

FUNCTIONAL ANATOMY OF THE FEEDING APPARATUS OF FOUR SOUTH AFRICAN CORMORANTS

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Accepted: September 1977

ABSTRACT

The functional anatomy of the head and anterior neck region of the cormorants *Phalacrocorax lucidus*, *P. neglectus*, *P. capensis* and *P. africanus* was investigated. There are significant differences in absolute size of the muscle and bone elements between the four species. The relative proportions of these elements are, however, very similar and indicate adaptations for capturing active prey under water. Kinetic movements of the upper jaw are large in all species, particularly *P. capensis*. The effective forces acting on the tip of the bill correlate well with the mass of prey taken by each species. Specific differences in jaw mechanism efficiency were viewed as adaptations for specific prey preferences. *P. lucidus* and *P. africanus*, although very different in body size, have similar adaptations for capturing slow-moving, benthic fish. *P. neglectus* has possibly the most generalized feeding apparatus which may correlate with the wide range of food taken. The jaws and neck of *P. capensis* appear most adapted for taking small, active prey which correlates with the preference for fast-moving pelagic fish. Differences in body size and jaw force are thought to reduce competition for food between the four species.

INTRODUCTION

This paper deals primarily with the structure and function of the head region in four species of cormorant: the white-breasted cormorant *Phalacrocorax lucidus*, the bank cormorant *P. neglectus*, the Cape cormorant *P. capensis* and the crowned cormorant *P. africanus*. Any two or more of these species commonly occur sympatrically in South Africa, and all four are similar in general body form (Rand 1960; McLachlan & Liversidge 1970; Siegfried *et al.* 1975). A degree of ecological segregation of the four species in the marine environment exists through differences in food and feeding (Siegfried *et al.* 1975). Since a bird's head is most intimately involved in feeding, anatomical adaptations related to feeding are most likely to be found there (Burton 1974).

The interdependence of anatomical form and function with an animal's environment has been emphasized by Bock & von Wahlert (1965). Adaptations of an organ system involve modification of its form and function in relation to the selection pressures of the environment. Although the head and jaws of birds have many biological roles, including feeding, preening, nest-building, display and defence, this paper focuses on adaptations for feeding.

MATERIALS AND METHODS

Following Goodman & Fisher (1962), linear dimensions were obtained from cleaned, adult

Zoologica Africana 13(1): 81-102 (1978)

skulls of ten *P. capensis*, six *P. lucidus*, three *P. neglectus*, and three *P. a. africanus* specimens. Sexes were combined for each species, since there is little dimorphism in size (McLachlan & Liversidge 1970). All measurements were correct to 0.1 mm.

Since it houses the brain and sensory organs, the cranium is considered to be subject to the least amount of adaptive modification (Goodman & Fisher 1962). For this reason cranial length was used to calculate proportions so that skulls of different sizes could be compared.

Kinesis in birds is the action of protraction and retraction of the upper jaw, relative to the cranium, about the nasal-frontal hinge (Figure 1). The degree of kinesis can be estimated by measuring the angle through which the upper jaw can move, relative to its resting position. This can only be done successfully using fresh, undissected skulls (Fisher 1955; Goodman & Fisher 1962). The maximum angles of protraction and retraction were measured using skulls which had previously been kept frozen. The skull, with all muscles, ligaments and integument present, was held firmly above a protractor and movement of the upper jaw effected by pressing upwards against the anterior tip of the beak. Since kinesis in cormorants is not restricted by the development of lacrimal or quadrate bone "stops" (Fisher 1955), the upper jaw was moved until distortion of the bones appeared imminent. In live birds, angles of protraction and retraction would of course be less.

Dissections of the muscles of the jaws and anterior neck were made, using three *P. lucidus*, three *P. capensis*, two *P. neglectus* and two *P. africanus*. The nomenclature of George & Berger (1966) was used for the description of jaw and neck muscles. However for the jaw adductors, the terminology of Hofer (1950) and Owre (1967) was adopted.

The movement of birds' jaws involves both simple and complex lever systems and Goodman & Fisher (1962) provide formulae whereby the moment of torque acting about one or more pivots can be analysed. The distance between the pivot (fulcrum) of a bone and the point of insertion of the muscle is known as the force arm of that muscle, whereas the distance between pivot and the point of resistance (beak tip) is known as the resistance arm. The moment of torque (T) is determined by the simple lever law:

$$T = F \times \sin \hat{a} \times d$$

where F is the relative force of the muscle, \hat{a} its angle of insertion on the force arm, and d the length of the force arm. The force (t) acting on the tip of the bill is then calculated as follows:

$$t = T/L$$

where L is the length of the resistance arm (anterior mandible length for adduction and abduction; upper jaw length for protraction and retraction; Figure 1).

Adductor and abductor muscles produce torque on the mandible, about its articulation with the quadrate bone, for which the simple lever law applies. All retractor muscles and *M. protractor pterygoidei* act directly upon the palatine or pterygoid bones to produce torque on the upper jaw about the nasal-frontal hinge. The torque on the upper jaw is thus calculated as follows:

$$T = F \times \cos \hat{a} \times d$$

with F as before, \hat{a} the angle between the muscle and the palatine-ptyergoid plane, and d the

force arm (upper jaw depth). The force on the upper jaw is calculated from the torque as before.

