

STRUCTURAL ADAPTATIONS OF THE  
HEAD AND NECK  
IN THE BLACK SKIMMER

*Rynchops nigra* Linnaeus

PUBLICATIONS OF THE NUTTALL ORNITHOLOGICAL CLUB, NO. 3

EDITOR, OSCAR M. ROOT

STRUCTURAL ADAPTATIONS OF  
THE HEAD AND NECK  
IN THE BLACK SKIMMER,

*Rynchops nigra* Linnaeus

by <sup>Lawrence</sup>  
RICHARD L. ZUSI

CAMBRIDGE, MASSACHUSETTS

Published by the Club

1962

Wisconsin.

an Herons.  
aid.

, *Rynchops*  
0 postpaid.

QL  
696  
C4Z96  
Birds

#### ACKNOWLEDGMENTS

Many people have helped me during this investigation. I am indebted to the late Josselyn Van Tyne for his guidance and encouragement during the early phase of the study. Andrew J. Berger, Claude W. Hibbard, Frederick H. Test, and, especially, Robert W. Storer gave generously of their time in reading and criticizing the manuscript.

Luther Goldman and Don Eckelberry extended their hospitality and invaluable assistance to me during my field work. Through the former's courtesy I was able to work on the Laguna Atascosa National Wildlife Refuge during the summer of 1956. Financial assistance for field work was provided by the Mae P. Smith Research Fund of the American Museum of Natural History.

For the use of specimens, I wish to thank the curators of the University of Michigan Museum of Zoology, the American Museum of Natural History, the Chicago Museum of Natural History, and the United States National Museum.

Among those who have given advice, criticism, encouragement, technical assistance, and help with translations, I should like to thank especially Philip S. Humphrey, Robert R. Miller, A. D. Moore, Peter Stettenheim, Harrison B. Tordoff, Rolf Vik, and Eva Wolfe. Mrs. Jennie Boynton generously typed the entire manuscript.

The present paper is a modification of a Doctoral Dissertation presented to the Faculty of the University of Michigan in partial fulfillment of the requirements for the degree of Doctor of Philosophy, 1959. For critically reading this manuscript and for making many excellent suggestions I am indebted to Harvey I. Fisher and Oscar M. Root.

I am particularly indebted to my wife Luvia for her constant encouragement and constructive criticism.

RICHARD L. ZUSI

University of Maine  
Orono, Maine  
February 1, 1962

from the  
y, Harvard

SMITHSONIAN  
INSTITUTION

JUL 6

1960

## CONTENTS

INTRODUCTION .....	1
METHODS AND FIELD WORK .....	2
PART 1. FEEDING BEHAVIOR .....	5
LITERATURE .....	5
SKIMMING .....	5
CATCHING PREY .....	11
SPEED OF SKIMMING .....	13
TIME OF SKIMMING .....	13
FEEDING HABITAT .....	13
FEEDING OF YOUNG .....	14
GULL-BILLED TERN, <i>Gelochelidon nilotica</i> .....	15
ROYAL TERN, <i>Thalasseus maximus</i> .....	16
LAUGHING GULL, <i>Larus atricilla</i> .....	18
PART 2. STRUCTURAL ADAPTATIONS .....	20
ADAPTATIONS OF THE BILL .....	20
ADAPTATIONS OF THE HEAD .....	28
SKULL AND JAWS .....	28
FORCES .....	28
PROPORTIONS .....	29
ARTHROLOGY .....	32
LOWER JAW .....	33
UPPER JAW AND PALATE .....	36
JAW MUSCULATURE .....	41
M. DEPRESSOR MANDIBULAE .....	44
M. PROTRACTOR QUADRATI .....	47
M. ADDUCTOR MANDIBULAE EXTERNUS .....	49
M. ADDUCTOR MANDIBULAE POSTERIOR .....	53

## INTRODUCTION

Highly specialized animals provide excellent material for the study of structural adaptation. Their range of behavior patterns is extremely limited, and we may say with fair assurance that some structures and some habits are mutually adaptive. Specializations in feeding and locomotion, for example, are frequently correlated with striking modifications in body form. Any modification of a structure that makes it particularly suited to its role in the life of an animal may properly be called an "adaptation." By emphasizing the adaptive nature of structural features, we obtain a clearer picture of the pathways along which present structures have evolved, and of the selective forces guiding their evolution.

The Black Skimmer, *Rynchops nigra* Linnaeus,<sup>1</sup> presents one of the most remarkable feeding specializations among birds. My purpose is to describe the feeding behavior of this species and to elucidate some of its associated structural modifications. In the absence of information about the genetic systems controlling the development of the structures I have studied, it is impossible to say that selection has produced a particular character, or to know what complexes of characters and behavior may be genetically associated. Nevertheless I shall regard as an adaptation each minute feature that, in itself or in combination with other characters, seems to be modified for feeding. This approach will emphasize the subtleties of structural modification without implying that there is a separate genetic system for each adaptation.

