NUMERICAL TAXONOMY AND THE SMELT FAMILY, OSMERIDAE

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INTRODUCTION

BEFORE the methods and principles of numerical taxonomy are accepted in their entirety or in part, it is necessary to compare their results with those of conventional taxonomy and to evaluate the differences. Using some of the methods of numerical taxonomy this paper makes a re-analysis of a recent conventional revision of the smelt family, Osmeridae (McAllister, 1963) and compares the results of the two studies. The source of the methods of numerical taxonomy used herein is Sokal and Sneath (1963). For further background material see the symposium *Phenetic and phylogenetic classification* of the Systematics Association (1964) and discussions in the pages of Systematic Zoology of recent years.

According to the principles of numerical taxonomy the selection of characters should be random; a minimum of 60 characters would seem advisable and never less than 40 should be used. It should be made clear that the data for the numerical taxonomic portions of this paper are drawn from a previous taxonomic study in which only 48 characters were analyzed. The data are, therefore, not ideal, though adequate for a numerical taxonomic study. But by using the same basic data for the two studies, the differences may more easily be attributable to the methods, rather than to the characters selected.

METHODS

The methods used in this similarity study are among those outlined in Sokal and Sneath (1963) (to which the following page references refer).

The characters were coded by a simple present (+) or absent (0) scheme (p. 76). Every character was known and applicable so NC entries were not necessary (p. 74). The characters were arranged along one axis of the table, the taxa (or operational taxonomic units) along the other. For example, four axinosts were present (scored +) in all forms except *Mallotus* (scored 0), in which there are six. Subspecies were not included in this study since their differences, of a partially overlapping nature, were not amenable to + or 0 scoring.

The following characters were coded; the alternative to each is "not", e.g. proethmoids double (proethmoids *not* double). Which of the alternatives is indicated by + or 0 is of no significance (in this method). The characters are: glossohyal teeth canine; maxillary extends past mid-eye; proethmoid double; otic bulla wide anteriorly; posterior myodome opening narrow; with parasphenoid wing joining prootic; mandible shallow; palatine dumbbell-shaped; dorsal edge of pterygoid straight; metapterygoid with dorsal vane over

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	S. 1.	S. t.	S. s.	0. e.	Т. р.	A. e.	Н. р.	H. t.	Н. о.	M. v.
S. 1.	х				1					
S. t.	31 1 1 15	x								
S. s.	$\begin{array}{r} 30 1 \\ 2 15 \end{array}$	$\begin{array}{r} 30 1 \\ 2 15 \end{array}$	x							
O. e.	24 4 8 12	24 4 8 12	22 6 9 11	x						
Т. р.	26 6 6 10	23 8 9 8	$\begin{array}{ccc} 21 & 10 \\ 10 & 7 \end{array}$	$\begin{array}{r} 24 & 7 \\ 4 & 13 \end{array}$	x					
А. е.	26 6 6 10	25 7 7 9	$\begin{array}{ccc} 26 & 6 \\ 5 & 11 \end{array}$	24 8 4 12	24 8 7 9	x				
Н. р.	12 7 20 9	13 6 19 10	12 7 19 10	12 7 16 13	9 10 22 7	10 9 22 7	x			
H. t.	12 7 20 9	$\begin{array}{ccc}12&3\\20&13\end{array}$	$\begin{array}{ccc}11&4\\20&13\end{array}$	10 5 18 15	6 9 25 8	7 8 25 8	$\begin{array}{rrr}15 & 0\\4 & 29\end{array}$	x		
Н. о.	$\begin{array}{ccc}11&4\\21&12\end{array}$	$\begin{array}{ccc}12&3\\20&13\end{array}$	$\begin{array}{ccc}10&5\\21&12\end{array}$	$\begin{array}{ccc} 10 & 5 \\ 18 & 15 \end{array}$	6 9 25 8	7 8 26 7	$\begin{array}{ccc}15&0\\4&29\end{array}$	$\begin{array}{ccc}14&1\\&1&32\end{array}$	x	
M.v.	$\begin{array}{ccc}12&14\\20&2\end{array}$	$\begin{array}{ccc}12&14\\20&2\end{array}$	$\begin{array}{ccc}11&14\\21&2\end{array}$	$\begin{array}{ccc} 12 & 14 \\ 16 & 6 \end{array}$	$\begin{array}{ccc} 14 & 12 \\ 17 & 5 \end{array}$	13 13 19 3	14 12 5 17	10 16 5 17	10 16 5 17	x

