THE PHYLOGENY OF THE ALCIDAE

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ABSTRACT.—An estimate of the phylogeny of 22 extant and 1 extinct species of the Alcidae
was determined from compatibility analyses of 33 cladistic characters of the skeleton, integ-
ument, and natural history. The puffins were found to be a sister-group to all other alcids.
Cerorhinca was found to be a puffin. The auklets were found to be a sister-group to the
remaining species. *Brachyramphus* was found to represent a phyletic line separate from that
including the other murrelets. *Cepphus* was found to be a member of the phyletic line in-
cluding *Endomychura* and *Synthliboramphus*. *Alle* was found to be a sister-group of the auks.
A compatibility analysis of muscle characters of Hudson et al. (1969) yielded a phylogenetic
tree in agreement with that found using my data. The relationships among *Cepphus* and the
murrelets were found to need further study. A classification based on these results is sug-
gested. It is recommended that the recent merging of genera by the A.O.U. (1982) be ac-
cepted, that *Cyclorrhynchus* be merged with *Aethia*, and that *Pinguinus* be merged with *Alca*.
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THE Alcidae, a distinct group of marine, wing-
propelled diving birds, have been classified
during the past 150 years (literature reviewed
by Sibley and Ahlquist 1972) with the loons
(Gaviidae), grebes (Podicipedidae), diving pe-
trels (Pelecanoididae), and penguins (Sphenis-
cidae). The modern consensus is that they are
members of the Charadriiformes (Wetmore
1930, Mayr and Amadon 1951, Kitto and Wil-
son 1966, Storer 1971, Sibley and Ahlquist 1972,
Stegmann 1978, Strauch 1978, Cracraft 1981);
however, a few recent authors (Verheyen 1958,
Gysels and Rabaey 1964) have disputed this
opinion. The assumed monophyly of the Cha-
radriiformes is based on their sharing a com-
plex of character states (Zusi 1974, Strauch
1976), but it never has been tested by a phy-
logenetic analysis of the orders of birds. Fur-
thermore, the limits of the order still are un-
resolved. Storer (1956) and Sibley and Ahlquist
(1972) presented evidence that the loons also
may be charadriiforms (but see Cracraft 1982).
Olson and Feduccia (1980) asserted that the fla-
mingos (Phoenicopteridae) are closely related
to Charadriiformes, and Olson and Steadman
(1981) presented evidence that *Pedionomus* is a
charadriiform. Maclean (1967) and Fjeldså
(1976) argued that sandgrouse (Pteroclididae)
are charadriiforms, but their evidence and con-
clusions have been challenged by Olson (1970)
and Strauch (1979) and are not supported by
the findings of Kitto and Wilson (1966). Sibley
and Ahlquist (in press), however, have new

evidence that sandgrouse are charadriiforms.
Although current evidence indicates that the
composition of the Charadriiformes is close to
that proposed by Wetmore (1930), future reso-
lution of the higher relationships of birds may
show this conclusion to be oversimplified.

Given that the Alcidae are charadriiforms,
there is still a question of their affinities within
the order. Most authors have suggested that al-
cids are most closely related to gulls (Storer
1960, Kozlova 1961). Ahlquist (1974) reported
that the isoelectric focusing in polyacrylamide
(IFPA) patterns of egg-white proteins of *Uria*
"shows an unmistakable likeness to those of
gulls." Evidence that the ancestor of the alcids
may have been more like a shorebird has been
reported by Stettenheim (1959), Hudson et al.
(1969), and Stegmann (1978). However, be-
cause there is considerable evidence that *Dro-
mas* is closely related to the Lari (Strauch 1978,
Sibley and Ahlquist in press), a shorebird-like
common ancestor of alcids and larids may not
conflict with earlier ideas. Strauch (1978) and
others (Stegmann 1978, Cracraft 1981) were un-
able to identify the closest relatives of the al-
cids. On the basis of DNA-DNA hybridization
studies, Sibley and Ahlquist (in press) found
that the Alcidae and Lari are sister-groups.

The Alcidae are distinguished among cha-
radriiform birds by their compact form, short
wings, and feeding habits (Coues 1868). Some
of the characteristics (sternum long and narrow
with long, rounded metasternum; wing bones

flattened) used to define them (Verheyen 1958, Zusi 1974) may be related to their marine and diving habits; others (large supraorbital grooves, basipterygoid processes absent in adults, anterior toes fully webbed, hind toe absent) are found in other charadriiform birds. Strauch (1978) found the Alcidae to be a monophyletic group defined by twisting of the brachial tuberosity of the coracoid so that it does not roof the triosseal canal and by lack of a lateral synsacral strut.

Coues (1868) used nostril feathering, bill form, and presence or absence of crests to divide the Alcidae into three subfamilies: Alcinae (*Pinguinus, Alca*), Phaleridinae (*Fratercula, Lunda, Cerorhinca, Ptychoramphus, Cyclorrhynchus, Aethia*), and Urinae (*Synthliboramphus, Endomychura, Brachyramphus, Cepphus, Alle, Uria*). Beddard (1898) used the number of rectrices, relative size of the right and left liver lobes, leg muscle formula, and form of the syrinx to divide the alcids into two families: Fraterculidae (*Cerorhinca, Lunda, Fratercula*) and Uriidae (all other genera). Shufeldt (1901), summarizing a series of papers on the osteology of the alcids (1888, 1889a–d), decided that Beddard's two families represented two subfamilies. Shufeldt (1889d) thought *Alle* closest to the auklets and *Uria* closest to the Laridae. Dawson (1920) used egg characteristics supplemented by other characters to divide the alcids into five families: Aethiidae (*Alle, Ptychoramphus, Cyclorrhynchus, Aethia*), Cepphidae (*Cepphus*), Alcidae (*Uria, Alca, Pinguinus*), Fraterculidae (*Cerorhinca, Lunda, Fratercula*), and Synthliboramphidae (*Synthliboramphus, Brachyramphus, Endomychura*). Storer (1945a) used pelvis and leg morphology supplemented by plumage, soft-part, egg, and breeding characters to divide the alcids into seven groups, which he later (1960) designated as tribes: Alcini (*Uria, Alca, Pinguinus*), Cepphini (*Cepphus*), Brachyramphini (*Brachyramphus*), Plautini (*Alle*), Aethiini (*Ptychoramphus, Cyclorrhynchus, Aethia*), Synthliboramphini (*Endomychura, Synthliboramphus*), and Fraterculini (*Cerorhinca, Lunda, Fratercula*). Storer (1952) suggested that *Alle* might be closest to his Alcini and that *Cepphus* was closer to the ancestral stock of the family than was *Uria*. Earlier, Storer (1945b) thought *Brachyramphus* the most primitive genus of alcid. Verheyen (1958) classified the Alcidae into four subfamilies: Fraterculinae (*Cerorhinca, Lunda, Fratercula*), Alcinae (*Pinguinus, Alca, Uria, Cepphus*), Plautinae (*Alle*),

and Aethiinae (the remaining genera). Yudin (1965) thought that there probably were two phyletic lines in the Alcidae but found insufficient grounds on which to divide them. He suspected that similarities in the jaw musculature of puffins and auklets were due to "parallel development." In a study of the wing and leg musculature, Hudson et al. (1969) found that the puffins differed markedly from other alcids, were probably the most primitive living alcids, and were closest to *Ptychoramphus*, among the genera studied. They found that *Brachyramphus* was not particularly close to any other genus, but was closer to *Uria* and *Alca* than to *Cepphus*, other murrelets, auklets, or puffins; and they found *Cepphus* to be closest to *Uria* and *Synthliboramphus*. Several authors (Storer 1945b, Sealy 1972, Binford et al. 1975, Jehl and Bond 1975) have concluded that among the murrelets *Endomychura* and *Synthliboramphus* are quite similar and that both are distinct from *Brachyramphus*.

It has long been agreed that the puffins (*Cerorhinca, Lunda, Fratercula*), the auklets (*Ptychoramphus, Cyclorrhynchus, Aethia*), and the auks (*Uria, Alca, Pinguinus*) are clusters of closely related species. The relationships among the murrelets (*Brachyramphus, Endomychura, Synthliboramphus*), the relationships of *Cepphus* and *Alle* to other alcids, and the relationships among all of these groups have been debated, however.

I reexamined the relationships among the species of the Alcidae using a modern, objective method to evaluate the characters on which the estimate of phylogeny is based.

