will be presented and compared to that established by Peterson (1971).

### The charadrii group

Since the males of the charadrii group are known to be morphologically indistinguishable and also produced a low cophenetic correlation (0.79), the females have been used exclusively for the classification of this group. A total of fifteen phenons were produced by draw-

ing a line at approximately the 0.50 level as discussed above. The following table is a comparison of these taxa which will now be referred to as species with those of Peterson (1971).

Table 5. Comparison of proposed species of the charadrii group with those of Peterson (1971).

Proposed species	Established species Peterson, 1971
Species 1 - <u>Brephosceles charadrii</u> Dubinin, 1951 includes: <u>B. inornatus</u> , <u>B. collaricus</u> <u>B. virginensis</u>	<u>Brephosceles charadrii</u> Dubinin, 1951 <u>Brephosceles inornatus</u> Peterson, 1971 <u>Brephosceles collaricus</u> Peterson, 1971 <u>Brephosceles virginensis</u> Peterson, 1971
Species 2 - <u>Brephosceles constrictus</u> Peterson, 1971	<u>Brephosceles constrictus</u> Peterson, 1971
Species 3 - <u>Brephosceles longistriatus</u> Peterson, 1971	<u>Brephosceles longistriatus</u> Peterson, 1971
Species 4 - <u>Brephosceles hoplopteri</u> Peterson, 1971	<u>Brephosceles hoplopteri</u> Peterson, 1971
Species 5 - <u>Brephosceles haematopi</u> Peterson, 1971	<u>Brephosceles haematopi</u> Peterson, 1971
Species 6 - <u>Brephosceles belonopteri</u> Peterson, 1971	<u>Brephosceles belonopteri</u> Peterson, 1971
Species 7 - <u>Brephosceles stephanibycis</u> Peterson, 1971	<u>Brephosceles stephanibycis</u> Peterson, 1971
Species 8 - <u>Brephosceles n. sp.</u>	

Table 5. continued.

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Species 9 - <u>Brephosceles afribycis</u> Peterson, 1971 includes: <u>B. lobivanelli</u>	<u>Brephosceles afribycis</u> Peterson, 1971 <u>Brephosceles lobivanelli</u> Peterson, 1971
Species 10 - <u>Brephosceles n. sp.</u>	
Species 11 - <u>Brephosceles chilensis</u> Peterson, 1971	<u>Brephosceles chilensis</u> Peterson, 1971
Species 12 - <u>Brephosceles n. sp.</u>	
Species 13 - <u>Brephosceles n. sp.</u>	
Species 14 - <u>Brephosceles vanelli</u> Gaud, 1959	<u>Brephosceles vanelli</u> Gaud, 1959
Species 15 - <u>Brephosceles n. sp.</u>	

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The four species of phenon 1 (figure 6) of the females may represent a species complex and are not thought to be valid species. Species 3, 5, 6, and 11 represent valid species which have been described previously. B. stephanibycis, represented by species 7, 8, and 10 has been split into three species. OTU 63 and especially OTU 70 of this species show less affinity with the rest of the group than one would expect at the species level. With the exception of OTU 87 B. afribycis appears to form a very distinct cluster. OTU 87 has been assigned to species 9 but also may represent a separate species. The large split in B. hoplopteri in both the males and the females indicates two distinct species. OTU 75 (phenon 15) of B. vanelli may represent a new species or may represent a very aberrant form .

The decapus group

With the exception of two species (B. marlae and B. puffini) both phenograms of the decapus group (figures 7 and 8) indicate a close association between the clusters and the established species. The following table is a comparison of the proposed species of the decapus group with those of Peterson, 1971.

Table 6. Comparison of the proposed species of the decapus groups with those of Peterson, 1971.