TABLE 1.-Two by Two Table for Computation of Coefficients of Association

hyomandibular head; dorsal fork of posttemporal long; frontal with lateral wings over orbit; vomerine teeth small; palatine teeth small; subopercle and/or opercle with striae; snout to dorsal length equals or exceeds dorsal to caudal; midlateral ridge in males; elongate midlateral scales; gill rakers 25 or more; pyloric caeca never more than 8(9); with blind stomach sac; midlateral scales always above 70; anal rays up to 23; pectoral rays 16-23; lateral line complete; length of adipose base never exceeds orbit; orbit 2/3 or less of caudal peduncle depth; mesethmoid simple; parietals not at all separated; pterosphenoid reaches parasphenoid wing anteriorly; no slit between hyomandibular and preopercle; actinosts 4; ventrals 8; dorsal 10-14; vertebrae 64 or more; branchiostegals 8-10; head 4.7 or less in standard length; pectoral always 70 per cent or more of distance to pelvic; pelvic origin anterior to dorsal; peritoneum silvery; marine; pyloric caeca obsolescent; ductus pneumaticus attaches to anteriormost end of gas bladder; gill rakers long; standard length exceeds 200 mm; mouth horizontal; range attains or exceeds 60° N. Lat.

In plus or minus coding some information is lost because the finer variations are excluded. This can be avoided to some extent by double coding. Note above the pyloric caeca are coded as 8(9) or less (or not) and obsolescent (or not).

	S. 1.	S. t.	S. s.	0. e.	Т. р.	A. e.	Н. р.	H. t.	Н. о.	M. v.
S. 1.	x									
S. t.	.96	x								
S. s.	.94	.94	x							
0. e.	.75	.75	. 69	x						
Т. р.	.75	.65	. 58	.77	x					
A. e.	.75	.71	.77	.75	. 69	x				
Н. р.	.44	.48	.46	. 52	.33	.35	x			
H. t.	.44	. 52	. 50	. 52	. 29	.31	.91	x		
Н. о.	.48	. 52	.46	. 52	. 29	. 29	.91	.96	x	
M. v.	. 29	. 29	. 29	.38	.40	.33	.65	. 56	. 56	x

TABLE 2.—Coefficients of Association (SM)

S.1. — Spirinchus lanceolatus S. t. — Spirinchus thaleichthys S. s. — Spirinchus starksi O. e. — Ösmerus eperlanus T. p. — Thaleichthys pacificus

A. e. — Allosmerus elongatus

H. p. - Hypomesus pretiosus

H. t. — Hypomesus transpacificus

H. o. — Hypomesus olidus M. v. — Mallotus villosus

After the coding basis is set up the different characters are recorded as + or 0 for the different species in a table (not shown, but above characters for all the species are recorded in McAllister, 1963). From this a two by two table for computation of coefficients of association is compiled, Table 1. This table compares, for all the possible different pairs of taxa (or operational taxonomic units), the number of characters which were ++ (positive in both taxa), +0 (positive in the first, negative in the second taxon), 0+ (negative in the first, positive in the second taxon) and 00 (negative in both taxa).

The simple matching coefficient used in this study is calculated by $S_{SM} =$ m/n = m/(m+u), where S_{SM} is the simple matching coefficient, m is the number of characters in "matched" cells (++ or 00) and u is the number of characters in "unmatched" cells (= 0 or 0+) and n is the total number of characters. In other words the simple matching coefficient is the number of characters which the two taxa share divided by the total number of characters.

The simple matching coefficients for all the pairs of taxa are calculated from the two by two table (Table 1) and presented in Table 2.

The coefficient is a measure of how close the two taxa are (i.e. how many characters they share). The higher the coefficient is, up to 1.00, the closer the two taxa. The lower the coefficient is, down to 0.00, the more distant the two taxa.

In order to more easily understand how the different genera are related to one another a further table is provided, Table 3. The pairs of genera are listed with the most closely related pairs at the top of the table. When a genus is polytypic the coefficient given is the mean of the coefficients between each of its species and the other genus.