MATERIALS AND METHODS

I examined skins and skeletons of each living species of alcid. A complete composite skeleton and several unassociated bones of *Pinguinus* also were examined. Integument characters for *Pinguinus* were obtained from Ridgway (1919). Natural history data were taken from the literature (Storer 1945a, Kozlova 1961, Sealy 1972, Simons 1980, Terres 1980). Natural history data for *Pinguinus* were obtained from Bengtson (1984). Character names follow Howard (1929), Bock and McEvey (1969), Zusi and Jehl (1970), and Strauch (1978).

A set of 33 cladistic characters was devised for the 22 extant and 1 extinct species studied. Primitive states were determined using other charadriiform birds, particularly the Lari, as outgroups (Strauch 1978). Character compatibility analysis employing the program CLINCH 5 (written by K. L. Fiala) was used to find the largest set of mutually compatible characters

TABLE 1. Character-state trees for the Alcidae.

No.	Character	State	Character-state tree
1	Maxillopalatine strut P		B → A
	Absent	B	
	Present	A	
2	Maxillopalatine shape		A → B
	Hollow and cup-shaped	A	
	Broad, flat plate	B	
3	Ventral end of interpalatine process		A → B
	Does not extend beyond ventral end of palatine shelf	A	
	Extends beyond ventral end of palatine shelf	B	
4	Secondary articulation of lower jaw		A → B
	Well developed	A	
	Absent	B	
5	Supraorbital rims		B → A
	Absent	B	
	Well developed	A	
6	Supraoccipital foramina		A → B
	Absent	A	
	Present	B	
7	Sclerotic ring		A → B
	Narrow, flat ring	A	
	Wide, conical ring with serrated edge	B	
8	Medial sternal notch		A → B
	Absent	A	
	Present	B	
9	Lateral sternal notch		A → B
	A notch	A	
	A fenestra	B	
10	Sternocoracoidal process of sternum		A → B
	Points caudally or dorsally	A	
	Points cranially	B	
11	Sternocoracoidal process of coracoid		A → B
	Well developed	A	
	Absent or poorly developed	B	
12	Number of sternal costal processes		A → B
	Six	A	
	Seven	B	
13	Coracoidal foramen		A → B
	Present	A	
	Absent	B	
14	Hypapophyses of thoracic vertebrae		A → B
	Well developed on all but last five vertebrae	A	
	Well developed on all but last three vertebrae	B	
15	Synsacral strut		A → B
	Well-developed strut	A	
	Absent or only a slight ridge	B	
16	Relative length of ischial angle and posterior projection of the ilium		A → B
	Ischial angle much longer	A	
	Both structures about the same length	B	
17	Pneumatic fossa II of humerus		A → B
	Well developed	A	
	Poorly developed	B	
18	Extensor process of carpometacarpus		A → B
	Short, rounded point	A	
	Long, flat structure	B	

TABLE 1. Continued.

No.	Character	State	Character-state tree
19	Tendinal canal No. 1 of hypotarsus		C ← B → A
	Bony canal	B	
	Deep channel	A	
	Shallow groove	C	
20	Trochlea		A → B
	Normal proportions for charadriiforms	A	
	Long and slender	B	
21	Claw of inner toe		A → B
	Normal alcid shape	A	
	Stout and strongly curved	B	
22	Nostril feathering		C → B → A
	Nostrils bare	C	
	Partly feathered	B	
	Feathered	A	
23	Head plumage		A → B
	Typical feathering	A	
	Velvety plumage	B	
24	Eye scales		A → B
	Absent	A	
	Present	B	
25	Incubation patches		A → B
	Two	A	
	One	B	
26	Secondaries		B → A
	Without white tips	B	
	With white tips	A	
27	Number of rectrices		A → B → C
	12	A	
	14	B	
	16 or more	C	
28	Shape of retrices		A → B
	Rounded at tips	A	
	Pointed at tips	B	
29	Scutellation		A → B
	Scutellate	A	
	Reticulate	B	
30	Clutch size		B → A
	Two	B	
	One	A	
31	Post-hatching development pattern		A ← C → B
	Semiprecocial	C	
	Intermediate	A	
	Precocial	B	
32	Nest sites		C → B → A
	In the open	C	
	In natural crevices	B	
	In burrows	A	
33	Nesting dispersion		A → B
	Colonial	A	
	Solitary	B	

in the data set (for details see Estabrook et al. 1977, Strauch 1978, Meacham 1980). This set of characters, called the primary characters or primary clique, uniquely defines a phylogenetic tree [i.e. one that "depicts actual patterns of ancestry and descent among a series of taxa" (Eldredge and Cracraft 1980)], the primary tree. It is hypothesized that the primary characters are free from homoplasy.

TABLE 2. Character states for species of Alcidae.

Species	Character number						
	1–5	6–10	11–15	16–20	21–25	26–30	31–33
Pinguinus impennis	B AAB A	B AAAA	AB ABB	ABB CA	AAB AB	ABB AA	ACA
Alca torda	B AAB A	AAAAA	AB ABB	ABB CA	AAB AB	AAB AA	ACA
Uria lomvia	B AAB A	AAAAA	AB ABB	ABB CA	AAB AB	AAAAA	ACA
Uria aalge	B AAB A	AAAAA	AB ABB	ABB CA	AAB AB	AAAAA	ACA
Alle alle	B AAB A	B AAAA	AAB AB	AB AB A	ABB AA	AAAAA	CB A
Cepphus grylle	B AAB B	B AAAA	AAAB B	AB AB A	AB AAA	B AAB B	CB A
Cepphus columba	B AAB B	AAAAA	AAAB B	AB AB A	AB AAA	BB AB B	CB A
Cepphus carbo	B AAB B	AAAAA	AAAB B	AB AB A	AB AAA	BB AB B	CB A
Brachyramphus marmoratus	B AAB B	B AAAA	ABB AB	AB AB A	AB AAB	BB AB A	CCB
Brachyramphus brevirostris	B AAB B	B AAAA	AAB BB	AB AB A	AB AAB	BB AB A	CCB
Endomychura hypoleucus	B AAB B	B AAAA	AB AB B	AB AB B	AB AAA	B AAB B	BB A
Endomychura craveri	B AAB B	B AAAA	AB AB B	AB AB B	AB AAA	B AAB B	BB A
Synthliboramphus antiquus	B AAB B	B AAAA	AB AB B	AB AB B	AB AAA	BB AB B	BB A
Synthliboramphus wumizusume	B AAB B	B AAAA	AAAB B	AB AB B	AB AAA	BB AB B	BB A
Ptychoramphus aleuticus	B AB AB	B AAAA	ABB AA	BB AB A	AB AAA	BB AB A	CAA
Cyclorrhynchus psittacula	B AB AB	B AAB A	AAB AA	BB AB A	AB AAA	BB AB A	CB A
Aethia cristatella	BBB AB	B AAB A	B AB AA	BB AB A	AB AAA	BB AB A	CB A
Aethia pusilla	BBB AB	B AAB A	B AB AA	BB AB A	AB AAA	BB AB A	CB A
Aethia pygmaea	BBB AB	B AAB A	B AB AA	BB AB A	AB AAA	BB AB A	CB A
Cerorhinca monocerata	AAAAB	BBB AB	BB AB A	AAAB A	ACAAA	B CAB A	CAA
Fratercula arctica	AAAAB	ABB AB	BB AB A	AAAAA	B CAB A	B CAB A	CAA
Fratercula corniculata	AAAAB	ABB AB	BB AB A	AAAAA	B CAB A	B CAB A	CAA
Lunda cirrhata	AAAAB	ABB AB	BB AB A	AAAAA	B CAAA	B CAB A	CAA

A series of secondary analyses was made on selected phyletic branches of the primary tree. In a secondary analysis the compatibility of the characters that vary among all taxa on a branch (a monophyletic group) is redetermined. This procedure may find additional characters that are compatible with the primary characters on the branch being analyzed but that are not compatible on the primary tree. The largest clique that includes all of the primary characters included in the secondary analysis is chosen as the set of most reliable characters. This restriction ensures consistency among the primary and secondary cliques. Secondary analyses are made progressively from large branches to smaller ones; the results accepted in each analysis must be consistent with all previous, more general analyses. Thus, relationships may be more fully resolved on smaller and smaller branches of the tree. As each branch is reanalyzed, it is replaced by the more fully resolved branch determined by the secondary analysis.

In each secondary analysis the character-state trees for primary and secondary characters accepted in a more general analysis of the branch being examined were taken as fixed. Character-state trees for rejected characters were reevaluated using the method of Strauch (1984). Their trees were redetermined according to the distribution of states in the sister-group of the branch being analyzed. If the evidence from the sister-group was ambiguous, the original form of the character-state tree was used.