Proposed species	Established species Peterson, 1971
Species 1 - <u>Brephosceles decapus</u> Gaud, 1953	<u>Brephosceles decapus</u> Gaud, 1953
Species 2 - <u>Brephosceles prolatus</u> Peterson, 1971	<u>Brephosceles prolatus</u> Peterson, 1971
Species 3 - <u>Brephosceles lunatus</u> Peterson, 1971	<u>Brephosceles lunatus</u> Peterson, 1971
Species 4 - <u>Brephosceles pterodromae</u> Peterson, 1971	<u>Brephosceles pterodromae</u> Peterson, 1971
Species 5 - <u>Brephosceles n. sp.</u>	
Species 6 - <u>Brephosceles pachyptilae</u> Peterson, 1971	<u>Brephosceles pachyptilae</u> Peterson, 1971
Species 7 - <u>Brephosceles puffini</u> Peterson, 1971 includes: <u>B. marlae</u>	<u>Brephosceles puffini</u> Peterson, 1971
Species 7 - <u>Brephosceles marlae</u> Atyeo and Peterson, 1970	<u>Brephosceles marlae</u> Peterson, 1971
Species 8 - <u>Brephosceles selenopeltatus</u> Peterson, 1971	<u>Brephosceles selenopeltatus</u> Peterson, 1971



Valid species include B. decapus, B. prolatus, B. pterodromae, B. pachyptilae, and B. selenopeltatus. B. lunatus is split in both phenograms and may actually represent two separate species. Both B. marlae and B. puffini form a species complex which suggests that B. marlae may be assigned to synonymy.

Species 8 - Brephosceles  
Peterson, 1971

Groups 3, 4, and 5

Brephosceles  
Peterson, 1971

With the exception of the split in B. disjunctus, all of the species and species groups in this study appear to be in agreement with established groups. The following table compares proposed species and species groups with those of Peterson, 1971.

Table 7. Comparison of proposed species groups with those of Peterson, 1971.

Proposed species	Established species Peterson, 1971
Species group 3	Species group 3
Species 1 - <u>Brephosceles disjunctus</u> Peterson, 1971	<u>Brephosceles disjunctus</u> Peterson, 1971
Species 2 - <u>Brephosceles parvatus</u> Peterson, 1971	<u>Brephosceles parvatus</u> Peterson, 1971
Species 3 - <u>Brephosceles n. sp.</u>	
Species 4 - <u>Brephosceles bilobatus</u> Peterson, 1971	<u>Brephosceles bilobatus</u> Peterson, 1971
Species 5 - <u>Brephosceles diomedei</u> Atyeo and Peterson, 1970	<u>Brephosceles diomedei</u> Atyeo and Peterson, 1970
Species 6 - <u>Brephosceles marginiventris</u> Trouessart, 1899	<u>Brephosceles marginiventris</u> Trouessart, 1899

Table 5 continued.

Species group 4	Species group 4
Species 7 - <u>Brephosceles lambda</u> Trouessart, 1885	<u>Brephosceles lambda</u> Trouessart, 1885
Species 8 - <u>Brephosceles anhima</u> Peterson, 1971	<u>Brephosceles anhima</u> Peterson, 1971
Species group 5	Species group 5
Species 9 - <u>Brephosceles geranoxenus</u> Peterson, 1968	<u>Brephosceles geranoxenus</u> Peterson, 1968

Phenogram 9 and table 7 shows that not only is there close agreement between the initial clusters and established species, but that there is also considerable resemblance between the larger clusters and the species groups. A line drawn at the 0.40 level in figure 9 would result in the production of phenons almost identical with established species groups.

#### Averaged charadrii phenons as OTU'S

The averaged charadrii phenons and the OTU's of groups 3, 4 and 5 (figures 11 and 12) show very clearly the higher taxonomic relationships of these groups. It is apparent that the species groups erected by Peterson, 1971 correspond very closely to those of the phenograms. When a line is drawn at the 0.30 level of figure 11, the average charadrii phenons with the exception of group 1 (B. haematopi) all cluster together to form a distinct group. Group 1 is clearly associated with













