Ideally, the Black Skimmer should be compared to the ancestral form from which it evolved, but with the scant fossil record of the gull-like birds (lariforms, from *Lari*: Skuas, Gulls, Terns, and Skimmers) this comparison is not possible at the present time. Instead, I have compared the Black Skimmer with the Royal Tern, *Thalasseus maximus* (Boddaert), the Gull-billed Tern, *Gelochelidon nilotica* (Gmelin), and the Laughing Gull, *Larus atricilla* Linnaeus. These three birds share a common structural plan with the Black Skimmer, indicating a close relationship, but they are, to varying degrees, less specialized in feeding habits and structure and in these respects are probably less modified from the ancestral condition. The Royal Tern and the Gull-billed Tern represent opposite extremes in the continuum of feeding

<sup>1</sup>Scientific names are from the *Check-List of North American Birds*, American Ornithologists' Union, Fifth Edition, 1957.

methods from diver to nondiver within the Sterninae, and consequently are well suited to illustrate structural diversity within this group.

The Black Skimmer is one of three species of the family Rynchopidae. This family has a wide distribution, and each species is geographically isolated. *Rynchops nigra* occurs in North and South America, *R. flavirostris* Vieillot in Africa, and *R. albigollis* Swainson in India, Burma, and Indochina. These birds are similar in form, but differ somewhat in size, bill color, and plumage pattern. Relatively little is known of the structure and habits of the African and Asian species.

#### METHODS AND FIELD WORK

I collected specimens for this study between June 26 and August 8, 1955, on the Bolivar Peninsula, Galveston County, Texas. From June 10 to August 9, 1956, I made an intensive analysis of the feeding behavior of the four species, primarily on the Laguna Atascosa National Wildlife Refuge in Cameron County, Texas, and on nearby offshore islands. Observations were supplemented by movies taken at 32, 48, or 64 frames per second. On July 11-13, 1957, I made further observations of Black Skimmers on Long Island, Suffolk County, New York, and at Stone Harbor, Cape May County, New Jersey, September 12-13, 1957.

I dissected four preserved specimens of each species, including both sexes, under a binocular microscope (9X). I photographed skeletal elements and traced all base drawings, with the exception of diagrammatic figures, from projected images.

In order to detect differences in relative development of particular structures in several species, one must first eliminate differences related to body size alone. Amadon (1943) has made a careful study of the use of body weight as an index of body size. Although his applications of this index were primarily taxonomic, the index is equally useful for functional-anatomical studies. The following passages are especially pertinent to this discussion:

Differences in general size of solids will always be reflected more accurately by an index such as weight, which is proportional to the mass or volume of the object, than by any single linear measurement. (p. 168)

The variability of volumes or weights will, to some extent, represent the cumulative variabilities of the linear dimensions of the object, and will inevitably have a larger value than that of any one linear dimension. It is usually advisable to use the cube roots of weights rather than the weights themselves as a standard of comparison for linear measurements. . . . Extracting the cube roots has the effect of reducing the variability to a value comparable with that of linear dimensions. (p. 171)

Simpson (1957:60) has further emphasized the need to have the same number of dimensions in both terms of a ratio used as an index of relative size.

I have used the mean body weight for each species as an index of its general size, and the mean cube root of body weight as a standard for comparing linear measurements. Body weights were obtained from the labels of skeletons and skins in the collections of the University of Michigan Museum of Zoology, from published data, and from my field catalog. Certain statistics of these weights and their cube roots are presented in Table I. The variabilities of many cube roots of body weight compare favorably with those of many linear measures of skeletal elements—for example, the measurements presented by Engels (1940) and Storer (1952).

TABLE I  
BODY WEIGHTS

Species	Sex	Mean (gms.)	Range	Mean Cube Root	S.D. of Cube Root	C.V. of Cube Root	Sample Size
Larus atricilla	♂	348	282-392	7.03	0.22	3.13	13
Gelocheidon nilotica	♂ ♀	166	150-190	5.50	0.14	2.55	11
Thalasseus maximus	♂ ♀	461	374-532	7.72	0.22	2.85	24
Rynchops nigra	♂	351	308-374	7.05	0.16	2.27	6
Rynchops nigra	♀	254	232-295	6.33	0.18	2.84	6

The following procedure served to adjust all drawings in a figure to the same body size: (1) a millimeter rule was photographed with each specimen; (2) the photograph of each specimen was projected on the drawing paper and the number of millimeters comparable to the cube root of body weight for that species was noted on the projected rule; (3) this length was altered, by moving the projector, until it equaled an arbitrary standard length; (4) each species in a given figure was altered in this way to conform to the same standard length before the drawing was made. The differences in proportions of parts of the species compared in an illustration are therefore independent of body size, and they represent adaptations to particular feeding methods in many instances.