TABLE 3 — Coefficients of Association	Between Pairs of Genera
Arranged in Order of Magnitude	(closest genera first)

_		
	Osmerus-Thaleichthys	77
	Osmerus-Allosmerus	75
	Allosmerus-Spirinchus	74
	Osmerus-Spirinchus	73
	Thaleichthys-Allosmerus	69
	Thaleichthys-Spirinchus	66
	Mallotus-Hypomesus	59
	Osmerus-Hypomesus	52
	Spirinchus-Hypomesus	48
	Thaleichthys-Mallotus	40
	Osmerus-Mallotus	38
	Allosmerus-Mallotus	33
	Allosmerus-Hypomesus	32
	Thaleichthys-Hypomesus	30
	Spirinchus-Mallotus	29

PRIMITIVENESS

The lack of fossil smelts different from extant species¹ forces use of other measures of primitiveness. Gosline (1960) suggests that the superfamily Salmonoidea gave rise to the Osmeroidea and the author agrees that this may be so. Of the Salmonidae, the Salmoninae appear to be closest to the required ancestor of the osmeroids, the Thymallinae and Coregoninae having various specializations which would bar them from ancestry. The paired proethmoids are clearly primitive, being paired in the esocoids. If the Salmoninae (see Norden, 1961 for some characters) are close to the ancestors of the smelts then certain characters may be regarded as primitive. The following character states may be regarded as primitive relative to the family Osmeridae: (1) branchiostegals numerous, more than 8; (2) mouth horizontal; (3) adipose fin oval; (4) scales numerous, more than 100; (5) mandible shallow; (6) glossohyal teeth not villiform; (7) peritoneum not black; (8) lateral line complete; (9) pyloric caeca numerous; (10) stomach without blind sac; (11) ventral rays numerous; (12) no opercular striae; (13) spawn in freshwater; (14) midlateral scales not elongate in male; (15) no anal shelf in male; (16) no midlateral ridge in male; (17) four simple axinosts; (18) parietals separated by supraoccipital; (19) vomerine teeth equal in size to palatines; (20) large adult size, more than 300 mm; (21) maxillary extending to mid-pupil or past; (22) proethmoids double, not fused.

Using the data in McAllister (1963) the number of primitive characters which are found in the different genera is given in Table 4. Then, according to this method, *Thaleichthys* would be the most primitive genus and *Mallotus* the most advanced.

¹See Appendix regarding Thaumaturus, and fossil otolith of Hypomesus.

TABLE 4 - Number of primitive characters in different genera

Thaleichthys	16
Osmerus	15
Spirinchus	12
Allosmerus	12
Hypomesus	10
Mallotus	8

DISCUSSION OF RESULTS

Comparison with Previous Studies

Classification involves categorization, erection of hierarchies and recognition of phylogeny (although some proponents of numerical taxonomy would not admit the latter). The distinctness of the taxonomic categories previously recognized is confirmed by the present study. The results of the last two operations in the two studies are compared below.

Hierarchies: The coefficients of association may be used to assess or establish the status of categories. The lower taxa will be more closely related, that is have higher coefficients of association.

In this regard the level of the taxa recognized in the last revision of the family appears to have been correctly assessed, relative to one another in the hierarchy. The species within a genus (in *Spirinchus* and *Hypomesus*) are more closely related, coefficients of 91-97, than the genera within a sub-family, 59-77, or than the genera between different subfamilies, 29-52.

Could other taxa have been recognized? In the foregoing study none of the species of the polytypic genera, Spirinchus and Hypomesus, were considered so highly distinguished as to warrant superspecific or subgeneric categories, nor with so few species was a need felt for such categories. The calculated coefficients agree with the conclusions from the previous study that the species of Spirinchus were very close, 94-96. So subgeneric categories do not seem to be indicated. In the genus Hypomesus the coefficient of association would indicate that H. pretiosus was more distinct, 91, than the other two species, 96. On this basis it might be possible to recognize a superspecies for H. pretiosus. It may be pointed out here that in the previous conventional study H. olidus was considered the most distinctive species in the genus (as indicated in the key, p. 27). The reasons for this are twofold. First, in coding, information was lost in differences in pyloric caeca. Secondly the point of juncture of the ductus pneumaticus, notably behind the anterior end of the gas bladder in H. olidus, is a feature unique in the family and was considered of more significance than the other characters (such as number of vertebrae which was found to vary within subspecies). However, the exact level of distinctness which might be recognized for superspecies is basically an arbitrary decision, as would be more readily apparent in a larger genus where a spectrum of differences would be found. It seems superfluous to recognize slightly marked species by superspecies when utility is not served. Minor degrees of affinity are best indicated in phylogenetic dendrograms (i.e. the author does not adhere to the cladistic

