

FORELIMB JOINT MOBILITY AND THE EVOLUTION OF WING-PROPELLED DIVING IN BIRDS

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ABSTRACT.—We measured wing joint mobility in penguins, alcids, diving-petrels, and non-diving fliers. Great reduction in mobility of the intrinsic wing joints was found in penguins, but not in alcids or diving-petrels. This reduction is correlated with simplification of the intrinsic wing musculature. In contrast, alcids and diving-petrels, which use their wings in both air and water, retain the full functional capacities for flight. Movement through the air probably requires a capability for subtle and varied motions, forces, and shape changes that preclude stiffening and simplification of the wing. Hence, the conversion of an aerial wing to a flipper, as in penguins, must be possible only after the evolutionary loss of flight. Received 23 September 1987, accepted 2 February 1988.

WING-PROPELLED diving has evolved at least five times in birds: in the penguins (Spheniscidae), auks (Alcidae), diving-petrels (Pelecanoididae), the extinct Plotopteridae (Olson and Hasegawa 1979), and the dippers (Cinclidae; Goodge 1959). The penguins are flightless, as were the plotopterids, the Miocene Lucas auks (Mancallinae), and the recent great auks (*Pinguinus*). The diving-petrels and all living alcids, however, practice both aerial and underwater locomotion. Simpson (1946: 84–92) maintained that living alcids and diving-petrels represent a stage in the evolution of flightlessness and wing-propelled diving through which the ancestor of penguins passed. Storer (1960) suggested further that flying auks and diving-petrels represent a “compromise” stage between birds well adapted for locomotion in air and in water.

Because the optimum design of the propulsive organs is different for the two media, which differ substantially in density and buoyancy, an intermediate adaptive stage probably would involve a loss of efficiency in each medium as the price of adequacy in the other. Neither Simpson nor Storer elaborated on the anatomical correlates of a “compromise” wing. If their views are correct, one might expect intermediate stages to approach some of the anatomical features of submarine specialists.

The extreme of underwater adaptation occurs

in penguins. The limb and its skeleton are flattened, and the wing is reduced in surface area by the loss of differentiated flight feathers, patagia, and the alula. The shoulder joint and the extrinsic muscles of the wing are functionally specialized (Bannasch 1986a, b, 1987), and the limb is relatively rigid because joint mobility is restricted. In all, the wing is converted to a “flipper” similar in external form to those of other aquatic tetrapods.

No detailed analyses of the relationship between wing structure and the idea of compromise has been made for forms such as the diving-petrels and volant alcids. Hudson et al. (1969) described the wing muscles of alcids and suggested (without functional explanation) that some features might be related to diving. Spring (1971) described underwater swimming in two species of the alcid genus *Uria*. Storer (1960: fig. 4) used illustrations of wing skeletons of a gull (*Larus*), Razorbill (*Alca*), Great Auk (*Pinguinus*), Lucas Auk (*Mancalla*), and penguin (*Spheniscus*) to represent stages in the evolution of the extreme aquatic specialization, showing a trend for increased flattening of the bones and loss of the alula. Pennycuik (1987) suggested that auks and diving-petrels have reduced wing areas as adaptations for propulsion through media of greatly different densities.

Storer did not address a concomitant specialization, the stiffening of the wing through a

reduction in the ranges of motion of the joints. Stiffening may prevent distortion of the wing during movement through the dense aquatic medium. That this is a problem is suggested by the observation that dippers and auks keep their wings partly folded when swimming (Goodge 1959, Spring 1971).

Studies of underwater propulsion indicate that alcids employ a different method from that of penguins. In alcids the manus stays in the flexed position during the propulsive stroke, in which the wing moves down and backward in a rowing action (Spring 1971). In penguins the manus is extended, the wing is rotated so that the leading edge is lower than the trailing edge in the downstroke, which entails little caudal movement of the wing, and the upstroke is used to generate thrust as well (Clark and Bemis 1979). Thus, with regard to method of underwater propulsion, alcids and penguins can be considered convergent only in the most general sense.

