A numerical taxonomic study of the Mallophagan genera *Cummingsiella* (= *Quadraceps*), *Saemundssonia* (Ischnocera: Philopteridae), and *Austromenopon* (Amblycera: Menoponidae) from alcids (Aves: Charadriiformes) of the northwest Atlantic[1] with reference to host–parasite relationships

ELDON S. EVELEIGH AND HIROSHI AMANO

Department of Zoology, University of Toronto, Toronto, Ont., Canada M5S 1A1

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Specimens of *Cummingsiella*, *Saemundssonia*, and *Austromenopon* recovered from the alcids of the northwest Atlantic were analyzed using the techniques of numerical taxonomy. Twenty-one morphological characters common to both sexes plus four genital characters in the males were measured and used in the analyses. Principal axis factor analysis (PAFA) and four clustering techniques were used to determine the phenetic relationships at various taxonomic levels.

The results supported the familial and generic classifications established by conventional taxonomists. The diagnostic value of genital characters at generic and specific levels were evaluated. The results from the analysis of each genus are presented and compared with existing classifications. With the exception of *Austromenopon*, the species groups formed within each genus were very similar for both sexes. Host–parasite relationships based on parasite interrelationships were investigated.

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On a utilisé les techniques de taxonomie numérique pour analyser des spécimens de *Cummingsiella*, *Saemundssonia* et *Austromenopon* prélevés chez des alcidés de la région du nord-ouest de l'Atlantique. On a mesuré et utilisé dans l'analyse 21 caractères morphologiques communs aux deux sexes et quatre caractères génitaux mâles. L'analyse factorielle en axes principaux (PAFA) et quatre analyses de groupements ont permis d'établir des relations phénétiques à divers niveaux taxonomiques.

Les résultats confirment les classifications familiale et générique établies par les méthodes taxonomiques classiques. On a évalué la valeur diagnostique des caractères génitaux aux niveaux générique et spécifique. On compare les résultats de l'analyse dans le cas de chaque genre avec ceux des classifications préalables. Les groupes spécifiques formés au sien de chaque genre, à l'exception d'*Austromenopon*, sont très semblables chez les deux sexes. On examine les liens hôte-parasite en se basant sur les relations inter-parasites.

[Traduit par le journal]

Introduction

The alcids of North America are infested with Mallophaga belonging to the genera *Cummingsiella* (= *Quadraceps*), *Saemundssonia*, and *Austromenopon* (Emerson 1972). While most papers written on these ectoparasites have been taxonomic (i.e. species descriptions), few attempts have been made to objectively study their classification. Timmermann (1957) provided a limited discussion of these genera on European alcids in a large study on the mallophagan parasites of the order Charadriiformes and, to date, this study contains the only work done on the *Saemundssonia* species from these hosts. Recently, the same author (Timmermann 1974) examined the *Cummingsiella* populations on 10 alcid species and erected 3 new species and subspecies. However, no formal classification of the parasites was presented. Clay (1959) erected a key to the *Austromenopon* parasites of charadriiform birds but she did not attempt to study those from alcids. Thus, no comprehensive taxonomic study of the forms infesting the alcids, particularly those from North America, has been attempted.

During an ecological study of the ectoparasites on six alcid species from the northwest Atlantic, Eveleigh and Threlfall (1976) reported 12 species belonging to these genera. While most parasites conformed to the data reported for these species in the literature, in some cases the host of a particular parasite differed and certain parasites were recovered from hosts other than those previously reported. Since most of the alcids (five of six) bred in the same colony where physical contact between certain species is possible, this suggests that through time certain mallophaga species may have made successful host transfers, resulting in the formation of previously unsuspected species complexes on these birds. Having representatives of these parasites from the same population provided us with an excellent opportunity to examine (1) the classification of the parasites and (2) host–parasite relationships.

To minimize the effect of character subjectivity and to obtain a more objective classification, the techniques of numerical taxonomy were used. The purpose of the study was fourfold: first, to examine the classification of the parasites at higher taxonomic levels; second, to determine the relative taxonomic importance of genital characters in the classification of males; third, to reach a satisfactory classification of each genus based on both male and female specimens; and fourth, to examine the relationship between parasite and host classifications using the groups formed within each parasite genus.

Materials and Methods

Materials

Eleven of the 12 species belonging to the three genera were available for study. Specimens of *Saemundssonia celidoxa* from the same population were unavailable. Details on the collection and examination of the hosts are given by Eveleigh and Threlfall (1976). Additional taxa from other charadriiform birds were included in the analyses as a check on the clusters formed by the various numerical techniques and to evaluate the degree of similarity between the parasites from the alcids. Details on the species examined are given in Table 1.

For the purpose of clarity each major taxon will be discussed separately.

Genus Cummingsiella Ewing, 1930

This genus was originally considered to occur only on hosts from the family Scolopacidae, those parasitizing the alcids belonging to the genus *Quadraceps* (Emerson 1972). Timmermann (1972) considers these genera synonymous and moved all of the forms on the alcids into the genus *Cummingsiella*. We have followed this move since a discussion of the relationships between these two forms is beyond the scope of this paper.

Four species were reported from the six alcid species by Eveleigh and Threlfall (1976). These included *aetherea klatti*, *alcae*, *helgovauki*, *obliqua obliqua*, and *obliqua aquilonis* (see Table 1). Two hosts (*Cepphus grylle* and *Plautus alle*) harboured populations of *aetherea klatti*. This is in disagreement with Timmermann (1974), who reported that *Plautus alle* and *Aethia pusilla* (not considered in this study) were parasitized by this species while *Alca torda* and *Cepphus grylle* were both parasitized by *alcae*. This discrepancy will be examined and discussed in the text.

With the exception of Timmermann's (1974) study, no detailed account of these parasites has been published.

Genus Saemundssonia Timmermann, 1935

This genus has been reported from a variety of hosts, five species occurring on the alcids, viz. *calva*, *celidoxa*, *fraterculae*, *grylle*, and *merguli* (Emerson 1972; Eveleigh and Threlfall 1976) (see Table 1). *Saemundssonia calva* had been previously reported from *Uria aalge* and *U. lomvia* by Timmermann (1957) but its presence on *U. lomvia* in North America was only recently demonstrated by Eveleigh and Threlfall (1976). It remains to be seen whether it is the same species on these hosts.