Another compatibility analysis was made using some of the data of Hudson et al. (1969). They described 108 wing and leg musculature characters for the Lari and Alcidae. Of these I used 17 that varied among the alcids and for which the primitive state could be determined from the states found in the Lari. In a few cases more than one state was found in a species; in such cases I used the state found in the majority of the specimens examined. The species studied by Hudson et al. are listed in Table 4. Only a primary analysis was done on those data.

The original data also were analyzed to find the most parsimonious tree in the data set using the method of Colless (1980, 1983).

CHARACTERS

The characters used in this study include 21 from the skeleton, 8 from the integument, and 4 from natural history. Homologies for structural characters were determined according to similarities in structure and location (Jardine 1969, Strauch 1978, Eldredge and Cracraft 1980); those for natural history characters were determined by the role they play in the life cycle of the species.

Although comparison was made with specimens of all other major groups of charadriiform birds to determine primitive states, when there were ambiguities because several states were found in the out-
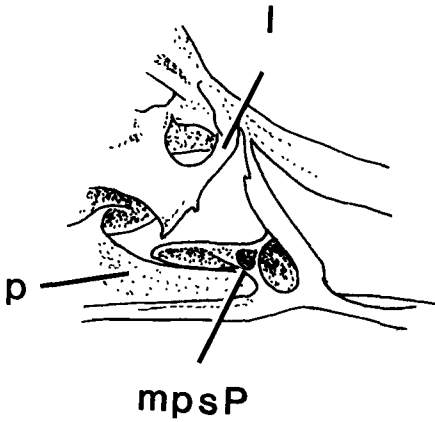
Fig. 1.   Right lateral view of the skull of *Cerorhinca monocerata*. l = lacrimal, mpsP = maxillopalatine strut P, p = palatine.
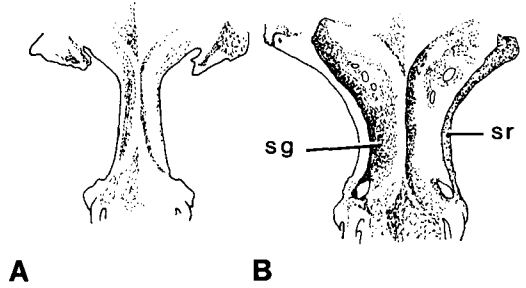

Fig. 3.   Dorsal view of the frontal region of *Cerorhinca monocerata* (A) and *Uria aalge* (B). sg = supraorbital groove, sr = supraorbital rim.

groups, greatest weight was given to the states found in the Lari.

The descriptions of the characters and their states, as well as the distribution of the states among the outgroups and in the Alcidae, are outlined below. In most cases the state found in the outgroup is hypothesized to be the primitive (plesiomorphic) state, while that found only in some alcids is hypothesized to be the derived (apomorphic) state. Complex situations are described in more detail. The character states and

character-state trees are given in Table 1. A table entry of A → B means that the primitive state is A and the derived state is B; the tree can be read as "state A is the ancestor of state B." The character states for the 23 species are given in Table 2.

Character 1.—Maxillopalatine strut P (Fig. 1). The maxillopalatine strut found in puffins does not appear to be homologous with any of those found in other charadriiforms (Lowe 1931, Bock 1958, Zusi and Jehl 1970, Strauch 1978). Its presence is considered to be derived.

Character 2.—Maxillopalatine shape (Fig. 2). In the Charadriiformes, except *Aethia*, the maxillopalatine is a hollow, cup-shaped structure; in *Aethia* it is a broad, flat plate that when viewed ventrally extends almost to the vomer.

Character 3.—Ventral end of the interpalatine process (Fig. 2). The ventral end of the interpalatine process does not extend as far ventrally as the ventral edge of the palatine plate in most charadriiforms. In the auklets, however, it extends beyond the edge of the palatine shelf.

Character 4.—Secondary articulation of the lower jaw. The Lari, auklets, and puffins have a well-developed secondary articulation of the lower jaw. The articulation is absent in the murrelets, *Cepphus, Alle,* and the auks. Kozlova (1961) reported the presence of the basisphenoid processes associated with this articulation in alcids. Bock (1960) reported the articu-

Fig. 2.   Ventral view of the palate of *Aethia cristatella*. j = jugal bar, mp = maxillopalatine, ps = palatine shelf, ipp = interpalatine process, v = vomer.
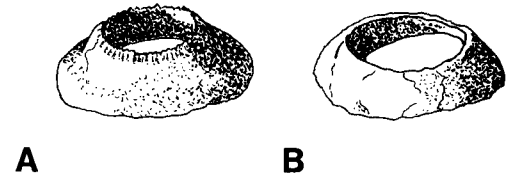

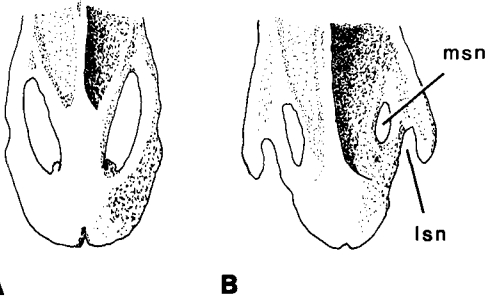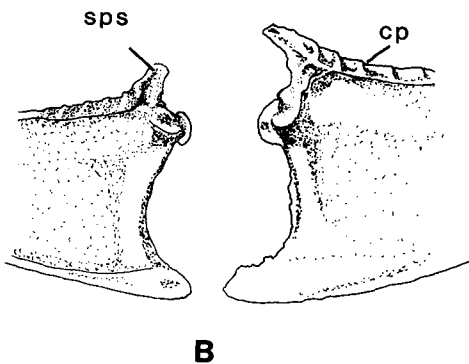Fig. 4.   Sclerotic rings of *Lunda cirrhata* (A) and *Uria aalge* (B).

Fig. 5. Ventral view of the caudal end of the sternum of *Aethia cristatella* (A) and *Cerorhinca monocerata* (B). lsn = lateral sternal notch, msn = medial sternal notch.
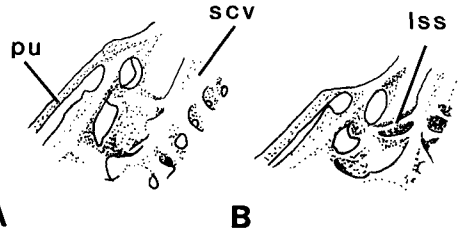

Fig. 7. Lateral ventral view of the right side of the synsacrum of *Uria lomvia* (A) and *Fratercula arctica* (B). lss = lateral sternal strut, pu = pubis, scv = sacral-caudal vertebrae.

lation absent in alcids, but did not report which taxa he examined.

Character 5.—Supraorbital rims (Fig. 3). The supraorbital rims are only partially developed in the Lari and some of the alcids. They are fully developed in the auks.

Character 6.—Supraoccipital foramina. Supraoccipital foramina are absent in the skulls of adult Lari and most other groups of charadriiforms; they are present in some species of alcids. Beddard (1898) reported that in alcids these foramina sometimes become obliterated with age. Shufeldt (1888) found them "by no means a constant character."

Character 7.—Sclerotic ring (Fig. 4). The sclerotic ring of most charadriiforms is a flattish, narrow ring. That of puffins, however, is distinctly conical and has a serrated inner edge. Shufeldt (1889d) was the first to describe this condition for the puffins. Curtis and Miller (1938) discussed the variation found in the sclerotic ring of North American birds.

Character 8.—Medial sternal notch (Fig. 5). Most

Fig. 6. Lateral view of the cranial end of the sternum of *Aethia cristatella* (A) and *Cerorhinca monocerata* (B). cp = costal process, sps = sternocoracoidal process of sternum.

charadriiforms have a medial sternal notch, but several, including members of the Lari and Alcidae, do not. Distribution of the states among other charadriiforms thus does not indicate which state is primitive in the alcids. Because the notch is absent in the Gruiformes (except the Otididae), which are probably a sister-group of the Charadriiformes, I hypothesized (Strauch 1978) that absence of the medial notch is primitive in charadriiforms. That coding is used here.

Character 9.—Lateral sternal notch (Fig. 5). Almost all charadriiforms (including all Lari) have a lateral sternal notch. In the auklets it is reduced to a fenestra, a condition assumed to be a derived state in the Alcidae. Shufeldt (1888, 1889a) and Lucas (1890) reported that in the auks the lateral sternal notch tends to become ossified with age. This condition clearly differs from that in the auklets; it is hypothesized to represent merely a variant of the state with the notch present. Kuroda (1954, 1955) illustrates the variation with age of the sternal notching of some alcids.