The second protractor muscle *M. protractor quadrati* causes protraction via a complex lever system. The muscle acts on the quadrate bone with a force calculated as follows:

$$\text{Force on the quadrate bone} = \frac{F \times \sin \hat{b} \times d_2}{L_2}$$

where F , \hat{b} and d_2 are respectively the muscle force, angle of insertion and the force arm on the quadrate bone. The resistance arm (quadrate bone length) has dimensions L_2 . This force is directed to the upper jaw via the palatine-ptyerygoid plane with a torque calculated as follows:

$$T = \frac{F \times \sin \hat{b} \times d_2 \times \cos (\hat{c} - 90^\circ) \times d}{L_2}$$

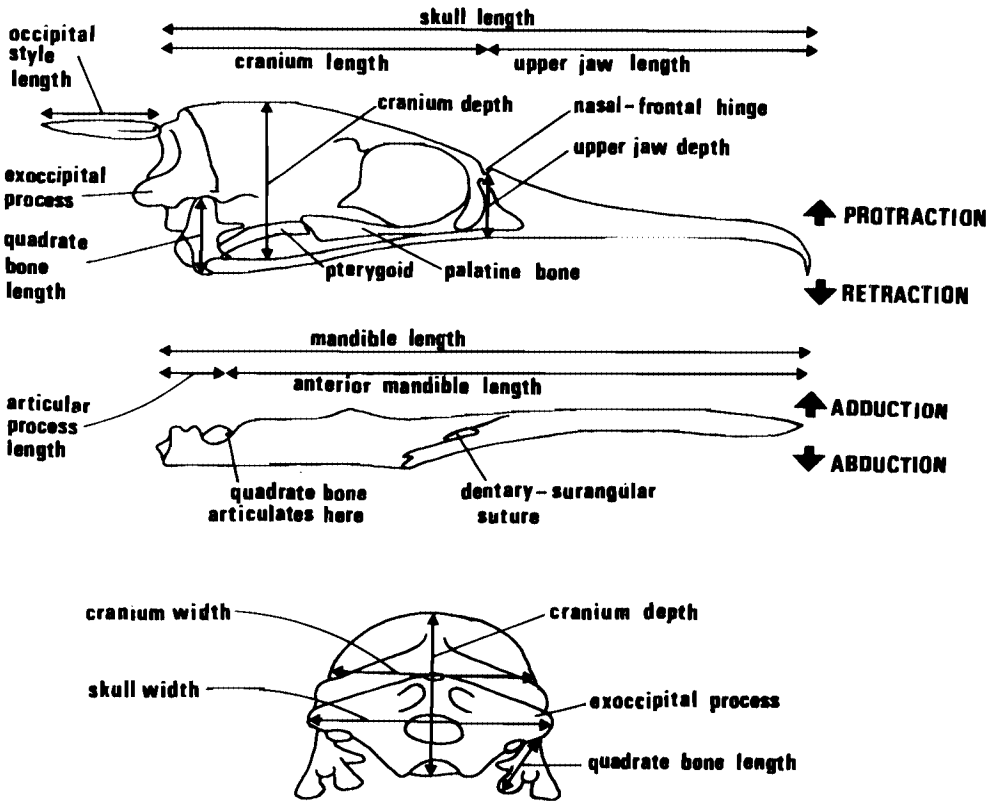


FIGURE 1

Lateral and posterior views of the skull of a cormorant (*P. lucidus*), showing features mentioned in the text.

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where \hat{c} is the angle between the quadrate and the pterygoid bones, and d is the force arm (upper jaw depth). The force at the tip of the upper jaw is calculated from the torque as before.

The dried mass of individual muscles was used as a measure of the relative force each muscle is capable of exerting. Muscles were oven-dried at 60 - 70 °C until a constant mass was attained. Muscles with pinnate and parallel fibres were treated alike, although the force, relative to size, of these muscle types is thought to differ (George & Berger 1966).

The mid-points of origin and insertion of each muscle, and the fulcrum of its force arm, were marked *in situ*. By triangulation of these points, the angles between the muscles and the force arms were obtained (Goodman & Fisher 1962). This procedure also provided the length of the force arm of each muscle. The angles of insertion of the pterygoid muscles, which insert on a sliding bone, and not directly on to a lever arm, were estimated using a protractor.

The mechanical advantage (the ratio of the force arm to the resistance arm) was calculated for all the muscles of the jaw. A large mechanical advantage indicates adaptation for strength rather than speed of action (Raikow 1970). The protractor and retractor muscles in each species have the same mechanical advantage, since they have the same force arm (upper jaw depth) and the same resistance arm (upper jaw length).

RESULTS

Anatomy

Linear dimensions of the skulls

The occipital style ranges in development from large (*P. lucidus*) to small (*P. neglectus*). The beak is proportionately larger in *P. capensis*, intermediate in *P. lucidus* and *P. neglectus* and smaller in *P. africanus*. With the exception of occipital style length, significant differences were found between the skull dimensions of the four species of cormorant (Table 1; ANOVA : $p < 0,05$). However, apart from occipital style and beak lengths, great similarity was found in the skull proportions, relative to cranial length (Table 2). The proportionate areas of muscle attachment are thus similar.

Kinesis

The angles of movement of the upper jaw (Table 3) indicate that kinesis is well developed in all four cormorant species, relative to other birds (Fisher & Goodman 1955a; Goodman & Fisher 1962). The former report a similar high degree of protraction (30°) in the double-crested cormorant *P. auritus*.

Muscles of the jaws

Twelve muscles and muscle divisions were recognized (Figures 2-3). No major differences in origin and insertion were noted between the four species. All muscles have parallel fibres

except the *temporalis posterior* and *caput nuchale* parts of *M. adductor mandibulae externus*, which are pinnate. The jaw muscles were treated as four groups.

Group A: Adductor muscles

1. *M. adductor mandibulae externus pars temporalis*. In the Phalacrocoracidae this muscle is recognizable as two parts, an anterior and a posterior (Owre 1967).
2. *M. adductor mandibulae externus caput nuchale*. Owre (1967) recognizes anterior and posterior parts of this muscle. These were evident in all four species considered, but, since both parts insert on a common tendon, they were considered as one muscle mass.

