

## THE FOSSIL LOON, COLYMBOIDES MINUTUS

By ROBERT W. STORER

In recent years, most taxonomic work on birds has been at the level of the species and subspecies, while the interrelationships of the major groups of birds have received relatively little attention. The classifications set up before Darwin's time were based purely on similarities in structure; but with the acceptance of the concept of organic evolution, the corollary of convergence slowly became understood. This idea that two or more unrelated groups of organisms could, in the course of evolution, become superficially similar in both habits and structure is, of course, very important. Thus in order to understand the true relationship between two groups, common characters which are the result of convergent evolution must be distinguished from more conservative features which are indicators of actual phylogenetic relationships.

The diving birds provide excellent examples of convergence. Until the appearance of the fourth edition of the Check-List of North American Birds in 1931, the loons, grebes, and auks were all grouped in one order by most American ornithologists. Members of the auk tribe, which, unlike the loons and grebes, regularly use their wings for propulsion under water, are now believed to be related to the gulls. The loons and grebes have been put in separate orders, which, however, are kept side by side in the classifications of most workers.

The reasons for separating loons from grebes are many and fundamental. Among them are the differences in the texture of the plumage, the form of the tail feathers, the location of the nest, the number of eggs, and the webbed versus lobed toes. Stolpe (1935) made detailed anatomical studies and listed a number of perhaps more deep-seated characters. For instance, when a swimming loon brings its foot forward prior to making a stroke, the toes are folded together and brought straight forward, whereas a grebe turns the whole foot through an arc of 90° and brings it forward sideways. In grebes, the extension of the tibia over the knee joint is made up of both the tibia itself and the patella. In loons, the patella is minute and does not form part of this cnemial crest.

Considering that the wings and pectoral girdle are little, if at all, modified for the birds' aquatic habits, the shape of the sternum, coracoid, and, in fact, all the wing elements of loons and grebes are strikingly different. This evidence that loons and grebes were not derived from a common swimming ancestor, however, was long in being discovered, and its significance was obscured for many years by the description of the fossil known as *Colymboides minutus*. This bird was found in Aquitanian deposits—late Oligocene or early Miocene in age—of France. Three elements, the femur, the humerus, and the ulna, were described by Milne-Edwards (1867–1868). Writing at a time when the role of convergence in evolution was not well understood, he said of the osteological characters of the family of the "Colymbides" [loons and grebes] "Cette famille, comprenant les Plongeurs proprement dits et les Grèbes, constitue un groupe parfaitement naturel, dont tous les membres présentent entre eux de grands traits de ressemblance." (p. 278). He described *Colymboides minutus* as having the characters of both loons and grebes and concluded that it was intermediate between these groups of birds.

Since from the description, *Colymboides* was obviously a diving bird and since it was my conviction that loons and grebes could not have come from a common swimming ancestor, I several years ago studied Milne-Edwards' description and plates and came to the conclusion that this bird was probably a loon which had reached a degree of specialization equivalent to that of modern grebes and that the characters said to have been grebelike were the result of this. These tentative conclusions were laid aside in

manuscript form in the hope that I could at some future date examine the fossils themselves.

In the course of the Eleventh International Ornithological Congress, I visited the Naturhistorisches Museum in Basel and there saw several bones of *Colymboides* on exhibition. Upon inquiring, I found that the museum had a large collection of fossils from Aquitanian deposits, and Dr. Schaub kindly invited me to examine it. Accordingly, Dr. Wetmore and I again visited the museum, where we found approximately fifty bones which we assigned to this species. Included were well-preserved examples of the coracoid, humerus, radius, ulna, carpometacarpus, sacrum, femur, tibiotarsus, and tarsometatarsus. Comparisons with recent material in Basel showed that *Colymboides* was, as suspected, a primitive loon. Dr. Schaub kindly offered to lend the material for further study, and I took it to Paris, where not only the type of the species is located but also about fifty more bones, most of which had come into Milne-Edwards' possession after he had described the species. Subsequently, I was able to compare the material from Basel with the type (a coracoid) of *Colymboides anglicus* at the British Museum. In all, 110 bones of *Colymboides minutus* have been examined as follows: 3 coracoids, 31 humeri, 28 ulnas, 8 radii, 10 carpometacarpi, 2 synsacra, 14 femurs, 9 tibiotarsi, and 5 tarsometatarsi. For comparison, skeletons of the following Recent loons and grebes have been available: 5 Red-throated Loons (*Gavia stellata*), 1 Arctic Loon (*G. arctica*), 18 Common Loons (*G. immer*), 2 Yellow-billed Loons (*G. adamsii*), 2 Dabchicks (*Podiceps ruficollis*), 2 Least Grebes (*P. dominicus*), 5 Horned Grebes (*P. auritus*), 2 Eared Grebes (*P. caspicus*), 2 Great Crested Grebes (*P. cristatus*), 4 Red-necked Grebes (*P. grisegena*), 1 Western Grebe (*Aechmophorus occidentalis*), and 16 Pied-billed Grebes (*Podilymbus podiceps*), all in the collections of the University of Michigan Museum of Zoology.

I am indebted to the staffs of the Naturhistorisches Museum in Basel, the Museum d'Histoire Naturelle in Paris, and the British Museum (Natural History) for permission to study the material under their care and for many other courtesies. I also wish to thank William L. Brudon for preparing the figures, Prof. J. Berlioz for making comparisons in the Museum d'Histoire Naturelle, Dr. Andrew J. Berger for assistance in interpreting muscle scars on the fossils, and Drs. C. W. Hibbard and J. Van Tyne for reading the manuscript and offering valuable suggestions.