point of view -see Mayr, 1965, p. 167). Supertaxa are useful when they help divide speciose groups. This is not to say that monotypic taxa should not be recognized when they are sufficiently distinctive.

A case might be made for the recognition of separate subfamilies for *Mallotus* and *Hypomesus*. The differences between genera of the two subfamilies presently recognized range from 29 to 52. The genera *Mallotus* and *Hypomesus* are only slightly less different, differing by a coefficient of 57. Deciding the level of coefficient at which to recognize subfamilies appears to be more arbitrary (in this family) than that between species and genera.

Phylogeny: Certain proponents of numerical taxonomy do not believe that phylogenies can be erected solely on the results of study of living species. These persons may regard the following discussions and figures as referring simply to the similarity of living species, not to their phylogeny.

In constructing a phylogeny of the subfamily Osmerinae tables 3 and 4 may be referred to. From the coefficients of association one may conclude that Osmerus and Thaleichthys are the most closely related genera and that Allosmerus is quite close to Osmerus. Allosmerus and Spirinchus are the next most closely related pair. The number of characters considered primitive would indicate that Thaleichthys is the most primitive, being closely followed by Osmerus. Allosmerus and Spirinchus are the most advanced and have achieved the same degree of advancement. The two sets of results appear compatable and are easily translated into a phylogenetic tree, with Thaleichthys at the bottom and Allosmerus and Spirinchus at the top, and with Osmerus in an intermediate position (see Figure 2).

Hypomesus and Mallotus obviously branch from a common stalk. As the most advanced genus, Mallotus must take the most distant position. Computing the mean coefficient of association for the subfamily Hypomesinae (average of its two genera) with each of the osmerin genera gives the following results: with Osmerus 45, Spirinchus 38.5, Thaleichthys 35 and Allosmerus 32.5. From these figures one would conclude that the Hypomesinae branched off from the Osmerinae close to Osmerus on the stem which gave rise to Spirinchus. The major features of all these relationships are depicted in the dendrogram given in Figure 2. (Although the relative positions can be indicated easily on a two dimensional figure, it does not appear practical to indicate the exact distances between all taxa without using three dimensions).

The major differences between the phylogenies suggested may be seen by comparing Figures 1 and 2. The first difference is that the positions of the genera *Spirinchus* and *Thaleichthys* are reversed, the latter being indicated as the most primitive by the numerical taxonomic study. Secondly the numerical taxonomic study suggests that the Hypomesinae are closer to *Osmerus* than to *Spirinchus*. Otherwise the generic relationships suggested by the two studies are similar.

A proper evaluation of the results of the two methods will only come when a knowledge of fossils will enable one to delineate the phylogenies on factual instead of theoretical bases. An evaluation might also be made when further taxonomic data are available, the author might suggest the worthiness of chromosome, blood and muscle protein¹ electrophoritic and serum studies. It is not suggested that any one of these will provide *the* answer but that each will contribute to a more certain phylogeny. The present author's personal subjective evaluation is that the new numerical analysis has contributed to the understanding of generic relationships. He is not sure that numerical analysis has correctly assessed the relationships within the genus *Hypomesus*.

COMMENTS ON NUMERICAL TAXONOMY

The following are some general critical comments on numerical taxonomy. They are not intended to comprise a complete critique. For further comments one may refer to the pages of Systematic Zoology.

