THE SYSTEMATIC POSITION OF THE MURRELET GENUS ENDOMYCHURA

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While one must admit that our most up-to-date concepts of the higher taxonomic categories make a reduction in the number of bird genera desirable, it is to be regretted that the current trend toward "lumping" should be accelerated to the point where taxonomic changes are made without at least a careful examination of skeletons of the forms involved. This practice not only might lead one to suspect systematists of attempting to be fashionable, but it also causes needless complications in the literature. The American Ornithologists' Union Check-list Committee's treatment of the murrelet genus *Endomychura* might be cited as an unfortunate example of this trend.

The Committee has voted (1944:449) to include *Endomychura* in the genus *Brachyramphus* and cites Peters (1934) as its authority for so doing. Peters in turn gives no reference or reason for his decision and hence one must look to the birds for an explanation for this change.

A casual examination of skins of the three murrelet genera reveals three genera of two closely related species each. All the forms are about the same size, and all have closely similar winter plumages. A further look reveals that *Synthliboramphus* has a deeper bill, which is light-colored in life, and elongated head feathers and a black throat in the breeding plumage. *Brachyramphus* on the other hand has a distinct, barred summer plumage and shorter tarsometatarsi. *Endomychura* resembles the former genus in its long tarsometatarsus and lack of barred summer plumage, and the latter genus in its lack of elongated head plumes and in the shape of its bill. As bill form is in many cases a good indication of relationship, it is understandable that *Endomychura* should be thrown toward *Brachyramphus*, even in the light of plumage and tarsal characters which hint strongly otherwise.

With this background, let us proceed to a deeper study of the group. In any taxonomic treatment of the Alcidae, two considerations should be kept in mind. First, the group is an old one, both in a geological and in an evolutionary sense as is shown by the fossil record and by the relatively large number of small genera and monotypic species; and second, the genera and species differ from each other in what at first sight appear to be a bewilderingly complex assortment of characters. These can, however, be broken down into three categories of varying importance in showing phylogenetic relationships. Some characters, such as the presence of a white patch on the side of the head, turn up more or less at random throughout the family. These seem best explained by the presence of an inherent germinal predisposition to mutations of a similar type, and should be considered as an indication of the relationship of all members of the family as a whole. Other characters, such as the deepening of the bill and the presence of elongated feathers on the head, appear as parallel trends which run through different groups of species within the family and which should be taken as indications of the relationship of the groups of species rather than that of immediate relationships of the species at equivalent evolutionary stages in different groups. The third type of character is that which has been developed in and is to be found exclusively in a single phyletic group. These characters are generally the oldest from a phylogenetic standpoint and may be illustrated by the egg shape in the auks and murres. There is some overlapping in these categories, but on the whole, they are sufficiently distinct to provide a basis for classification and evaluation. Certainly a lack of understanding of the parallel trends has been responsible for misinterpretations of the interrelationships within the family under consideration. These trends appear, by and large, to be nonadaptive and to be reflections of the inherent genetic constitution of the family as a whole.

Avian taxonomists have placed too much importance on the shape of the bill which, admittedly, is an important clue to the relationships of many birds, but which occasionally runs "hog wild" as in the Geospizidae and Drepanididae, and is even subject to considerable sexual dimorphism as in *Heteralocha acutirostris*. The principal variations in bill form in the Alcidae differ from those of the Geospizidae and Drepanididae in that they represent a series of parallel trends rather than a sort of adaptive radiation. These parallel trends appear analogous to those mentioned by Mayr (1942:279-280) as occurring in the Old World flycatchers (Muscicapidae), but involve deepening com-

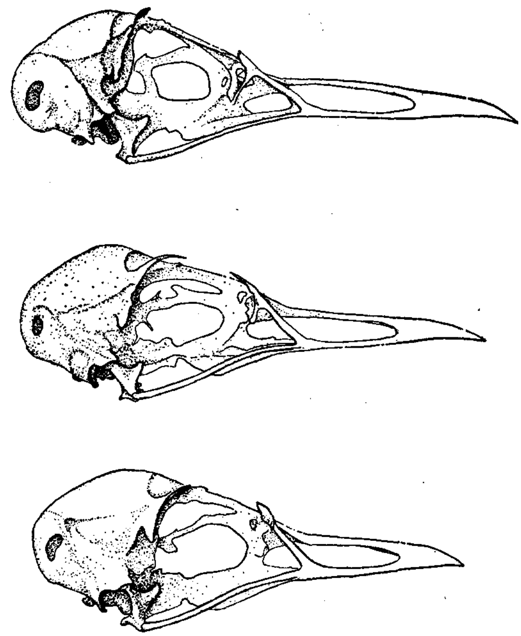

Fig. 27. Lateral aspect of the skulls of murrelets. Top, *Brachyramphus marmoratus* (M. V. Z. no. 70637); center, *Endomychura hypoleuca* (no. 46844); bottom, *Synthliboramphus antiquus* (no. 7658); all natural size.