Although the pictorial method of comparison has the disadvantages that variability is not presented and that comparison of data with those of other workers is difficult, the drawings nevertheless present many anatomical facts in a more striking, more meaningful, and more concise way than tables of measurements could do, especially when one is dealing with such complex structures as the skull and vertebrae. Accurate and useful measurements of weight, volume, or cross-sectional areas of the pennate jaw muscles, however valuable, would be difficult to obtain.



## Part I

### FEEDING BEHAVIOR

Knowledge of details of the feeding process of the Black Skimmer is important for an understanding of structural modifications. The following analysis of feeding behavior is based largely on my own observations and on a study of slow-motion movies taken by me in southern Texas.

#### LITERATURE

Numerous authors have expressed a variety of observations and theories concerning feeding methods of the Black Skimmer. Excellent accounts of these birds catching fish and crustaceans while skimming are those of Azara (1802:144), Audubon (1838:205), Wilson and Bonaparte (1878:34), Darwin (1888:170), Pettingill (1937:242), Davis (1951:259), and Tomkins (1951:237). Theories that cannot be accepted today are those of Lesson (1828:385-86), Housse (1945:148), Koenig (1932:35), Roberts (1940:123), Priest (1934:171), and Arthur (1921) concerning mollusc feeding, scooping up microorganisms, probing in the sand, and catching fish while wading.

Of 10 stomachs of the Black Skimmer examined by Leavitt (1957), 6 contained both fish and shrimp, and 4 contained only fish. He suspected that filamentous green algae found in several stomachs were inadvertently swallowed. There is general agreement in the literature that the food of *R. nigra* is largely fish and crustaceans, and there is little doubt that these are taken almost exclusively while skimming.

#### SKIMMING

While skimming, the Black Skimmer's body is horizontal or tilted slightly up in back and down in front, and the neck and head are angled downward (Figures 1, 6). The tail is usually spread, and it is sometimes rotated almost vertically when the bill strikes a submerged object (Figure 4). Ordinarily the feet remain folded under the tail, only rarely being lowered for paddling. The motion and position of the wings vary with the direction of skimming relative to the direction of the wind. While skimming, the bird may flap rapidly with regular beats, it may alternately flap and glide or it may glide for considerable periods. The wing tips seldom touch

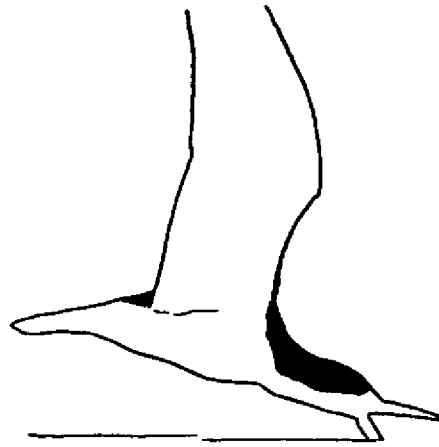


FIGURE 1. Lateral view of *Rynchops nigra*, showing typical skimming posture.

the water although they may come within an inch or two of the surface. The wing of a skimming bird travels through a maximum arc of about  $45^\circ$  (Figure 2), but as Young (1928:768) has pointed out, the arc is often less than this, giving skimming flight a fluttering appearance. One wing may travel through a larger arc than the

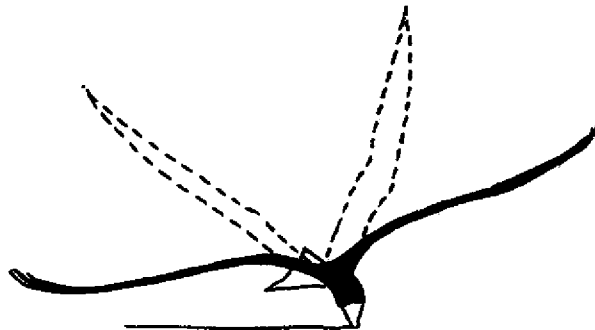


FIGURE 2. Anterior view of *Rynchops nigra* skimming, showing extent of wing beat.

other, or one may be flapped while the other is not. In gliding, the wings are held fully extended at a positive dihedral of about  $40^\circ$ . The longitudinal axis of the head and neck is sometimes turned to one side of the body's axis, the direction of the bird following that of the axis of the head and neck rather than that of the body.

When the lower jaw strikes something, a number of adjustments allow the bird to capture prey while maintaining the continuity of its flight. The head may be simply flexed on the neck at the occipital condyle so that only the bill and face are submerged (Figure 5). The head is then brought forward and raised to body height, and the bill is lifted out of the water. Also, the head may be submerged and doubled under the body so that the bill points directly backwards (Figures 3, 6, 7). The belly is held about two inches from

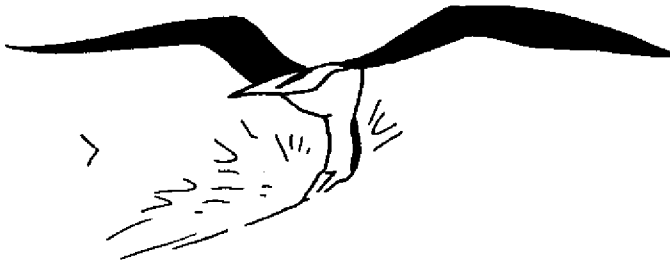


FIGURE 3. Posterolateral view of *Rynchops nigra* striking a submerged object.

the water, leaving room for withdrawal of the head from the water while it is still doubled under the body. The backward motion of the head is sometimes more or less to one side rather than along the median line.