We attempted to determine whether species capable of both flight and wing-propelled diving show attributes of wing structure convergent to those of penguins. We measured and compared wing-joint mobility in penguins, other wing-propelled divers, and nondiving fliers, and related these findings to differences in the wing musculature. The results are discussed in relation to the evolutionary transformation from aerial to submarine propulsion.

MATERIALS AND METHODS

The range of motion was measured at the shoulder, elbow, wrist, and major digit of specimens that were frozen while freshly dead and subsequently thawed in a refrigerator 2-5 days (depending on size) before measurement. Each specimen was placed on its back on a table, and the right wing was extended flat over a sheet of paper. To measure motion at each joint, the proximal element was held securely in place, the position of the joint was marked, and the distal element was moved through the range of motion until the joint resisted further movement. These points were marked, and the arc thus circumscribed was measured with a protractor. This was taken as an estimate of the normal arc of motion. To reduce variation in technique, one person (the senior author) moved the element through the range of motion while the other workers maintained the specimen in place and marked the positions. Replicate estimates varied, and each measurement was repeated 10 times and a mean arc of motion was calculated. Although the tissues were compliant, we observed no pattern of increase in the estimated arc during a series of replicates, indicating

that deformation through stretching of the tissues did not occur during measurement.

RESULTS

Joint mobility.—We obtained arcs of motion at four joints for 11 volant species that do not use their wings underwater, 2 species of diving-petrels, 9 of alcids, and 7 of penguins (Table 1). For all four motions the values in alcids, diving-petrels, and nondiving fliers were similar and overlapped broadly. In penguins the mean values for flexion of the forearm, manus, and major digit were substantially lower than those for alcids, diving-petrels, and nondiving fliers, and did not overlap the values for these groups. For protraction of the humerus, the values for penguins overlapped the lowest three values among the nondiving fliers and the lowest value of the set of alcids. The penguin average values, however, were lower than the values for these groups. Bannasch (1986a) reported a lower estimate (45°) for this motion but, unlike our method, limited the fully protracted position to a line perpendicular to the body axis.

The mean arc and 95% confidence limits of the mean for flexion of the forearm, protraction of the humerus, flexion of the manus, and flexion of the major digit for each species are depicted in Figs. 1-4. The reduction in forearm flexion of penguins differed dramatically from the other species (Fig. 1). This pattern was typical of flexion of the manus and major digit as well (Figs. 3 and 4). The values for flexion of the forearm in alcids and diving-petrels appeared slightly larger on average than for the nondiving fliers (Fig. 1). The penguins also had a slightly reduced protraction of the humerus compared with the other species (Fig. 2).

To test for these and other possible differences in the arcs of movement, the species (Table 1) were allocated to three categories: diving nonfliers (penguins), diving fliers (alcids and diving-petrels), and nondiving fliers (remaining species, including *Melanitta nigra*, a foot-propelled diver). For each measurement a group mean was calculated (Table 2), and a one-way analysis of variance was performed. For protraction of the humerus and flexion of the manus, the difference between the mean for penguins and that for each other category was statistically significant ($P < 0.05$). For flexion of the forearm and major digit the variances of the means were heteroscedastic (Bartlett's box F test