TABLE I
Mean linear dimensions (mm) of skulls of adult cormorants
*One standard deviation

	<i>lucidus</i>		<i>neglectus</i>		<i>capensis</i>		<i>africanus</i>	
	\bar{x}	SD*	\bar{x}	SD*	\bar{x}	SD*	\bar{x}	SD*
Skull length	139,2	7,8	128,4	1,6	112,3	2,5	81,5	4,2
Cranium length	64,6	3,2	59,8	0,9	50,5	1,2	43,3	2,7
Cranium width	31,5	1,7	33,5	0,5	28,7	0,7	24,6	1,6
Cranium depth	26,7	1,2	22,9	0,6	21,5	0,7	18,7	1,1
Skull width	33,7	1,6	29,7	0,7	25,5	0,9	20,4	1,5
Occipital style length	29,8	3,0	14,2	0,3	14,2	1,4	15,6	1,8
Upper jaw length	73,0	4,9	69,0	1,5	61,8	1,6	38,2	1,6
Upper jaw depth	14,8	1,1	11,3	0,4	8,5	0,4	7,9	1,6
Mandible length	130,4	8,7	119,5	0,5	104,7	2,7	73,0	3,7
Articular process length	13,7	1,1	11,5	1,0	9,5	0,6	7,2	0,4
Anterior mandible length	116,7	8,4	107,8	1,1	95,2	2,6	65,8	1,8
Quadrate bone length	14,0	0,3	12,3	0,7	9,9	1,3	8,7	0,4
No. specimens measured	6		3		10		3	

TABLE 2

Mean ratios of linear dimensions of skull to cranial length in adult cormorants. All values of standard deviation were less than 0,01

	<i>lucidus</i>	<i>neglectus</i>	<i>capensis</i>	<i>africanus</i>
Skull length	2,1	2,2	2,2	1,9
Cranium length	1,0	1,0	1,0	1,0
Cranium width	0,5	0,6	0,6	0,6
Cranium depth	0,4	0,4	0,4	0,4
Skull width	0,5	0,5	0,5	0,5
Occipital style length	0,5	0,2	0,3	0,4
Upper jaw length	1,1	1,2	1,2	0,9
Upper jaw depth	0,2	0,2	0,2	0,2
Mandible length	2,0	2,0	2,1	1,7
Articular process length	0,2	0,2	0,2	0,2
Anterior mandible length	1,8	1,8	1,9	1,5
Quadrate bone length	0,2	0,2	0,2	0,2
No. specimens measured	6	3	10	3

TABLE 3

Mean maximum angles (degrees) of protraction and retraction of the jaw in adult cormorants

Species	Protraction		Retraction		No. birds measured
	\bar{x}	range	\bar{x}	range	
<i>P. lucidus</i>	36	34 - 38	18	17 - 19	2
<i>P. neglectus</i>	36	34 - 37	22	20 - 23	2
<i>P. capensis</i>	47	43 - 52	25	20 - 28	3
<i>P. africanus</i>	37	36 - 38	23	20 - 25	2

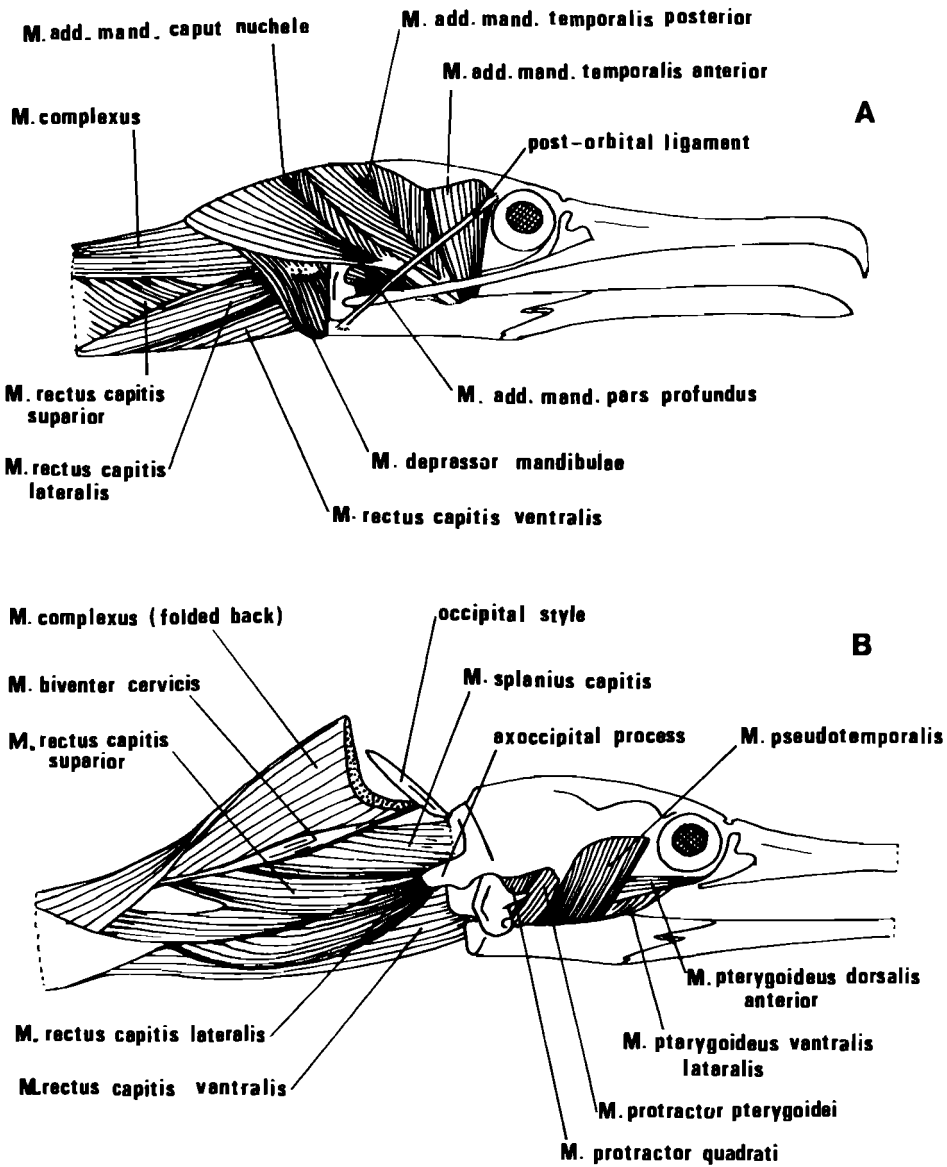


FIGURE 2

Lateral views of the jaw and anterior neck muscles of a cormorant (*P. lucidus*), showing (A) superficial muscles and (B) deep muscles.