Character 10.—Sternocoracoidal process of sternum (Fig. 6). In the Lari and most other charadriiforms the sternocoracoidal process of the sternum points caudally or dorsally; in the puffins it points distinctly cranially.

Character 11.—Sternocoracoidal process of coracoid. The sternocoracoidal process of the coracoid is well developed in the Lari and most other charadriiforms; it is absent or poorly developed in some of the auklets. These differences are illustrated by Kuroda (1954: Fig. 7) and are mentioned by Shufeldt (1889c).

Character 12.—Number of costal processes (Fig. 6). There are six costal processes on the sternum of the Lari and most other charadriiforms; some alcids have seven.

Character 13.—Coracoidal foramen. The Lari and most other charadriiforms have a coracoidal foramen; it is absent in some species of alcids.

Character 14.—Hypapophyses of thoracic vertebrae. The Lari and other nonalcid charadriiforms have poorly developed hypapophyses on their thoracic
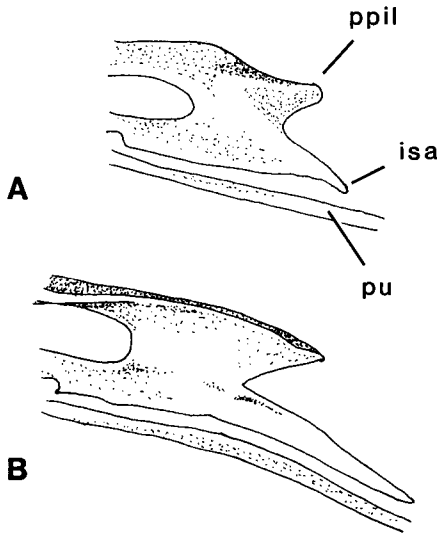
Fig. 8. Lateral view of the caudal end of the synsacrum of *Aethia cristatella* (A) and *Uria lomvia*(B). isa = ischial angle, ppil = posterior projection of ilium, pu = pubis.

vertebrae. Well-developed hypapophyses, most with bilateral flanged wings, are found in all alcids, but the number of vertebrae on which they occur varies among the species. It is hypothesized that a greater number of vertebrae with well-developed hypapophyses is a more derived condition. Similar structures are found in loons, grebes, penguins, and some anseriforms (Beddard 1898).

Character 15.—Synsacral strut (Fig. 7). In most charadriiforms a strut or brace extends from the fused sacral-caudal vertebrae to the acetabulum. In the alcids this strut may be well developed (contra Strauch 1978), it may be reduced to a very slight ridge, or it may be completely absent.
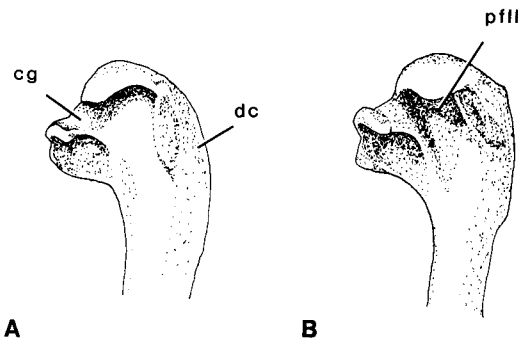

Fig. 9. Anconal view of the proximal end of the humerus of *Alca torda* (A) and *Lunda cirrhata* (B). cg = capital groove, dc = deltoid crest, pfII = pneumatic fossa II.
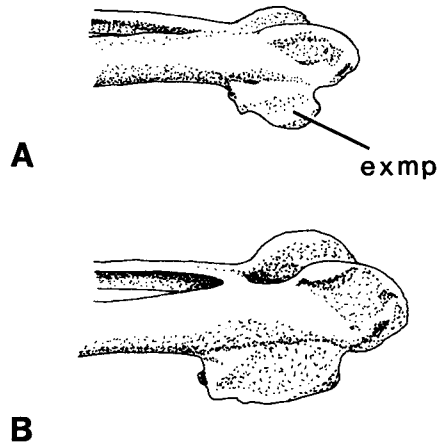

Fig. 10. Ventral view of the proximal end of the carpometacarpus of *Cerorhinca monocerata* (A) and *Uria lomvia* (B). exmp = extensor process of metacarpus.

Character 16.—Relative length of the ischial angle and posterior projection of the ilium (Fig. 8). In the Lari and most other charadriiforms the ischial angle is much longer than the posterior projection of the ilium; in the auklets the length of the ischial angle is much reduced, and the structures are almost the same length. These differences also are indicated by Storer's (1945a) measurements of alcid skeletons.

Character 17.—Pneumatic fossa II of humerus (Fig. 9). The Lari and most other charadriiforms have a well-developed pneumatic fossa II of the humerus; in some alcids, however, it is poorly developed or almost completely absent.

Character 18.—Extensor process of carpometacarpus (Fig. 10). The extensor process of the carpometacarpus is a short, rounded point in the Lari and most other charadriiforms; in some of the alcids it is long and flat.

Character 19.—Tendinal canal No. 1 of hypotarsus. The pattern of the canals in the hypotarsus of charadriiforms is discussed by Strauch (1978). Only the condition of the canal assumed to be for the tendon of M. flexor digitorum longus shows different states in the Alcidae. In most charadriiforms canal No. 1 is a bony canal; in the Lari it is either a bony canal or a deep channel. In the Alcidae it may be a bony canal (most species), a deep channel (some puffins), or a shallow groove (the auks). The bony canal in charadriiforms is hypothesized to be primitive (Strauch 1978). More open canals in the hypotarsus have been linked with greater specialization and probably represent derived states (Harrison 1976).

Character 20.—Trochlea. In the Lari and most alcids the proportions of the trochlea are similar. In some murrelets the trochleae are relatively long and somewhat compressed and give the tarsometatarsus a slender appearance (Storer 1945b).
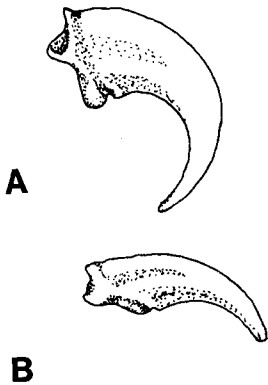
A

B

Fig. 11. Lateral view of the claw of the inner (second) toe of *Lunda cirrhata* (A) and *Alca torda* (B).

Character 21.—Claw of the inner (second) toe (Fig. 11). The claw of most charadriiforms is moderately arched, compressed, and acute (Coues 1868). In puffins that dig their own burrows, the inner (second) toe is usually stout and strongly curved. Figure 11 shows the toe with the claw attached; Shufeldt (1889d) illustrates the ungual phalanx with the claw removed. Although it has been assumed that this toe is used in digging burrows, I could not find a description of its use.

Character 22.—Nostril feathering. The nostrils of the Lari, some alcids, and most other charadriiforms are bare. Some alcids have partially feathered nostrils, and others have completely feathered ones. It is hypothesized that increasing feathering represents progressively derived states. This character was first used by Brandt (1837) to classify the alcids.

Character 23.—Head plumage. The head plumage of the Lari and most other charadriiforms consists of typical feathers; in some alcids the head plumage is distinctly velvety.

Character 24.—Eye scales. The Lari and most other charadriiforms have no eye scales; they are present in some puffins.

Character 25.—Number of incubation patches. Paired lateral incubation patches are found in shorebirds, Lari, and some alcids (Bailey 1952). Some alcids have only one patch.

Character 26.—White-tipped secondaries. In the Lari the secondaries may be solid-colored or white-tipped. The condition in the Lari thus does not indicate the primitive state in the Alcidae. Since dark-tipped secondaries are found in three of the four major groups of alcids ["widespread" according to the principles of Kluge and Farris (1969)], white tips are hypothesized to be a derived state.

Character 27.—Number of rectrices. The Lari have 12 rectrices. Alcid species may have 12, 14, 16, or 18 rectrices. The number appears to be constant within a species except for *Cerorhinca*, which may have 16 or

18. It is hypothesized that an increasing number of rectrices represents increasingly derived states.

Character 28.—Shape of rectrices. The rectrices of the Lari and most other charadriiforms have rounded tips. In some auks the rectrices are distinctly pointed.