Montagna (1945) presents evidence that the digits of the birds' hand should be numbered II, III, and IV. However, until his work has been confirmed, I prefer to use the more familiar system which numbers the digits I, II, and III, particularly because a change in the numbering of the digits requires several awkward changes in the nomenclature of the muscles. Therefore, I have followed the nomenclature of Howard (1929) for all the bones and their parts.

Rather than present detailed series of measurements of the bones, only measurements of the lengths of the long bones are presented (table 1), which, with the photographs of the bones (figs. 1-3), should give a clearer idea of the fossils than exhaustive descriptions and measurements.

#### LIMB STRUCTURE

*Limb proportions.*—Because the loons and grebes are primarily foot-propelled diving birds, it is to be expected that the relative lengths of the leg bones should reflect the degree of specialization for swimming and diving. On the other hand, it might be argued that differences in the wing proportions of loons and grebes would more probably indicate differences of a phylogenetic nature. This appears to be the case. In table 2, it will be seen that grebes have relatively long ulnas and correspondingly short metacarpi as

Table 1  
Lengths of Limb Bones of *Colymboides minutus* in Millimeters

Element	Number measured	Range	Mean
Humerus	18	62.0-66.0	63.8
Ulna	21	49.8-56.0	52.2
Radius	7	50.4-52.0	51.2
Carpometacarpus	10	31.0-34.5	32.8
Femur	6	28.9-33.0	30.9
Tibiotarsus without cnemial crest	3	55.0-59.2	56.8
Tarsometatarsus	4	30.8-32.8	32.2

compared with the loons. The agreement in these proportions within both the loons and the grebes is remarkable; and the resemblance of *Colymboides minutus* to the loons in these proportions is extremely close.

The ratio of total length of leg to total length of wing increases from the larger to the smaller species in both groups. This is to be expected because of the surface-volume ratio. That is, with an overall increase in length, weight increases more rapidly than wing area, hence in large birds, there must be a disproportionate increase in wing size in order to make flight possible. On the other hand, no such disproportionate increase in foot area is necessary because the force required to move a body through the water is

Table 2  
Limb Proportions of *Colymboides minutus* and of Recent Loons and Grebes Expressed as Per Cent of the Lengths of the Limbs and Their Elements

	<i>Podiceps cristatus</i>	<i>Podilymbus podiceps</i>	<i>Podiceps dominicus</i>	<i>Colymboides minutus</i>	<i>Gavia adamsii</i>	<i>Gavia immer</i>	<i>Gavia stellata</i>
Number of individuals	2	16	2	*	2	18	5
<u>Femur</u>							
Total leg <sup>1</sup>	20.5	26.3	24.7	25.8	20.1	19.5	17.3
<u>Tibiotarsus<sup>2</sup></u>							
Total leg	49.4	46.6	45.5	47.4	49.5	49.0	50.5
<u>Tarsometatarsus</u>							
Total leg	30.1	27.1	29.8	26.8	30.4	31.5	32.2
<u>Femur + cnemial crest</u>							
Total leg	29.7	33.8	32.7	33.2	37.2	37.2	37.8
<u>Total leg</u>							
Total wing <sup>3</sup>	81.3	83.8	88.3	80.6	63.6	65.6	70.5
<u>Humerus</u>							
Total wing	42.7	41.9	41.4	42.9	43.2	43.7	42.6
<u>Ulna</u>							
Total wing	38.9	39.1	40.3	35.1	34.7	37.7	34.4
<u>Carpometacarpus</u>							
Total wing	18.3	19.0	18.4	22.0	22.1	22.6	23.0

\* Calculations based on average measurements of 6 femurs, 3 tibiotarsi, 4 tarsometatarsi, 18 humeri, 7 ulnas, and 10 carpometacarpi.

<sup>1</sup> The sum of the lengths of the femur, tibiotarsus (minus the cnemial crest), and the tarsometatarsus.

<sup>2</sup> The length of the bone minus the length of the cnemial crest.

<sup>3</sup> The sum of the lengths of the humerus, ulna, and carpometacarpus.

