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## *Diving Birds of North America: 1* General Attributes and Evolutionary Relationships

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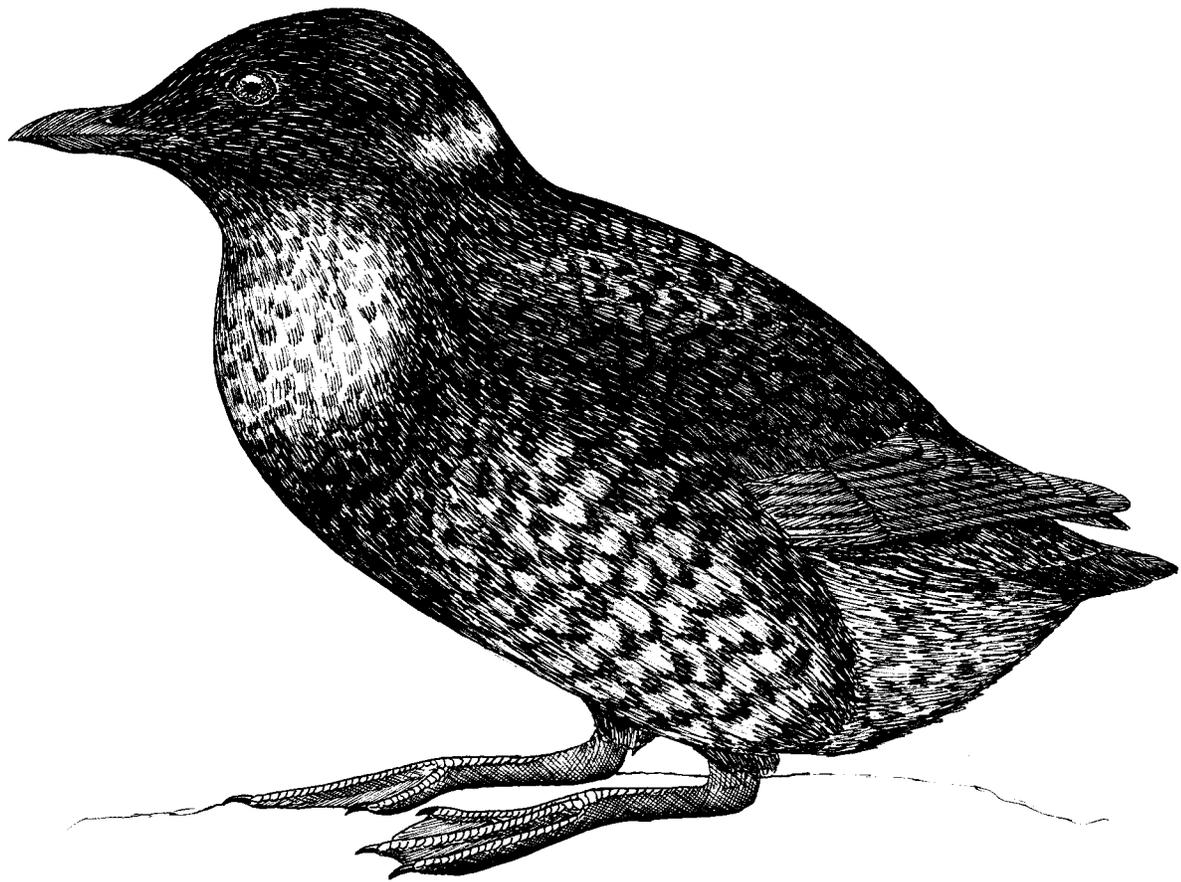
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# I. General Attributes and Evolutionary Relationships

Loons, grebes, and auks comprise a rather large number of species of aquatic diving birds that are fairly unfamiliar to most people, inasmuch as they tend to spend much of their time well away from shore and, when approached on the water, usually dive inconspicuously and reappear a considerable distance away. Thus in many areas grebes, simply called "helldivers," are often confused with coots or even diving ducks. Many people know loons only by their wild, penetrating cries and romantically associate them with northern woods and lakes, while auks are symbolic of arctic coastal cliffs. But ornithologists can find fascinating examples of convergent or parallel evolution in avian locomotory and foraging behaviors among these bird groups. They also offer a host of problems of more general ecological and behavioral interest to biologists. Nevertheless, all these groups have been largely neglected in terms of their comparative biology, and not a single inclusive book has dealt with them since Bent's 1919 monograph on their "life histories."