## APPENDIX II - CONTINUED

CHARACTER	OTU				APPENDIX III					
	91	92	93	94	5	6	7	8	9	10
1	99.	99.	92.	95.	100.	108.	113.	106.	90.	90.
2	112.	108.	108.	106.	105.	108.	103.	108.	82.	82.
3	79.	81.	77.	77.	95.	100.	109.	98.	111.	111.
4	70.	73.	68.	68.	55.	57.	58.	58.	55.	58.
5	90.	90.	86.	86.	2.	2.	2.	1.	2.	2.
6	117.	116.	112.	112.	24.	36.	31.	24.	21.	24.
7	14.	13.	13.	14.	1.	1.	1.	1.	2.	2.
8	270.	274.	259.	264.	130.	134.	139.	127.	130.	187.
9	84.	81.	77.	81.	10.	10.	10.	10.	10.	43.
10	33.	30.	31.	33.	1.	1.	1.	1.	2.	2.
11	84.	81.	77.	81.	166.	182.	180.	168.	173.	170.
12	48.	46.	41.	51.	1.	1.	1.	1.	1.	1.
13	70.	70.	70.	73.	36.	41.	36.	38.	36.	31.
14	40.	39.	40.	42.	77.	79.	79.	82.	70.	72.
15	33.	33.	33.	33.	36.	38.	43.	41.	43.	43.
16	79.	84.	79.	79.	115.	113.	122.	120.	146.	134.
17	22.	18.	20.	20.	149.	151.	170.	144.	202.	216.
18	60.	60.	42.	59.	26.	29.	31.	24.	67.	62.
19	123.	121.	115.	119.	67.	74.	67.	53.	68.	46.
20	70.	68.	66.	66.	82.	84.	84.	79.	69.	60.
21	22.	29.	26.	24.	48.	48.	50.	53.	43.	40.
22	145.	150.	141.	143.	2.	2.	2.	2.	1.	1.
23	31.	33.	33.	33.	103.	113.	96.	82.	70.	58.
24	40.	40.	35.	42.	245.	269.	264.	250.	254.	269.
25	48.	51.	48.	48.	225.	290.	299.	221.	312.	322.
26	70.	73.	70.	70.	185.	206.	211.	197.	264.	275.
27	20.	20.	20.	19.	82.	77.	82.	82.	107.	102.
28	110.	116.	115.	125.	299.	278.	283.	264.	336.	291.
29	15.	14.	14.	13.	308.	361.	245.	322.	328.	325.
30	40.	40.	37.	42.	43.	48.	48.	46.	48.	43.
31	51.	52.	48.	51.	1.	1.	1.	1.	1.	1.
32	55.	60.	57.	59.	2.	2.	2.	2.	2.	2.
33	270.	274.	259.	277.	103.	113.	96.	82.	70.	58.
34	387.	396.	382.	390.	245.	269.	264.	250.	254.	269.
35	165.	176.	176.	176.	225.	290.	299.	221.	312.	322.
36	88.	92.	85.	90.	185.	206.	211.	197.	264.	275.
37	322.	333.	336.	326.	82.	77.	82.	82.	107.	102.
38	234.	224.	216.	222.	299.	278.	283.	264.	336.	291.
39	2.	2.	2.	2.	308.	361.	245.	322.	328.	325.
40	2.	2.	2.	2.	43.	48.	48.	46.	48.	43.