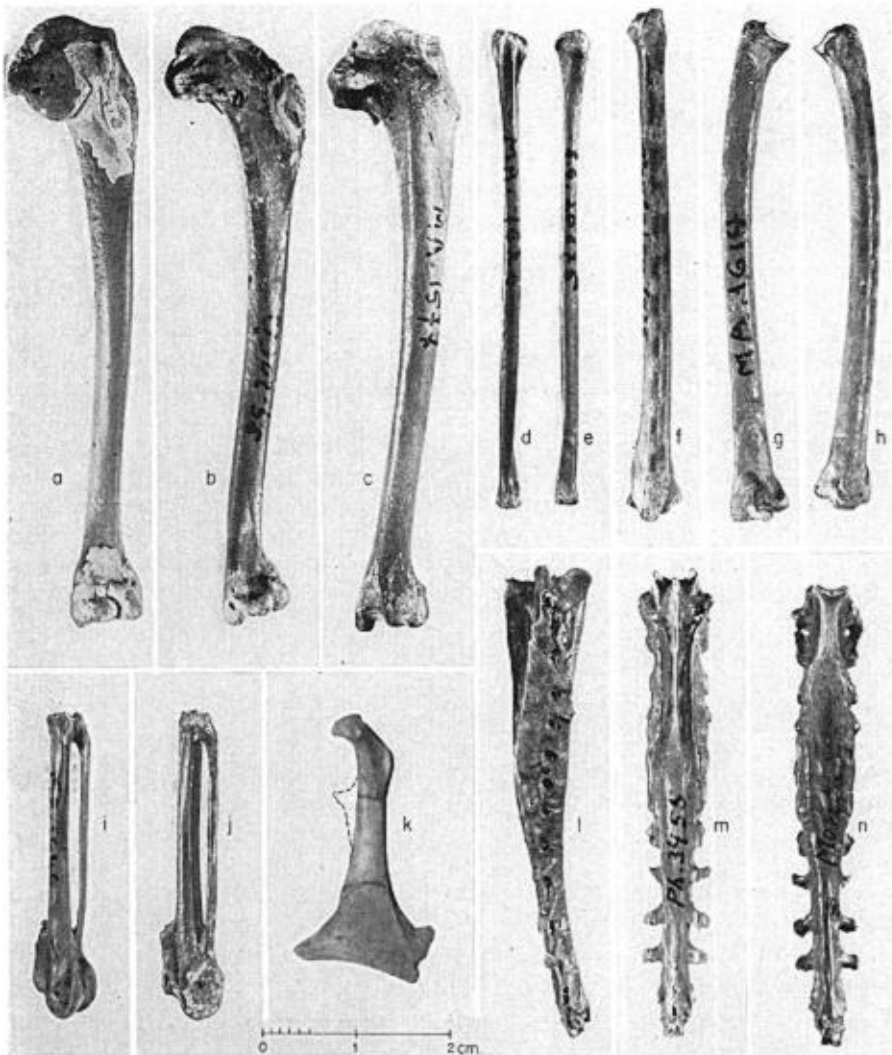


Fig. 1. Wing elements, coracoid, and synsacrum of *Colymboides minutus*: a (Ph. 2005), b (S.G. 20613), and c (M.A. 1577), humeri; d (M.A. 1626) and e (S.G. 20675), radii; f (S.G. 20652), g (M.A. 1614), and h (M.A. 9784), ulnas; i (M.A. 1646) and j (S.G. 5614), carpometacarpi; k, coracoid; l, m, and n (all Ph. 3455), synsacrum. Coracoid from the Museum d'Histoire Naturelle in Paris, other specimens from the Naturhistorisches Museum in Basel.

proportional to its cross-sectional area. In geometrically similar birds, the cross-sectional area and the area of the foot, which provides the propulsive power, increase at the same rate as the overall size of the bird increases.

When due allowance for the sizes of the different species is made, it becomes apparent that loons have a relatively low leg/wing ratio and that this ratio in *Colymboides* is significantly lower than that of grebes of approximately the same size. A relatively short femur and long tibiotarsus are found in both loons and grebes, and it is probable

that these proportions are indicative of the degree of adaptive modification for submarine locomotion. Using this as a criterion of the degree of modification, the loons can be regarded as more highly modified than the grebes. *Colymboides* resembles *Podilymbus* in this respect.

*Colymboides* also resembles *Podilymbus* in the combined relative lengths of the femur and cnemial crest. The proportion of this sum to the total length of the leg may be taken as an indication of the size of the attachment, and hence the size, of the gastrocnemius, the muscle most important in retracting the foot in swimming. In this, as in the relative lengths of the leg bones, the Recent loons are more modified adaptively than are the grebes and *Colymboides*.

*Coracoid*.—This element, more than any other part of the skeleton, proves *Colymboides* to have been a loon and eliminates any possibility of affinity with the grebes. Figures 1 and 4 show clearly the loonlike form of this bone. In grebes, the coracoid is relatively much longer and narrower, the procoracoid and the sternocoracoid process are but slightly developed, and there is a very large ventral sternal facet. Indeed, it is surprising to find such differences in birds which are so similarly adapted.

Had the coracoid of *Colymboides minutus* been known to Milne-Edwards when he described the species, I doubt that he would have suggested that this bird had any relationship with the grebes. Subsequently, he must have examined this element, for a beautifully preserved coracoid (fig. 1) in the Paris Museum bears a label which reads "Colymboides minutus A. M-Ed. Coracoidien. St. Gerand. Col. A. M. Edw. 1906-17." I cannot find any evidence of his having published a description of it.

*Colymboides anglicus*, described by Lydekker (1891:192-193) from the "Upper Eocene (Lower Oligocene) of Hordwell, Hampshire," England, is known from a coracoid (the type), shown in figure 4, and an "imperfect anterior portion of a sternum probably referable to this species." Of the latter, Lydekker states (p. 193) "the left coracoidal groove fits the preceding specimen [the type]. In the presence of a deep concavity in the middle line between the coracoidal grooves, the inner surface of this specimen agrees with the sternum of *Colymbus* [= *Gavia*], to which it approximates in the slight development of the episternal process." This fragmentary sternum may be lost, for it could not be found during my visit to the British Museum (Natural History) in June and July of 1954. Unfortunately, it has never been figured.

The coracoid of *C. anglicus* is approximately one-third larger than that of *C. minutus*, and the shaft of the bone is relatively more slender. Otherwise, the resemblance between the coracoids of these two species is remarkably close, and they almost certainly represent species belonging to the same genus. It is interesting that Lydekker should have placed *anglicus* in the genus *Colymboides*, because at the time he described this species, the coracoid of *C. minutus* was apparently unknown.

*Humerus* (figs. 1 and 3).—Both loons and grebes have slender humeri compared with birds which fly better and more frequently. This bone in *Colymboides minutus* is somewhat stouter than the humeri of either loons or grebes and thus appears to represent a condition intermediate between that of the Recent loons and an ancestral stock with more powerful wings.