bined with lateral compression instead of flattening. The least differentiated bills in the family are to be found in the genera *Brachyramphus*, *Endomychura*, and *Uria* although there is a tendency toward lengthening visible in *Uria aalge* and *Endomychura craveri*, a development which reaches an extreme in *Cepphus carbo*. Trends toward deepening and lateral compression are to be found in *Synthliboramphus* and the auklets, auks, and puffins.

When viewed in this light, the similarity of the bills of *Endomychura* and *Brachyramphus* loses its significance, for it is clear that the retention of an obviously "primitive" character by two groups of birds is not necessarily an indication of close relationship. In fact the two genera under consideration are rather widely divergent in other skeletal as well as plumage characters.

Aside from the differences in bill form, the major differences in the skulls of the three murrelet genera are to be found in the temporal region. Immediately posterior to the orbit there is a shallow depression which runs posteriorly and ventrally from the depression in which the nasal glands lie. In *Brachyramphus* this depression is separated dorsally from the bed of the nasal gland and posteriorly from the temporal fossa by sharp ridges. In *Synthliboramphus* the depression is also set off by ridges, but the dorsal ridge does not approach the bed of the nasal gland. In *Endomychura* it is confluent with the temporal fossa and is separated from the bed of the nasal gland by a low, broad ridge. Furthermore, the temporal fossae of *Synthliboramphus* and *Endomychura* are considerably more extensive than that of *Brachyramphus*, the ridges forming the upper and posterior borders lying nearer the top and rear of the cranium, respectively, in the two former genera (see fig. 27).

The significance of the characters of the pelvis and hind limb of the Alcidae has been largely overlooked. In these structures there are two possible classes of adaptational development. The first of these is for swimming and diving, but as the wings are, as far as we know, the sole means of submarine propulsion, very great diving modifications in the hind limb are not to be expected. And outside of a few characters in *Synthliboramphus, Endomychura, Alca,* and *Pinguinus,* there is little to suggest this type of adaptation.

The second class of modifications includes those connected with breeding habits. Here an interesting group of radiating adaptations has developed, beginning with the generalized guillemots (*Cepphus*) which show a variety of nesting habits and branching to the auks and murres which nest on open ledges, to the dovekie and most auklets which nest in crevices, and to the puffins and *Synthliboramphus* which use burrows. I have elsewhere (Storer, in press) divided the family into seven natural groups largely on the basis of pelvic and hind limb structure and characters connected with breeding habits. The two categories are in most cases so well correlated that I am strongly convinced that characters in the hind limb are important in showing relationships even where their relation to breeding habits has yet to be fully determined.

As the afore-mentioned paper describes the differences in pelvic and hind limb structure in some detail, it will be unnecessary to give here more than a brief discussion of those characters of the murrelets. The accompanying photograph (fig. 28) clearly shows the broad, flat preacetabular ilium, the relatively short postacetabular ilium, ischium, and pubis, and the generally broad, weakly fused pelvis of *Brachyramphus*. The relatively long, narrow pelves of *Synthliboramphus* and *Endomychura* plus the long, slender tarsometatarsus with its "streamlined" articulations for the toes are strikingly different from the same bones of *Brachyramphus* and are suggestive of diving and swimming modifications such as are found developed to a much higher degree in *Gavia, Colymbus,* and the extinct *Hesperornis*. In the accompanying drawing (fig. 29) showing the tarsometatarsi of *Brachyramphus, Endomychura* and *Synthliboramphus,* the similarity of the last two genera and the difference between them and the marbled murrelet is obvious.

The short tarsometatarsus of *Brachyramphus* as measured on the skin has long been used as a character for separating this genus from the other murrelets. Shufeldt (1889), in his description of the murrelet skeletons, has indicated the principal differences between the tarsometatarsi of *Brachyramphus* and *Synthliboramphus* and has given a table of measurements of the leg bones of these genera. Unfortunately, the measurements for *Brachyramphus* are listed after *Synthliboramphus,* and vice versa, and no conclusions regarding the relationship of these genera with each other or the other alcids were drawn from the data.