TABLE 1. Range of motion in avian wing joints.*

Species no.	Protraction of humerus	Flexion of forearm	Flexion of manus	Flexion of major digit
Spheniscidae				
1 <i>Aptenodytes patagonica</i>	103 (97-106)	23 (17-34)	22 (18-26)	12 (11-15)
2 <i>Aptenodytes forsteri</i>	92 (88-102)	14 (13-18)	13 (10-15)	14 (12-19)
3 <i>Pygoscelis papua</i>	65 (57-72)	26 (20-34)	29 (24-34)	25 (20-31)
4 <i>Pygoscelis adeliae</i> 1	100 (91-106)	25 (20-32)	25 (22-29)	17 (13-21)
5 <i>Pygoscelis adeliae</i> 2		27 (20-32)	23 (19-26)	19 (11-23)
6 <i>Pygoscelis antarctica</i>	73 (67-82)	25 (20-30)	21 (19-22)	21 (16-27)
7 <i>Eudyptes crestatus</i>	92 (83-106)	34 (28-37)	30 (25-35)	26 (22-30)
8 <i>Eudyptes chrysolophus</i>	62 (57-68)	26 (22-31)	27 (24-31)	16 (14-20)
Pelecanoididae				
9 <i>Pelecanoides urinatrix</i>	144 (120-155)	149 (142-155)	112 (95-122)	78 (63-91)
10 <i>Pelecanoides georgicus</i>	157 (148-173)	149 (144-156)	106 (99-119)	83 (65-100)
Alcidae				
11 <i>Uria aalge</i>	158 (144-173)	157 (149-165)	109 (102-120)	76 (72-84)
12 <i>Uria lomvia</i>	136 (125-154)	152 (145-163)	110 (98-117)	63 (55-70)
13 <i>Cephus columba</i>	114 (87-135)	160 (158-162)	101 (93-109)	53 (47-60)
14 <i>Synthliboramphus antiquus</i>	155 (130-180)	143 (136-152)	107 (95-114)	71 (64-82)
15 <i>Ptychoramphus aleuticus</i>	137 (119-150)	161 (151-170)	114 (110-117)	63 (45-75)
16 <i>Cyclorhynchus psittacula</i>	124 (102-157)	158 (153-164)	119 (112-128)	67 (56-84)
17 <i>Aethia cristatella</i>	154 (136-168)	142 (135-148)	117 (105-128)	62 (52-68)
18 <i>Fratercula cirrhata</i>	135 (115-148)	155 (147-160)	113 (100-120)	65 (58-68)
19 <i>Fratercula corniculata</i>	92 (76-131)	158 (154-164)	97 (90-105)	68 (50-75)
Nondiving fliers				
20 <i>Larus occidentalis</i>	137 (113-148)	143 (137-151)	119 (103-126)	60 (49-67)
21 <i>Rissa tridactyla</i>	159 (150-169)	159 (147-168)	119 (90-135)	56 (46-75)
22 <i>Melanitta nigra</i>	129 (102-139)	132 (120-143)	117 (111-130)	58 (40-72)
23 <i>Colinus virginianus</i>	151 (135-164)	155 (142-171)	109 (92-121)	64 (58-71)
24 <i>Porzana carolina</i>	141 (130-155)	146 (130-153)	113 (100-130)	77 (65-85)
25 <i>Columba livia</i> 1	120 (113-130)	125 (117-132)	114 (107-128)	48 (40-63)
26 <i>Columba livia</i> 2	106 (95-115)	124 (111-134)	134 (125-144)	45 (39-50)
27 <i>Columba livia</i> 3	99 (87-115)	113 (102-123)	129 (120-137)	57 (51-75)
28 <i>Coccyzus americanus</i>	149 (135-160)	152 (140-160)	104 (87-117)	81 (64-98)
29 <i>Ramphastos ambiguus</i>	126 (109-140)	142 (126-152)	113 (90-138)	66 (59-75)
30 <i>Colaptes auratus</i>	99 (88-107)	125 (103-135)	103 (95-122)	34 (29-43)
31 <i>Hylocichla mustelina</i>	85 (71-107)	112 (98-122)	99 (91-107)	43 (36-53)
32 <i>Gracula religiosa</i>	145 (120-165)	134 (123-141)	116 (96-130)	68 (57-79)

* Values are in degrees, with mean and range for 10 measurements at each joint in each species.

for homogeneity of variances; $P < 0.05$), and the one-way ANOVA model was thus inappropriate. An approximate test of equality of means, using the Games and Howell method (Sokal and Rohlf 1981: 409-410), indicated that for these two motions the means of penguins differed

significantly from those of nondiving fliers and of diving fliers ($P < 0.01$). The difference between the means for flexion of the forearm in diving and nondiving fliers was also statistically significant ($P < 0.05$); the value in diving fliers was larger than in nondiving fliers. None