The humeri of loons and grebes differ in several characters. On the proximal end of the bone, the bicipital furrow is deeper and narrower, the deltoid crest is more arched, and the head of the humerus is relatively larger in loons than in grebes. On the distal part of the bone, both the external and internal tricipital grooves are wider, slightly deeper, and extended further proximally on the shaft in loons than in grebes. In the loons, the shaft of the humerus is more S-shaped than it is in most species of grebes. The humerus of *Colymboides* agrees with those of Recent loons in all these characters,

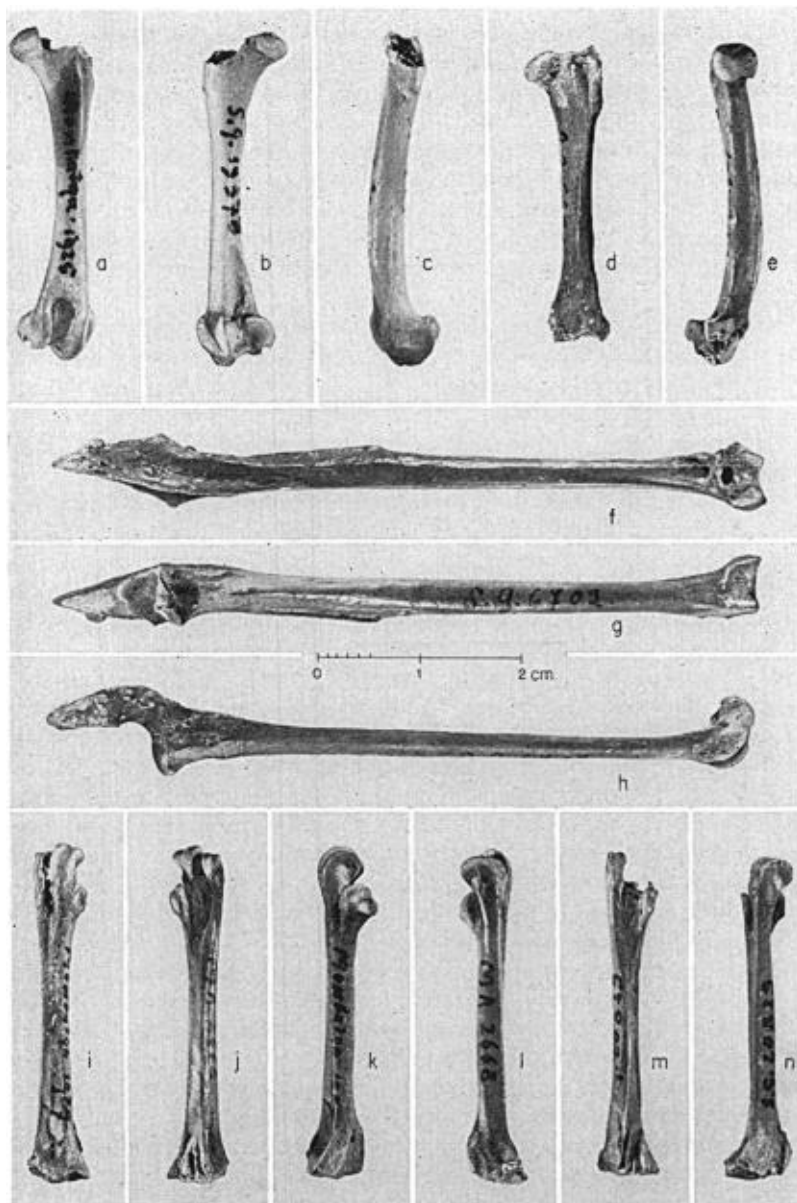


Fig. 2. Leg elements of *Colymboides minutus*: *a*, *b*, and *c* (all S.G. 19373), *d* (S.G. 6686), and *e* (M.A. 2627), femurs; *f*, *g*, and *h* (all S.G. 6702), tibiotarsi; *i*, *j*, *k*, and *l* (all M.A. 2668) and *m* and *n* (both S.G. 20829), tarsometatarsi. All from the Naturhistorisches Museum in Basel.

although the arching of the deltoid crest is even more pronounced than it is in any Recent loon.

*Ulna* (figs. 1 and 3).—The ulnas of loons and grebes differ in several important respects. Those of loons are much heavier and more circular (less triangular) in cross section. The ulna of *Colymboides* is quite loonlike in these respects and also in the

arrangement of the longitudinal intermuscular ridge on the anterior face of the bone. A striking feature of the ulnas of loons is the very much expanded carpal tuberosity. In *Colymboides*, this process is much larger than that of grebes, and although resembling that of loons in general form, it is less well developed. On the proximal end of the bone, the prominence for the anterior articular ligament is broad, high, and bordered posteriorly by a deep groove; in grebes, this prominence is narrower and less raised, and



Fig. 3. End views of limb bones of *Colymboides minutus*: *a* (M.A. 1646), proximal end of carpometacarpus; *b* (S.G. 6686), proximal end of femur; *c* (S.G. 19373), distal end of femur; *d* (S.G. 20829), proximal end of tarsometatarsus; *e* (M.A. 2668), distal end of tarsometatarsus; *f* (M.A. 1577), proximal end of humerus; *g* (S.G. 20613), distal end of humerus; *h* (M.A. 1614), proximal end of ulna; *i* (M.A. 2538), distal end of ulna. All specimens from the Naturhistorisches Museum in Basel.

there is no groove behind it. The corresponding prominence in *Colymboides* is broader than even those of Recent loons, but the posterior groove is not present. Milne-Edwards' description of the ulna of *Colymboides* (1867-1868:298) is very brief, mentioning only the laterally compressed distal end of the bone, its shortness as compared with the humerus, and its generally loonlike form.