I do not know whether the downward and backward motion of the head results primarily from voluntary contraction of the ventral neck muscles or whether it is a passive motion caused by the inertia



FIGURE 4. Series showing *Rynchops nigra* striking a submerged object. Numbers in brackets indicate number of movie frames omitted.

of the prey. It seems likely that the initial movement after impact is followed by a voluntary downward head-thrust, during which the bill is snapped shut.

When the bill strikes a submerged object, the tail is spread and depressed for a fraction of a second, producing a momentary braking effect (Figures 6, 7). During the downstroke, which is not completed until the head has bent under the body and is out of the

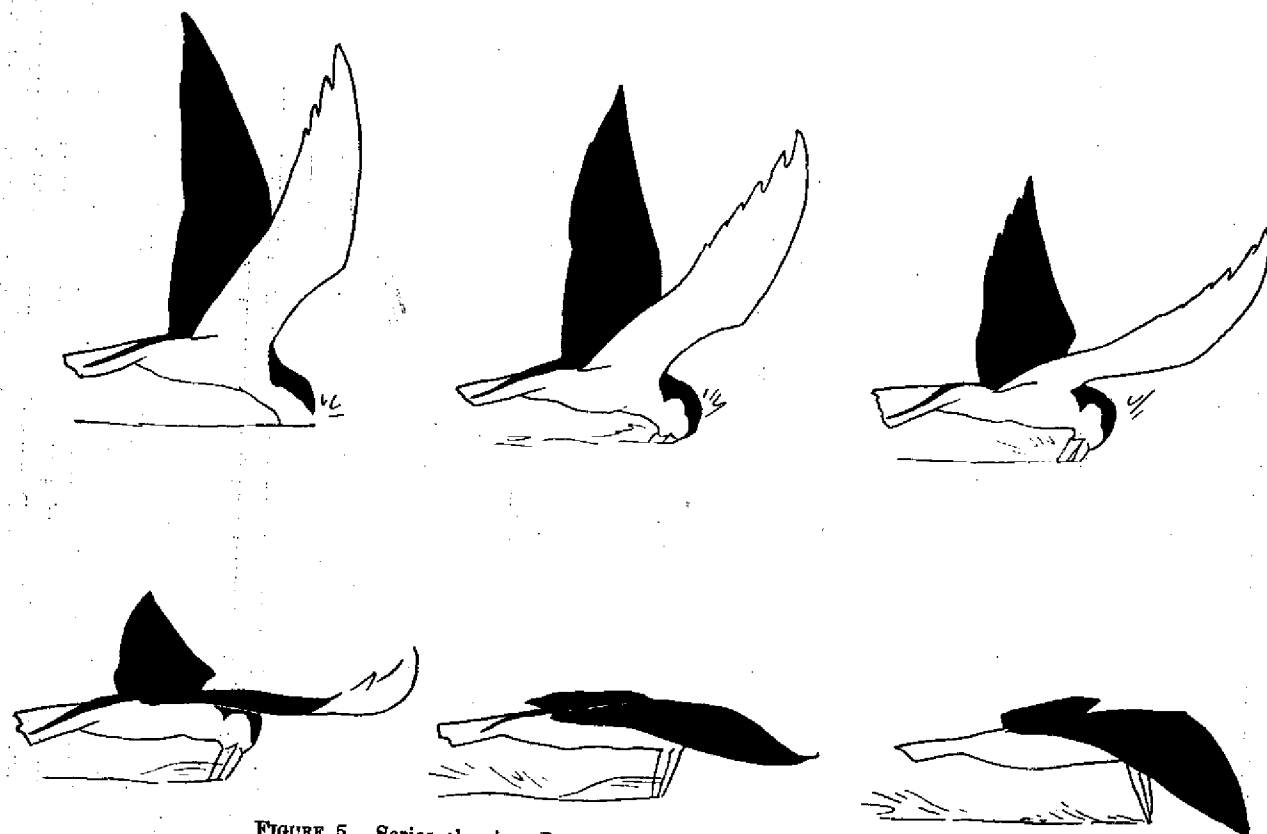


FIGURE 5. Series showing *Rynchops nigra* striking a submerged object.