## APPENDIX III - CONTINUED

CHARACTER	OTU									
	11	12	13	14	15	16	17	18	19	20
1	2.	2.	2.	2.	2.	2.	2.	2.	2.	2.
2	58.	58.	60.	58.	55.	53.	56.	53.	58.	60.
3	120.	127.	120.	120.	120.	110.	113.	132.	118.	122.
4	127.	130.	118.	127.	122.	120.	122.	139.	122.	130.
5	94.	98.	102.	94.	98.	92.	93.	95.	98.	94.
6	70.	72.	65.	67.	67.	67.	62.	74.	65.	65.
7	2.	2.	2.	2.	1.	2.	2.	2.	2.	2.
8	20.	17.	17.	20.	22.	22.	19.	20.	26.	24.
9	3.	3.	3.	3.	3.	3.	3.	3.	3.	3.
10	132.	132.	122.	125.	127.	134.	144.	139.	149.	142.
11	8.	8.	8.	8.	8.	8.	8.	9.	8.	8.
12	1.	1.	1.	1.	1.	1.	1.	1.	1.	1.
13	170.	190.	180.	192.	175.	187.	182.	192.	202.	202.
14	1.	1.	1.	1.	1.	1.	1.	1.	1.	1.
15	67.	62.	60.	58.	62.	55.	62.	60.	72.	67.
16	89.	86.	84.	84.	84.	86.	94.	86.	96.	94.
17	38.	38.	38.	36.	43.	38.	46.	36.	41.	46.
18	156.	156.	144.	144.	154.	158.	156.	163.	168.	163.
19	139.	120.	149.	144.	142.	132.	125.	139.	137.	139.
20	62.	56.	60.	60.	53.	58.	55.	58.	44.	43.
21	74.	70.	77.	70.	67.	70.	67.	70.	89.	91.
22	29.	24.	29.	29.	29.	20.	22.	24.	38.	34.
23	62.	67.	58.	55.	62.	65.	55.	65.	60.	58.
24	2.	2.	2.	2.	2.	2.	2.	2.	2.	2.
25	120.	110.	118.	106.	103.	110.	103.	118.	118.	123.
26	292.	298.	288.	283.	293.	288.	283.	307.	307.	302.
27	254.	254.	250.	245.	259.	245.	245.	254.	245.	259.
28	216.	216.	211.	203.	216.	206.	202.	216.	216.	211.
29	105.	108.	98.	101.	100.	103.	113.	106.	122.	113.
30	288.	288.	283.	283.	288.	278.	275.	288.	293.	293.
31	274.	267.	289.	280.	288.	270.	243.	272.	240.	260.
32	55.	55.	50.	53.	53.	60.	55.	60.	62.	60.
33	1.	1.	1.	1.	1.	1.	1.	1.	1.	1.
34	2.	2.	2.	2.	2.	2.	2.	2.	1.	1.
35	122.	120.	120.	137.	120.	132.	113.	122.	134.	130.
36	38.	38.	38.	55.	36.	48.	38.	38.	50.	46.
37	113.	113.	110.	115.	115.	108.	108.	120.	127.	125.
38	21.	21.	21.	22.	22.	21.	21.	54.	17.	17.
39	2.	2.	2.	2.	2.	2.	2.	5.	2.	2.
40	1.	1.	1.	1.	1.	1.	1.	4.	1.	1.





## APPENDIX III - CONTINUED

CHARACTER	OTU						
	41	42	43	44	45	46	47
1	2.	2.	2.	2.	2.	2.	2.
2	50.	55.	53.	50.	50.	48.	53.
3	103.	108.	108.	98.	103.	98.	110.
4	101.	110.	108.	98.	103.	101.	108.
5	102.	98.	100.	100.	100.	97.	102.
6	53.	41.	55.	50.	53.	53.	58.
7	2.	2.	2.	2.	2.	2.	2.
8	22.	10.	22.	19.	22.	22.	5.
9	3.	3.	3.	3.	3.	3.	3.
10	106.	113.	110.	103.	108.	101.	110.
11	5.	5.	5.	5.	8.	8.	8.
12	1.	1.	1.	1.	1.	1.	1.
13	158.	158.	180.	150.	170.	168.	175.
14	1.	1.	1.	1.	1.	1.	1.
15	48.	48.	41.	34.	50.	48.	43.
16	72.	67.	70.	62.	72.	70.	72.
17	27.	29.	30.	29.	31.	26.	31.
18	122.	130.	136.	125.	132.	120.	135.
19	127.	134.	117.	115.	122.	130.	134.
20	34.	38.	50.	48.	38.	43.	38.
21	50.	53.	62.	62.	55.	65.	55.
22	29.	31.	17.	20.	34.	26.	31.
23	48.	50.	55.	53.	43.	46.	48.
24	2.	2.	2.	2.	2.	2.	2.
25	70.	77.	89.	91.	74.	89.	77.
26	249.	250.	264.	245.	254.	245.	245.
27	213.	220.	209.	201.	216.	206.	221.
28	187.	194.	180.	170.	184.	180.	190.
29	84.	89.	89.	89.	89.	86.	94.
30	249.	254.	250.	235.	245.	238.	259.
31	296.	291.	280.	264.	275.	277.	276.
32	50.	48.	72.	43.	48.	46.	55.
33	1.	1.	1.	1.	1.	1.	1.
34	1.	1.	1.	1.	1.	1.	1.
35	98.	103.	137.	96.	113.	110.	114.
36	34.	41.	67.	34.	48.	42.	43.
37	113.	98.	100.	96.	108.	101.	96.
38	21.	21.	16.	17.	14.	14.	17.
39	1.	1.	2.	2.	1.	1.	1.
40	1.	1.	1.	1.	1.	1.	1.