On several ulnas of *Colymboides*, scars for the papillae of 11 secondaries can be counted, evidence of the remarkably fine state of preservation of these fossils. In both loons and grebes, there is variation in the number of these scars, so I doubt their value in macrotaxonomic work, at least in these two orders of birds.

*Radius* (fig. 1).—Like the ulnas, the radii of loons are relatively stouter than those of grebes. They are also straighter, having little of the pronounced "S" shape of grebes' radii. The radii of *Colymboides* closely resemble those of loons in both of these respects. Perhaps the most distinctive character in the radii of loons is the presence of a groove lying anterior and parallel to that for the tendon of the extensor metacarpi radialis muscle. This groove is present in *Colymboides* but absent in the grebes; and furthermore, the groove for the tendon of *M. extensor metacarpi radialis* extends well up onto the shaft of the radius in Recent loons (and in *Colymboides*) but little or not at all in grebes.

*Carpometacarpus* (figs. 1 and 3).—The most conspicuous feature of this bone in the loons is the long, narrow first metacarpal, which is approximately 33 per cent of the length of the whole bone as opposed to 16 per cent in grebes and 23 to 24 per cent in *Colymboides*. In grebes, the proximal end of the first metacarpal is expanded into a

prominence for the extensor attachment, whereas in loons this part of the bone is nearly straight and the extensor attachment is a flat, slightly depressed area. On the external face of the distal end of the carpometacarpus of loons, there are conspicuous tendinal grooves between the second and third metacarpals; these are not present in the carpometacarpus of grebes. In these characters, and also in the relatively wide intermetacarpal space and the shape of the carpal trochlea, *Colymboides* is loonlike. The relative shortness (for a loon) of the first metacarpal may be taken as evidence of an evolutionary tendency in loons.

*Gaviella pusilla* (Shufeldt), known from the proximal end of a carpometacarpus collected at Lusk, Wyoming, has been tentatively assigned to the White River Oligocene by Wetmore (1940). This fragment differs from the carpometacarpus of *Colymboides minutus* in being considerably larger, in having metacarpal I relatively higher, and in having the fused proximal portions of metacarpals II and III even longer, relatively, than those of *Gavia immer*. This bird appears to have been an off-shoot of the loons and has been given subfamilial status by Wetmore (*op. cit.*).

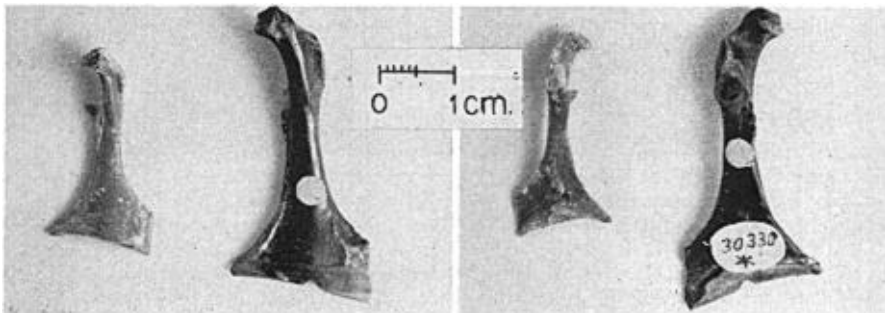


Fig. 4. Coracoids of *Colymboides minutus* (smaller) and *Colymboides anglicus* (larger), the former, an uncatalogued specimen in the Naturhistorisches Museum in Basel, the later, the type in the British Museum (Natural History). Photographs, courtesy of the British Museum.

*Synsacrum* (fig. 1).—Like the leg bones, the synsacrum indicates that *Colymboides* was a loon and was not nearly so modified for underwater locomotion as are the Recent loons. The synsacrum of *Colymboides* is broader than that of *Gavia*, especially in the caudal region, and the lateral processes of the caudal vertebrae are relatively longer and weaker. The pelvis was thus considerably broader in the fossil form.

In Recent loons, the extreme narrowing of the synsacrum and the accompanying shortening or disappearance of the lateral processes of the vertebrae make it difficult to classify the vertebrae. In *Colymboides* this is somewhat easier. Anteriorly in *Colymboides*, there is one thoracic vertebra bearing costal facets. In *Gavia*, there may be one, two, or three, two being the usual number in adults. Apparently there is some fusion as the birds get older. There are three lumbar vertebrae immediately anterior to the acetabulum in both genera; and although without costal facets, the anteriormost of these is intermediate between the other lumbar vertebrae and the last thoracic one in structure. Behind the lumbar series come three vertebrae which lack lateral processes and appear to be sacral vertebrae. The next vertebra bears a small process and is intermediate between the sacrals and the succeeding fused caudals in character. Counting this vertebra of intermediate type, there are usually seven fused caudals in *Gavia* and at least six in *Colymboides*. (The synsacra of both specimens available to me are broken in this region.) As in the case of the fused thoracic vertebrae, the number of fused caudal verte-



brae in *Gavia* increases with age. The number of fused vertebrae in *Colymboides* falls within the range of variation in *Gavia* but would appear to average less. It might be expected that in the process of becoming better adapted for diving, there would be an increase in the number of vertebrae fused into the synsacrum, and this appears to have been the case in the loons. One of the important differences between the synsacra of grebes and of loons (including *Colymboides*) is that in the former the lateral processes of one lumbar vertebra form the principal attachment with the ilia whereas in the latter, the processes of two lumbar vertebrae share in this attachment.