Timmermann (1957) examined the known European species from alcids but no comprehensive study of this genus has been published as to the validity of the species groups that he proposed.

Genus Austromenopon Bedford, 1939

Emerson (1972) listed three species from the alcids in North America (*nigropleurum*, *uriae*, and *merguli*). Eveleigh and Threlfall (1974) erected *phippsi* from *U. lomvia* and suggested that *merguli* and *nigropleurum* were synonyms. Another species, *A. fraterculae*, was described by Timmermann (1954) from *Fratercula arctica* but is regarded by Clay (1959) as a straggler from another host and not a species from the alcids. Eveleigh and Threlfall (1976) reported *nigropleurum* from this host and also from two others (*A. torda* and *P. alle*) (see Table 1).

It is generally agreed by taxonomists that all the species are closely related and belong to one species group, the *nigropleurum* group. *Austromenopon phippsi* is regarded by Eveleigh and Threlfall (1974) to be closely related to *A. uriae* and hence part of this *nigropleurum* group.

Of the three genera occurring on the alcids, this genus is by far the most troublesome and a complete revision is certainly in order.

Methods

The number of specimens of each taxon to be used was arbitrarily decided because in many cases only a limited number of good, undistorted specimens was available for study. If many specimens of certain taxa existed then five or six of each sex were chosen for examination. In a few cases only one sex of a taxon was available. Only adult specimens were considered.

Twenty-one characters common to both sexes were selected with four genital characters added in the males. These were chosen for ease and repeatability of measure-

[1]The alcids of the northwest Atlantic include: *Fratercula arctica*, *Uria aalge*, *Uria lomvia*, *Plautus alle*, *Cepphus grylle*, and *Alca torda*.

TABLE 1. The species of Mallophaga examined in this study and their hosts

Species name	No. examined ♂	No. examined ♀	Host	Host family	Host locality
Cummingsiella					
aetherea klatti	3	5	*Plautus alle*	Alcidae	Nfld.*
	1	1	*Cepphus grylle*	Alcidae	Nfld.
alcae	4	3	*Alca torda*	Alcidae	Nfld.
helgovauki	3	4	*Fratercula arctica*	Alcidae	Nfld.
obliqua obliqua	5	3	*Uria aalge*	Alcidae	Nfld.
obliqua aquilonis	5	5	*Uria lomvia*	Alcidae	Nfld.
falcigerus	2	1	*Totanus flavipes*	Scolopacidae	Ont.†
nigrolimbatus	—	1	*Limnodromus griseus*	Scolopacidae	Ont.
ravus	—	1	*Actitis macularia*	Scolopacidae	Ont.
normifer normifer	—	1	*Stercorarius parasiticus*	Stercorariidae	Ont.
Saemundssonia					
calva	5	4	*Uria lomvia*	Alcidae	Nfld.
	2	—	*Uria aalge*	Alcidae	Nfld.
fraterculae	5	6	*Fratercula arctica*	Alcidae	Nfld.
grylle	—	1	*Cepphus grylle*	Alcidae	Nfld.
merguli	3	3	*Plautus alle*	Alcidae	Nfld.
lari	2(2)‡	2(2)	*Larus argentatus*	Laridae	Nfld.(Ont.)
lari gonothorax	5	5	*Larus marinus*	Laridae	Ont.
tringae ?	—	2	*Limnodromus griseus*	Scolopacidae	Ont.
platygaster islandica ?	1	—	*Crocethia alba*	Scolopacidae	Ont.
Austromenopon					
nigropleurum	3	5	*Fratercula arctica*	Alcidae	Nfld.
	—	5	*Plautus alle*	Alcidae	Nfld.
	—	1	*Alca torda*	Alcidae	Nfld.
phippsi	5	5	*Uria lomvia*	Alcidae	Nfld.
uriae	5	5	*Uria aalge*	Alcidae	Nfld.
transversum ?	—	1	*Xema sabini*	Laridae	Ont.

*Nfld. = Newfoundland.
†Ont. = Ontario.
‡Number in parentheses indicates number examined from corresponding host locality in parentheses.

ment, and overall morphological representation. A list of the characters used is given in Table 2 and illustrated in Fig. 1.

All measurements were taken using a Reichert interference microscope and were recorded in microns (μm).

It should be noted that a few characters were invariant in certain taxa and were deleted from the analyses. Details on this will be given in the text if and when appropriate.

Since the characters were not all expressed in the same units, each character was standardized according to the method of Sokal and Sneath (1963).

The data for each specimen was processed on the IBM 370-165 computer at the University of Toronto Computer Center. Ordination of the data in reduced dimensions was performed using principal axis factor analysis (PAFA), a multivariate method developed and described by Veldman (1967). The phenetic relationships between the operational taxonomic units (OTUs), based on correlation coefficients (r), were determined by using four cluster techniques from the NT-SYS package developed by Rohlf, Kishpaugh, and Bartcher. These included the unweighted pair-group method using arithmetic averages (UPGMA), weighted pair-group method using arithmetic averages (WPGMA), complete linkage, and single linkage. Distortion of the original correlation matrix by the clustering procedures was estimated by computing the cophenetic value between each phenogram and the original correlation matrix. The clustering method producing the least distortion is presented.

To aid in the interpretation and discussion of various phenograms, a phenon line was chosen. These lines are purely group defining with no special taxonomic significance attached to them.

Three-dimensional diagrams showing the positions of the OTUs relative to the first three axes were obtained from a perspective program developed by A. R. Gibson, University of Toronto.

In most analyses the results from both the PAFA and the clustering method are presented and discussed for the following reasons: (1) the PAFA allows the relationships of the OTUs to be viewed in a three-dimensional space with little loss of information and the characters influencing the separation of the OTUs along each axis can be determined from the factor scores; (2) the clustering method depicts the relationship of the taxa within clusters with reasonable accuracy, but unlike PAFA, may distort the relationships between clusters. Therefore, the presentation of both techniques enables a fuller discussion of the data.