Before dealing with the many specific attributes of loons, grebes, and auks that are of special interest to ornithologists, let me define each of them in a formal but rather broad manner and point out their overall similarities as well as some of their differences.

Loons are large diving birds having long, straight, and acutely pointed bills, with feathers covering the lores (region between eye and bill) and extending to the linear nostrils. There are 10 functional primaries and 22–23 secondaries, the inner secondaries shorter than the primaries. Molting of the remiges (flight feathers) is simultaneous, and the wings are not used for underwater propulsion. The 16–20 rectrices (tail feathers) are short and stiff. The body feathers are shiny and water-resistant; aftershafts and adult down feathers are present. The legs are set extremely far back on the body, making standing very difficult and walking or takeoff

from land nearly impossible. The tarsus is laterally compressed, with reticulated (networklike) scales, and is unserrated behind. The lobed hallux (hind toe) is long and slightly elevated, the front toes are fully webbed, and all the toes have sharp claws. The wings are long and pointed, and the body is somewhat elongated, with a fairly long neck. The adults have white underparts, and in most species both sexes are spotted or striped with black and white on the back and neck during the breeding season. All species are monogamous, with distinct breeding and wintering plumages that lack sexual dimorphism. The nests are built of vegetational debris and placed at the water's edge. The eggs (usually 2) are spotted and are elliptical to ovate, and the young are unpatterned and nidifugous, with two successive coats of uniformly brownish down. The family has a Holarctic distribution, and all the species are migratory, wintering primarily on salt water and breeding solitarily on freshwater lakes or large tundra ponds. Their foods are primarily fish and aquatic invertebrates, but they also eat small amounts of plant materials. Four extant species are usually recognized, all having breeding ranges that include North America, primarily in boreal and arctic regions (table 1).

Grebes are small to medium-sized diving birds having bills that vary from short and rather blunt tipped to long and acutely pointed, with bare lores and head feathers not extending to the linear or oval nostrils. There are 11 functional primaries and 17–22 secondaries, the inner secondaries longer than the primaries. Molting of the primaries is simultaneous; the wings are not used for underwater propulsion, which is provided by the feet. The rectrices are soft, rudimentary, and hidden. The body feathers are small, water-resistant, and shiny. Aftershafts and adult down feathers are present. The legs are set extremely far back on the body, making walking difficult and takeoff from land impossible. The

Table 1: Taxonomy and Geographic Distributions of the Loons and Grebes of the World