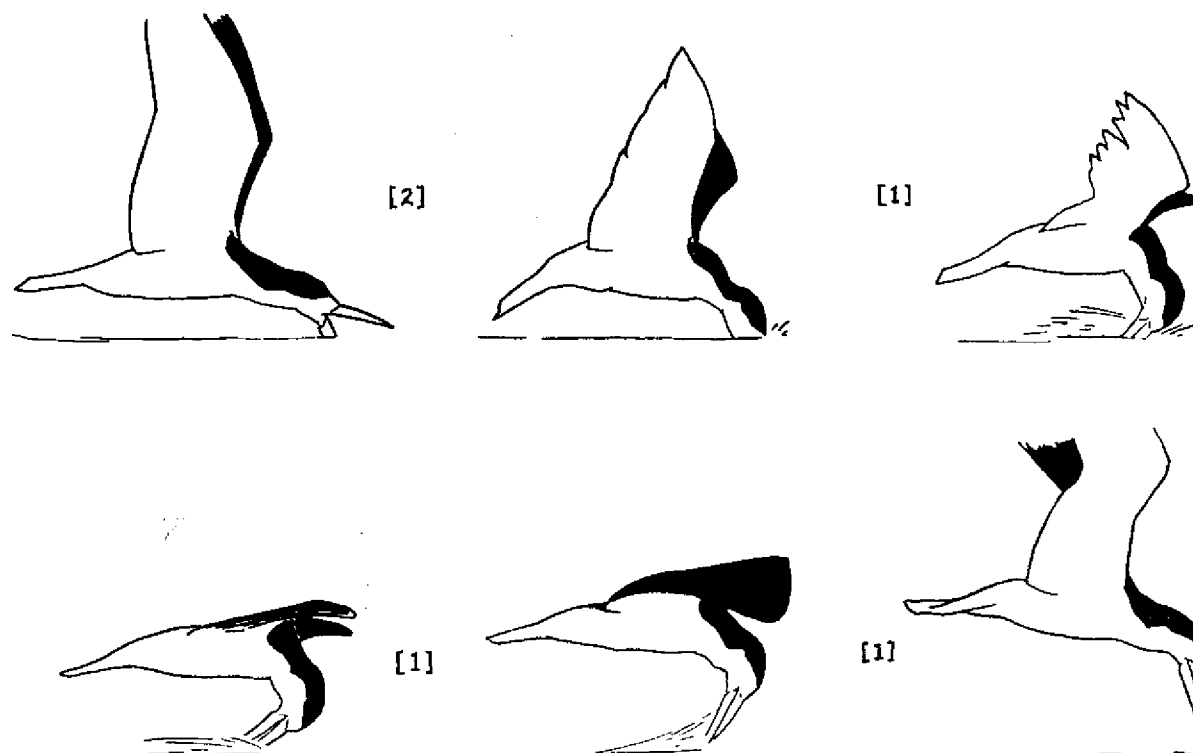


FIGURE 6. Series showing *Rynchops nigra* striking a submerged object. Numbers in brackets indicate number of movie frames omitted.