TABLE 2. Characters used in the analyses. Last four characters are for males only

Character no.	Description
1	Body length
2	Body width (taken at widest point)
3	Ratio of body length to body width
4	Head length
5	Head width (taken at widest point)
6	Ratio of head length to head width
7	Ratio of body length to head length
8	Prothorax length
9	Porthorax width
10	Ratio of prothorax width to prothorax length
11	Distance between head tip and mouthpart bases
12	Distance between mouthpart bases
13	Length of femur of leg III
14	Length of tibia of leg II
15	Degree of sclerotization (ratio of width of nonsclerotized zone of fourth spiracle-bearing segment (x) to total width of that segment of abdomen (y) (x:y))
16	Presence or absence of maxillary palps
17	No. of segments in antenna
18	No. of setae on femur of leg II (dorsal and ventral)
19	No. of setae on tibia of leg III (dorsal and ventral)
20	No. of setae on second spiracle-bearing abdominal segment (dorsal and ventral)
21	No. of setae on fifth spiracle-bearing abdominal segment (dorsal and ventral)
22	Length of paramere
23	Width of paramere
24	Length of endomere
25	Width of mesosomal structures

Results and Discussion

Analyses of Higher Taxonomic Structure

To examine the classification of the parasites at higher taxonomic levels, the first analysis performed was on the mean data of males and females using 21 characters common to both sexes (genitalia excluded). The results are shown in Figs. 2 and 3.

The results from UPGMA (Fig. 2) show a clear distinction between the two recognized families: Philopteridae (OTUs 1–33) represented by the genera *Cummingsiella* (OTUs 1–17) and *Saemundssonia* (OTUs 18–33), and *Menoponidae* (OTUs 34–42) represented by the genus *Austromenopon*.

The three-dimensional plot of PAFA (Fig. 3) also shows a clear distinction between the two families and the three genera. The continuous but distinct clusters of *Cummingsiella* (OTUs 1–17) and *Saemundssonia* (OTUs 18–33) along factor II indicate that they are very similar and probably belong to the same subfamily Cummingsiellinae as suggested by Timmermann (1972). In both figures *Austromenopon* (OTUs 34–42) forms a homogeneous cluster.

An examination of the factor scores from PAFA revealed that the two clusters formed along factor I have been influenced by characters 4, 5, 16, 17, 18, 20, and 21. The separation of *Cummingsiella* and *Saemundssonia* along factor II was due to variations in characters 1, 2, 4, 5, and 19.

The difference in the level of clustering displayed by the ischnocerans (*Cummingsiella* and *Saemundssonia*) and the amblyceran (*Austromenopon*) is interesting. It is generally believed that members of the latter type are less closely adapted to particular habitats on their hosts and consequently display lesser divergence than the ischnocerans which have become adapted to particular habitats on their hosts (Rothschild and Clay 1961). This hypothesis is supported by the analyses since the levels of clustering of the taxa in the ischnocerans is quite low in comparison with the amblyceran (Fig. 2). From a taxonomic point of view, this suggests that species differences in the ischnocerans are more clearly defined than in the amblycerans and that the taxonomic structure within these two forms is probably quite different. Evidence of this will be seen in later analyses.

It is also interesting that sexual dimorphism, which is clearly exhibited in individual taxa of all three genera, is not reflected to the same degree within each genus. In the ischnocerans the males and females do not form distinct clusters, whereas in the amblyceran the males (OTUs 35, 37, and 39) and females (OTUs 34, 36, 38, 40, and 41) from the alcids do form distinct clusters. This is probably because the males and females of the ischnocerans show a wider divergence resulting in a 'bridging over' of the variation between the sexes when all the taxa are compared. Conversely, in the amblyceran, the variation between taxa is small and the sexes show clear separation.

The Relative Taxonomic Importance of Genital Characters on the Classification of Males

As indicated by the preceding analyses, the three genera could be separated without considering genital characters. However, no attempt

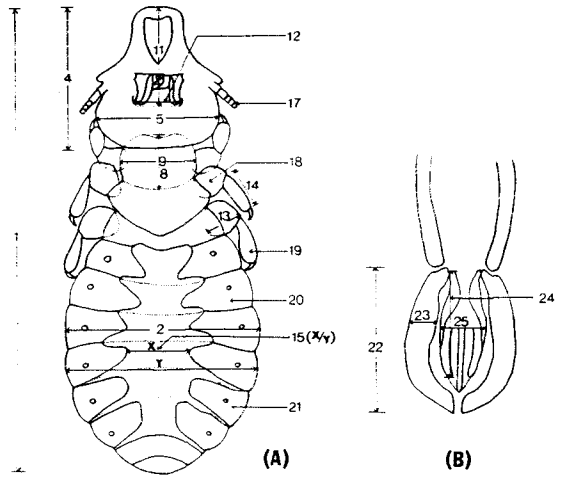

FIG. 1. Schematic diagram of a Mallophaga showing characters used in the analysis. (A) Adult specimen; (B) male genitalia. See Table 2 for character description.

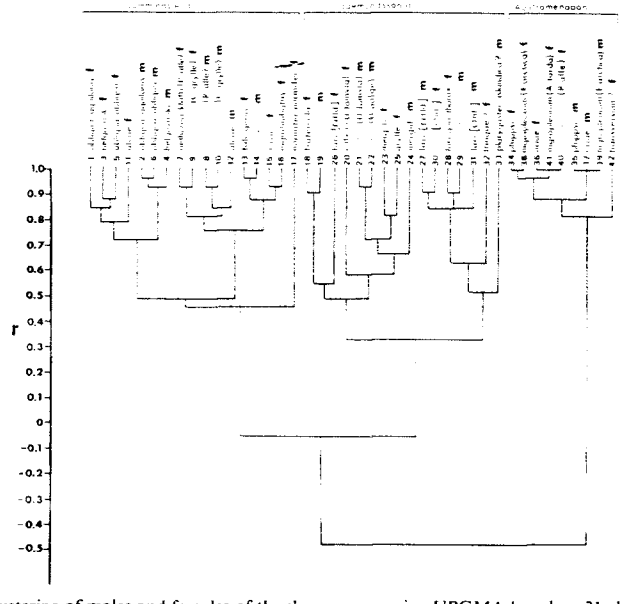

FIG. 2. Clustering of males and females of the three genera using UPGMA based on 21 characters. Cophenetic correlation = 0.917. *f* = female; *m* = male; hosts are given in parentheses; host locations are in square brackets.