Scientific and Vernacular Names	Distribution	References
<i>Gavia</i>		
<i>stellata</i> (red-throated loon)	Circumpolar Holarctic tundra	This work
<i>arctica</i> (arctic loon) <sup>a</sup>	Circumpolar Holarctic tundra and taiga	This work
[ <i>immer</i> (common loon)	Boreal Nearctic and western Palearctic	This work
<i>adamsii</i> (yellow-billed loon)	Circumpolar Holarctic tundra	This work
<i>Rollandia</i>		
<i>rolland</i> (white-tufted grebe)	South America	Fjeldså 1985
<i>microptera</i> (Titicaca grebe)	South America (Titicaca area)	Fjeldså 1985
<i>Tachybaptus</i>		
[ <i>novaehollandiae</i> (Australian dabchick)	East Indies, Australia	Frith 1976
[ <i>ruficollis</i> (little grebe)	Eurasia, Africa, Madagascar, East Indies	Cramp and Simmons 1977
<i>rufolavatus</i> (Alaotra grebe)	Madagascar (Lake Alaotra)	Voous and Payne 1965
<i>pelzelni</i> (Madagascan grebe)	Madagascar	Voous and Payne 1965
<i>dominicus</i> (least grebe)	North America, South America	This work
<i>Podilymbus</i>		
[ <i>podiceps</i> (pied-billed grebe)	North America, South America	This work
[ <i>gigas</i> (giant pied-billed grebe)	Guatemala (Lake Atitlan)	Bowes 1969
<i>Poliiocephalus</i>		
[ <i>poliocephalus</i> (hoary-headed grebe)	Australia	Fjeldså 1983b
[ <i>rufopectus</i> (New Zealand dabchick)	New Zealand	Storer 1971
<i>Podiceps</i>		
<i>major</i> (great grebe)	South America	Storer 1963
<i>auritus</i> (horned grebe)	North America, Eurasia	This work
<i>grisegena</i> (red-necked grebe)	North America, Eurasia	This work
<i>cristatus</i> (great crested grebe)	Eurasia, Africa, Australia, New Zealand	Cramp and Simmons 1977
[ <i>nigricollis</i> (eared grebe) <sup>b</sup>	North America, South America, Eurasia, Africa	This work
[ <i>occipitalis</i> (silvery grebe)	South America	Fjeldså 1982a
[ <i>taczanowskii</i> (puna grebe)	Peru (Lake Junin)	Fjeldså 1982a
<i>gallardoi</i> (hooded grebe)	Argentina	Storer 1982
<i>Aechmophorus</i>		
<i>occidentalis</i> (western grebe) <sup>c</sup>	North America	This work

NOTE: Taxonomy of Storer 1979; brackets connect probable superspecies groups.

<sup>a</sup>The form *pacifica* has recently been recognized by the AOU as a distinct species (*Auk*, 102:680).

<sup>b</sup>The now apparently extinct South American form (*andinus*) is sometimes considered a distinct species.

<sup>c</sup>The form *clarkii* has recently been recognized by the AOU as a distinct species (*Auk*, 102:680).

tarsus is laterally compressed, with a scutellated scale pattern, and is serrated behind. The hallux is long and elevated; it and the front toes are separately lobed, and the claws are flat and naillike. The wings are somewhat rounded to rather elongated, and most species have a white patch or "speculum" on the secondaries. The body is short, with a variably long neck and silvery white plumage on the underparts. Facial tufts or crests are usually present in both sexes during the breeding season. All species are monogamous and lack apparent sexual dimorphism; most have distinct breeding and wintering plumages. Their nests are built of floating and emergent vegetation anchored in shallow water. The eggs (3 to 9) are unspotted whitish and are elliptical to nearly fusiform. The young are covered with dense down and typically have complex color patterning. As with loons, the young have extended fledging periods and often are carried about on their parents' backs. The family has a nearly cosmopolitan distribution, and the species are mostly migratory, usually wintering on salt water and breeding colonially or solitarily in shallow and reedy freshwater habitats. Their foods include fish, aquatic invertebrates, and some plant materials; for uncertain reasons feathers are also often swallowed. There are at least twenty species, six (or seven) of which breed in part or entirely in North America, mainly in temperate-latitude marshes (table 1).