## APPENDIX IV - CONTINUED

DATA MATRIX FOR 37 MALES (GROUPS 3, 4, AND 5)

CHARACTER	OTU	1	2	3	4	5	6	7	8	9	10
1	108.										
2	112.										
3	60.	2.	2.	2.	2.	2.	2.	2.	2.	2.	2.
4	60.	34.	34.	36.	36.	36.	23.	36.	59.	60.	
5	60.	82.	80.	78.	80.	82.	74.	74.	101.	108.	
6	71.	72.	68.	68.	68.	61.	51.	62.	101.	99.	
7	4.	114.	118.	115.	118.	134.	145.	119.	100.	118.	
8	314.	46.	46.	46.	44.	38.	28.	16.	65.	60.	
9	98.	1.	1.	1.	1.	1.	1.	1.	1.	1.	
10	37.	12.	13.	40.	8.	10.	9.	12.	29.	29.	
11	70.	2.	2.	2.	2.	2.	2.	2.	2.	2.	
12	43.	84.	86.	86.	82.	72.	59.	65.	142.	140.	
13	79.	6.	8.	7.	7.	5.	5.	8.	8.	8.	
14	44.	2.	2.	2.	2.	2.	2.	2.	2.	2.	
15	20.	113.	108.	104.	99.	97.	74.	98.	201.	199.	
16	73.	1.	1.	1.	1.	1.	1.	1.	1.	1.	
17	37.	24.	24.	24.	23.	19.	17.	22.	43.	35.	
18	44.	45.	45.	46.	42.	44.	36.	28.	91.	71.	
19	108.	22.	20.	21.	21.	23.	24.	27.	30.	25.	
20	86.	90.	90.	91.	97.	104.	95.	91.	130.	124.	
21	59.	84.	86.	82.	84.	65.	55.	101.	127.	124.	
22	167.	38.	34.	46.	40.	28.	22.	31.	33.	28.	
23	24.	39.	36.	46.	40.	29.	22.	31.	30.	28.	
24	64.	10.	14.	12.	11.	11.	16.	17.	50.	30.	
25	46.	1.	1.	1.	1.	1.	1.	1.	1.	1.	
26	68.	1.	1.	1.	1.	1.	1.	1.	1.	1.	
27	44.	55.	51.	67.	59.	45.	34.	48.	94.	101.	
28	119.	182.	181.	178.	181.	195.	176.	173.	273.	284.	
29	46.	152.	148.	146.	152.	137.	125.	163.	235.	226.	
30	23.	129.	129.	124.	130.	112.	99.	144.	180.	180.	
31	57.	59.	57.	59.	59.	51.	43.	60.	108.	103.	
32	57.	176.	178.	172.	179.	165.	148.	192.	264.	259.	
33	324.	302.	312.	292.	303.	324.	344.	320.	244.	251.	
34	450.	31.	34.	30.	30.	23.	21.	26.	48.	53.	
35	166.	1.	1.	1.	1.	1.	1.	1.	1.	1.	
36	96.	2.	2.	2.	2.	2.	2.	2.	2.	2.	
37	320.	81.	79.	67.	67.	53.	38.	58.	156.	110.	
38	271.	40.	29.	25.	24.	21.	15.	26.	79.	36.	
39	2.	74.	70.	68.	67.	78.	65.	67.	93.	108.	
40	2.	8.	10.	8.	8.	8.	7.	1.	16.	10.	
	2.	2.	2.	2.	2.	2.	2.	1.	1.	2.	
	2.	2.	2.	2.	2.	1.	1.	2.	2.	2.	