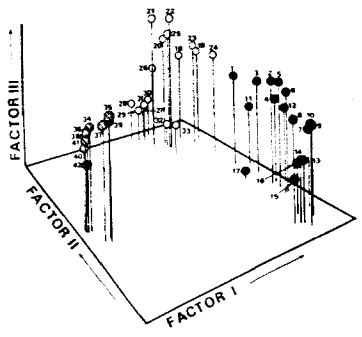

FIG. 3. Three-dimensional plot of PAFA for the males and females of the three genera based on 21 characters. The percentages of variation accounted for on factors I, II, and III are 41.13, 27.25, and 9.56% respectively. ● = *Cummingsiella*; ○ = *Saemundssonia*; ◔ = *Austromenopon*. See Fig. 2 for explanation of numbers.

was made at that time to examine the effects of the addition of genital characters on the phenetic relationships between the males of these taxa. Since conventional taxonomists heavily weight male genital characters in these genera, it is desirable to have some indication of their taxonomic importance in the classification of these parasites.

To achieve this aim, the data on the males of *Cummingsiella* and *Saemundssonia* were selected for analysis. *Austromenopon* was not included since it has already been established that this genus has no close affinity to the other genera based on nongenital characters and furthermore, their genitalia bear no resemblance to those of the other genera.

Three data sets were analyzed: the first, using only genital characters with the data nonstandardized; the second, using only nongenital characters; and the third, using all characters including those from the genitalia. In the latter two analyses the data were standardized. The four cluster analyses were used with each specimen representing an OTU. The antennal and maxillary palp characters were excluded in the latter analyses, being invariant in both taxa.

The results obtained when the genital characters were heavily weighted were completely meaningless, with little or no separation between genera and all of the taxa being essentially contained within one cluster. This indicates that, in this type of analysis, the size of the genital structure has no particular taxonomic importance. However, we realize that if it was possible to examine more characters and (or) describe the shape of the genital structures, as is done in conventional taxonomy, then more meaningful results may have been obtained.

The results obtained from the analysis of the nongenital characters and the complete data set indicated that the addition of genital characters did not affect the separation of *Cummingsiella* and *Saemundssonia*. It is evident, therefore, that genital characters are of no more taxonomic importance than characters associated with other body structures in separating taxa at higher taxonomic levels.

A closer examination of the results revealed that in both data sets six clusters have been formed: two in *Cummingsiella* and four in *Saemundssonia*. These clusters were formed at the same phenon level in both analyses, indicating that the inclusion of genital characters had little effect on the formation of clusters within genera. Differences did occur, however, in the phenetic relationships between the clusters and also in the composition of the taxa within each cluster. Hence it appears that genital characters do have some taxonomic value, if combined with other characters, and for more meaningful results they should be included in classifications at lower taxonomic levels.

In summary, we feel that from the point of view of describing new forms and constructing keys, genital characters are probably essential, but for the purpose of recognizing species groups and their interrelationships, it is necessary that these characters be given equal weight with other characters in an attempt to arrive at a more meaningful and objective classification. Moreover, one cannot hope to objectively establish the affinities between taxa if certain characters are emphasized while others are considered to have little importance.

Analysis of the Genera Cummingsiella, Saemundssonia, and Austromenopon Based on Both Sexes

The females in these genera appear to contain few diagnostic characters and are often regarded by conventional taxonomists as being indistinguishable in closely related species. Therefore, this sex has received little attention in species descriptions and in the construction of keys. It

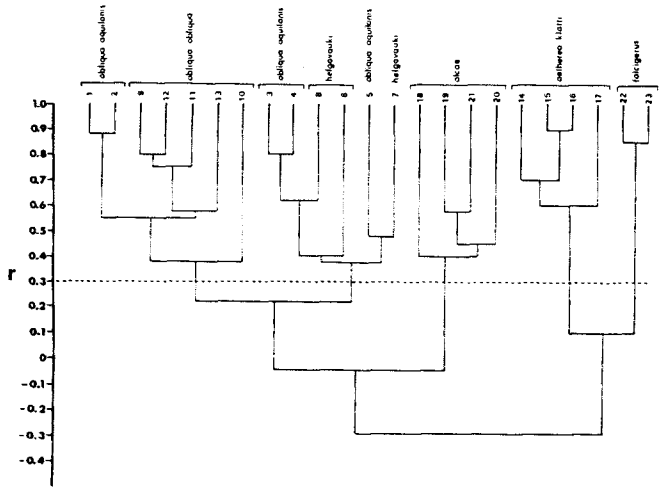

FIG. 4. Clustering of *Cummingsiella* males using UPGMA based on 23 characters. Cophenetic correlation = 0.868.

was hoped that through the use of numerical taxonomic techniques this situation could be improved and that a more natural classification based on both sexes could be obtained. Furthermore, the sexes warrant separate analyses since sexual dimorphism is not consistent within each genus (see Fig. 2).

In the analyses which follow, an attempt will be made to classify the species belonging to each genus. Twenty-three characters were used for the males and 19 for the females with each specimen representing an OTU. The maxillary palps and antennal characters were excluded, being invariant in all taxa.

Genus Cummingsiella

Males

The results obtained from the analyses of males are shown in Figs. 4 and 5. Using the 0.30 phenon line (Fig. 4), five groups are defined, four of which comprise the alcid parasites and the other consisting of specimens from a host of the family Scolopacidae. An examination of these groups reveals that the first consists primarily of *obliqua obliqua* (OTUs 9–13) plus two specimens of *obliqua aquilonis* (OTUs 1–2), and the second group, a mixture of *obliqua aquilonis* (OTUs 3–5) and *helgovauki* (OTUs 6–8). The other groups are exclusive to *alcae* (OTUs 18–21), *aetherea klatti* (OTUs 14–17), and *falcigerus* (OTUs 22–23) respectively.

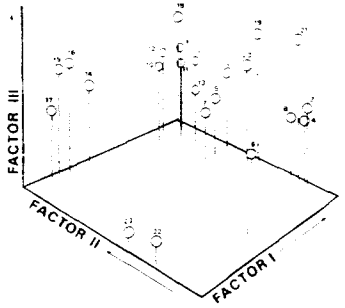

FIG. 5. Three-dimensional plot of PAFA for *Cummingsiella* males based on 23 characters. The percentages of variation accounted for factors I, II, and III are 33.95, 16.61, and 12.43% respectively. See Fig. 4 for explanation of numbers.