Numerical taxonomy has criticised conventional taxonomy on a number of scores. Some of its charges have been valid, but others apply only to certain workers in conventional taxonomy and should not be made against the field of conventional taxonomy. Take for example the number of characters employed. Many poor conventional studies do employ too few characters. However there are many conventional studies which have employed the minimum number of characters or well above the minimum which numerical taxonomists consider necessary. To cite a few examples in the field of ichthyology: Briggs (1955) used a least 50 in his revision of the Order Gobiesociformes; Norman (1934) used at least 60 characters in his revision of the flatfishes; Katayama (1960) in his revision of the Japanese Serranidae used at least 75 characters. Moreover, the minimum suggested by Sokal and Sneath, perhaps valid for their groups, may not be valid for other groups. My colleague, Dr. Arthur H. Clarke, Jr., informs me that for the freshwater molluscs on which he is working at the moment it would be difficult to find 30 meaningful taxonomic characters, let alone the suggested absolute minimum of 40.

At present the coding of data in numerical taxonomy does not seem wholly capable of absorbing all data available. For example body part ratios of different species may be discrete at any one size, but the ratios over the whole size range (which would be used for coding) overlap. A series of overlapping ranges of meristic or proportional characters for different forms would be quite difficult to code, but can be dealt with in conventional studies. However, these difficulties in coding may not prove insurmountable and could be dealt with now by setting these characters aside for special handling, at least in smaller groups.

The non-weighting of characters has been one of the most difficult of principles of numerical taxonomy for others to accept. The present author can see certain cases where he might consider that characters are of approximately equal value, e.g. where in certain groups the dorsal and anal fin ray counts might be equivalent, and they to a scale count differences, or perhaps to a colour or even a behavior pattern. In higher classification it would be difficult to weight certain of the more important characters such as protrusibility of the jaws, presence of maxilla in gape of the jaws, presence of true

¹Dr. Hiroshi Tsuyuki and the author are engaged in a joint study using muscle proteins in the Osmeridae to help determine relationships.

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FIGURE 1. Phylogenetic dendrogram derived from a conventional taxonomic study (McAllister, 1963).

fin spines, physostomous or physoclistic gas bladder, etc. But other characters are clearly of different worth, e.g. the principal caudal rays as opposed to the variability in anal rays in many groups, or of a trenchant osteological character as opposed to a colour pattern. This would make one less willing to equate all characters with one another. It must be admitted that there would be some difficulty in deciding how much to weight characters. However it would 1966



FIGURE 2. Phylogenetic dendrogram based on the present study using methods of numerical taxonomy.

be relatively easy to make a rule of the thumb ratio, 2:1, 3:1 or other simple ratio, after preliminary study of a group, for weighting — before any systematic decisions had been made. Nor is it difficult to conceive of some basis for a less subjective weighting formula. This would weight characters more strongly when they displayed constancy within taxa and showed correlation with other independent characters². By weighting some characters the loss of valuable information might thereby be avoided. In this regard taxonomists might be reminded that they need not accept all the precepts of numerical taxonomy. The suggestion to separate phylogeny and classification is probably a century too late.

The simple consideration of the number of diagnostic characters will not permit deciding whether a form is a species or subspecies. Here must be

²Ignoring taxonomically spurious correlations such as those due to large size in the close parts because of a common growth centre, those resulting solely from inhabiting the same ecological niche, etc.

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evaluated factors such as percentage separation, degree of interbreeding, sympatry, information on behaviour and ecology, etc. Information may be incomplete for any one factor. The geographical distribution of intermediates between two types will influence interpretation of status. Sibling species may differ little morphologically³. Here it will be difficult for numerical taxonomy to supplant the experienced systematist. It is probably in the establishing of comparable taxa above the species level that numerical taxonomy will have its greatest use. Also in the use of many characters to establish relationships in morphologically complex groups; here it is difficult for the systematist to hold all the characters in his mind in analyzing affinities.

There are a number of features of value in numerical taxonomy. It provides a standard approach which may be taken for all groups. It provides a rational series of steps and bases on which to proceed. These assist toward attaining repeatability and objectivity. The use of numerous characters, which it advocates, should raise the quality of classification.

While all of the tenets of numerical taxonomy may not be acceptable, these and the restating of the bases of taxonomy will challenge zoologists to rethink the philosophy of systematics. The quality of taxonomy will still depend to a large degree on the care and accuracy of the taxonomists, the adequacy of the series of specimens he studied in terms of number, geographic representation, sex, etc., and his thoroughness in studying even the less accessable characters. While numerical taxonomy will probably not supplant conventional taxonomy it will perhaps help make and rejuvenate it, and lead the way to a new and superior systematics.