3. *M. adductor mandibulae externus pars profundus*
4. *M. pseudotemporalis*

Group B: Abductor muscles

5. *M. depressor mandibulae*. This large muscle is responsible for abduction of the mandible. Recently, its role as a protractor of the upper jaw has been explained in birds, including cormorants, having "coupled" kinesis (Bock 1964; Zusi 1967).

Group C: Protractor muscles

6. *M. protractor pterygoidei*. The posterior end of this muscle is continuous with *M. protractor quadrati*. Separation of the two was possible by following the fibres of the pterygoid part from their insertion on the pterygoid bone. This muscle causes protraction of the upper jaw, by pulling the pterygoid bone forward.

7. *M. protractor quadrati*. This small muscle aids in protraction of the upper jaw by pulling the quadrate bone forward. This causes forward movement of the pterygoid and palatine bones. An additional function is to keep the quadrate bone firm during opening of the jaws (Bock 1964).

Group D: Retractor muscles

8. *M. pterygoideus*. Four subdivisions of this muscle were recognized, based on the origins, insertions and angles of action of each section: *M. pterygoideus ventralis medialis*, *M. pterygoideus ventralis lateralis*, *M. pterygoideus dorsalis anterior* and *M. pterygoideus dorsalis posterior*. This complex of muscles causes retraction of the upper

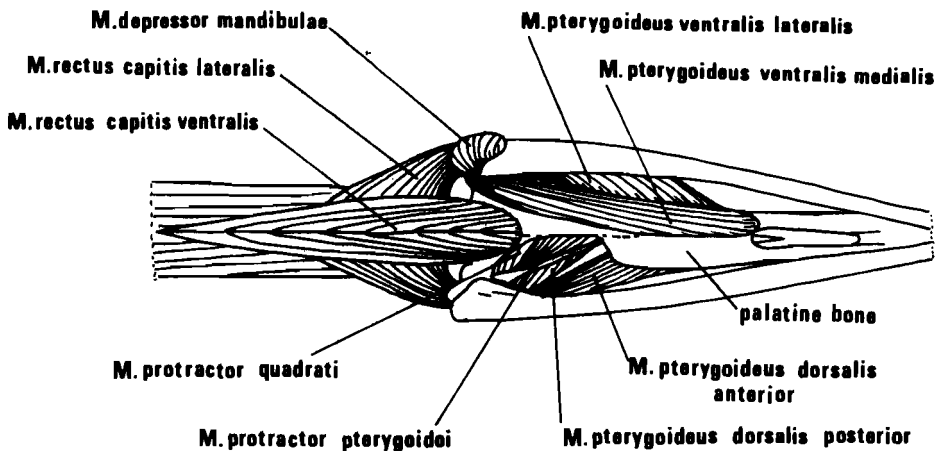


FIGURE 3

Ventral view of the jaw and anterior neck muscles of a cormorant (*P. lucidus*). *M. depressor mandibulae* and *M. pterygoideus ventralis* have been removed on the left side.

jaw by pulling the palatine and pterygoid bones backward. It also pulls the rami of the mandibles together as the jaw closes.

Size of the jaw muscles

The oven-dried masses of the jaw muscles are given in Table 4. Analysis of variance showed that the mean mass of each muscle differed significantly between the four species ($p < 0.05$). When expressed as a percentage of the total jaw musculature, the four jaw muscle systems have similar proportions in the four species (Table 5). These proportions are also similar to those in the double-crested cormorant *P. auritus*, yet differ from those of the American darter *Anhinga anhinga* (Owre 1967).

Total jaw muscle mass was compared with the total body mass of each species (Table 6). *Phalacrocorax lucidus* has relatively well-developed jaw muscles followed by *P. africanus* and *P. neglectus*. *Phalacrocorax capensis* has the smallest jaw muscles relative to body mass.

Forces of the jaw muscles

Preliminary calculations indicated that the maximum forces at the tip of the beak could be expected to occur with the jaws closed. This is due to the decrease in the angle of insertion of

TABLE 4
Mean mass (mg) of jaw muscles on one side of the skull in cormorants

Muscle	<i>lucidus</i>	<i>neglectus</i>	<i>capensis</i>	<i>africanus</i>
<i>M. add. mand. temp. anterior</i>	354	206	76	71
<i>M. add. mand. temp. posterior</i>	892	359	192	141
<i>M. add. mand. caput nuchale</i>	1493	540	334	258
<i>M. add. mand. pars profundus</i>	170	75	52	42
<i>M. pseudotemporalis</i>	339	147	72	49
<i>M. protractor pterygoidei</i>	204	124	63	45
<i>M. protractor quadrati</i>	68	27	24	13
<i>M. pterygoideus ventralis medialis</i>	542	278	175	118
<i>M. pterygoideus ventralis lateralis</i>	423	168	85	66
<i>M. pterygoideus dorsalis anterior</i>	219	100	48	30
<i>M. pterygoideus dorsalis posterior</i>	41	35	14	10
<i>M. depressor mandibulae</i>	509	268	158	87
Mean total jaw muscles	5228	2328	1288	930
No. specimens measured	5	2	3	2

the jaw muscles as the jaws open. For this reason, the moments of torque and the maximum forces resultant at the beak tip on closing, were calculated. The forces of adduction are considerably larger than other forces in the four species (Table 7). In all the species, *M. adductor mandibulae caput nuchale* makes the greatest contribution to the force of adduction (See Appendix). The forces of protraction are relatively small in all four species with *M. protractor pterygoidei* contributing the major force. The forces of retraction are large,

TABLE 5
Mean mass of the jaw muscle systems expressed as a percentage (\pm one SD) of the total jaw muscle mass in adult cormorants