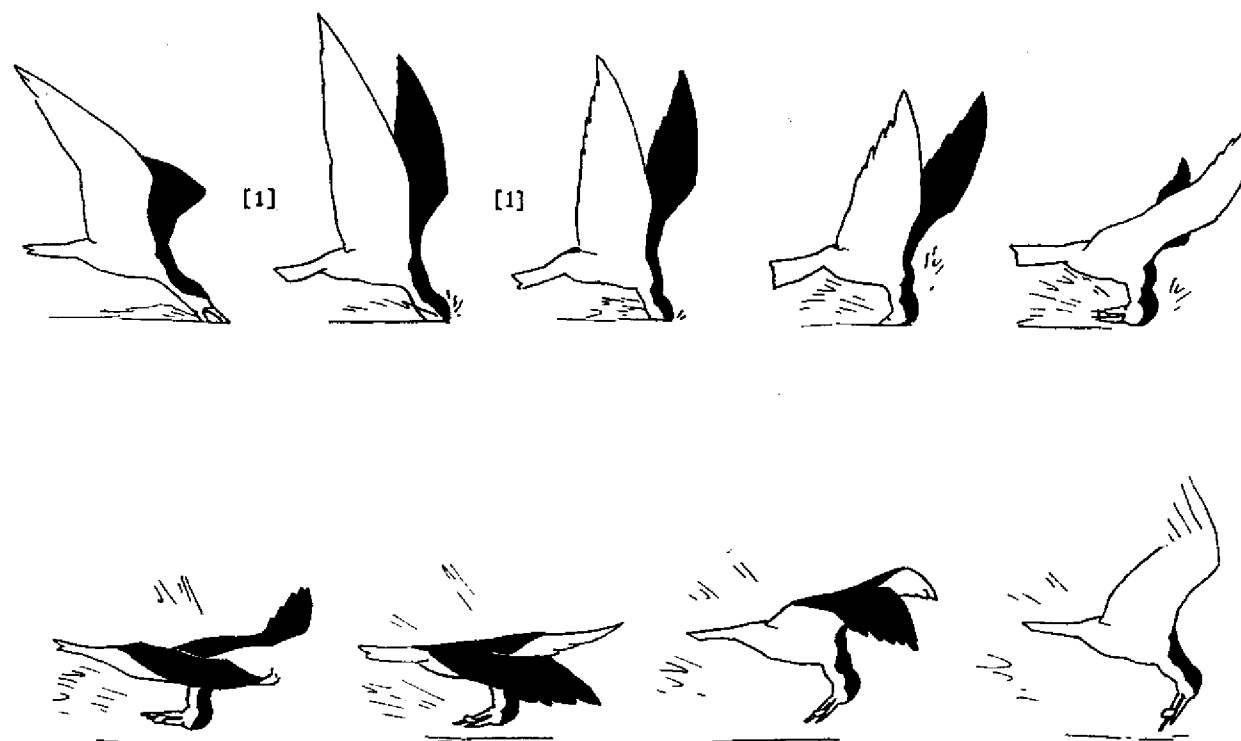


FIGURE 7. Series showing *Rynchops nigra* catching a fish. Numbers in brackets indicate number of movie frames omitted.

water, the wings are drawn forward, thus providing lift anterior to the center of gravity (Figure 7). This lift counteracts water pressure on the head and air pressure on the tail that tend to rotate the bird downward anteriorly. The immediate return of the tail to its normal position also helps to counteract the rotary motion of the bird. During this period of disrupted equilibrium the wing beat is accelerated, or, if the bird has been gliding, the wings are flapped. An aspect of the skimming position scarcely altered at this time is the position of the body (Figures 6, 7).

I have measured the angle of the tomium of the lower jaw relative to the water surface on drawings traced from projected motion-picture frames. The birds were moving at right angles to the camera in every case, and the error of the measurements is probably within  $\pm 3^\circ$ . Forty-seven measurements taken from birds that were skimming with the lower jaw rather deeply immersed averaged  $60^\circ$  (range,  $35^\circ$  to  $99^\circ$ ). Audubon (1838:205) and Roosevelt (1916:275) stated that the angle is  $45^\circ$ , and Davis (1951) estimated  $40^\circ$ . In general, the angle decreases as the depth of immersion of the lower jaw decreases, but an angle of  $35^\circ$  is probably minimal even when the bill is only slightly submerged. Ordinarily, the distal one-third to two-thirds of the rhamphotheca of the lower jaw is held under water, although sometimes it is submerged completely. Tomkins (1951) claimed that the lower jaw is depressed very little during skimming. While this is often true, it may at times be moderately depressed.

From projected motion picture frames I could not find a reliable standard for measuring the angle of protraction of the upper jaw. The Black Skimmer usually holds the upper jaw above the water, and the extent to which it is protracted tends to increase as the depth and the angle of the lower jaw increase. Sometimes, however, the distal portion, or even the entire upper jaw is submerged during skimming, and considerable spray may be thrown up as the jaw moves through the water.

#### CATCHING PREY

The upper jaw clamps down when the lower jaw strikes a submerged object. My observations indicate that the head almost invariably moves downward and backward whether the prey is large or small. This movement allows the bird to grasp prey originally struck beyond the reach of the upper jaw (Figure 8), and also cushions the fish's resistance to the forward motion of the bird.

Probably some of the food items struck by the lower jaw are not seized, for the head may be bent under the body many times with no food being caught. Fish struck obliquely or close to the head or

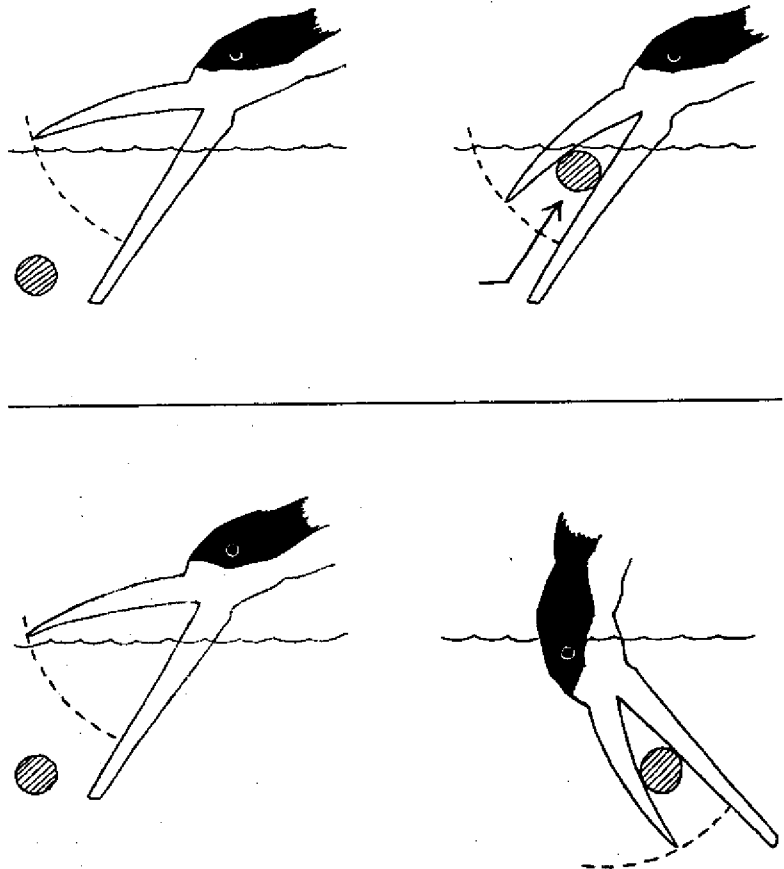


FIGURE 8. Diagram showing the methods of grasping prey by *Rynchops nigra*. Above, method seldom if ever used, in which prey slides up jaw. Below, method usually employed, in which downward motion of head enables bird to grasp prey.