Auks are small to medium-sized diving birds having bills that are variably pointed and compressed but never acuminate and are sometimes covered with colorful horny sheaths in breeding adults. Feathering densely covers the lores and often extends to the nostrils, which vary from linear to oval. There are 10 functional primaries and 15–19 secondaries; the greater secondary and primary coverts are usually lengthened. Molting of the primaries is usually simultaneous but is gradual in some species; the wings are used for underwater propulsion, and the feet are then used mainly for steering. The 12–18 rectrices are short and normal in shape. The feathers are dense, water-resistant, and shiny; after-shafts and adult down feathers are present. The legs are set fairly far back on the body; walking is done in an erect posture with the weight on the toes (digitigrade). Takeoff from level ground is difficult and infrequent; the birds usually take flight from cliffs or into the wind from water. The tarsus is compressed laterally, is reticulated or scutellated, and is usually shorter than the middle toe. The hallux is absent or vestigial, and the front toes are fully webbed. The wings are relatively short (one recently extinct species and several fossil species were flightless), bowed, and pointed, and the body is robust, with a short neck and large head. Adults have white to dark grayish underparts and usually are black-

ish dorsally. Adults of most species exhibit crests, facial tufts, or other distinctive plumage or horny bill adornments in both sexes during the breeding season. All species are monogamous and monomorphic, often having distinct breeding and wintering plumages. The eggs are laid on rock ledges, in crevices or burrows, or rarely among the branches of trees. The eggs (1 or 2) are often spotted and are pyriform to ovate. The young are down-covered, unpatterned to bicolored, and are nidifugous to seminidicolous. The family is Holarctic in distribution, and the species are entirely marine in winter but usually breed colonially (sometimes solitarily) along coastlines. Their foods mainly consist of fish, plankton, and other marine fauna. There are twenty-two extant species, twenty of which breed in North America, particularly along the northern Pacific coast (table 2).

The relative evolutionary relationships among these three groups of diving birds have been a source of continuing controversy, which has not slackened but indeed has intensified as more recent information has become available. There are, to be sure, many similarities that unite each of the three groups with one or both of the other two groups (table 3), but there are also substantial numbers of unique or nearly unique characteristics exhibited by each of the three (table 4). During the late 1800s and until the early decades of the current century, all three groups were usually placed in a single order "Pygopodes." This group was formed in 1880 by W. Sclater to accommodate the earlier family "Colymbidae" (a family erected by T. Huxley that included the loons and grebes) and also the Alcidae. Coues (1882) characterized the Pygopodes in some detail, assigning each of the three groups considered in this book to separate suborders but excluding the penguins, which some had considered part of the same general assemblage. In 1919 Ridgway separated the auks from the loons and grebes, assigning them to a suborder (Alcae) of the Charadriiformes. He said that the anatomical evidence indicated a close relationship of the auks with the gulls rather than with the loons, though he admitted that the loons and auks evidently are also fairly closely related.

Later studies by authors such as Shufeldt (1904) still supported the general position that loons and grebes are closely related; indeed, Shufeldt regarded the two groups as part of a single family (Podicipidae) and the sole component of his "Pygopodes," an order he considered most probably related to the gull-like birds. However, Stolpe (1935) undertook an anatomical comparison of the hind-limb structure of loons, grebes, and the fossil diving bird *Hesperornis* and concluded that inasmuch as loons and grebes differ by so many of their hind-limb structures and their leg movements during swimming, they are not closely related to one another.