Muscles	<i>lucidus</i>	<i>neglectus</i>	<i>capensis</i>	<i>africanus</i>
Adductors				
<i>M. add. mand. (all parts)</i>	55,0 \pm 1,5	50,8 \pm 0,8	50,4 \pm 0,8	56,3 \pm 1,0
<i>M. pseudotemporalis</i>	6,5 \pm 0,4	6,3 \pm 0,3	5,6 \pm 0,4	5,3 \pm 0,7
Total	61,5 \pm 0,9	57,1 \pm 0,7	56,0 \pm 0,6	61,6 \pm 1,6
Abductors				
<i>M. depressor mandibulae</i>	9,7 \pm 0,5	11,5 \pm 0,3	12,3 \pm 0,7	9,4 \pm 0,1
Protractors				
<i>M. protr. quadrati et pterygoidei</i>	4,7 \pm 0,4	6,5 \pm 0,1	6,8 \pm 0,3	6,2 \pm 0,1
Retractors				
<i>M. pseudotemporalis (all parts)</i>	23,4 \pm 0,5	25,1 \pm 0,6	25,1 \pm 1,2	24,0 \pm 0,1
No. specimens measured	5	2	3	2

TABLE 6
Mass of jaw and neck muscles in relation to whole body mass in cormorants
*Data from Rand (1960)

	<i>lucidus</i>	<i>neglectus</i>	<i>capensis</i>	<i>africanus</i>
Fresh body mass (g)*	2884	1867	1204	756
Dried jaw muscles (g)	10,46	4,65	2,58	1,86
Dried anterior neck muscles (g)	6,22	3,57	2,39	1,45
Ratio of jaw muscles to body mass	36 X 10 ⁻⁴	25 X 10 ⁻⁴	21 X 10 ⁻⁴	25 X 10 ⁻⁴
Ratio of neck muscles to body mass	21 X 10 ⁻⁴	19 X 10 ⁻⁴	20 X 10 ⁻⁴	19 X 10 ⁻⁴

emphasizing the importance of kinetic jaw movement. Approximately one-third of the force exerted at the tip of the beak, as it closes, originates from the complex *M. pterygoideus* (Table 7).

In *P. lucidus* and *P. africanus* the forces of the muscles are more effectively transmitted to the tip of the beak than in the other two species (Table 7). This relates to the larger mechanical advantage of the jaw muscle system of *P. lucidus* and *P. africanus* (Table 8). Thus, although all four species show adaptations for rapid rather than powerful biting, this is less evident in *P. lucidus* and *P. africanus* than in *P. neglectus* and *P. capensis*.

TABLE 7
Effective force at the tip of the beak and efficiency of the jaw muscle systems in adult cormorants (details in Appendix)

Species	Adductor muscles		Protractor muscles		Retractor muscles		Abductor muscles	
	Force (mg)	% efficiency	Force (mg)	% efficiency	Force (mg)	% efficiency	Force (mg)	% efficiency
<i>P. lucidus</i>	844	13	56	10	483	20	79	8
<i>P. neglectus</i>	307	12	22	7	176	15	45	8
<i>P. capensis</i>	173	12	10	6	91	14	27	9
<i>P. africanus</i>	160	14	11	10	90	20	21	12

TABLE 8
Mechanical advantage of the jaw muscles in adult cormorants

Muscle	<i>lucidus</i>	<i>neglectus</i>	<i>capensis</i>	<i>africanus</i>
<i>M. add. mand. temporalis anterior</i>	0,20	0,19	0,17	0,22
<i>M. add. mand. temporalis posterior</i>	0,18	0,17	0,16	0,16
<i>M. add. mand. caput nuchale</i>	0,16	0,15	0,15	0,21
<i>M. add. mand. pars profundus</i>	0,09	0,09	0,08	0,09
<i>M. pseudotemporalis</i>	0,09	0,09	0,09	0,12
All protractor muscles	0,21	0,16	0,15	0,21
All retractor muscles	0,21	0,16	0,15	0,21
<i>M. depressor mandibulae</i> (abductor)	0,08	0,08	0,08	0,12

Muscles of the neck

Only the anterior neck muscles which act upon the skull were considered, and six pairs were isolated (Figures 2-3). The superficial dermal muscle *M. dermatotemporalis* was not considered to be significant in head movement (Owre 1967).

1. *M. complexus*. Acting together this muscle and the one from the other side extend (raise) the head; when acting singly it turns the head laterally.

2. *M. biventer cervicis*. This muscle is very reduced in cormorants, and lacking in *Anhinga anhinga* (Owre 1967). Although very small, it provides a tendinous connection with the base of the neck, which may restrict forward or dorsal movement of the occipital style when the *M. adductor mandibulae caput nuchale* contracts.

3. *M. splenius capitis*. This stout triangular muscle lies deep to *M. complexus*, and acts to extend and rotate the skull.

4. *M. rectus capitis lateralis*. This is a superficial muscle on the lateral side of the neck; its main function is to effect lateral movements of the head.

TABLE 9

Mean mass (mg) of the anterior neck muscles and the percentage (figures in parentheses) of the total neck musculature inserting on the skull in adult cormorants. The muscles on both sides of the neck were combined.

Muscle	<i>lucidus</i>		<i>neglectus</i>		<i>capensis</i>		<i>africanus</i>	
<i>M. complexus</i>	1469	(23)	975	(27)	592	(25)	371	(25)
<i>M. biventer cervicis</i>	47	(1)	50	(1)	28	(1)	14	(1)
<i>M. splenius capitis</i>	963	(15)	479	(13)	296	(12)	155	(11)
<i>M. rectus capitis superior</i>	1038	(17)	665	(19)	322	(14)	178	(12)
<i>M. rectus capitis lateralis</i>	1231	(20)	676	(19)	473	(20)	269	(19)
<i>M. rectus capitis ventralis</i>	1472	(24)	727	(21)	674	(28)	460	(32)
No. specimens measured	2		1		2		1	

5. *M. rectus capitis superior*. Much of this muscle lies deep to *M. rectus capitis lateralis*. Simultaneous contraction on both sides of the neck muscles flexes the head, while unilateral contraction depresses the head to one side.

6. *M. rectus capitis ventralis*. This large muscle lies ventral to the vertebrae and the other neck muscles and causes flexion of the head. It may also help to rotate the head.