Character 29.—Scutellation. The scutellation on the podotheca of the Lari is scutellate. In alcids it may be either scutellate or reticulate. Coues (1868), Ridgway (1919), and Verheyen (1958) describe several subclasses of scutellation for alcids, and sometimes disagree about them. A. J. Baker (pers. comm.) and I found only two major types in the specimens we examined.

Character 30.—Clutch size. The Lari and almost all other charadriiforms lay a clutch of two or more. Although some alcids lay two eggs, most species lay only one.

Character 31.—Post-hatching development pattern. Alcids have three distinct post-hatching development patterns: precocial, intermediate, and semiprecocial (Sealy 1973). The pattern for *Pinguinus* is unknown. Bengtson (1984), in a review of the literature on *Pinguinus*, estimated that chicks leave the nest at about 10 days old, which would agree with an intermediate pattern. In the Lari the pattern is semiprecocial; it is hypothesized that shortening of the nestling period in alcids represents a derived condition.

Character 32.—Nest sites. The Lari nest in the open, as do some alcids. Other alcids nest in crevices or in burrows. Kozlova (1961) thought that the original nest sites of alcids were "on open rocks or coastal cliffs." It is hypothesized that nesting in crevices or in burrows represents increasingly derived conditions.

Character 33.—Nesting dispersion. The Lari and most of the alcids nest in colonies. Some species of alcids, however, nest solitarily.

Characters considered but rejected because more than one state was found in a species were the fusion of the interorbital septum and brain case [Shufeldt (1901) reported this to vary with age], the presence of a mandibular fossa, the number of caudal and cervical vertebrae, and the diet (see Bédard 1969). I found insufficient information for every species to use color of the eye or mouth lining, the shedding of the bill plates, the shape of the first bronchial semirings, the size of the two lobes of the liver, the tongue or palate characters of Bédard (1969), or the barring of the juvenal plumage. I could not devise a credible character-state tree for the egg categories of Dawson (1920).

The character descriptions and character-state trees for the data of Hudson et al. (1969) are given in Table 3. The character states for the 12 species they studied are given in Table 4.

RESULTS

The compatibility analysis of the 33 characters for the 23 species of alcids found one larg-

TABLE 3.   Character-state trees for wing- and leg-musculature characters of Hudson et al. (1969).

No.	Character	State	Character-state tree
H1	M. pectoralis abdominalis		A → B
	Insertion on tendon of M. pectoralis thoracica	A	
	Insertion on humerus	B	
H2	M. subcoracoideus		A → B
	Small or absent anterior head	A	
	Anterior head short or long	B	
H3	M. propatagialis longus		A → B
	Dilation at wrist unossified	A	
	Dilation at wrist ossified	B	
H4	M. propatagialis		A → B
	2 tendons	A	
	1 tendon	B	
H5	Patagial fan sesamoid		A → B
	Present	A	
	Absent	B	
H6	M. deltoideus minor		A → B
	Dorsal head present	A	
	Dorsal head absent	B	
H7	Swelling in M. triceps tendons		A → B
	Unossified	A	
	Ossified	B	
H8	Swelling in humero-ulnar pulley		A → B
	Ossified	A	
	Unossified	B	
H9	M. biceps brachii		C ← A → B
	Divided lengthwise	A	
	Divided distally	B	
	Undivided	C	
H10	M. flexor digitorum sublimis		A → B
	Dilation at base of phalanx 1 ossified	A	
	Dilation at base of phalanx 1 unossified	B	
H11	M. ulnimetacarpalis dorsalis		A → B
	Ventral head present	A	
	Ventral head absent	B	
H12	M. ambiens		A → B
	Present	A	
	Absent	B	
H13	Pars iliofemoralis of M. piriformis		A → B
	Absent	A	
	Present	B	
H14	Pars interna of M. gastrocnemius		A → B
	Extends around anterior surface of knee	A	
	Does not extend around anterior surface of knee	B	
H15	Pars interna of M. gastrocnemius		A → B
	No extra head from tibia	A	
	Extra head from tibia	B	
H16	Pars medialis of M. gastrocnemius		A → B
	Present	A	
	Absent	B	
H17	M. plantaris		A → B
	Present	A	
	Absent	B	

TABLE 4. Character states for species of Alcidae; data of Hudson et al. (1969).

Species	H character number			
	1–5	6–10	11–15	16–17
Alca torda	A B B A B	B A A C A	A B B B B	A A
Uria lomvia	A B A A B	B A A C B	A B B B B	A A
Uria aalge	A B A A B	B A A C B	A B B B B	A A
Cepphus grylle	A B A A B	A A B C B	A B B B B	A A
Cepphus columba	A B A A B	A A B C B	A B B B B	A A
Brachyramphus marmoratus	A B B A B	A A A C B	A B B B A	B B
Synthliboramphus antiquus	A B B B A	A A A C B	B B B B B	A A
Ptychoramphus aleuticus	B A B B B	A A A A B	B B A B A	A A
Cerorhinca monocerata	A A A A B	A B A B A	A A A A A	A A
Fratercula arctica	A A A A B	A B A B A	A A A A A	A A
Fratercula corniculata	A A A A B	A B A B A	A A A A A	A A
Lunda cirrhata	A A A A B	A B A B A	A A A A A	A A

est clique of 23 characters: 1–5, 7–10, 15–24, 26, 28, 31, 33. The tree defined by this clique is shown in Fig. 12. It shows that the earliest split in the alcid phylogenetic tree gave rise to two branches: one leading to the puffins and one leading to the auklets, murrelets, *Cepphus*, *Alle*, and the auks. The second branch divided further, the first split giving rise to a branch leading to the auklets and one leading to the murrelets, *Cepphus*, *Alle*, and the auks. *Endomychura* and *Brachyramphus* are found on different phyletic lines. The relationships of *Cepphus* are unresolved. [The occurrence of extant taxa on intermediate nodes does not necessarily imply that these taxa are ancestors of other extant taxa, only that none of the characters used in the study distinguishes them from their hypothetical ancestor. Strauch (1978) discussed how to interpret the estimates of phylogenetic trees developed from compatibility analysis.]

A secondary analysis was made of the auklets, murrelets, *Cepphus*, *Alle*, and the auks. Before this analysis was made the character-state trees for the ten characters rejected in the primary analysis (6, 11–14, 25, 27, 29, 30, 32) were reevaluated (Strauch 1984). The reevaluation used puffins as an outgroup. On this basis the character-state trees for characters 11, 12, 14, 27, 29, 30, and 32 were revised (Table 5). A compatibility analysis of the 26 characters that varied among the 19 species used in this analysis gave one largest clique of 18 characters: 2–5, 9, 15, 16, 18–20, 22, 23, 26, 28–31, 33. This clique includes the 16 primary characters included in the analysis plus 2 of the revised characters (29 and 30). The tree defined by this

clique (Fig. 13) shows that on the basis of character 30 *Cepphus* is a member of the phyletic line that includes *Endomychura* and *Synthliboramphus*.

A secondary analysis was made of the murrelets, *Cepphus*, *Alle*, and the auks, using the auklets as an outgroup. For this analysis the character-state trees for characters 6, 13, and 14 were recoded (Table 5). The compatibility analysis of the 19 characters that varied among the 14 species of murrelets, *Cepphus*, *Alle*, and the auks gave a largest clique of 12 characters: 5, 18–20, 22, 23, 26, 28–31, 33. This clique contains all of the primary and previously accepted secondary characters used in the analysis, but no new characters.

The reciprocal of the previous analysis was made using the murrelets, *Cepphus*, *Alle*, and the auks as the outgroup for the auklets. Character 11 was recoded (Table 5) to its original form. The compatibility analysis of the 5 characters that varied among the 5 species of auklets gave one largest clique of 5 characters: 2, 9, 11, 12, 32. This clique contains all of the characters used in the analysis: the primary characters 2 and 9 plus the previously rejected characters 11, 12, and 32. No new transitions were identified by the tree determined by this clique.