Table 2: Taxonomy and Geographic Distributions of the Auks of the World

Scientific and Vernacular Names	Distribution	References
Tribe Allini		
<i>Alle</i>		
<i>alle</i> (dovekie)	North Atlantic and adjacent areas	Glutz and Bauer 1982
Tribe Alcini		
<i>Uria</i>		
[ <i>aalge</i> (common murre)]	Circumpolar Holarctic	Glutz and Bauer 1982
[ <i>lomvia</i> (thick-billed murre)]	Circumpolar Holarctic	Glutz and Bauer 1982
<i>Alca</i>		
<i>torda</i> (razorbill)	North Atlantic and adjacent areas	Glutz and Bauer 1982
<i>Pinguinus</i>		
<i>impennis</i> (great auk)	Extinct since 1844	Bengtson 1984
Tribe Cepphini		
<i>Cepphus</i>		
[ <i>grylle</i> (black guillemot)]	North Atlantic and adjacent areas	Glutz and Bauer 1982
[ <i>columba</i> (pigeon guillemot)]	North Pacific and Bering Sea	This work
[ <i>carbo</i> (spectacled guillemot)]	Coasts of northeastern Asia	Thoreson (in press)
Tribe Brachyramphini		
<i>Brachyramphus</i>		
<i>marmoratum</i> (marbled murrelet)	Coastlines of North Pacific	This work
<i>brevirostris</i> (Kittlitz murrelet)	Coastlines of North Pacific	This work
Tribe Synthliboramphini		
<i>Synthliboramphus</i>		
[ <i>hypoleucus</i> (Xantus murrelet)]	Pacific Coasts of California and Baja California	This work
[ <i>craveri</i> (Craveri murrelet)]	Gulf of California	This work
[ <i>antiquus</i> (ancient murrelet)]	North Pacific and Bering Sea	This work
[ <i>wumizusume</i> (Japanese murrelet)]	Coasts of Japan	Thoreson (in press)
Tribe Aethini		
<i>Ptycoramphus</i>		
<i>aleuticus</i> (Cassin auklet)	Aleutian Islands to Baja California	This work
<i>Cyclorhynchus</i>		
<i>psittacula</i> (parakeet auklet)	North Pacific and Bering Sea	This work
<i>Aethia</i>		
<i>pusilla</i> (least auklet)	North Pacific and Bering Sea	This work
<i>pygmaea</i> (whiskered auklet)	Commanders, Kuriles, Aleutians	This work
<i>crstatella</i> (crested auklet)	North Pacific and Bering Sea	This work
Tribe Fraterculini		
<i>Cerorhinca</i>		
<i>monocerata</i> (rhinoceros auklet)	North Pacific	This work
<i>Fratercula</i>		
<i>cirrhata</i> (tufted puffin)	North Pacific and Bering Sea	This work
[ <i>arctica</i> (Atlantic puffin)]	North Atlantic and adjacent areas	Glutz and Bauer 1982
[ <i>corniculata</i> (horned puffin)]	North Pacific and Bering Sea	This work

NOTE: Taxonomy of AOU *Check-list* 1983; brackets connect superspecies.

Table 3: Characteristics That Variably Serve to Associate Loons, Grebes, and Auks

Traits That Associate All Three Groups	Traits That Associate Two of the Three Groups
<ol style="list-style-type: none"> <li>1. Consume aquatic animal life</li> <li>2. Prey captured by extended dives</li> <li>3. Bill sharply pointed in most species; skull with schizognathous palate</li> <li>4. Legs variably placed toward rear, affecting standing and walking efficiency, pelvis variably narrowed</li> <li>5. Predominantly temperate to arctic in North American breeding distribution</li> <li>6. Mostly migratory; primarily marine in winter</li> <li>7. Sexes monogamous and monomorphic</li> <li>8. Distinctive nuptial and winter plumages in most species</li> </ol>	<p>A. <i>Traits shared by loons and grebes</i></p> <ol style="list-style-type: none"> <li>1. Hallux present and paddlelike</li> <li>2. Pelvis strongly narrowed; underwater propulsion by feet alone</li> <li>3. Nest situated very close to water</li> <li>4. Young tended for extended periods and carried on backs of both parents</li> </ol> <p>B. <i>Traits shared by loons and auks</i></p> <ol style="list-style-type: none"> <li>1. Rectrices normally developed</li> <li>2. Toes palmate and sharply clawed</li> <li>3. Loes fully featured</li> </ol> <p>C. <i>Traits shared by grebes and auks</i></p> <ol style="list-style-type: none"> <li>1. Nuptial head tufts present in many species</li> <li>2. Variably colonial nesting frequent</li> </ol>