Relative sizes of the neck muscles

The total anterior neck musculature is of similar size, relative to body weight, in all four species (Table 6). The proportions of each pair of muscles are also similar in the four species (Table 9). *Phalacrocorax lucidus* and *P. neglectus*, however, have a proportionately larger *M. rectus capitis superior* and *P. capensis* and *P. africanus* have a proportionately larger *M. rectus capitis ventralis*. In all four species the neck muscle proportions are similar to those in *P. auritus* (Owre 1967).

Ecology

Food and foraging

Phalacrocorax lucidus is a marine and freshwater species (McLachlan & Liversidge 1970). The marine birds take fairly large fish (*Chilodactylus*, *Pachymetopon* and *Pterogymnus*) and crustaceans (including *Plagusia*) associated with shallow, inshore waters (Rand 1960; Siegfried *et al.* 1975). Inland, the species feeds on frogs and fish in lakes and vleis (McLachlan & Liversidge 1970). *Phalacrocorax neglectus* is strictly marine, foraging in the littoral zone (Siegfried *et al.* 1975). The species' diet includes slow-moving "rock fish", crustaceans and cephalopods (Table 10). *Phalacrocorax capensis* is a marine species, feeding mainly on fast-moving pelagic, shoaling fish (Table 10; Siegfried *et al.* 1975). *Phalacrocorax africanus* has marine and freshwater populations. The marine birds take small, slow-moving, benthic fish found close inshore (Table 11; Siegfried *et al.* 1975). The major food item in the diet of the freshwater birds is slow-moving, lurking fish (Table 11), and frogs are also frequently included (McLachlan & Liversidge 1970). Data on mass of prey and size of meal for the four cormorant species are given in Table 12.

Prey capture

Due to the cormorants' underwater feeding habits, little is known about their actual methods of prey capture. The available evidence suggests that most species swim rapidly through the water and prey is taken by surprise or actively pursued (Van Dobben 1952; Bowmaker 1963; Owre 1967). Van Dobben (1952) and Takashima & Niima (1957) analysed the wounds inflicted on fish by *Phalacrocorax carbo* and *P. capillatis* respectively. Both workers concluded that these cormorants invariably seized the fish just behind the gills, from above. A catch in this position secures the best hold on a wriggling fish and rapidly incapacitates the prey (Van Dobben 1952).

In the four South African cormorants a significant correlation occurs between the biting force (adduction + retraction) of each species and the mean mass of prey items ($r = 0,99$; $p < 0,001$; based on data in Tables 7 and 12). This relationship is represented by the linear regression equation

$$y = 0,15 x - 12,06$$

where y is prey mass (in grams) and x is relative biting force (in mg).

DISCUSSION

Skull and jaws

The skull proportions of the four cormorants indicate streamlining, a necessary prerequisite for efficient, rapid movement underwater. Beaks are long and the jaw muscles are situated farther back on the skull than in most birds (Fisher & Goodman 1955b; George & Berger 1966; Burton 1974). This results in poor mechanical advantage, indicating adaptations for rapid rather than powerful jaw movements. Owre (1967) considered the posterior situation of the adductor muscles to possibly facilitate "mouthing" of food objects by cormorants. Such mouthing would permit food to be drawn deeper into the beak.

The broad posterior region of the cormorant skull affords a large area for attachment of jaw muscles. The large muscle mass ensures that, in spite of poor mechanical advantage, a

TABLE 10

Stomach contents (percentage aggregate mass) of *P. capensis* and *P. neglectus* from the south-western Cape (Davies 1956; Rand 1960) and from Namibia (Mathews 1961; Berry 1976).

¹*Trachurus, Pterosmaris, Scomber, Etrumeus, Sardinops & Engraulis*; ²*Gonorhynchus, Ammodytes & Heteromycteris*; ³Triglidae; ⁴Clinidae, Blennidae, *Chorisochismus & Conger*

Prey	<i>P. capensis</i>				<i>P. neglectus</i> Rand
	Davies	Rand	Mathews	Berry	
Pelagic shoaling Fish ¹	89	58	97	99	1
Inshore sandy-bottom fish ²	0	30	0	0	12
Benthic fish ³	0	1	0	0	7
Littoral/kelp-bed fish ⁴	5	3	0	1	61
Others or unidentified	5	5	3	1	0
Invertebrates	1	4	0	1	21
Sample sizes	77	204	210	93	73

powerful bite is still possible. The presence of an occipital style, and greatly enlarged *M. adductor mandibulae caput nuchale*, is unique to the Phalacrocoracidae and the Ahhingidae (Owre 1967). This arrangement is clearly a means of increasing the mass of the adductor muscles without reducing streamlining of the head. A large sagittal crest would allow increased muscle attachment, but would reduce streamlining. The occipital style articulates on the back of the skull; if it were fused to the skull the movement of the head and neck would be restricted. The specific size of the *caput nuchale* muscle correlates well with the size (length) of the occipital style.

In each species the forces of adduction and retraction are far in excess of the forces of protraction and abduction. The maximum force of adduction occurs when the jaws are least open, during the final stages of the biting action. The wide gape and throat can accommodate fairly large prey, swallowed whole. The dentary-surangular suture forms a hinge on the

TABLE II

Prey consumed by *P. africanus* in freshwater lakes (A) and at sea (B). Data for (A) from Bowmaker (1963), based on stomach-contents of 83 specimens. Data for (B) from Rand (1960), based on stomach-contents of 9 specimens

Prey	% aggregate mass	% frequency of occurrence	Mean mass (g) of prey objects
A) FRESHWATER FISH			
Mormyridae	35	21	24,5
Characidae	2	5	5,2
Schilbeidae	19	16	28,1
Clariidae	13	13	18,5
Machokidae	3	3	31,5
Cichlidae	24	35	14,6
Anabatidae	4	7	17,0
B) MARINE FISH			
Centracantidae	—	3	—
Clinidae	—	12	—
Syngnathidae	—	18	—
Gobiesocidae	—	1	—
Soleidae	—	34	—
"Shrimps"	—	32	—

mandible ramus which can bend outward to allow passage of large prey into the gullet. The gular membrane itself is very flexible.