In the three-dimensional plot of PAFA (Fig. 5) four of the five groups indicated above can be readily distinguished. One group appears to form a continuous cluster along factor II and is composed of specimens of *obliqua obliqua* (OTUs 9–13), *obliqua aquilonis* (OTUs 1–5), and *helgovauki* (OTUs 6–8). While the results indicate that *obliqua obliqua* and *helgovauki* are separate taxa, *obliqua aquilonis* shows an affinity to both of these taxa. This prevents us from determining the exact taxonomic placement of *obliqua aquilonis* at this time.

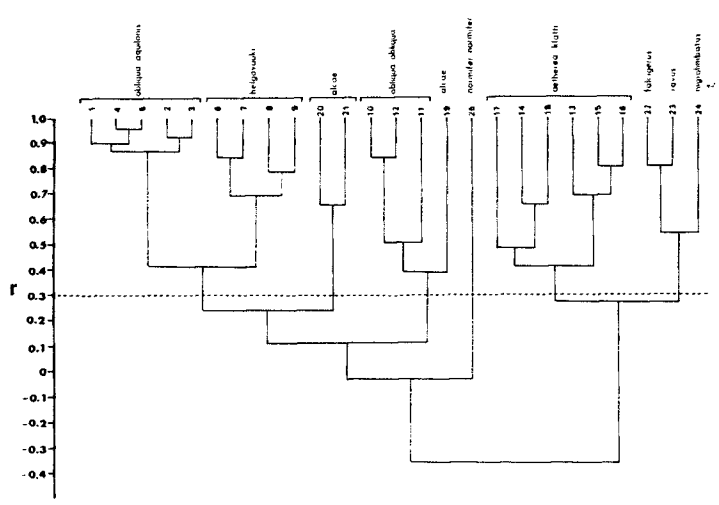

FIG. 6. Clustering of *Cummingsiella* females using UPGMA based on 19 characters. Cophenetic correlation = 0.855.

The *alcae* and *aetherea klatti* groups remain distinct in both analyses. The *aetherea klatti* group is represented by specimens from two hosts, *P. alle* (OTUs 14–16) and *C. grylle* (OTU 17). It is quite clear that they are the same parasite: the specimens from *C. grylle* being only slightly different from those from *P. alle*. This disagrees with the findings of Timmermann (1974) who reported *alcae* from *C. grylle*. However, this discrepancy may be attributed to the fact that different host populations were sampled in these studies and it may be possible for the same host to harbour different parasite populations in different geographical locations.

The specimens of *falcigerus* (OTUs 22–23) form a separate group in both analyses.

Based on the factor scores in PAFA, the groups have been separated out on factor I by variations in characters 2, 4, 8, 11, 18, and 24. Along factor II variations in characters 11, 19, 20, 22, and 23 have been stressed. Factor III emphasized characters 7, 8, 10, and 21.

In his taxonomic study of this genus, Timmermann (1974) obviously considered *obliqua aquilonis* to be closely related to *obliqua obliqua*. As mentioned above, our results indicate that it is intermediate between *obliqua obliqua* and *helgovauki* but we were unable to accurately determine its closest relative. Timmermann, in the same study, considered *helgovauki* to be closely related to *ambestrix*, a species found on the rhinoceros auklet (*Cerorhinca monocerata*). Since this study is confined to the northwest Atlantic alcids, this host was not examined, but in the context of this study it appears that *helgovauki* is similar to the *obliqua* spp. and can be placed with these parasites in a single group, the '*obliqua* group.'

Specimens of *alcae* are somewhat intermediate in their phenetic relationship with the '*obliqua* group' and *aetherea klatti*. However, in both analyses it shows greater affinity to the former group and perhaps should be considered a part of this group.

Cummingsiella aetherea klatti demonstrated only a remote phenetic relationship to the other alcid parasites and we do not hesitate to place it in a separate group. Furthermore, since *falcigerus* shows a closer affinity to *aetherea klatti* than to the alcid parasites as a whole, this separation is warranted. This probably supports Timmermann's (1974) decision to place *klatti* as a subspecies of *aetherea*, a parasite found on the least auklet (*Aethia pusilla*).

Females

The results obtained from the analyses of females are shown in Figs. 6 and 7. Using the same phenon line (0.30 in Fig. 6) as in the males, six groups are formed. Again four of these are

formed within the alcid parasites, the other two being composed of specimens from hosts of the families Scolopacidae and Stercorariidae. Within the first group are specimens of *obliqua aquilonis* (OTUs 1–5) and *helgovauki* (OTUs 6–9). The second group is exclusive to *alcae* (OTUs 20–21), and the third, although consisting primarily of *obliqua obliqua* (OTUs 10–12), contains one *alcae* specimen (OTU 19). The other three groups are composed of *normifer normifer* (OTU 25), *aetherea klatti* (OTUs 13–18), and specimens from the family Scolopacidae (OTUs 22–24) respectively.

The results from the three-dimensional plot of PAFA (Fig. 7) also demonstrate these groups well. The factor scores revealed that the separation of the groups along factor I has been influenced by variations in characters 3, 4, 6, 7, 11, and 21. Factor II emphasized the variations in characters 13, 14, 18, and 19. Along factor III variations in characters 6, 10, 13, 15, and 19 have been stressed.

As in the males, certain taxa exhibit wide variation and fail to form a homogeneous group. In both analyses (Figs. 6 and 7), two of the three *alcae* specimens cluster together but the other specimen (OTU 19) falls in the *obliqua obliqua* group. A detailed examination of this specimen using the characters outlined by Timmermann (1974) revealed that the specimen is indeed *alcae* although in overall similarity it is closer to *obliqua obliqua*.

The *aetherea klatti* specimens cluster consistently throughout the analyses. As in the males, the specimens from *P. alle* (OTUs 13–17) and *C. grylle* (OTU 18) are the same parasite as reported by Eveleigh and Threlfall (1976). The specimens from hosts of the families Scolopacidae (OTUs 22–24) and Stercorariidae (OTU 25) form distinct groups in the analyses, these occurring on the periphery in the three-dimensional plot of PAFA.