## APPENDIX V

## BASIC DATA MATRIX FOR 37 MALES (GROUPS 3, 4, AND 5)

CHARACTER	OTU	12	13	14	15	16	17	18	19	20
	1	2	3	4	5	6	7	8	9	10
1	2.	2.	2.	2.	2.	2.	2.	2.	2.	2.
2	36.	34.	34.	36.	36.	36.	25.	36.	55.	60.
3	82.	82.	80.	78.	80.	82.	74.	74.	101.	108.
4	72.	72.	68.	68.	68.	61.	51.	62.	101.	98.
5	114.	114.	118.	115.	118.	134.	145.	119.	100.	110.
6	48.	46.	46.	46.	44.	36.	28.	36.	65.	60.
7	1.	1.	1.	1.	1.	1.	1.	1.	1.	1.
8	12.	12.	13.	40.	8.	10.	9.	12.	29.	29.
9	2.	2.	2.	2.	2.	2.	2.	2.	2.	2.
10	89.	84.	86.	86.	82.	72.	59.	65.	142.	140.
11	6.	6.	8.	7.	7.	5.	5.	8.	8.	8.
12	2.	2.	2.	2.	2.	2.	2.	2.	2.	2.
13	119.	113.	108.	104.	99.	97.	74.	98.	201.	199.
14	1.	1.	1.	1.	1.	1.	1.	1.	1.	1.
15	24.	24.	24.	24.	23.	19.	17.	22.	43.	35.
16	48.	45.	45.	46.	42.	44.	36.	48.	91.	91.
17	23.	22.	20.	21.	21.	23.	24.	27.	50.	46.
18	103.	90.	90.	91.	97.	104.	95.	91.	154.	151.
19	86.	84.	86.	82.	84.	65.	55.	101.	117.	115.
20	48.	38.	34.	46.	40.	28.	22.	31.	53.	46.
21	47.	39.	36.	46.	40.	29.	22.	31.	72.	77.
22	17.	10.	14.	12.	11.	11.	16.	17.	50.	50.
23	1.	1.	1.	1.	1.	1.	1.	1.	1.	1.
24	1.	1.	1.	1.	1.	1.	1.	1.	1.	1.
25	67.	55.	51.	67.	59.	45.	34.	48.	94.	101.
26	192.	182.	181.	178.	181.	195.	176.	173.	273.	288.
27	153.	152.	148.	146.	152.	137.	125.	163.	235.	226.
28	130.	129.	129.	124.	130.	112.	99.	144.	180.	180.
29	65.	59.	57.	59.	59.	51.	43.	60.	108.	103.
30	182.	178.	178.	172.	179.	165.	148.	192.	264.	259.
31	280.	302.	312.	292.	303.	324.	344.	320.	244.	251.
32	33.	31.	34.	30.	30.	23.	21.	26.	48.	53.
33	1.	1.	1.	1.	1.	1.	1.	1.	1.	1.
34	2.	2.	2.	2.	2.	2.	2.	2.	3.	3.
35	68.	81.	70.	67.	67.	53.	38.	58.	156.	110.
36	26.	40.	29.	25.	24.	21.	15.	26.	79.	36.
37	70.	74.	70.	68.	67.	78.	65.	67.	93.	108.
38	8.	8.	10.	8.	6.	8.	7.	1.	16.	10.
39	2.	2.	2.	2.	2.	2.	2.	1.	2.	2.
40	2.	2.	2.	2.	2.	1.	1.	2.	2.	2.





## APPENDIX V - CONTINUED

CHARACTER	OTU						
	31	32	33	34	35	36	37
1	2.	2.	2.	2.	2.	2.	2.
2	53.	55.	58.	55.	55.	55.	53.
3	101.	101.	96.	96.	96.	101.	98.
4	101.	102.	100.	101.	101.	106.	103.
5	100.	99.	96.	95.	95.	95.	95.
6	72.	74.	77.	74.	74.	77.	74.
7	1.	1.	1.	1.	1.	1.	1.
8	7.	26.	19.	31.	31.	26.	29.
9	2.	2.	2.	2.	2.	2.	2.
10	127.	125.	132.	129.	129.	127.	130.
11	14.	16.	17.	17.	17.	15.	19.
12	2.	2.	2.	2.	2.	2.	2.
13	161.	180.	163.	166.	166.	163.	173.
14	1.	1.	1.	1.	1.	1.	1.
15	41.	43.	43.	41.	41.	41.	38.
16	65.	72.	74.	70.	70.	72.	70.
17	62.	62.	60.	62.	62.	60.	60.
18	216.	213.	199.	208.	208.	211.	200.
19	122.	130.	127.	130.	130.	134.	132.
20	18.	17.	19.	17.	17.	18.	15.
21	41.	40.	41.	36.	36.	34.	38.
22	94.	105.	98.	100.	100.	106.	106.
23	1.	1.	1.	1.	1.	1.	1.
24	1.	1.	1.	1.	1.	1.	1.
25	67.	55.	67.	58.	60.	58.	62.
26	317.	331.	307.	326.	312.	326.	317.
27	278.	288.	264.	283.	245.	278.	273.
28	211.	225.	206.	221.	190.	220.	211.
29	96.	91.	98.	91.	96.	98.	91.
30	331.	336.	321.	336.	307.	336.	326.
31	345.	370.	326.	370.	320.	343.	358.
32	38.	38.	38.	36.	41.	38.	38.
33	1.	1.	1.	1.	1.	1.	1.
34	3.	3.	3.	3.	3.	3.	3.
35	76.	110.	79.	91.	79.	79.	122.
36	43.	77.	48.	62.	48.	46.	74.
37	122.	130.	120.	137.	134.	125.	120.
38	22.	17.	18.	17.	15.	15.	14.
39	2.	2.	2.	2.	2.	2.	2.
40	4.	4.	4.	4.	4.	4.	4.