Table 4: Characteristics That Variably Serve to Separate Loons, Grebes, and Auks

Traits of Loons	Traits of Grebes	Traits of Auks
1. Foot-propelled divers	1. Foot-propelled divers	1. Wing-propelled divers
2. Carpometacarpus elongated and narrow	2. Caropometacarpus short and narrow	2. Carpometacarpus long and robust
3. Long cnemial process on tibiotarsus; no separate patella	3. Long cnemial process on tibiotarsus; separate patella	3. Tibiotarsus lacking cnemial process
4. Large foot area relative to body weight	4. Large foot area relative to body weight	4. Small foot area relative to body weight
5. Synsacrum longer than sternum; very narrow at acetabulum	5. Synsacrum as long as sternum; narrow at acetabulum	5. Synsacrum shorter than sternum; broad at acetabulum
6. Two generations of natal down	6. One generation of natal down	6. One generation of natal down
7. 16–20 normally developed rectrices	7. Rectrices vestigial	7. 12–18 normally developed rectrices
8. 10 functional primaries; 22–23 secondaries	8. 11 functional primaries; 15–21 secondaries	8. 10 functional primaries; 15–19 secondaries
9. Large supraorbital glands	9. Small supraorbital glands	9. Large supraorbital glands
10. Skeleton nonpneumatic	10. Skeleton virtually nonpneumatic	10. Skeleton slightly pneumatic
11. 14–15 cervical vertebrae	11. 17–21 cervical vertebrae	11. 15 cervical vertebrae

This conclusion has been rather widely adopted and has been fairly recently supported by Storer (1960), who went so far as to question the possibility that the loons, grebes, and hesperornithiform birds even had a common swimming ancestor. Storer's study and other historically important studies on the loon-grebe question have been admirably summarized by Sibley and Ahlquist (1972).

These authors furthermore reported on their own egg-white protein studies, indicating that the starch-gel electrophoretic patterns of loons and grebes do not provide unequivocal evidence of their evolutionary relationships. However, more recent and unpublished work on DNA hybridization conducted in their laboratory supports the position that the loons share a common if distant ancestry with the penguins and tube-nosed swimmers, while the grebes appear to be extremely isolated from all other extant bird groups. As expected, the alcids exhibit close DNA affinities with gulls and terns (C. Sibley, pers. comm.). Korzun (1981) has also recently concluded from anatomical evidence that any evolutionary connection between the loons and grebes is probably a very ancient one.

Recent but still unpublished osteological studies by Boertmann (1980), whose conclusions have been summarized by Glutz and Bauer (1982), point to an even closer relation between loons and shorebirds than has been judged by Sibley and Ahlquist or by earlier authors. Boertmann has recommended merging the loons into the order Charadriiformes and reducing them to family status within the superfamily Laroidea. Within this superfamily he recognizes five distinct families: Glareolidae, Dromadae, Laridae, Alcidae, and Gaviidae.

Thus several recent morphological studies strongly support the existence of an evolutionary affinity between the loons and the gull-like birds and a separate but essentially unknown evolutionary origin of the grebes. However, Cracraft (1982) has recently generated a new cycle of controversy by taking the position not only that are loons and grebes monophyletic but that this evolutionary assemblage also includes the flightless Cretaceous divers *Hesperornis* and *Baptornis*. He has proposed that loons and grebes be regarded only as families in the order Gaviiformes and that this order and the extinct Hesperornithiformes be encompassed within a superorder Gaviomorphae. He did not deal with the anatomical evidence suggesting a charadriiform relationship of the loons but rather offered the suggestion that the Gaviomorphae are instead most closely related to the Sphenisciformes (penguins) and less closely related to the Procellariiformes (tube-nosed swimmers) and Pelecaniformes (totipalmate swimmers).