A final analysis was made of *Alle* and the auks using the murrelets and *Cepphus* as outgroups. Character 14 was revised (Table 5) for this analysis. The compatibility analysis of the 12 characters that varied among the 5 species in this analysis found two largest cliques of 10 characters each: (A) 12–14, 18, 19, 22, 25, 28, 31, 32; (B) 6, 12–14, 18, 19, 22, 25, 31, 32. Only clique
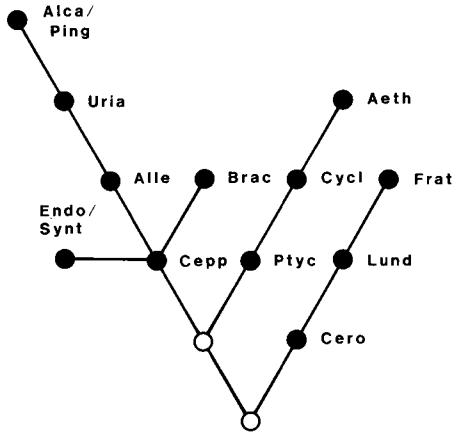
Fig. 12. Primary phylogenetic tree of the Alcidae, defined by 23 characters. Aeth = *Aethia*, Brac = *Brachyramphus*, Cepp = *Cepphus*, Cero = *Cerorhinca*, Cycl = *Cyclorhynchus*, Endo = *Endomychura*, Frat = *Fratercula*, Lund = *Lunda*, Ping = *Pinguinus*, Ptyc = *Ptychoramphus*, Synt = *Synthliboramphus*.
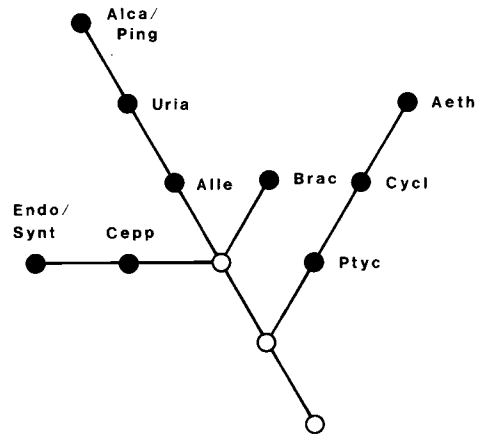

Fig. 13. Secondary phylogenetic tree of the nonpuffin alcids. Abbreviations as in Fig. 12.

A included all of the primary and previously accepted secondary characters used in this analysis. Characters 12–14, 25, and 32 are newly accepted on this branch. The tree determined by this clique (Fig. 14) shows a new transition separating *Alle* from the common ancestor it shares with the auks.

The final phylogenetic tree for the Alcidae found from these analyses is shown in Fig. 15.

The analysis of the 17 wing- and leg-muscle characters for 12 species derived from the study of Hudson et al. (1969) gave one largest clique of 12 characters: H1, H2, H6–H9, H12–H17. The

tree determined by this clique is shown in Fig. 16. This tree includes a transition not found in my data set that indicates that *Cepphus*, *Synthliboramphus*, *Uria*, and *Alca* share a most recent common ancestor not shared with *Brachyramphus*.

The tree from the data of Hudson et al. (1969) is consistent with that found from my data, as shown by a compatibility analysis using the two phylogenetic trees (Figs. 15, 16) as character-state trees for the taxa common to both data sets. The two trees are compatible and determine the tree shown in Fig. 17.

A nonexhaustive search using the parsimony program of Colless (1980, 1983) found 33 different, shortest, equal-length trees (one of which was found by the Wagner-78 program).

TABLE 5. Recoded character-state trees for characters rejected in the primary analysis, as recoded for indicated secondary analysis.

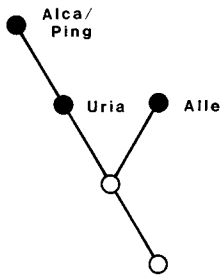| Character no.	Secondary analysis			
	Nonpuffin alcids	Murrelets, *Cepphus*, *Alle*, and auks	Auklets	*Alle* and auks
6	A → B	B → A	—	B → A
11	B → A	—	A → B	—
12	B → A	B → A	B → A	B → A
13	A → B	B → A	—	B → A
14	B → A	A → B	—	B → A
25	A → B	A → B	—	A → B
27	C → B → A	C → B → A	—	C → B → A
29	B → A	B → A	—	—
30	A → B	A → B	—	—
32	A → B → C	A → B → C	A → B → C	A → B → C

Fig. 14. Secondary phylogenetic tree of *Alle* and the auks. Abbreviations as in Fig. 12.

I estimate that there are at least 45 trees of this length if only dichotomies are allowed. These trees had several features in common. The earliest split in the alcid tree was the same as determined by the compatibility analyses, and showed the same relationships among the species of puffins as determined by the compatibility analyses; they place *Alle* and the auks on the same branch, but they indicate three different sets of relationships among the auks; they place the auklets on the same branch and show the same relationships among them as found in the compatibility analyses; and they show *Endomychura* and *Synthliboramphus* to be closely related. As for the relationships among *Cepphus*, the murrelets, and the auklets, however, the trees show 15 different patterns, some of which place the species of *Cepphus* on different phyletic lines.

DISCUSSION

PHYLOGENY

My earlier finding (Strauch 1978) that the Alcidae are defined by a twisted brachial tuberosity of the coracoid is supported by this study; that they also are defined by lack of a synsacral strut is not, because the strut is found in the puffins and auklets. Additionally, I found that alcids are also defined by the presence of well-developed hypapophyses on the thoracic vertebrae (character 14).

The phylogenetic tree obtained in this study supports many previously held ideas about the relationships among the alcids: that the puffins are a monophyletic group that includes *Cerorhinca*; that the auklets are a monophyletic group; that *Brachyramphus* and *Endomychura* are not closely related; and that *Alle* is closely re-
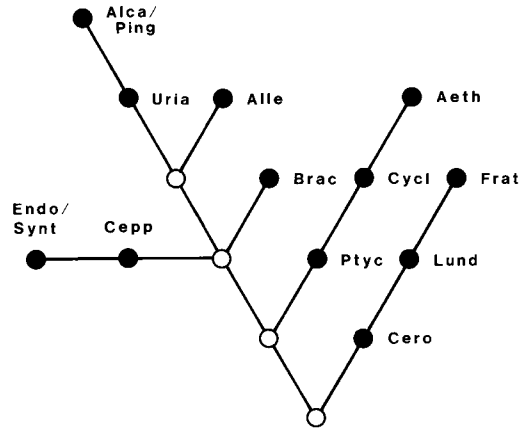

Fig. 15. Final phylogenetic tree of the Alcidae. Abbreviations as in Fig. 12.

lated to the auks. On the other hand, the phylogeny found here differs substantially from Storer's (1960), although it agrees in the composition of some of his phyletic lines.

These results show that the earliest split in the alcid phylogenetic tree gave rise to two phyletic lines: one leading to the puffins and one leading to the auklets, murrelets, *Cepphus*, *Alle*, and the auks. The puffins are defined by the presence of maxillopalatine strut P (character 1); a wide, conical sclerotic ring with a serrated inner edge (7); medial sternal notches (8); and cranially pointing sternocoracoidal processes of the sternum (10). *Lunda* and *Fratercula* are further defined by tendinal canal No. 1 of the hypotarsus, a deep channel (19); and a stout, strongly curved inner toe (21). *Fratercula* is defined by the presence of eye scales (24).
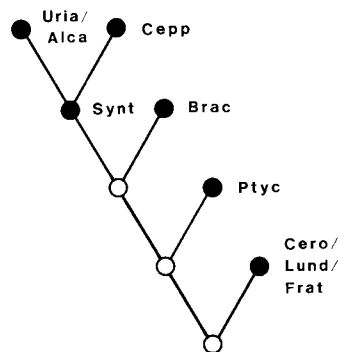

Fig. 16. Primary phylogenetic tree from the data of Hudson et al. (1969). Abbreviations as in Fig. 12.

These are all states of primary characters, and all but one are skeletal characters.

Various authors have suggested that the puffins are either the most primitive or the most advanced alcids. That they are the only living representatives of one of the branches of the earliest split in the alcid phylogenetic tree, however, does not indicate that they are necessarily primitive. The idea that they are advanced arises from a tendency to think of the most numerous and familiar group of species in a family as somehow representing the generalized and primitive condition from which smaller distinct groups have been derived. Among the alcids, the auks, *Cepphus,* and the murrelets have long been the norm against which the other members have been judged. Although the puffins are indeed quite different from the auks, their differences combine the retention of primitive states absent in the auks with the possession of derived states not found in other alcids. Representatives of all the alcid phyletic lines found here are known from the Upper Miocene (Olson 1985); the earlier record is too fragmentary to indicate when these lines first appeared. There is thus no evidence for designating any group of alcids as primitive. In any case, modern puffins and modern auks are both modern representatives of phyletic lines that have been evolving for ten million years.