tail, as well as some of those struck by the distal tip of the lower jaw, are likely to escape. When birds skim through dense surface concentrations of small fish, the latter are sometimes deflected out of the water to either side of the bill. Apparently these fish are not struck squarely by the lower jaw, or perhaps they are thrown up by the stream of water on either side of the bill. Motion-picture frames show that the upper jaw clamps down in rapid succession under these conditions (although the position of the head does not change), probably in response to the sight of the fish.



Small fish are swallowed quickly and effortlessly. Large fish, although sometimes swallowed in flight, are usually manipulated for a while after the bird alights. The bird takes a fresh grip on the fish several times, each time closer to the head, while the position of the fish changes from transverse to oblique, with its head toward the bird's mouth. Once the head has entered the mouth the fish is swallowed rapidly.

#### SPEED OF SKIMMING

While feeding, the Black Skimmer usually flies into the wind, sometimes cross-wind, and rarely with the wind. Its flight speed varies considerably. Using an automobile I measured the speed of birds skimming in shallow water along the edge of a beach on six occasions. The speed on four occasions was close to 11 m.p.h., once between 12 and 14 m.p.h., and once between 15 and 18 m.p.h. Estimates made by timing birds with a stop watch along a pond of known length revealed that the birds skimmed about 16 m.p.h., although they sometimes attained a speed of 24 m.p.h. when skimming only at intervals. Longstreet (1930) followed two feeding birds by car for 3 miles at 18 m.p.h., and Davis (1951) gave the same figure. Probably most skimming is done at 10 to 20 m.p.h. Although the slowest measured speed was 11 m.p.h., birds sometimes skim more slowly, especially into a strong wind or in irregular shallow stretches of water where submerged objects are frequently struck.

#### TIME OF SKIMMING

The Black Skimmer feeds at night as well as during the day. Nicholson (1948) has recorded nocturnal skimming at Orlando, Florida, during spring, summer, and winter months. Tomkins (1951) also noted night feeding in fall and winter, as well as in summer. At a fresh-water pond in Texas, July 21-22, 1956, I observed that skimmers fed from 6:30 p.m. until 7:45 a.m. CST. The birds were as active after the setting of the moon (3:30 a.m.) as before.

Skimmers may feed at any hour of the day, but feeding activity is noticeably greater in the early morning and at dusk.

#### FEEDING HABITAT

Most of the feeding areas of Black Skimmers are characterized by relatively smooth water surface, lack of obstructions above the surface, and little or no submerged vegetation near the surface. At times they skim in relatively deep water. I noted in southern Texas, for example, that large schools of fish swam at the surface where they were available to the birds in water five feet or more in depth.

More often, however, the Black Skimmer feeds in shallow water. Tidal pools, edges of sand bars, and edges of coves and bays are favored skimming areas along the coast. In southern Texas birds fly several miles inland to feed along the shallow ponds, cayos, roadside ditches, and the edges of shipping canals, which may contain salt, brackish, or fresh water.

On the Laguna Atascosa National Wildlife Refuge, these birds usually fed in water less than a foot deep, sometimes less than one inch deep, where the bottom varied from compact sand to exceedingly soft mud. Under these conditions the rhamphotheca may cut through the muddy bottom at times. Black Skimmers frequently skimmed in the thin sheet of water cast on the beach by a breaking wave, sometimes traveling a mile or more along the beach before going elsewhere or retracing their path. Although the average density of fish in this thin sheet of water is probably small, I have nevertheless seen skimmers catch fish there. In many other situations, however, the rate of catch is moderate or very high (Zusi, 1959a).

#### FEEDING OF YOUNG

Authors disagree as to how the Black Skimmer feeds its chicks. Arthur claimed that downy chicks eat food regurgitated onto the ground by adults. The chicks avidly pick at the parent's bill as the fish is being dropped (in Bent, 1921:314-15). However, Tomkins (1933) observed chicks, too small to run from the nest, with fish tails protruding from their mouths. He pointed out that adults regurgitate undigested matter and that young birds pecking at it may appear to be feeding. Pettingill (1937:240) wrote: "I did not see any cases where it seemed that the food was regurgitated. The young took the food directly from the beak, although, if it were dropped, they were capable of picking it up and devouring it."