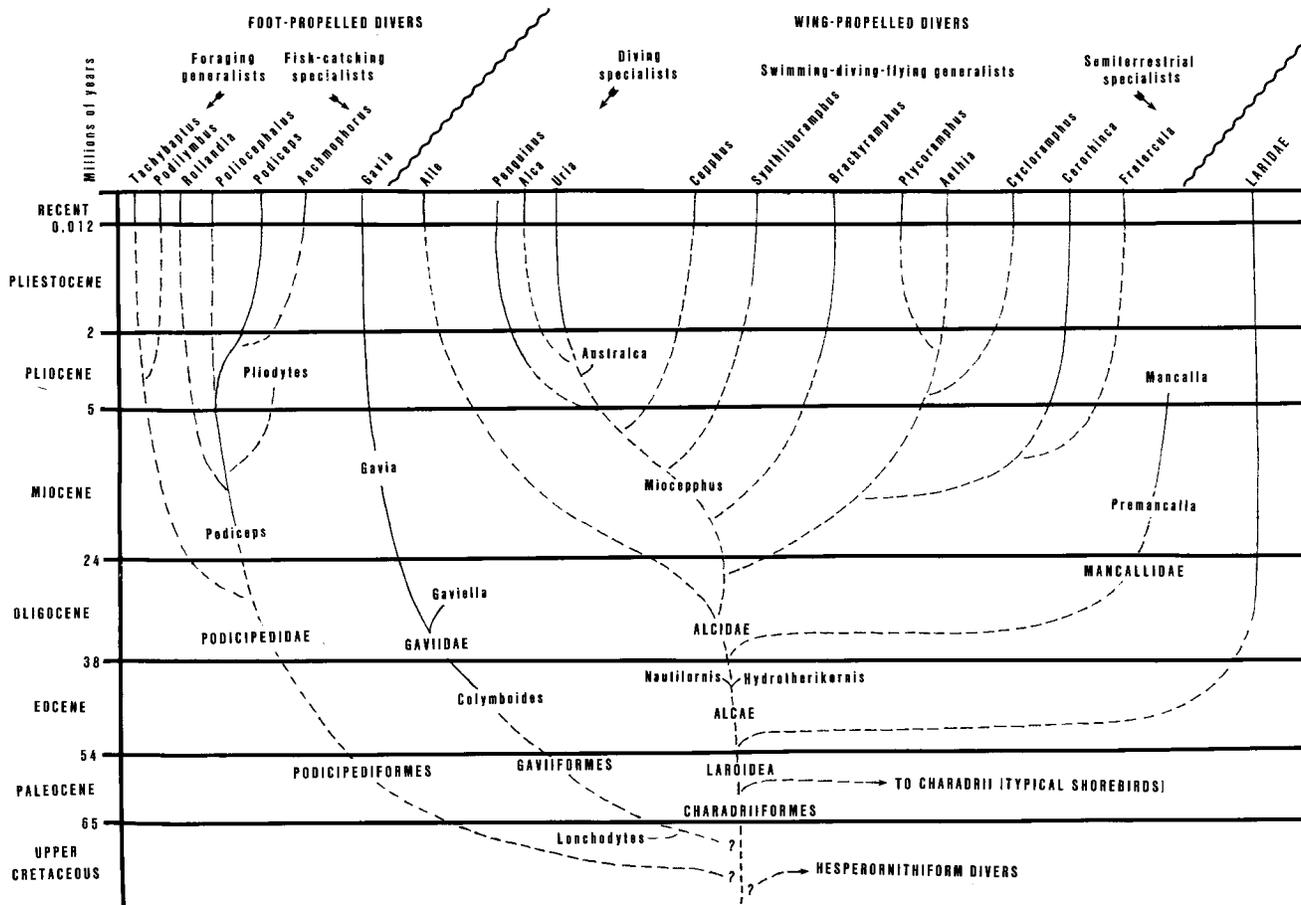
Unfortunately the fossil record does little to help re-

solve this general controversy. The fossil record of grebes is especially weak, with the genus *Podiceps* extending back only to the Lower Miocene, while in Lower Pliocene strata the related *Pliodytes* also has been found (Brodkorb 1963).