In connection with the tarsometatarsal length, it should be noted that in the same list of taxonomic changes in which *Endomychura* and *Brachyramphus* were combined, the American Ornithologists' Union Check-list Committee accepted Murphy's separa-

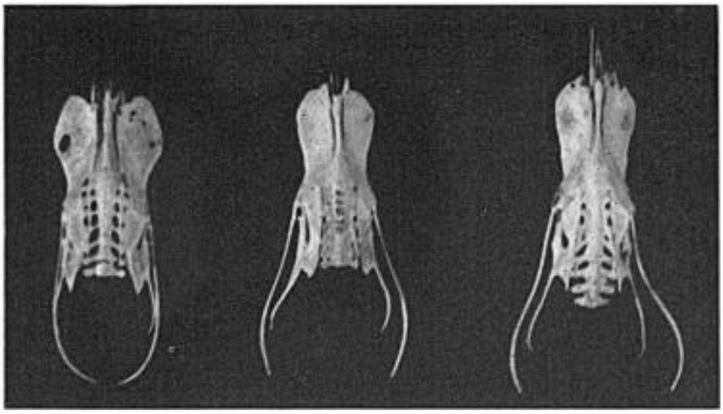

Fig. 28. Dorsal aspect of the pelves of murrelets. Left, *Brachyramphus marmoratus* (M. V. Z. no. 27096); center, *Endomychura hypoleuca* (no. 46844); *Synthliboramphus antiquus* (no. 19045).

tion of *Loomelania* from *Oceanodroma*. Murphy (1936:744-745) bases his conclusions primarily on the ratio of the length of the tarsometatarsus to that of the femur. In the accompanying table, I have shown this proportion for four species of murrelets. The difference between *Brachyramphus* and *Endomychura* is self-evident as is the similarity between the latter and *Synthliboramphus*. Furthermore, *Loomelania* is intermediate between *Oceanodroma* and *Occanites*, whereas *Brachyramphus* and *Endomychura* represent the extremes of the whole family Alcidae (a statement based on measurements of skeletons of representatives of all fourteen alcid genera). The Committee's precedent in the case of *Loomelania* should not be disregarded in the case of *Endomychura* in which there exist important differences in pelvic, plumage, and other characters which have yet to be demonstrated in the case of *Loomelania*.

Species	Number	Range	Average
Brachyramphus marmoratus	7	68.9 to 73.8	71
Endomychura hypoleuca	2	109.5 to 109.9	110
Endomychura craveri	4	104.8 to 106.5	106
Synthliboramphus antiquus	14	102.0 to 105.0	103

As might be expected from the similarity of the general habits of the birds, no significant differences in the three genera were found in the proportions of the wing segments expressed as per cent of the humerus. However, the total length of the wing (obtained by adding the over-all length of the humerus, radius, carpometacarpus, and the two phalanges of digit two) expressed as per cent of the body length (the distance between the anterior articular surface of the acetabulum and the anterior articular surface of the first thoracic vertebra) appears to be significant. In five skeletons of *Brachyramphus marmoratus*, this ratio varies from 183 to 192 with an average of 187, whereas seven specimens of *Synthliboramphus antiquus* vary from 202 to 222 with an average of 212. The two available specimens of *Endomychura craveri* and the one of *E. hypoleuca* fall in or near the range of *Synthliboramphus*, the ratios being 220, 223, and 204, respectively.

The difference in wing length is further shown in the ratio of the length of the wing measured on the skin, using the distance between the carpal joint and the tip of the longest primary. For this purpose ten specimens each of *S. antiquus*, *E. craveri*, and *B. marmoratus* were selected at random from the collection of the Museum of Vertebrate Zoology, the wing lengths measured and averaged, and this figure divided by the average body length obtained by averaging the body lengths used in the preceding ratios. The percentages thus found are *Synthliboramphus* 200, *Endomychura* 197, and *Brachyramphus* 171.

Reduction of the wings has occurred frequently and independently in diving birds which use their wings for underwater "flying." The value of this adaptation is due to the density of the liquid medium in which the optimum wing size as illustrated by the penguins and the great auk is considerably smaller than that required to engage in aerial

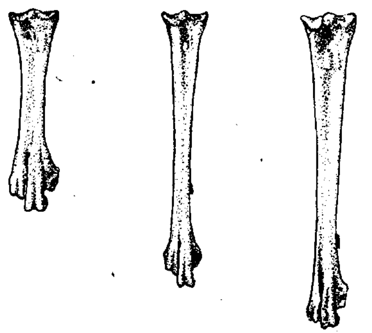

Fig. 29. Anterior aspect of tarsometatarsi of murrelets. Left, *Brachyramphus marmoratus* (M. V. Z. no. 70637); center, *Endomychura craveri* (no. 54725); right, *Synthliboramphus antiquus* (no. 19045); all approximately × 1½.

flight. As the wings of all alcids are small in proportion to the body weight, and as there has been great reduction in the size of the wing in the great auk and presumably in the fossil *Mancalla*, it is natural to expect some reduction in the wings of other alcids. Such changes are another example of parallel trends, and as such should not in themselves be considered important in determining relationships of genera within the family. However, I am giving the above figures because they add weight to the other evidence presented.