The phyletic line that leads to the auklets, murrelets, *Cepphus, Alle,* and the auks is defined by a poorly developed pneumatic fossa II of the humerus (17) and partly feathered nostrils (22), both states of primary characters. This line further splits into one line leading to the auklets and one leading to the remaining taxa. The auklets are defined by the extension of the ventral end of the interpalatine process beyond the ventral end of the palatine shelf (3) and nearly equal lengths of the ischial angle and posterior projections of the ilium (16). *Cyclorrhynchus* and *Aethia* are further defined by the reduction of the lateral sternal notch to a fenestra (9), six costal processes on the sternum (12), and nesting in natural crevices (32). *Aethia* is defined by broad, flat, platelike maxillopalatines (2) and an absent or poorly developed sternocoracoidal process of the coracoid (11). All of these groups are defined by states of primary characters, supplemented by those of secondary characters for *Cyclorrhynchus* and *Aethia.*
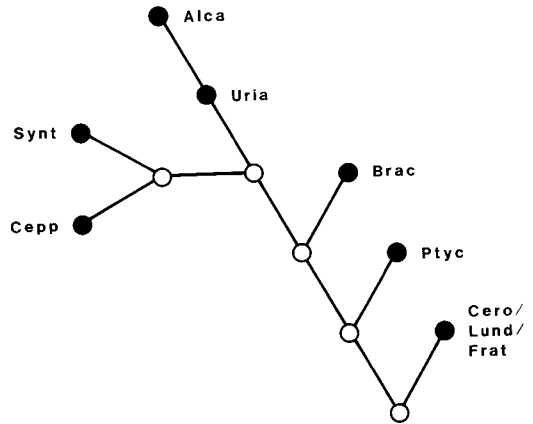

Fig. 17. Phylogenetic tree resulting from combining the results of this study and that of Hudson et al. (1969). Abbreviations as in Fig. 12.

The murrelets, *Cepphus, Alle,* and the auks are defined by a lack of the secondary articulation of the lower jaw (4) and loss of a well-developed synsacral strut (15), states of primary characters. This line splits into branches (Fig. 15) leading to *Brachyramphus,* defined by solitary nesting (33); to *Cepphus, Endomychura,* and *Synthliboramphus,* defined by a two-egg clutch (30); and to *Alle* and the auks, defined by well-developed supraorbital rims (5), velvety head plumage (23), white-tipped secondaries (26), and a scutellate tarsus (29). The line leading to *Brachyramphus* and that leading to *Alle* and the auks are defined by primary characters; the line leading to *Cepphus, Endomychura,* and *Synthliboramphus* is defined by a secondary character.

Most of the lineages identified are defined by primary characters. Of the three lines found in the group consisting of the murrelets, *Cepphus, Alle,* and the auks, however, only one is defined by a primary skeletal character; the other two are defined by natural-history characters, only one of which is a primary character. This testifies to the structural similarities of these birds.

The final phylogenetic tree (Fig. 15) supports the findings of several authors (Storer 1945b, Sealy 1972, Binford et al. 1975, Jehl and Bond 1975) that *Endomychura* and *Brachyramphus* are not closely related and further shows them to be members of different phyletic lines. *Endomychura* and *Synthliboramphus* are defined by long, slender trochleae (20) and a precocial post-

hatching development pattern (31), both states of primary characters. Perhaps most interesting is the finding that *Cepphus* is not closely related to the auks, but rather is a member of one of the murrelet lines. *Cepphus* is placed with *Endomychura* and *Synthliboramphus* because it shares a two-egg clutch, a state of a secondary character. This is the only major transition on the phylogenetic tree defined only by a secondary character. However, this character (30) shows no homoplasy on the alcid phylogenetic tree. It is a clear example that using outgroups can lead to errors in the estimation of primitive states (Meacham 1984, Strauch 1984). Although a clutch size greater than one may be primitive for the Charadriiformes, it appears that a clutch of one is primitive for alcids. If the secondary coding had been used in the primary analysis, character 30 would have been compatible with all of the primary characters. The same argument applies to character 29 (scutellation).

The ventral feathers of the juvenal plumage of *Cepphus* and *Brachyramphus* have dark tips that give the plumage a distinct barred appearance (Ridgway 1919, Kozlova 1961). Similar dark-tipped feathers recently have been found on the flanks of juvenile specimens of *Synthliboramphus antiquus* and *Endomychura hypoleucus* (Storer in litt.). The phylogenetic significance of this character state cannot be evaluated until the juvenal plumages of all alcids are better known.

The line leading to *Alle* and the auks splits into one branch leading to *Alle*, defined by six costal processes (12) and by hypapophyses on all but the last five thoracic vertebrae (14; both states of secondary characters), and one leading to the auks, defined by presence of a coracoidal foramen (13), a long, flat extensor process of the carpometacarpus (18), tendinal canal No. 1 a shallow groove (19), completely feathered nostrils (22), one incubation patch (25), an intermediate post-hatching development pattern (31), and nesting in the open (32). *Alca* and *Pinguinus* are further defined by pointed rectrices (28). This result supports a closer relationship of *Alle* to the auks than to the auklets.

Olson (1985) notes the curious absence of fossils of *Uria* in Atlantic deposits before the Pleistocene, in spite of the presence of abundant fossils of *Alca*-like auks in the Pliocene and perhaps related birds from Middle Miocene deposits. He suggests that this is evidence that *Uria* may not be closely related to *Alca*. To

me the fossil evidence is not irreconcilable with the phylogenetic tree presented here. The fossil evidence is consistent with a Pacific origin and early radiation of the Alcidae (Olson 1985). Conceivably, an *Alca*-like ancestor entered the Atlantic much earlier than *Uria*, but only after the lineages leading to the two genera had split.

The phylogenetic tree (Fig. 16) derived from the data of Hudson et al. (1969) supports the one derived from my data. The first split in the alcid tree gives rise to a branch leading to the puffins that is defined by an ossified swelling in the M. triceps tendons (H7) and a distal division of M. biceps brachii (H9), and one to the other alcids that is defined by the absence of M. ambiens (H12) and no extension of M. gastrocnemius around the anterior surface of the knee (H14). The second branch splits further into one leading to the auklets that is defined by insertion of M. pectoralis abdominalis on the humerus (H1), and one leading to the murrelets, *Cepphus*, and the auks that is defined by the presence of a head of M. subcoracoideus (H2), an undivided M. biceps brachii (H9), the presence of Pars medialis of M. gastrocnemius (H16), and the absence of M. plantaris (H17). The branch leading to *Synthliboramphus*, *Cepphus*, and the auks is defined by an extra head from the tibia for Pars interna of M. gastrocnemius (H15). Finally, the branch leading to *Cepphus* is defined by an unossified swelling in the humero-ulnar pulley (H8), and that leading to the auks is defined by the lack of a dorsal head of M. deltoideus minor (H6).

The tree from the data of Hudson et al. (1969) indicates that the auks, *Cepphus*, and *Synthliboramphus* share a most recent common ancestor not shared with *Brachyramphus*. This result suggests a resolution to the trichotomy found on my tree. The phylogenetic trees (Figs. 15, 16) produced from independent data sets are in full agreement, each showing different details of the phylogeny of the Alcidae.

In this study 76% of the skeletal characters, 62% of the integument characters, and 50% of the natural-history characters were included in the primary clique. In the analysis of the muscle characters (Hudson et al. 1969), 71% of the characters were included in the primary clique. This result supports the idea that structural characters are better indicators of relationships than those of the integument or natural history. However, if characters 29 and 30 had been used in what I believe is their correct form in

the primary analysis, 75% of the integument and 75% of the natural-history characters would have been accepted in the primary clique. Thus, the percentage of characters accepted fails to indicate that a particular type of character is a better estimator of relationship. There are further considerations, however.

I used fewer characters of the integument and natural history than of the skeleton. It was more difficult to identify distinct character states for, and to form logical character-state trees from, integument and natural-history characters than it was for skeletal characters. For example, alcids have at least seven distinct bill types, but I could not arrange them in a credible evolutionary sequence. Coues (1868) used bill form to classify the alcids, but his classification agrees poorly with the phylogeny found here.

Another problem is variation of character states in a species. Although I eliminated from consideration skeletal characters in which more than one state was found in a species, several of the muscle characters of Hudson et al. (1969) were used even though they reported some variation within a species. Furthermore, for natural-history characters the state characteristic of a species was used even though variation is known. *Cepphus* is a particularly frustrating genus in this regard. Guillemots usually lay two-egg clutches, but one-egg clutches are found regularly in all populations studied and may represent up to 9% of the clutches in some populations (Drent 1965). One-egg clutches may come from young birds breeding for the first time or older individuals entering senescence, or they may represent an environmental adaptation. There is no evidence favoring any of these alternatives, however. In addition, *Cepphus* occasionally uses nest sites as diverse as those represented in the entire family (Cramp et al. 1974), and on the Pacific Northwest coast of North America it sometimes digs burrows (Dawson and Bowles 1909, Thoresen and Booth 1958, Drent 1965). Many of the colonial species occasionally nest solitarily.