The phenetic relationships of these groups are somewhat different from those of the males. In Figs. 6 and 7 *obliqua aquilonis* and *helgovauki* are closely associated but separated from *obliqua obliqua* by *alcae*, whereas in the males *obliqua aquilonis*, *obliqua obliqua*, and *helgovauki* were a single group with *alcae* intermediate between this group and *aetherea klatti*. The females of *aetherea klatti* are remote from the other alcid parasites as in the males. *Cummingsiella normifer normifer* (OTU 25) (host family Stercorariidae) shows an affinity to the '*obliqua* group', while *falcigerus* (OTU 22), *ravus* (OTU 23), and *nigrolimbatus* (OTU 24) (host family Scolopacidae) cluster with *aetherea klatti*. It would be expected that if the alcid parasites were a homogeneous group then these species should form a distinct cluster remotely related to the alcid parasites. Similar results were noted in the males.

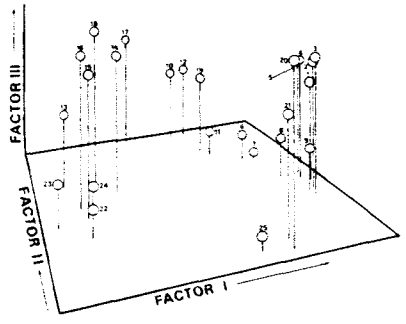

FIG. 7. Three-dimensional plot of PAFA for *Cummingsiella* females based on 19 characters. The percentages of variation accounted for on factors I, II, and III are 41.7, 16.24, and 12.89% respectively. See Fig. 6 for explanation of numbers.

Although it appears that the differences in the species interrelationships in both sexes are not sufficient to warrant separate discussions, it is necessary to take these differences into account in making a final decision on the classification of this genus.

The close similarity of *helgovauki* and *obliqua aquilonis*, especially in the females, suggests that possibly the latter form should be more appropriately regarded as a subspecies of *helgovauki*. This close similarity was also suggested in the males but the results were too inconclusive to allow a final decision at that time. Although *alcae* behaves somewhat differently in both sexes, its close affinity to *helgovauki*, *obliqua obliqua*, and *obliqua aquilonis*, especially in the females, suggests that it be combined with these parasites to form a single group. *Cummingsiella aetherea klatti* clusters consistently in both sexes and its close association with the nonalcid parasites warrants its placement in a separate group.

Genus Saemundssonia

Males

The results from the analyses are shown in Figs.

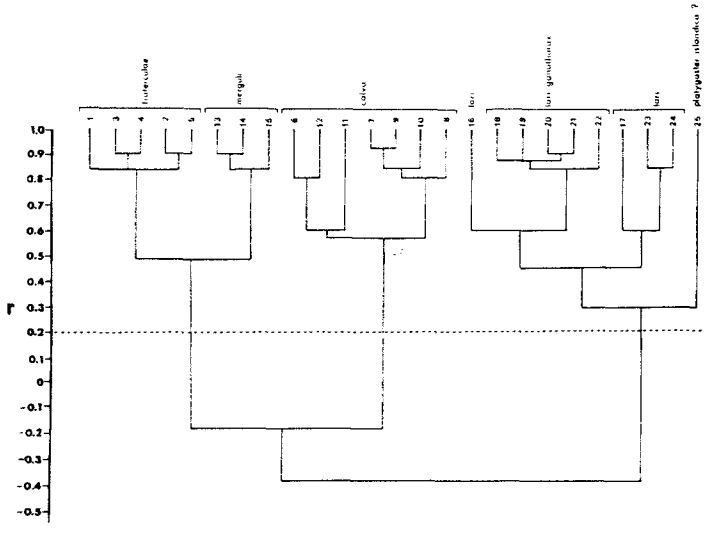

FIG. 8. Clustering of *Saemundssonia* males using UPGMA based on 23 characters. Cophenetic correlation = 0.938.

and 9. Using the 0.20 phenon line in the UPGMA dendrogram (Fig. 8), three groups are formed: two within the alcid parasites and the other consisting of specimens from hosts of the families Laridae and Scolopacidae. The first group contains specimens of *fraterculae* (OTUs 1–5) and *merguli* (OTUs 13–15), while the second is exclusive to *calva* (OTUs 6–12). The third group is a conglomeration of *lari* (OTUs 16–17, 23–24), *lari gonothorax* (OTUs 18–22), and *platygaster islandica* ? (OTU 25).

These groups are also very distinct in the three-dimensional plot of PAFA (Fig. 9) and have been separated out on factor I by variations in characters 3, 5, 6, 11, 15, 21, 22, and 25. Factor II emphasized the variations in characters 15, 18, 20, 23, and 24. The characters emphasized on factor III are 1, 4, 9, and 19.

In both analyses it is evident that while *fraterculae* and *merguli* are very similar, they nevertheless form distinct clusters. Although specimens of *celidoxa* from *A. torda* were unavailable for study, previous studies on this parasite (Eveleigh and Threlfall 1976) indicate that it is probably closely associated with the '*fraterculae-merguli* group.' Males of *grylle* were also unavailable but this parasite will be discussed in the analysis of females.

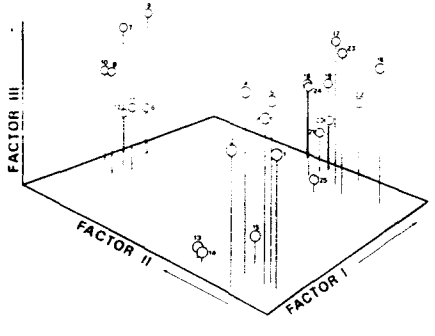

FIG. 9. Three-dimensional plot of PAFA for *Saemundssonia* males based on 23 characters. The percentages of variation accounted for on factors I, II, and III are 41.83, 26.60, and 11.07% respectively. See Fig. 8 for explanation of numbers.

The *calva* group is represented by specimens from two hosts, *U. lomvia* (OTUs 6–10) and *U. aalge* (OTUs 11–12). The specimens from *U. lomvia* show a slight separation from those on *U. aalge*, but this separation is insufficient to justify the erection of a new subspecies. Timmermann (1957) also considered these parasites to be identical on European hosts.