TABLE 2. Mean values in degrees of arc \pm 1 SD for joint movements in diving nonfliers (penguins), diving fliers (alcids and diving-petrels), and nondiving fliers. n indicates the sample size.

	n	Protraction of humerus	Flexion of forearm	Flexion of manus	Flexion of major digit
Diving nonfliers	8	83.9 \pm 23.3 ^a	25.0 \pm 5.5	23.8 \pm 5.4	18.8 \pm 5.0
Diving fliers	13	126.6 \pm 23.3	153.1 \pm 6.6	109.6 \pm 6.6	68.1 \pm 8.5
Nondiving fliers	11	136.9 \pm 20.6	135.5 \pm 15.4	114.5 \pm 9.8	58.2 \pm 13.4

^a Sample size = 7; see Table 1.

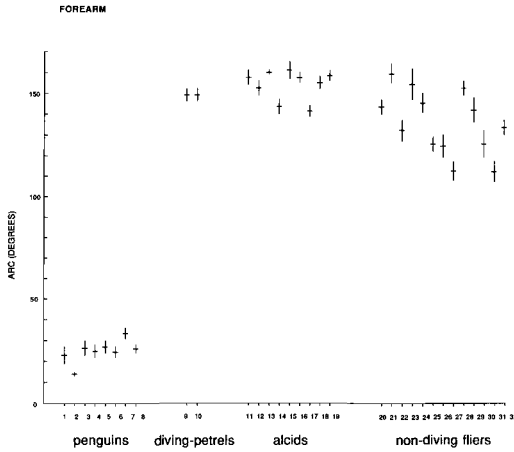


Fig. 1. Arcs of flexion of the forearm in penguins, diving-petrels, alcids, and volant species that do not engage in wing-propelled diving. The horizontal bars represent mean arcs based on 10 measurements, and the vertical lines are the 95% confidence intervals of the means. The numbers along the abscissa correspond to species numbers listed in Table 1.

of the other differences among the means for each motion (Table 2) was statistically significant ($P > 0.05$).

We were unable to measure accurately rotation at the shoulder or elevation and depression of the wing. Bannasch (1986a) measured rotation in penguins as part of a functional analysis but did not measure other groups of birds. Manipulation of our specimens suggested that none of the species has substantial (if any) reduction of the arc of elevation and depression.

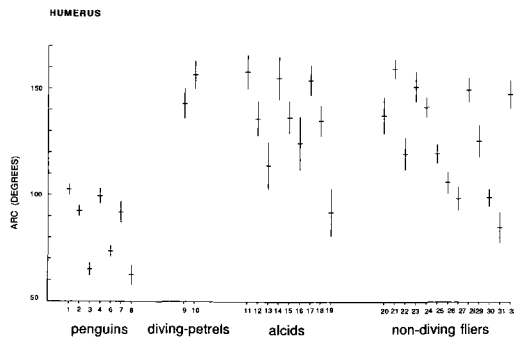


Fig. 2. Arcs of protraction of the humerus in penguins, diving-petrels, alcids, and volant species that do not engage in wing-propelled diving. The format is as in Fig. 1. The second specimen of *Pygoscelis adeliae* (5) was not suitable for this measurement.

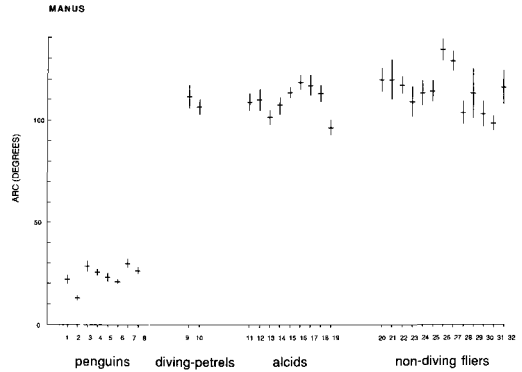


Fig. 3. Arcs of flexion of the manus in penguins, diving-petrels, alcids, and volant species that do not engage in wing-propelled diving. The format is as in Fig. 1.