*Femur* (figs. 2 and 3).—Some of the important differences between the femurs of loons and those of grebes are found on the lateral face of the head of this bone. In grebes, the tendon of the ischiofemoralis muscle inserts in a conspicuous, nearly circular depression, which usually has a lip extending posteriorly; in the loons, the corresponding depression is usually elongate and never has a lip. In the grebes, the trochanteric ridge rises in a conspicuous, rounded projection distally, whereas it is nearly straight in the loons. In all of these characters, and also in the form of the rotular groove, the femur of *Colymboides minutus* is loonlike.

Although there is considerable variation from species to species, the femoral shafts of Recent loons are heavier than those of the grebes and *Colymboides*, particularly anteroposteriorly. I think that the relative thickness of the shaft is an expression of the degree of modification for diving and swimming and that the resemblance of *Colymboides* to some grebes, especially to *Podilymbus*, in this respect does not imply a phylogenetic relationship. It stands to reason that the loons must have passed through a stage comparable in its degree of adaptive modification to that now seen in *Podilymbus*.

The raised crest described by Milne-Edwards (1867–1868:298) as forming the internal border of the area of attachment of the “internal” (= medial) head of the gastrocnemius muscle is quite distinct in all the specimens which I have examined and has no counterpart in either the loons or the grebes.

As Milne-Edwards noted (*loc. cit.*), some of the femurs of *Colymboides* are shorter and heavier than others. There is also considerable variation in the position of the ridges in the region of the attachment of Mm. flexores perforati digiti II, III, and IV on the posterior surface of the femur. Milne-Edwards suggested that two species might be involved or that the observed differences might be sexual or individual. In the Common Loon, there is a considerable sexual difference in the length of the femur: those of 7 males and 11 females average 56.3 and 52.1 mm., respectively. This sexual difference is relatively greater than that found in any other limb element of the Common Loon. The coefficient of variation of 14 femurs (7 of males and 7 of females) of the Common Loon is  $5.5 \pm 1.0$ ; that for 6 femurs of *Colymboides minutus*,  $4.6 \pm 1.3$ . The latter figure, although a rather crude estimate owing to the smallness of the sample, does not suggest that we are dealing with more than one species of *Colymboides*. In the Common Loon, there is considerable variation in the size and location of the ridge marking the area of attachment of the Mm. flexores perforati digiti II, III, and IV, and this variation does not appear to be correlated with sex or age. On the basis of the condition in this Recent species, I believe that the differences in the size of the known femurs of *Colymboides minutus* are probably in part sexual, whereas those in the sculpturing of the posterior surface of the bone are individual in nature.

It must be pointed out, however, that the coefficient of variation for the lengths of 18 humeri of *Colymboides minutus* is very low,  $2.0 \pm 0.3$  as compared with  $4.2 \pm 0.9$  for 14 Common Loons (7 males and 7 females). This suggests a much greater degree of sexual difference in the femurs of *Colymboides* than was present in the humeri; in the Common Loon, this difference in degree of sexual variation between these two limb

elements is apparent though less marked. It is possible that this relatively great difference is correlated with corresponding sexual differences in the pelvis and synsacrum, but there is not enough material available at present to determine this.

*Tibiotarsus* (figs. 2 and 3).—In the degree of development of the cnemial process, this element of *Colymboides minutus* resembles the corresponding bone in grebes, but in characters which are more important from a phylogenetic standpoint it is loonlike. The lateral surface of the outer cnemial crest in the grebes is smooth and convexly rounded, and it is with this surface that the large patella articulates. In contrast, this surface of the outer cnemial crest of loons is concave and covered with a network of low ridges; the patella of loons, a minute splinter of bone, embedded in the tendons for the femorotibialis, pars externus, and the iliotibialis (Wilcox, 1952:543), does not articulate with the cnemial process. In *Colymboides*, the lateral surface of the outer crest is concave, as in the loons, and is roughened. There is no indication of an articulation with a patella. The general outline of the inner cnemial crest and the form of the posterior surface of the tibia, on which the ridge from the distal end of the outer cnemial crest continues distad beyond the fibular crest, are again loonlike as is the foramen through which the medullary artery emerges into a groove on the anterolateral part of the bone just distal from the fibular crest. In grebes this foramen is situated on a small ridge. The external ligamental prominence, the groove for the peroneus profundus, and the scar for the mesial end of the anterior ligament (Wilcox, 1952:547) all resemble the corresponding parts of the tibiotarsus of *Gavia* and differ from those of *Podiceps*.

The distal part of a tibiotarsus which Milne-Edwards (1867–1868, pl. 25, figs. 14–18) assigned with doubt to *Anas natator* may be that of *Colymboides*. However, it appears shorter; the distance from the distal end of the fibular crest to the distal end of the bone measures between 33.5 and 34.0 mm. on Milne-Edwards' figures 14 and 16, whereas this measurement on two specimens of *Colymboides* is 35.7 and 36.8 mm. It is difficult to assess the accuracy of these figures, and until direct comparisons with Milne-Edwards' material can be made, we cannot be certain that it is actually *Colymboides*.

In the original description of *Anas natator*, Milne-Edwards (1867–1868:148–149) failed to designate a type, although he stated that the existence of this species "was revealed to me by the discovery of an ulna of small size and perfectly preserved, which presented all the proper characters of the Anatidae; a short time later I collected from the same locality the distal end of a humerus and a nearly complete tibia, which perhaps belonged to this species" (my translation). This implies that he considered the ulna as the type. Because of this, because it is the only complete element, and because it is clearly that of a duck, I formally designate the ulna as the type of *Anas natator*. Thus, should the tibiotarsus prove referable to *Colymboides*, no change in the name of the duck will be necessary.