The specimens from [illegible]

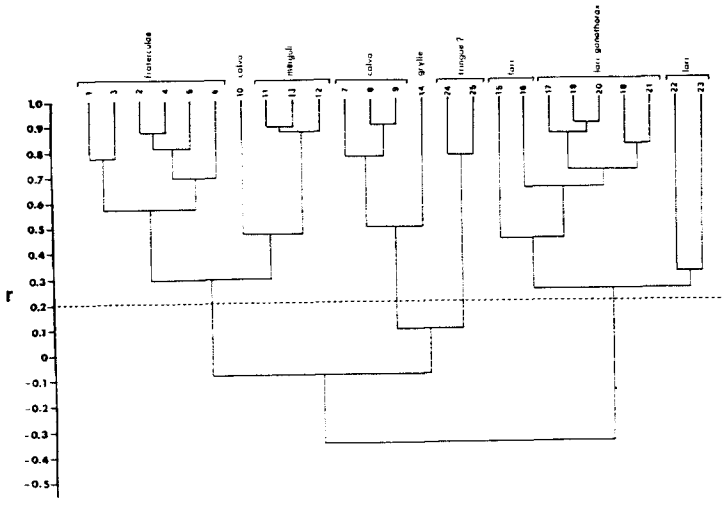

FIG. 10. Clustering of *Saemundssonia* females using UPGMA based on 19 characters. Cophenetic correlation = 0.858.

Laridae form a distinct cluster in both analyses. Although the purpose of this study is confined to the alcid parasites, these specimens deserve comment. *Saemundssonia lari gonothorax* (OTUs 18–22) exhibits little variability and appears to be slightly isolated from *lari* (OTUs 16, 17, 23, and 24) and it is difficult to decide, at this time, whether they are distinct taxa. It is hoped that the females will provide additional information. Emerson (1972) considered the subspecies invalid, stating that the species found on all gulls is *S. lari*. It is also interesting to note that *platygaster islandica* ? from a host of the family Scolopacidae shows a closer similarity to the larid parasites than to the alcid forms. This indicates that the alcid parasites are rather homogeneous taxa.

Altogether the results indicate that *fraterculae* and *merguli* are very similar and can be regarded as belonging to a single group. *Saemundssonia calva* exhibits a loose association with this group and forms a separate entity.

Females

Figures 10 and 11 show the results from the analyses of females. Using the same phenon line (0.20 in Fig. 10) as in the males, four groups are defined. As in the males, the alcid parasites contain two groups, the other two being composed of specimens from hosts of the families

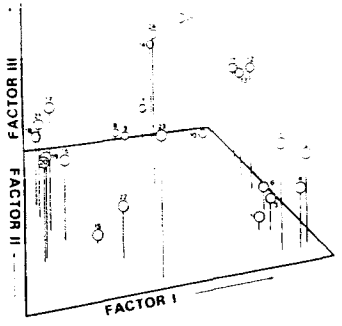

FIG. 11. Three-dimensional plot of PAFA for *Saemundssonia* females based on 19 characters. The percentages of variation accounted for on factors I, II, and III are 39.85, 20.18, and 13.98% respectively. See Fig. 10 for explanation of numbers.

Scolopacidae and Laridae. The first group contains specimens of *fraterculae* (OTUs 1–6), *merguli* (OTUs 11–13), and *calva* (OTU 10). Within the second group are specimens of *calva* (OTUs 7–9) and *grylle* (OTU 14) with the third group being exclusive to *tringae* ? (OTUs 24–25). The last group contains specimens of *lari* (OTUs 15, 16, 22, and 23) and *lari gonothorax* (OTUs 17–21). These groups are also clearly depicted in the three-dimensional plot of PAFA (Fig. 11).

An examination of the factor scores revealed that the groups were separated out on factor I by variations in characters 3, 5, 6, 8, 12, 13, 15, and 18. Factor II emphasized the variations in characters 4, 7, 8, 11, 15, 18, and 19. The groups were separated out on factor III by variations in characters 1, 11, 20, and 21.

The analyses show that *fraterculae* and *merguli* form distinct clusters with one specimen of *calva* being closely allied to these forms. However, most specimens of *calva* form a distinct group that is segregated from the other two parasites. This is particularly evident in the PAFA plot (Fig. 11) where all the *calva* specimens, including OTU 10, are separated out on factors II and III. The *grylle* specimen is distinct in both analyses but has a close affinity with the *calva* group. The *tringae* ? specimens also cluster consistently in the analyses and show more affinity with the alcid parasites than to those from the larids.

As in the males, *lari gonothorax* forms a rather homogeneous cluster which is now clearly separated from *lari*. Two *lari* specimens (OTUs 22 and 23) are from *Larus argentatus* in Ontario, Canada while the other two specimens (OTUs 15 and 16) are from the same host in Newfoundland, Canada. In both figures the former *lari* specimens are distinctly separated from *lari gonothorax* which were also collected in Ontario, while the latter fall in an intermediate position between them. It appears that *lari gonothorax* may be subspecifically distinct from *lari* in the Ontario populations but a conclusive decision cannot be made owing to the position of the Newfoundland specimens. Whether geographical variation can occur in a species from the same host in different localities has not been documented, but it may be a factor influencing the results in this study and it could account for the large number of subspecies on these hosts. This certainly warrants further investigations.

As in the genus *Cummingsiella*, the differences in the species associations in both sexes are not sufficient to warrant separate considerations. The results in both sexes show that *fraterculae* and *merguli* are very similar and can be considered as belonging to one group. Based on the male data, the *calva* specimens from *U. lomvia* and *U. aalge* are identical. *Saemundssonia grylle* is closely associated with *calva* and they are placed together in a separate group.

Timmermann (1957) erected a key to the European species from the alcids and divided the species into species groups. He considered *fraterculae* and *celidoxa* to be closely related and placed them in a single group; *grylle* and *merguli* were considered as a related but separated group and *calva* as constituting a third group. Despite the fact that *celidoxa* was not studied, there is little agreement between the two classifications. This is not surprising since this study is based on overall similarity using many characters while Timmermann's study was based almost exclusively on the male genital characters.

Genus Austromenopon

In the following analyses, 20 characters were used in the males and 18 in the females. Because the endomeres and mesosomal structures were absent in the males and the degree of sclerotization was invariant, these characters were excluded. Only the results from PAFA will be presented since the cluster analyses contained considerable distortion.