The fossil record of loons is appreciably better, with *Gavia* remains extending back to the Miocene and with the related *Gaviella* of Oligocene age. Even older is the Eocene *Colymbiodes*, which some have believed represents an intermediate link between the loons and grebes (Howard 1950). However, Storer (1956) judged *Colymbiodes* to be an ancestral type of loon, with no affinities to grebes but instead with probable charadriiform affinities. Some even older loonlike fossils of Upper Cretaceous age, now assigned to the family Lonchodytidae (Brodkorb 1963), have also fairly recently been found, suggesting that separation of the loons from the typical charadriiform assemblage must have occurred in pre-Cenozoic times.

The fossil record of the alcidlike group is also moderately extensive (Brodkorb 1967) and provides at least some clues to the early radiation of the auks. The earliest known alcid fossils are the Eocene *Nautilornis* and *Hydrothericornis*, known from Utah and Oregon respectively. Both had well-developed wings and were thus probably excellent fliers. However, reduction of wing surface for more efficient diving probably began fairly early in auk evolution and led to an early separation of a group of flightless "Lucas auks" that are generally recognized as the Mancallidae but sometimes are considered a subfamily of the Alcidae (Brodkorb 1967). This fossil lineage extends forward only to the Pliocene, when the group became extinct, possibly through competition with more typical alcid diving specialists. These perhaps included the ancestors of *Pinguinus*, which had already become differentiated by this time.

An attempt has been made to present some of this information in graphic form (fig. 1), as a hypothetical evolutionary dendrogram that represents my interpretation of the information available on the probable relation of the loons and grebes to auks, as well as the more definite affinities of the genera of living auks. Much of the basis for the evolutionary organization of the auks is dependent on information to be discussed in the species accounts, and at this point it is only important to note that the surviving auks seem to consist of three fairly recognizable morphological types. First, there are the relatively generalized forms that have not greatly modified their wings for diving or their legs for walking. These include the auklets, murrelets, and guillemots and the similar but rather distantly related dovekie. Second, there are the forms that have become better adapted for walking at the expense of diving profi-



1. Hypothetical evolutionary dendrogram of the loons, grebes, and auks, including known fossil representatives of these groups.

ciency; these consist of the puffins and the rhinoceros auklet. Last, there are the auks that have modified their body and wing configuration to facilitate diving, at the expense of increased wing loading and decreased ability for walking. These include the murre, the razorbill, and especially the great auk, which became completely flightless and eventually extinct.

On the basis of anatomical evidence, Stettenheim (1959) concluded that the alcids evolved from an undifferentiated shorebird ancestral stock that was as distantly related to the gulls and terns as to the more typical shorebirds. He judged that these may have been wading rather than plunge-diving birds, which initially used diving to escape from danger and only later began to forage by this means. Kozlova (1961), however, judged that gulls and alcids shared a common ancestry and that

the earliest alcids specialized on marine fish and only later began to eat various marine invertebrates. She stated that, at least on the basis of skull conformation, the guillemots, murrelets, murre, razorbill, and dovekie are the least modified (most gull-like), whereas in the auklets and puffins the skull has become greatly modified, apparently in part at least because of its role (in typical puffins) in digging nesting sites. Such a role for the bill might help explain the original source of selection for increased bill size, which might later have been supplemented by the influence of sexual selection. Kozlova outlined a highly plausible evolutionary history of alcids and their geographic dispersion during Cenozoic times.

Relationships within the grebe family are less clear-cut, but recent studies by Fjelds  (1982a, 1983a) support

the general view that the genus *Rollandia* approaches the ancestral stem of grebe evolution, from which the dabchicks (*Polioccephalus*) and pied-billed grebes (*Podilymbus*) have diverged in one direction, while the remaining genera have diverged in another direction, toward the relatively specialized *Podiceps* and *Aechmophorus* types that largely constitute the North American grebe fauna. Fjeldså (1982a) has published a provisional phylogeny of all the grebe species that has an independent origin from figure 1 and differs from it in minor respects.