*Tarsometatarsus* (figs. 2 and 3).—In the museum in Basel Dr. Wetmore and I found three hitherto unidentified tarsometatarsi which we referred to *Colymboides*. I was able to find only two examples of this element in the material identified as *Colymboides minutus* in the Paris Museum, although it seemed odd to me that with all the other material of this species there should be so few tarsometatarsi. Later, on looking through Milne-Edwards (1867–1868), I noticed illustrations (pl. 57, figs. 18–22) of a bone which appeared to be identical with the tarsometatarsi of *Colymboides*. The bone illustrated was described by Milne-Edwards (pp. 362–364) as *Hydrornis natator*. After pointing out superficial resemblances between this bone and the corresponding elements of ducks and tubinares, Milne-Edwards concluded "I have preferred to adopt a name which does not indicate the zoological position of this fossil and its natural affinities because I find that they are not sufficiently known" (my translation).

Professor Jacques Berlioz very kindly compared one of the tarsometatarsi from the museum in Basel with the type and other material of *Hydrornis natator* in the Paris Museum. In a letter of April 7, 1956, he states

"I have been able, at the Laboratory of Paleontology, to make the comparisons you requested.

"It is certain that the bone (tarsometatarsus) which you have sent me is entirely similar to the type of *Hydrornis natator* Milne-Edwards. It even appears, from what is written on this bone, that it came from exactly the same lot of tarsometatarsi as the four others which are in our museum. (This is all which is catalogued under the name of *Hydrornis natator*.)

"I have also compared the more numerous bones catalogued as *Colymboides minutus* (tarsometatarsi, tibias, coracoids, etc.), and there is scarcely any doubt that they belong to the same species of fossil bird, the differences between the tarsometatarsi being of the slightest and only individual. In addition, I must call to your attention that on the label of '*Hydrornis natator*,' a manuscript notation in pencil (but unsigned), apparently quite old, mentions: '*Hydrornis natator* = *Colymboides minutus*.'"

It is thus apparent that *Hydrornis natator* and *Colymboides minutus* are the same species. *C. minutus* was described from three different elements; *Hydrornis natator*, from only the tarsometatarsus. A second species, *anglicus*, has been described in *Colymboides*. *C. minutus* has page priority over *H. natator* and is the better known name. Therefore, as first revisor, I designate *Colymboides minutus* the name to be used. This will involve only one nomenclatural change, placing *Hydrornis natator* in the synonymy of *Colymboides minutus*; and in the unlikely event that page priority may again be used, no further change will be necessary.

Although more compressed laterally than this bone in ducks, the tarsometatarsus of *Colymboides* is much less compressed than that of Recent loons and resembles that of grebes in general proportions. Other characters in which this element of *Colymboides* differs from that of Recent loons are the much shallower grooves on the anterior and posterior surfaces of the bone and the lower calcaneal ridges, which do not meet in the midline (see fig. 3). In the evolution of Recent loons, the tarsometatarsus appears to have become more elongated than that of *Colymboides* in the region between the hypotarsus and the metatarsal facet. Aside from these differences, which are all attributable to a lesser degree of specialization for diving and swimming and are therefore primarily adaptive, the tarsometatarsus of *Colymboides* resembles that of Recent loons. It differs from the corresponding element of grebes in such fundamental characters as the arrangement of the canals through the hypotarsus and the conformation of the trochleae for the digits.

#### DISCUSSION

From the foregoing descriptions, it will be seen that *Colymboides minutus* was a small loon, some 10 to 12 inches in length. Its hind limbs were not as highly adapted for swimming rapidly and powerfully under water as are those of living loons. They had, instead, reached a level of adaptive development approaching those of a Pied-billed Grebe. Although their webbed feet were set far back on the body, these birds could probably walk somewhat better than grebes. Even so, their activities on land must have been quite limited, and they probably nested near the waters' edge as do living loons. Their relatively strong wings suggest that they flew more strongly and more frequently than their modern relatives, but I have found nothing in the structure of the wings to suggest that they were used under water like those of the alcids or diving petrels.

The diet of *Colymboides* was probably primarily animal, and its degree of adaptation for underwater swimming indicates that it could have captured small fish. It is unfortunate that the skull and bill of this bird are unknown.

The Aquitanian deposits of France from which *Colymboides minutus* comes are particularly rich in bird remains (Lambrecht, 1933). In spite of their antiquity, the species and genera of birds found in these deposits are similar enough to living forms to permit us to draw some general conclusions concerning the climatic and ecological conditions under which these birds lived. That the climate was warm is suggested by the presence of a trogon (*Paratrogon*), a parrot (*Archaeopsittacus*), a crowned crane (*Probalearica*), a secretary bird (*Amphiserpentarius*), six flamingos (*Phoenicopterus croizeti*) and five species of the primitive, straight-billed group known as *Palaelodus*, and five genera of storks and ibises. The presence of the flamingos, the storks and ibises, at least two dabbling ducks (*Anas blanchardi* and *A. consobrina*), two cranes (*Probalearica* and *Palaeogrus*), two rails (*Palaeoaramides* and *Paraortygometra*), five genera of shorebirds (three scolopacids, a thick-knee, and a stilt), and three small gulls (*Larus elegans*, *L. desnoyersi*, and *L. totanoides*) indicate the presence of marshes and mud flats. Two marine forms, a shearwater (*Puffinus arvernensis*) and a gannet (*Sula arvernensis*), suggest a coastal situation. Other groups of birds represented include a pelican, two cormorants, a heron, a kite, two small eagles, a vulture, several partridges, a small dove, a sandgrouse, three owls, two swifts, two woodpeckers, a hoopoe-like bird, and at least three passerines.