Males

Figure 12 shows the results from the analysis of males. Although none of the taxa form homogeneous clusters, it appears that *phippsi* (OTUs 1–5) and *nigropleurum* (OTUs 11–13) are separated out on factors I and III. *Austromenopon uriae* (OTUs 6–10) forms two widely separated clusters, one being associated with *phippsi* and the other with *nigropleurum*. Thus, *phippsi* and *nigropleurum* are probably separate taxa but the position of *uriae* makes it impossible

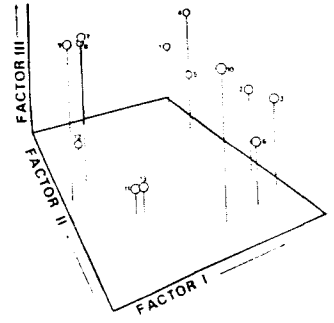

FIG. 12. Three-dimensional plot of PAFA for *Austromenopon* males using 20 characters. The percentages of variation accounted for on factors I, II, and III are 28.14, 19.66, and 15.49% respectively. 1–5, *phippsi*; 6–10, *uriae*; 11–13, *nigropleurum*.

to draw any definite conclusions about its status. Eveleigh and Threlfall (1974) considered *uriae* and *phippsi* to be related.

From the factor scores these taxa have been separated out on factor I owing to variations in characters 13, 14, 19, 20, and 23. Factor II emphasized the variations in characters 2, 4, 6, and 10 while characters 1, 6, 9, and 11 were stressed on factor III.

Females

The results from the analysis of females (Fig. 13) reveals a conglomerate of specimens in which no definite clusters are discernible. Even the specimen of *transversum* ? (OTU 22) from a host of the family Laridae is not separated from the alcid parasites.

The results from both sexes indicate that the *Austromenopon* parasites from the alcids are very homogeneous and that species complexes do exist. Unlike in the other two genera discussed, the females could not be as clearly separated as the males. This supports the conventional taxonomists' decision to rely on the males for diagnostic characters, and especially the genitalia. However, in this study we feel that it is inappropriate to propose a classification based solely upon the males. Moreover, since the same characters were used in analysing each genus it appears that the species concept is not as clearly defined in this genus as in the other two genera and a reanalysis is needed taking into consideration more characters and their variation in the various taxa before a classification is proposed.

In summary, the results indicate that while it may not have been possible by conventional taxonomy to classify females using a few specific characters, by using numerical techniques we were able to successfully classify both females and males. The only exception is *Austromenopon* where specimens were not conclusively demarcated in either sex and the taxa were poorly defined.

Host–Parasite Relationships

Many mallophagan taxonomists have attempted to use host–parasite relationships as a means of determining the classification of hosts and as an important clue to the identification of the parasite. Ward (1957) reported that the classification of the Tinamiformes conformed almost perfectly with the divisions shown by their Mallophaga and concluded that "the Mallophaga species groups define host genera and provide exact data on their relationships." Since the specimens studied here include almost all of the species reported from alcids of the northwest Atlantic and the phenetic relationships between the parasite species have been established, it should be possible to examine the affinities of the hosts at lower taxonomic levels.

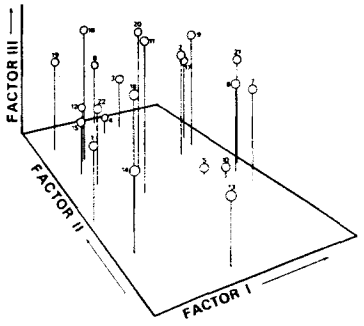

FIG. 13. Three-dimensional plot of PAFA for *Austromenopon* females using 18 characters. The percentages of variation accounted for on factors I, II, and III are 26.14, 20.22, and 12.41% respectively. 1–5, *phippsi*; 6–10, *uriae*; 11–21, *nigropleurum*; 22, *transversum* ?

Examining each mallophagan genus separately, the groups in *Cummingsiella* suggest that *U. aalge*, *U. lomvia*, *F. arctica*, and *A. torda* are closely associated and separated from *C. grylle* and *P. alle*. Those in *Saemundssonia* indicate that *U. aalge*, *U. lomvia*, and *C. grylle* are associated with *F. arctica* and *P. alle* in a separate group. The affinity of *A. torda* cannot be established since specimens from this host were unavailable. Although the results from *Austromenopon* were inconclusive they suggest even different affinities. *Fratercula arctica*, *P. alle*, and *A. torda* are probably closely allied and distinct from *U. aalge* and *U. lomvia*. *Cephus grylle* would constitute a separate group since it has no recorded *Austromenopon* parasites. It can be concluded, therefore, that with the exception of *U. aalge* and *U. lomvia* parasitological evidence fails to demonstrate any consistent host groups. Hence the use of parasitological evidence as a method of alleviating the controversy surrounding the taxonomic relationships of the Alcidae seems questionable. The results do show, however, that species from other host families could be separated from the alcid parasites and research in this area may aid in determining the taxonomic placement of the family itself.

The ecology of the hosts may be the important factor in explaining the disagreement between Ward's findings and those reported in this study. The alcids that we examined breed in large colonies where opportunities for physical contact between different bird species are possible. This probably resulted in the establishment of a parasite species on hosts which are not necessarily related but possess similar feather structures. In this type of situation the taxonomist cannot rely on the host for significant taxonomic information on the parasite since they are not exhibiting host specificity. Likewise, the relationships between the hosts will not be reflected in the parasite interrelationships. Undoubtedly, the hosts that Ward examined did not demonstrate such an ecological arrangement and his results portray an excellent example of parasite phylogeny paralleling host phylogeny. This is certainly not the case in the alcids since all three parasite genera depicted different host interrelationships and we do not know a priori which of the genera, if any, actually evolved with the hosts.

Kethley and Johnston (1975) discussed host–parasite relationships in bird and mammal ectoparasites. They concluded that successful host transfers of ectoparasites are most likely to occur between hosts that have similar topographical features and that the establishment of noncongruent host–parasite relationships is probably quite common. Our results support their conclusions. Furthermore, Eveleigh and Threlfall (1976) showed that the habits and habitat of the hosts influence their mallophagan orden and it seems quite possible that these factors could also contribute to the noncongruent host–parasite relationships shown in this study.

It is evident that careful attention must be paid to the ecology of both the host and its parasites before attempts are made to use host–parasite relationships as a means of making taxonomic decisions about either the host or its parasites. Moreover, it appears that host–parasite relationships may also depend upon the host's geographical location as demonstrated earlier in certain *Cummingsiella* species.

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