Wing musculature.—Penguins possess virtually a full complement of extrinsic muscles, those that arise on the pectoral girdle or other structures and insert on the humerus (Table 3). These muscles control the operation of the wing as a whole, and their retention as a functional system is consistent with the wide range of movements at the shoulder.

The reduction in intramembral mobility of penguins is closely correlated with modification of the corresponding intrinsic muscles (Table 3). Most of these muscles either are converted to tendons that lack contractile function or are lost entirely (Schreiweis 1982). These changes, however, occur in a pattern that retains the capability of providing limited activity at each joint. No joint is immobilized, but each is reduced to a restricted arc of movement (Table 1).

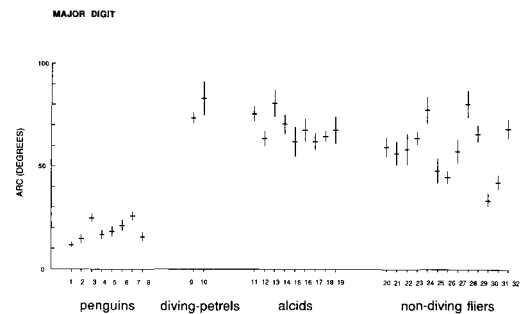


Fig. 4. Arcs of flexion of the major digit in penguins, diving-petrels, alcids, and volant species that do not engage in wing-propelled diving. The format is as in Fig. 1.

TABLE 3. Muscles of the wing in penguins.

Muscles ^a	Condition ^b
Humerus	
Scapulohumeralis cranialis	Absent
Scapulohumeralis caudalis	Normal
Subscapularis	Normal
Subcoracoideus	Normal
Coracobrachialis cranialis	Weak or vestigial
Coracobrachialis caudalis	Normal
Pectoralis	Normal
Supracoracoideus	Normal
Latissimus dorsi pars cranialis	Normal
Latissimus dorsi pars caudalis	Normal
Deltoideus major	Weak
Deltoideus minor	Normal
Forearm	
Extension	
Triceps brachii	Normal
Flexion	
Biceps brachii	Absent
Brachialis	Normal
Rotation	
Pronator superficialis	Absent
Pronator profundus	Absent
Supinator	Weak
Ectepicondylo-ulnaris	Tendinous
Entepicondylo-ulnaris	Absent
Manus	
Extension	
Extensor metacarpi radialis	Weak
Extensor longus alulae	Normal
Extensor longus digiti majoris	Tendinous
Flexion	
Flexor carpi ulnaris	Tendinous
Flexor digitorum superficialis	Tendinous
Flexor digitorum profundus	Tendinous
Extensor digitorum communis	Tendinous
Extensor metacarpi ulnaris	Tendinous
Ulnometacarpalis dorsalis	Normal
Ulnometacarpalis ventralis	Absent
Alula	
Extensor brevis alulae	Absent
Abductor alulae	Absent
Flexor alulae	Absent
Adductor alulae	Absent
Extensor digitorum communis	Tendinous
Major digit	
Extension	
Interosseus dorsalis	Tendinous
Abductor digiti majoris	Weak
Extensor longus digiti majoris	Tendinous
Extensor digitorum communis	Tendinous
Flexor digitorum superficialis	Tendinous
Flexor digitorum profundus	Tendinous
Flexion	
Interosseus ventralis	Normal
Flexor digiti minoris	Normal

^a Functional groupings follow Raikow (1985).^b Data from Schreiweis (1982).