The extent of kinetic jaw movement in cormorants is large relative to other birds. In addition, approximately a third of the biting force (adduction and retraction) results from forces of retraction, delivered by the *M. pterygoideus* complex. This illustrates the importance of kinesis in these cormorants. Bock (1964) has pointed out some of the advantages of kinetic movement in avian skulls. With both jaws able to move, both the gape and the speed of movement of the jaws are increased. There is more favourable distribution of jaw musculature and greater force is possible. Bock also pointed out that movement of the upper jaws permits a bird to grasp prey directly in front of it, without any change in the orientation of the head axis. These characteristics can be viewed as adaptations for catching fast-moving prey.

Anterior neck region

The large anterior neck muscles, which insert on the back of the skull, are responsible for movement of the head relative to the neck. Considerable mobility of the head is required in grasping and manipulating prey. Cormorants usually bring the prey to the surface and manipulate it into position for swallowing, mainly by the action of the neck and jaws (Van Dobben 1952; Bowmaker 1963; Owre 1967). The tongue and tongue muscles of the four cormorants are small. The tongue probably plays little part in the manipulation of prey after capture. In this respect cormorants differ from penguins, which have well-developed tongues and which ingest prey underwater (Zusi 1975).

The four cormorants have well-developed muscles on all sides of the neck. These muscles, inserting on the broad occiput, produce powerful movements of the head. The proportions of the muscles are similar to those of *P. auritus* (Owre 1967). Owre believed this species to have the potential for extensive movements of the head in all directions. Most neck muscles act in complex combinations. Consequently, it is difficult to explain differences in relative size of neck muscles in relation to any specific head movement. The large dorsal neck muscles in *P. lucidus* and *P. neglectus* may be adaptations for manipulating large prey above the water. The proportionately large ventral neck muscles of *P. capensis* and *P. africanus* indicate greater potential for flexion of the head. The four South African species appear to have adaptations for rapid and powerful movement of the head in all directions. The presence of a long neck in all the species enhances this ability.

Differences and similarities in head anatomy

The significant differences in skull dimensions between the four species appear to be due to the absolute size differences, and not to modifications of osteological development. The skull dimensions, relative to cranial length, are remarkably similar for all four species. Similarly, the jaw muscles and necks of the four cormorants are significantly different in absolute size, but are similar in relative size.

Although widely used for comparative purposes (Goodman & Fisher 1962; Owre 1967), the dimensions of the muscles themselves are not necessarily the most accurate indicators of

jaw function and adaptation. The feeding action of the jaws is also affected by the linear dimensions and proportions of the skull, the points and angles of insertion and origins of the muscles, and the presence of ligaments (Goodman & Fisher 1962; Bock 1964). A mode of comparison which encompasses these variables is the comparison of the effective forces exerted on the beak by the jaw muscles.

The calculated effective forces at the tip of the beak are clearly different for each species. These forces correlate well with the average mass of prey taken. The greater forces of adduction and retraction of the larger species of cormorant presumably permit capture and handling of larger prey. The ratio of jaw muscle mass (and thus the force at the beak tip) to body mass is relatively constant between species (Table 6 and Appendix). It seems to be the size difference between the cormorants *per se* which results in differentiation of the prey size.

Although the relative proportions of the skulls, jaw muscles and neck muscles of the four species are similar, slight differences were found in some parameters. These differences are thought to be linked to the specific feeding methods and prey types.

Phalacrocorax lucidus is not only the largest of the four species, but also has the largest jaw and neck musculature relative to body mass. The adductor muscles of the jaws are particularly well developed. The forces of the adductor and retractor muscles are efficiently converted to a biting force at the tip of the beak. This is achieved by the relatively large mechanical advantage of the jaw muscle-lever systems. Kinesis is less well developed than in the other three species. The jaw system appears to be adapted for more powerful biting than in the other cormorants considered, although, as in all the cormorants, adaptations for rapid jaw movement are evident. The few data available suggest that *P. lucidus* takes fairly large prey, relative to body mass.

Phalacrocorax neglectus and *P. capensis* are intermediate in the range of body size for South African cormorants. *Phalacrocorax neglectus* differs, however, in that the total jaw musculature is larger, relative to body mass. The forces of these muscles are not efficiently transmitted to the beak tip, due to the fairly low mechanical advantage of the jaw muscle-lever systems. Kinesis is moderately well developed. From the available data, it would appear that *P. neglectus* has a wider range of food types than the other three cormorants. A substantial part of its diet appears to be crustaceans and cephalopods. The somewhat generalized structure of the jaws and neck muscle systems may be linked with this diet.

The total jaw musculature of *P. capensis* is smaller, relative to body mass, than in the other three species. Muscle forces are also least efficiently transmitted to the beak tip. This is due to the proportionately longer beak and lower mechanical advantage of the jaw muscle systems, suggesting that the jaws are adapted for rapid, rather than powerful movement. This species has the greatest kinetic movement of the four species. This is enhanced by proportionately large abductor, protractor and retractor muscles. Adaptations for securing fast-moving prey are evident in all the anatomical features of the head region. It is hardly surprising then to note that the prey most often taken by this species is indeed relatively small, fast-moving, pelagic fish.

The relative proportions of the head region of *P. africanus* are somewhat similar to those

of *P. lucidus*, in spite of the great size difference between the two species. The jaw adductor muscles of both are proportionately well developed. The efficiency of the jaw muscle-lever systems in transmitting force to the tip of the beak is greatest in *P. africanus*. This is due to the proportionately short beak, which results in a higher mechanical advantage than in the other three species. The small forces resultant at the tip of the beak would allow relatively small prey to be taken. The kinetic jaw movements are large in *P. africanus*, but still smaller than in *P. capensis*. Adaptations for taking fast-moving prey are thus more similar to those of *P. lucidus*. Bowmaker (1963) showed that *P. africanus* did not take the common, fast-moving fish in inland lakes. Although both *P. africanus* and *P. lucidus* seem to have similar adaptations of the head region and frequently occur sympatrically, competition could be reduced by the great difference in body size between the two species. The size range of prey taken by each species does not overlap significantly (Table 12).

Adaptations for feeding in animals are not limited to the head region. Adaptations and differences in limb and axial anatomy probably exist among the four South African cormorant species. Behavioural differences are known to occur, particularly in relation to foraging and nesting habits (Rand 1960; McLachlan & Liversidge 1970; Siegfried *et al.* 1975).