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SUMMARY

The data of a conventional taxonomic study of the smelt family (Mc-Allister, 1963), Osmeridae, was re-analyzed using some of the methods of numerical taxonomy as propounded by Sokal and Sneath (1963). A primitiveness score was introduced. The results of the two studies were then compared. The allotment of species to genera, and status of the various taxa in the studies agreed closely. The (phylogenetic) relationships shown were close, but not identical, differing in reversal of positions of *Thaleichthys* and *Spirinchus* (the former now being considered primitive, the latter advanced) and in the derivation of the subfamily Hypomesinae from the stem closer to *Osmerus* than to *Spirinchus*. The use of classical and numerical methods have resulted in very

³A student at the University of Ottawa, Claude Delisle, has discovered two populations of Osmerus eperlanus mordax in a lake in the Gatineau area, Quebec, one composed of giant-, the other of normalsized individuals. Brief examination of a series of these by the author showed several differences, the most significant of which was the number of gill rakers. However, the number of gill rakers did overlap. Data like this is difficult to handle with numerical taxonomy. See also Svardson (1961) who reports morphologically similar populations spawning at different times.

similar taxonomic pictures. Comments are made about numerical taxonomy and its future.

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APPENDIX

The Miocene fossil genus *Thaumaturus* was first placed in the family Salmonidae. Later it was accorded familial distinction close to the Salmonidae by Voigt (1934) and Berg (1947). Norden (1961) in his study of the osteology of the Salmonidae considered the Thaumaturidae were likely allied to the Argentinidae or Osmeridae, judging by a description and figure of a single caudal vertebral centrum. However Voigt (1934) figures a specimen with 2 or three upturned caudal vertebrae which would distinguish *Thaumaturus* from even the superfamily Osmeroidae. Other characters of Voigt's material also distinguish it from the Osmeridae: 40 instead of 51-78 vertebrae; lack of flanges on the posterior neural spines; posterior position of the dorsal fin partly overlying the anal base; body deep instead of slender; presence of intermuscular bones; shallowly forked caudal; lack of dermethmoids; premaxillary bordering 2/3 of gape (instead of 1/3) presence of teeth on the shaft of the vomer; lack of supramaxillary. Further differences may be seen in comparing Chapman

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(1941) and Rembiszewski (1964) with Voigt (1934). These characters together indicate a rather distant relationship of *Thaumaturus* to Osmeridae.

In agreement with McAllister (1963), Bigelow (1964) reduces the Atlantic American form of smelt to a subspecies, *Osmerus eperlanus mordax*. He reduced the Pacific capelin (considered consubspecific by McAllister, 1963) to a subspecies of the Atlantic form but realized that Arctic specimens might change the conclusions.

Stinton (1963) has described a new species, *Hypomesus glaber* from otoliths in Miocene deposits, Victoria, Australia. Zoogeographically this would be an interesting find, as all previously-known living and fossil osmerids were in the northern hemisphere. One wonders if the otoliths might actually belong to one of the southern hemisphere families closely related to the Osmeridae – the Galaxiidae, Retropinnidae or Aplochitonidae. However an otolith from a New Zealand specimen of *Galaxias* and from one of *Retropinna* were quite different.

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SIEVE MESH SIZE AS RELATED TO VOLUMETRIC AND GRAVIMETRIC ANALYSIS OF CARIBOU RUMEN CONTENTS

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ANALYSIS of rumen content is probably the most common method employed to determine the food habits of ruminants. The method offers obvious advantages when dealing with a highly mobile species, such as barren-ground caribou (*Rangifer tarandus groenlandicus*), which may move several miles per day. Other methods, such as direct observation of feeding, require long hours of field work and cause many problems in logistics. In contrast, rumen analysis can be completed in the laboratory. Buechner (1950) listed some of the limitations of feeding minute studies as applied to pronghorn antelope (*Antilocapra americana*). Most of the limitations also would apply to a study of the feeding activities of barren-ground caribou.

The present study was undertaken to determine which sieve mesh size, if any, would separate the forage into portions representative of that within the rumen of barren-ground caribou during the winter months. A second purpose was to compare results obtained using wet volume and air-dry weight as methods of measurement.



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