In the alcids, the general plumage pattern is fairly constant within each group, although parallel trends toward elongated head plumes occur and white patches on the side of the head appear at random. Hence the occurrence in *Brachyramphus* of a white scapular patch and of a type of summer plumage unique among alcids in its type of feather pattern and equalled only by one genus (*Cepphus*) in its extent, is indicative of the distinctness of this genus and suggests unusual breeding habits. The lack of seasonal differences in plumage in *Endomychura* is also unique in the family. *Synthliboramphus* is intermediate, having a partial prenuptial molt. *Endomychura* also differs from the other two genera in the number of rectrices (12 as opposed to 14).

The eggs of murrelets of the genus *Endomychura* are variable in color, markings, and shape. Those of the ancient murrelet (*Synthliboramphus*) are larger (as is to be expected in a larger bird) and are rather uniform in shape, color, and markings. They can, however, be matched in these three respects by some eggs of *Endomychura*. Two eggs appear to be the normal number for a set in both genera. This, and the color and markings should be considered primitive characters if, as it is usually assumed, the alcids are derived from laro-limicoline ancestors. The scant available data on the eggs of *Brachyramphus marmoratus* and *B. brevirostris* indicate that a single egg is the rule in this genus. The shape of the egg is similar to that of *Synthliboramphus* (and hence some eggs of *Endomychura*) whereas the ground color and markings of eggs of the genus as illustrated in Bent (1919, pls. 48 and 49) differ from those of *Endomychura* and *Synthliboramphus*. However, until a series of eggs of *B. marmoratus* and *B. brevirostris* can be secured and the extent of the variation in the eggs of these forms can be determined, the use of oölogical characters in speculations on the relationships of these forms is ill-advised.

From the evidence herewith presented, it will be seen that the murrelets of the genus *Endomychura* are most closely related to the ancient and Japanese murrelets (*Synthliboramphus*). The reason for their having been included in the genus *Brachyramphus* appears to lie in their both having a small, primitive type of bill. *Endomychura* appears to be the most primitive genus of the Alcidae. This is evidenced by the shape of the bill, the lack of seasonal differences in plumage, nesting habits, number and color of eggs, and small size. *Synthliboramphus* is an offshoot of this genus, differing in having elongated head plumes and a black throat in the breeding plumage, a deepened and partly colored bill, in being slightly larger, and in digging a nesting burrow. *Brachyramphus*, if derived from the same genus (which I doubt) has diverged much more widely as is evidenced by the barred summer plumage, short tarsus, and pelvic and cranial differences; it should be placed in a group by itself.

The relationship between *Endomychura* and *Synthliboramphus* parallels that between *Ptychoramphus* and *Aethia* or *Cyclorrhynchus*. In each case the more primitive genus (*Endomychura* or *Ptychoramphus*) agrees with the more advanced (*Synthliboramphus* or *Aethia* or *Cyclorrhynchus*) in skeletal structure and eggs, and differs in having a less deepened bill, in lacking elongated plumes on the head, and in having a more southern distribution. In connection with the last, it will be remembered that Matthew (1915) postulated that the more highly evolved forms of a group develop near the center of dispersal of the group and force the more primitive forms to occupy the peripheral parts of the range of the group. As the center of dispersal of the Alcidae certainly lies on the northern fringe of the Pacific Ocean, the fact that the most primitive genus of both the murrelets and the auklets has in each case the most southern distribution is further evidence to support Matthew's hypothesis.

As the genus is a purely artificial category adopted by the systematist for his own convenience, the inconvenience of unnecessary or erroneous changes should be seriously weighed in making any proposed alteration in generic names. This I fear has been all too often neglected by over-eager taxonomists. Combination of the genera *Endomychura* and *Synthliboramphus* is a borderline case which "splitters" could never attempt to propose and which "lumpers" would jump to make. The gap between these two genera is so distinct that each name suggests a definite series of characters applicable to the two species of each genus. Hence it would be no inconvenience to keep these genera separate at least until a definitive study can be made. Such a study should at least include dissections of the pelvic region and leg and of the musculature of the temporal region, a careful analysis of the plumage differences, and a study of the courtship pattern and breeding habits of the forms involved. This work should also be done with an eye to solving the further problems of the relationships of *Ptychoramphus, Cyclorrhynchus* and *Aethia, Fratercula* and *Lunda,* and of *Pinguinus* and *Alca.*

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