DISCUSSION

We found that the diving-petrels and extant species of alcids are not intermediate in intrinsic wing mobility between nondiving fliers and penguins. Furthermore, alcids retain a full complement of wing muscles, as diving-petrels probably do, in contrast to penguins, which have a highly reduced set of muscles and but a vestige of contractile force at each intrinsic joint. Thus, the living alcids and diving-petrels represent adaptive intermediates only in the limited sense that they have balanced a reduced wing area (Pennycuick 1987) with the structural specializations necessary for flight and the behavioral modifications required for wing-propelled diving. In addition, studies of underwater propulsion indicate that alcids employ a different method from penguins (Spring 1971, Clark and Bemis 1979). Thus, the interpretation of alcids as an adaptive compromise is overly simplistic (see also Raikow 1985: 81).

The lack of wing rigidity and muscular simplification in volant alcids implies constraints on the evolution of a flipper-like wing that probably relate directly to the requirements of flight. Maintenance of the pressure gradients entailed in flight requires changes in the shape and orientation of the wing surfaces during the flapping cycle. These involve rapid and variable movements provided by a combination of joint mobility and varied muscular actions. Thus, the capacity for flight probably precludes structural modifications like those of the wings of penguins.

We submit that the reduction and loss of intrinsic muscles, and the stiffening of the wing, cannot evolve in flying birds. Penguins probably passed through an auklike stage in which they used their wings for both aerial and underwater propulsion, but they must have abandoned aerial flight before they developed their morphological specializations of reduced musculature and restricted joint mobility.

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LITERATURE CITED

- BANNASCH, R. 1986a. Morphologisch-funktionelle Untersuchung am Lokomotionsapparat der Pinguine als Grundlage für ein allgemeines Bewegungsmodell des "Unterwasserfluges," teil I. Gegenbaurs Morphol. Jahrb. 132: 645-679.
- . 1986b. Morphologisch-funktionelle Untersuchung am Lokomotionsapparat der Pinguine als Grundlage für ein allgemeines Bewegungsmodell des "Unterwasserfluges," teil II. Gegenbaurs Morphol. Jahrb. 132: 757-817.
- . 1987. Morphologisch-funktionelle Untersuchung am Lokomotionsapparat der Pinguine als Grundlage für ein allgemeines Bewegungsmodell des "Unterwasserfluges," teil III. Gegenbaurs Morphol. Jahrb. 133: 39-59.
- CLARK, B. D., & W. BEMIS. 1979. Kinematics of swimming of penguins at the Detroit Zoo. J. Zool. London 188: 411-428.
- GOODGE, W. R. 1959. Locomotion and other behavior of the dipper. Condor 61: 4-17.
- HUDSON, G. E., K. M. HOFF, J. VANDEN BERGE, & E. C. TRIVETTE. 1969. A numerical study of the wing and leg muscles of Lari and Alcae. Ibis 111: 459-524.
- OLSON, S. L., & Y. HASEGAWA. 1979. Fossil counterparts of giant penguins from the North Pacific. Science 206: 688-689.
- PENNYCUICK, C. J. 1987. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: ornithodolite observations. J. Exp. Biol. 128: 335-347.
- RAIKOW, R. J. 1985. Locomotor system. Pp. 57-147 in Form and function in birds, vol. 3 (A. S. King and J. McLelland, Eds.). London, Academic Press.
- SCHREIWEIS, D. O. 1982. A comparative study of the appendicular musculature of penguins (Aves: Sphenisciformes). Smithsonian Contrib. Zool. 341: 1-46.
- SIMPSON, G. G. 1946. Fossil penguins. Bull. Am. Mus. Nat. Hist. 87: 1-100.
- SOKAL, R. R., & F. J. ROHLF. 1981. Biometry, 2nd ed. San Francisco, W. H. Freeman.
- SPRING, L. 1971. A comparison of functional and morphological adaptations in the Common Murre (*Uria aalge*) and Thick-billed Murre (*Uria lomvia*). Condor 73: 1-27.
- STORER, R. W. 1960. Evolution in the diving birds. Proc. 12th Int. Ornithol. Congr.: 694-707.