TABLE 12

Mean mass of meal and prey objects consumed by four species of cormorant

*Data from Rand (1960)

†Data from Bowmaker (1963)

Species	Mean mass (g) of meal	Mean mass (g) and range of prey objects	Mean mass of prey objects as percentage of bird's mean mass
<i>P. lucidus</i> *	270	187 29-458	6,5
<i>P. neglectus</i> *	146	68 5-214	3,6
<i>P. capensis</i> *	104	37 2-125	3,1
<i>P. africanus</i> (at sea)*	21	17 2-31	2,3
<i>P. africanus</i> (inland)†	24	20 3-50	2,7

ACKNOWLEDGEMENTS

I am grateful to Peter Frost, Jenny Jarvis and Roy Siegfried for their encouragement, advice and help. The Council for Scientific and Industrial Research and the University of Cape Town provided financial assistance and the latter provided aid for publication.

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APPENDIX

The moments of torque of the jaw muscle systems and the forces resultant at the tip of the bill in the four cormorants. The muscle force from both sides of the jaw were considered. Superscripts: 1, upper jaw depth at the nasal-frontal hinge (from Table 1); 2, torque on the quadrate bone; 3, torque on the upper jaw calculated from 2.

Muscle:	Muscle mass (mg)	Length of force arm (mm)	Muscle angle	Torque (mg x mm)	Force at bill tip (mg)
<i>P. LUCIDUS</i>					
M. add. mand. temporalis anterior	708	24	91	16989	146
M. add. mand. temporalis posterior	1784	21	64	33672	289
M. add. mand. caput nuchale	2986	19	44	39411	338
M. add. mand. pars profundus	340	11	56	3101	27
M. pseudotemporalis	678	11	137	5086	44
TOTAL ADDUCTORS	6496			98259	844
M. protractor pterygoidei	408	15 ¹	56	3422	47
M. protractor quadrati a)	136	7	42	(637) ²	—
b)	(46)	15 ¹	10	680 ³	9
TOTAL PROTRACTORS	544			4102	56
M. pterygoideus ventralis medialis	1084	15 ¹	9	16060	220
M. pterygoideus ventralis lateralis	846	15 ¹	13	12365	169
M. pterygoideus dorsalis anterior	438	15 ¹	23	6048	83
M. pterygoideus dorsalis posterior	82	15 ¹	48	823	11
TOTAL RETRACTORS	2450			35296	483
M. depressor mandibulae	1018	9	90	9162	79

Muscle:	Muscle mass (mg)	Length of force arm (mm)	Muscle angle	Torque (mg x mm)	Force at bill tip (mg)
<i>P. NEGLECTUS</i>					
M. add. mand. temporalis anterior	412	21	74	8317	77
M. add. mand. temporalis posterior	718	18	50	9900	91
M. add. mand. caput nuchale	1080	16	40	11108	103
M. add. mand. pars profundus	150	10	46	1079	10
M. pseudotemporalis	294	10	104	2853	26
TOTAL ADDUCTORS	2654	—	—	33257	307
M. protractor pterygoidei	248	11 ¹	62	1281	19
M. protractor quadrati a)	54	6	45	(229) ²	—
b)	(19)	11 ¹	20	196 ³	3
TOTAL PROTRACTORS	302			1477	22
M. pterygoideus ventralis medialis	558	11 ¹	8	6078	88
M. pterygoideus ventralis lateralis	336	11 ¹	14	3586	52
M. pterygoideus dorsalis anterior	200	11 ¹	26	1977	29
M. pterygoideus dorsalis posterior	70	11 ¹	51	485	7
TOTAL RETRACTORS	1164			12126	176
M. depressor mandibulae (ABDUCTOR)	536	9	89	4823	45

P. CAPENSIS

M. add. mand. temporalis anterior	152	16	88	2431	26
M. add. mand. temporalis posterior	384	15	60	4988	52
M. add. mand. caput nuchale	668	14	50	7164	75
M. add. mand. pars profundus	104	8	50	637	7
M. pseudotemporalis	144	9	109	1225	13
TOTAL ADDUCTORS	1452			16445	173

Muscle:	Muscle mass (mg)	Length of force arm (mm)	Muscle angle	Torque (mg x mm)	Force at bill tip (mg)
M. protractor pterygoidei	126	9 ¹	64	497	8
M. protractor quadrati a)	48	5	40	(154) ²	
b)	(16)	9 ¹	16	138 ³	2
TOTAL PROTRACTORS	174			635	10
M. pterygoideus ventralis medialis	350	9 ¹	7	3127	51
M. pterygoideus ventralis lateralis	170	9 ¹	12	1497	24
M. pterygoideus dorsalis anterior	96	9 ¹	24	789	12
M. pterygoideus dorsalis posterior	28	9 ¹	50	162	3
TOTAL RETRACTORS	644			5575	91
M. depressor mandibulae	316	8	88	2526	27
<i>P. AFRICANUS</i>					
P. add. mand. temporalis anterior	142	15	76	2067	31
P. add. mand. temporalis posterior	282	11	60	2686	40
P. add. mand. caput nuchale	516	14	43	4927	73
P. add. mand. pars profundus	84	6	54	408	6
P. pseudotemporalis	98	8	118	692	10
TOTAL ADDUCTORS	1122			10780	160
M. protractor pterygoidei	90	8 ¹	62	338	9
M. protractor quadrati a)	26	4	40	(67) ²	
b)	(8)	8 ¹	18	61 ³	2
TOTAL PROTRACTORS	116			399	11
M. pterygoideus ventralis medialis	236	8 ¹	6	1878	49
M. pterygoideus ventralis lateralis	132	8 ¹	15	1020	26
M. pterygoideus dorsalis anterior	60	8 ¹	22	445	12
M. pterygoideus dorsalis posterior	20	8 ¹	40	123	3
TOTAL RETRACTORS	448			3466	90
M. depressor mandibulae (ABDUCTOR)	174	8	86	1389	21