The problems raised by the study of *Colymboides minutus* alone are proof enough that this remarkable fauna needs to be studied in greater detail. Until such monographic study can be made and the taxonomic positions of all the species determined with greater precision, it is probably not safe to conclude more about the conditions under which these birds lived than I have outlined.

It is evident that *Colymboides minutus* was a primitive loon. Having established this, it should be possible to shed new light on the ancestry of the loons and their relationship to other groups of birds. Two lines of reasoning might be used to do this: it might be possible to work back from their present habits and adaptations through *Colymboides* to a hypothetical ancestor, or it might be possible to find which other groups share relatively non-adaptive morphological characters with the loons. Further, each method might also be used as a check on the other.

If we assume that the resemblances between loons and grebes are the results of convergent evolution, then the most striking morphological differences between them may be considered oldest from a phylogenetic standpoint. Some of these old, "non-adaptive" characters in loons (including *Colymboides*) are the form of the coracoid, the expanded carpal tuberosity on the ulna, the two tendinal grooves near the distal end of the radius, the elongated first metacarpal, and the two proximal foramina and the arrangement of the tendinal canals on the hypotarsus. To begin with, these characters were looked for in representative examples of the grebes, tubinares, steganopodes, herons, ibises, flamingoes, ducks, galliformes, gruiformes, and charadriiformes. The arrangement of tendinal grooves near the distal end of the radius is not shared by any other group examined, although the alcids have two such grooves. In most of the groups studied, the carpal tuberosity on the ulna is developed but not similar to that of the loons in form, and most groups agree in having two proximal foramina on the tarsometatarsus. The grebes, tubinares, steganopodes, and galliformes share none of the other characters with the loons. This is particularly interesting in view of Mayr and Amadon's unsupported statement (1951:5) on the position of the loons. "Since, however, the grebes have been thought to be remote allies of the petrels, and since McDowell (oral communication)

thinks that loons may be a specialized offshoot of petrel stock, it is possible that the grebes and loons have some distant or indirect relationship."

The shaft of the coracoid of *Colymboides anglicus* (fig. 4) is narrower than that of *C. minutus*. This suggests that the ancestors of the loons had even narrower coracoids. In contrast, the coracoid of *Puffinus*, a genus which goes back to Aquitanian times, is even shorter and broader than that of Recent loons. The coracoids of the tubinares in general also differ from those of the loons in the more proximal position of the coracoidal fenestra and the conformation of the sternal end of the bone. The tubinares also differ in having three proximal foramina on the tarsometatarsus and two tendinal canals in the anteriormost row on the hypotarsus. These, plus the entirely different structure of the wing bones in the tubinares, admittedly highly modified for soaring flight, preclude close relationship.

The coracoid of loons is most similar to that of shorebirds and gulls, and birds of these groups also have two proximal foramina on the tarsometatarsus and three anterior hypotarsal canals. Thus, the loons may have their closest relationship with the great charadriiform complex. However, the loons constitute an old and well-marked group, and their affinities are still by no means certain.

The evolutionary history of the loons may be reconstructed thus: In some period between the late Cretaceous and the early Eocene, loons became separated from a very primitive larine stock and evolved the diving habit. The coracoid of *Colymboides anglicus* of the late Eocene is sufficiently similar to that of *C. minutus* for us to infer that, like the latter species, it was a foot-propelled diving bird. There is a gap in the fossil record from the late Eocene to Aquitanian times (late Oligocene or early Miocene) when *Colymboides minutus* was found. By this time, loons had reached a level of specialization for diving equivalent to that of the Pied-billed Grebe. *Gaviella pusilla*, provisionally assigned by Wetmore (1940) to the White River formation (Oligocene), does not appear to be closely related to either *Colymboides* or to modern loons, and as it is known from only a fragmentary carpometacarpus, it is not possible to make inferences about its diving ability. No other fossil loons are known from deposits earlier than those of the Pliocene, in which four species of the modern genus *Gavia* (*G. concinna*, *G. howardae*, *G. palaeodytes*, and *G. portisi*) occurred (Brodkorb, 1953). Two Recent species, the Common Loon (*G. immer*) and the Red-throated Loon (*G. stellata*), are known from deposits of Pleistocene age.

Finally, the question of the taxonomic position of *Colymboides* within the order Gaviiformes must be considered. The morphological differences between *Colymboides* and *Gavia* are many and rather great, but they are largely ones of size and of degree of specialization. With the present gaps in the fossil record, it would be unwise to state dogmatically that *Colymboides* was ancestral to *Gavia*, but I think that it must at least have been near the ancestral stock of modern loons. If we had a series of intermediate forms linking *Colymboides* and *Gavia*, all would be considered part of a single subfamily. Thus, until we have strong evidence to the contrary, I believe that *Colymboides* should be placed in the Gaviinae.

The loons should be classified as follows:

- Order Gaviiformes
  - Family Gaviidae
    - Subfamily Gaviinae
      - Genus *Colymboides*
      - Genus *Gavia*
    - Subfamily Gaviellinae
      - Genus *Gaviella*

## SUMMARY

*Colymboides minutus*, from Aquitainian deposits (late Oligocene or early Miocene in age), was a primitive loon. Its resemblance to the grebes results from its having reached an adaptive level comparable to that of the grebes.

*Hydrornis natator* is a synonym of *Colymboides minutus*.

The loons and the grebes did not have a common swimming ancestor. The loons appear to be distantly related to the Charadriiformes.

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