## APPENDIX VI - CONTINUED

CHARACTER	OTU									
	11	12	13	14	15	16	17	18	19	20
1	95.	79.	97.	81.	84.	84.	70.	85.	81.	86.
2	79.	72.	95.	77.	75.	66.	68.	70.	68.	73.
3	59.	52.	64.	59.	55.	52.	53.	51.	53.	53.
4	55.	48.	59.	57.	53.	50.	51.	48.	51.	51.
5	53.	48.	62.	53.	51.	46.	46.	54.	47.	48.
6	70.	62.	81.	66.	63.	59.	58.	61.	53.	61.
7	7.	7.	11.	7.	7.	6.	4.	6.	5.	6.
8	176.	157.	265.	230.	225.	220.	215.	211.	206.	225.
9	60.	59.	97.	81.	79.	79.	73.	77.	80.	77.
10	24.	21.	40.	28.	26.	24.	25.	26.	24.	54.
11	37.	37.	77.	64.	57.	57.	57.	58.	62.	59.
12	40.	35.	55.	55.	51.	53.	51.	44.	48.	40.
13	33.	31.	75.	68.	64.	66.	57.	62.	62.	64.
14	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
15	9.	9.	22.	29.	24.	26.	22.	20.	20.	24.
16	33.	31.	75.	55.	62.	55.	48.	60.	55.	51.
17	20.	21.	31.	24.	24.	29.	28.	24.	33.	29.
18	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
19	86.	81.	131.	112.	101.	106.	103.	103.	102.	117.
20	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
21	9.	13.	20.	18.	18.	20.	15.	20.	15.	20.
22	95.	94.	151.	130.	119.	126.	118.	123.	117.	137.
23	9.	9.	15.	15.	13.	13.	13.	13.	15.	15.
24	40.	33.	51.	48.	51.	50.	51.	51.	51.	55.
25	18.	15.	22.	26.	23.	22.	23.	24.	23.	26.
26	24.	23.	55.	46.	46.	44.	40.	44.	42.	44.
27	9.	9.	22.	15.	13.	13.	13.	13.	13.	13.
28	79.	81.	125.	90.	88.	84.	84.	84.	86.	92.
29	4.	2.	2.	1.	2.	2.	1.	2.	2.	2.
30	24.	20.	29.	33.	26.	24.	23.	23.	22.	22.
31	28.	26.	42.	30.	31.	30.	29.	30.	26.	29.
32	48.	35.	50.	55.	46.	46.	44.	44.	44.	46.
33	176.	157.	265.	221.	223.	216.	208.	211.	199.	218.
34	294.	240.	382.	314.	323.	314.	304.	304.	294.	323.
35	125.	157.	166.	127.	132.	120.	100.	118.	112.	122.
36	120.	110.	102.	105.	112.	127.	403.	121.	119.	119.
37	296.	266.	273.	284.	285.	278.	295.	274.	258.	292.
38	568.	153.	230.	247.	245.	262.	304.	258.	263.	265.
39	1.	1.	1.	1.	1.	2.	1.	1.	1.	1.