These observations suggest that integument and natural-history characters are more plastic than those of bones and muscles and may be more difficult to identify and use. The results from the compatibility analyses, however, show that some integument and natural-history characters are better than some skeletal characters. To reject them because of their variability may result in ignoring good indicators of

relationship. The strength of the hypothesis of relationship suggested by a character thus is based not on an a priori belief that some characters are better than others, but rather on how well it agrees with the hypotheses suggested by other characters.

One of the 33 trees found in the parsimony analysis was similar to the results of the compatibility analyses, but there is no objective method to choose it as a better tree than any of the others. The parsimony trees use characters 6 and 27, which were rejected in all of the compatibility analyses in which they were tested. Other than agreeing that the earliest split in the alcid tree gives a branch leading to the puffins and that *Alle* is close to the auks, the results of the parsimony analysis offer little insight into the phylogenetic relationships among the alcids.

The results of this study place the phylogeny of the Alcidae on a firm empirical base. The major problem remaining is to resolve the relationships among the murrelets and *Cepphus*. Expansion of the work of Hudson et al. (1969) to other species would allow muscle characters to be included in a larger compatibility analysis. Unfortunately, there appears to be no specimen of *Pinguinus* to include in such a study (Hahn 1963). New characters must be identified to test the relationships found here. A biochemical study that estimated genetic distances among the species would be particularly interesting.

CLASSIFICATION

Critics of compatibility analysis (e.g. Wiley 1981) have confused the process of deriving a phylogenetic tree and the process of deriving a classification from it. Compatibility analysis is an objective method for deriving phylogenetic trees from sets of character-state trees and not a method of classification.

The derivation of classifications has been highly controversial. Though some have asserted that a classification is an information retrieval system that somehow gives the reader considerable information on the attributes of the taxa listed, the reader needs a firm knowledge of the biology and structure of the taxa if a classification is to impart much information. Furthermore, different phylogenetic trees may have the same classification.
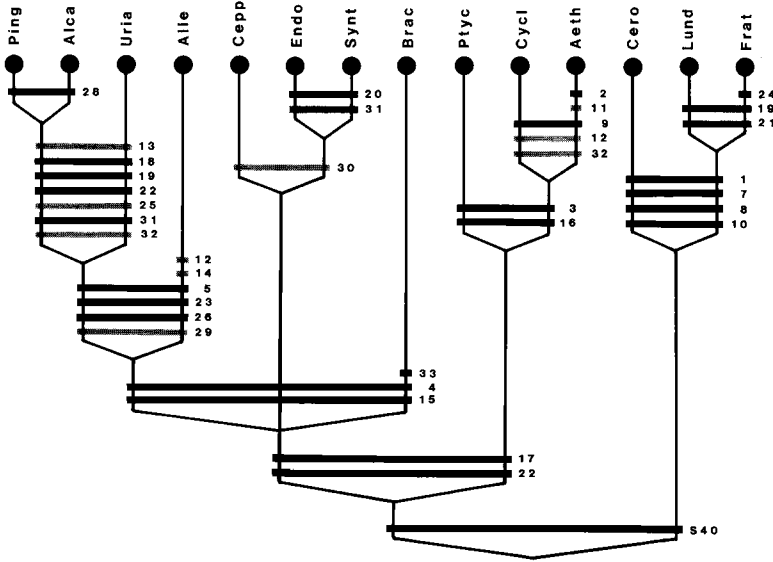
Fig. 18. Cladogram of the Alcidae. Horizontal bars represent the characters defining the various branches, numbers represent characters, solid bars represent primary characters, and halftone bars represent secondary characters. Abbreviations as in Fig. 12.

The derivation of phylogenetic relationships, in spite of the uncertainties and difficulties, is the biologically interesting problem:

For, it goes without saying, the taxonomist's task is to reconstruct the course of biological history. He is seeking not alone a formally ordered, or traditional body of knowledge, but an understanding of the actual facts. If he is honest, he is not constructing some ideal filing system; but he is reconstructing the outline of the tree of life. He is trying to discover phylogenetic relationships . . . . (Dawson 1920).

Figure 18 is a cladogram derived from the phylogenetic tree (Fig. 15) on which are indicated the characters used to define the various groups. A cladogram is a convenient tree (Hendy and Penny 1984) from which to develop a classification. It tends to overstate the evidence, however. For example, *Endomychura* and *Synthliboramphus* appear as distinct in Fig. 18, but there is no evidence in this study to separate them and they appear on the same node in the phylogenetic trees.

The Alcidae may be classified using the subordination scheme of Hennig (1966), in which each sister-group is assigned the same taxonomic rank; however, that system requires far too many categorical ranks to be practical, even

for a family as small as the Alcidae. I prefer to use the phyletic sequencing scheme (Eldredge and Cracraft 1980), in which taxa in a sequence are assigned the same rank. The apparent trichotomy involving the murrelets, *Cepphus, Alle,* and the auks probably represents two unresolved dichotomies, as suggested in the analysis of the data of Hudson et al. (1969). Until their relationships are better resolved I prefer to recognize the three branches as three equivalent taxa of the rank given the puffins and auklets. The cladogram in Fig. 18 thus supports the classification shown in Table 6.

The A.O.U. (1982, 1983) does not indicate what phylogenetic hypothesis forms the basis of its classification [a situation that prevails in spite of Storer's (1945b) complaint that the A.O.U. Check-list Committee combined *Endomychura* and *Brachyramphus* without supporting evidence]. The A.O.U. (1983) rules for the sequence of genera and species indicate that it is not based on the phylogenetic tree of Storer (1960). If the A.O.U. rules are followed, its classification agrees generally with that found here. The main disagreement concerns the details of the arrangement of *Cepphus* and the murrelets. The A.O.U. sequence rules, however, are at variance with those more generally followed

TABLE 6. A classification of the Alcidae.

Family Alcidae
Tribe Fraterculini
Cerorhinca monocerata. Rhinoceros Auklet
Fratercula arctica. Atlantic Puffin
Fratercula corniculata. Horned Puffin
Fratercula cirrhata. Tufted Puffin
Tribe Aethiini
Ptychoramphus aleuticus. Cassin's Auklet
Aethia psittacula. Parakeet Auklet
Aethia pusilla. Least Auklet
Aethia pygmaea. Whiskered Auklet
Aethia cristatella. Crested Auklet
Tribe Brachyramphini
Brachyramphus brevirostris. Kittlitz's Murrelet
Brachyramphus marmoratus. Marbled Murrelet
Tribe Cepphini
Cepphus grylle. Black Guillemot
Cepphus columba. Pigeon Guillemot
Cepphus carbo. Spectacled Guillemot
Synthliboramphus hypoleucus. Xantus' Murrelet
Synthliboramphus craveri. Craveri's Murrelet
Synthliboramphus antiquus. Ancient Murrelet
Synthliboramphus wumizusume. Japanese Murrelet
Tribe Alcini
Alle alle. Dovekie
Uria aalge. Common Murre
Uria lomvia. Thick-billed Murre
Alca torda. Razorbill
Alca impennis. Great Auk

(Eldredge and Cracraft 1980, Wiley 1981); the latter indicate a reversed order of the A.O.U. tribes.

A genus has been defined (Mayr 1969) as a monophyletic group of species separated from other genera by a decided gap. The problem lies in how to estimate the gap. Voous (1975) briefly discusses the rather loose system of genera traditionally used in ornithology. Even if the rules for naming taxa suggested by Eldredge and Cracraft (1980) are followed, there is room for subjective evaluation on the limits of genera. Because I favor genera that emphasize the phylogenetic relationships of species, I would reduce the number of genera recognized in the Alcidae to about six; however, a more conservative approach may be necessary to promote the acceptance of new ideas (A.O.U. 1983). I accept the merging of genera recommended by the A.O.U. (1982) and recommend the following additional combinations: *Cyclorrhynchus* into *Aethia* and *Pinguinus* into *Alca*. Olson (1977) argues that *Pinguinus* and *Alca* should

be kept separate, but because there are fossil intermediates (Olson 1985) and because I found no qualitative differences between them, I disagree.

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