## APPENDIX VII - CONTINUED

CHARACTER	OTU						
	11	12	13	14	15	16	17
1	2.	2.	2.	2.	2.	2.	2.
2	60.	59.	62.	51.	52.	60.	79.
3	100.	96.	100.	83.	86.	91.	86.
4	126.	117.	122.	103.	106.	106.	108.
5	79.	82.	82.	80.	81.	86.	80.
6	103.	97.	103.	84.	88.	91.	87.
7	1.	1.	1.	1.	1.	1.	1.
8	36.	37.	12.	26.	26.	24.	34.
9	1.	1.	1.	1.	1.	3.	1.
10	147.	137.	136.	116.	129.	125.	125.
11	14.	10.	14.	10.	11.	40.	10.
12	1.	1.	1.	1.	1.	1.	1.
13	197.	185.	168.	156.	168.	156.	156.
14	1.	1.	1.	1.	1.	1.	1.
15	39.	39.	43.	35.	38.	35.	31.
16	81.	79.	79.	65.	74.	70.	70.
17	50.	47.	53.	36.	40.	43.	38.
18	185.	184.	197.	150.	159.	163.	156.
19	96.	88.	106.	86.	74.	82.	84.
20	41.	47.	39.	34.	27.	26.	34.
21	84.	75.	2.	51.	54.	48.	53.
22	61.	38.	48.	50.	44.	67.	53.
23	1.	1.	1.	1.	1.	1.	1.
24	1.	1.	1.	1.	1.	1.	1.
25	108.	102.	84.	75.	77.	91.	77.
26	328.	310.	297.	255.	266.	274.	267.
27	243.	225.	240.	195.	193.	220.	199.
28	193.	177.	187.	157.	147.	178.	161.
29	93.	93.	100.	84.	84.	81.	77.
30	286.	261.	288.	228.	232.	259.	232.
31	268.	279.	288.	274.	274.	320.	301.
32	55.	51.	50.	47.	47.	46.	48.
33	1.	1.	1.	1.	1.	1.	1.
34	3.	3.	3.	3.	3.	3.	3.
35	110.	98.	86.	79.	92.	82.	79.
36	45.	42.	40.	37.	41.	36.	34.
37	126.	120.	110.	101.	105.	100.	115.
38	18.	19.	20.	20.	16.	17.	19.
39	2.	1.	1.	1.	1.	1.	1.
40	3.	3.	3.	3.	3.	3.	3.



APPENDIX VIII - CONTINUED

CHARACTER	OTU				
	11	12	13	14	15
1	98.	98.	90.	95.	86.
2	113.	108.	103.	112.	98.
3	83.	78.	77.	76.	70.
4	75.	70.	69.	68.	64.
5	98.	88.	87.	91.	81.
6	122.	114.	108.	116.	101.
7	11.	13.	11.	12.	9.
8	289.	269.	255.	259.	215.
9	101.	82.	88.	103.	90.
10	41.	32.	40.	44.	22.
11	93.	82.	78.	89.	79.
12	52.	44.	44.	49.	46.
13	78.	71.	63.	71.	60.
14	53.	40.	42.	47.	44.
15	33.	33.	25.	23.	20.
16	82.	80.	69.	73.	64.
17	23.	20.	20.	23.	20.
18	56.	55.	52.	44.	42.
19	119.	118.	87.	98.	95.
20	74.	68.	59.	62.	57.
21	35.	27.	33.	32.	26.
22	153.	145.	134.	130.	121.
23	34.	33.	31.	25.	22.
24	45.	39.	41.	46.	44.
25	50.	50.	44.	39.	35.
26	75.	72.	65.	65.	57.
27	23.	19.	24.	22.	22.
28	129.	119.	116.	129.	117.
29	16.	14.	15.	15.	13.
30	36.	39.	34.	33.	26.
31	52.	50.	48.	52.	44.
32	53.	57.	46.	52.	42.
33	291.	273.	259.	262.	220.
34	408.	390.	362.	373.	323.
35	188.	179.	171.	178.	147.
36	87.	90.	87.	84.	88.
37	284.	325.	290.	250.	239.
38	216.	217.	211.	210.	220.
39	2.	2.	2.	1.	2.



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