On a sand pit near Stone Harbor, New Jersey, I watched a flock of about 450 adult and recently fledged Black Skimmers. Several juveniles persistently approached adults, with heads lowered, bills open and pointed slightly upward, and with the wings folded but held far from the body at the wrist, evidently begging for food. But the adults carried no food, and offered none. Other juvenile birds skimmed in the troughs between breakers, along the beach edge, and in a shallow inlet, or attempted to skim the dry beach sand, striking the ground periodically with a downward jerk of the head.

On the Texas coast I observed a recently fledged Black Skimmer, whose lower jaw projected noticeably beyond the upper, poking at the sand while opening and closing its beak. After several futile attempts to pick up objects, it flew up, skimmed a foot or two, and settled again on the beach. On a number of occasions I have seen

young birds skimming in company with one or two adults, probably the parents. The skimming behavior of these juveniles resembled that of the adults.

These observations suggest that the juvenile bird learns, as its bill differentiates, that it can no longer obtain food from the ground by pecking. Black Skimmers exhibit skimming behavior soon after they first fly, and perfect the skimming technique rapidly through practice. Juveniles probably learn where to skim through trial and error as well as by accompanying adult birds.

#### GULL-BILLED TERN, *Gelochelidon nilotica*

A brief description of the feeding behavior of the Gull-billed Tern, Royal Tern, and Laughing Gull will contribute to a better interpretation of structural differences between these three birds and the Black Skimmer. The following descriptions are based both on the literature and on my field notes and motion pictures.

Unlike many terns, *G. nilotica* seldom plunges into the water, although at times it does feed in this manner. Audubon (1839:129), Wetmore (1926:136), Bannerman (1931:245), and Archer and Godman (1937:519) have made statements, some of them conflicting, concerning plunging by this tern.

This species usually feeds by swooping toward the ground or water, taking the prey in the bill with a single downward nod of the head. The swoop is uninterrupted, and momentum carries the bird upward almost to its original height. Analysis of my motion picture films shows that the downward nod of the head is preceded by neck extension and head raising. The downward nod carries the head well under the body with only the bill submerged. Small fish are captured in this manner, with a high percentage of success.

The swoop is often made over open patches of ground. I was unable to observe how the head and neck are used in taking food from the ground.

In areas where dense vegetation prevents a swoop, I have often seen these terns hover or pause in their flight, then descend vertically on their prey with the body horizontal, wings extended and raised, and head and neck pointed downward. The birds lower their feet, bounce once on the ground while picking up their prey, and then fly upwards.

The literature and my own examination of stomach contents indicate that the food of this species includes invertebrates, particularly insects, crustaceans, and molluscs; also small fish, amphibians, reptiles, birds, birds' eggs, and mammals. A number of authors state that the Gull-billed Tern frequently catches flying insects on the wing.

ROYAL TERN, *Thalasseus maximus*

The Royal Tern secures its food most frequently by plunging into the water for fish and crustaceans that are near the surface. The plunge varies from a steep, rapid dive, in which the bird submerges its body completely, to shallow dives in which only the belly and head are submerged. In addition, this species sometimes swoops low over the water with uninterrupted flight, catching its prey with a single downward nod of the head in the manner of the Gull-billed Tern. They may rob one of their own species, taking the food from the other bird's bill in flight, or harassing the bird in the air until the fish is dropped. Sometimes they join the large flocks of gulls picking scraps from the surface of the water behind fishing boats. Audubon (1835: 506) has written that Royal Terns sometimes alight on banks of raccoon oysters in inlets and feed on crabs and fish in small shallow pools.

While searching for food, Royal Terns usually fly with measured wing beats in wide circles, from 15 to 40 or more feet above the water. They hunt individually or in loose flocks. Sometimes the cries of an individual hovering over a school of fish will attract other Royal Terns fishing in the same area. Together they hover over the school, plunging repeatedly into the water and screaming excitedly. Eventually the birds disperse and circle about until the next school is sighted.

From level flight over the water a Royal Tern may go directly into a dive, it may hover for varying lengths of time before diving, or it may swoop up abruptly to poise briefly with wings raised, body tilted upward anteriorly, and the head and neck pointed downward. The dive is not always an uninterrupted plunge; on the contrary, the bird may break the dive once or several times to hover or poise before diving further. Although these birds sometimes fly at heights of about 100 feet, the final plunge is seldom from an altitude greater than 40 feet.

The initial phase of a dive involves rapid adjustments of the wings and tail, the latter being elevated, depressed, or rotated while the bird aims its body. At the same time the feet are brought forward flat against the belly. In the second phase, the tail is stabilized and the partially extended wings are gradually angled posteriorly until they seem to trail behind the bird. At the moment of striking the water the wings are raised, and their tips remain above the surface while the body is submerged. Before the head appears above the surface, the wings are partially folded, but when the head and body emerge, the wings are extended for the first beat (Figure 9).

Unlike the Gannet, *Morus bassanus* (Linnaeus), the Royal Tern is not a deep diver. The birds probably seldom reach a depth greater

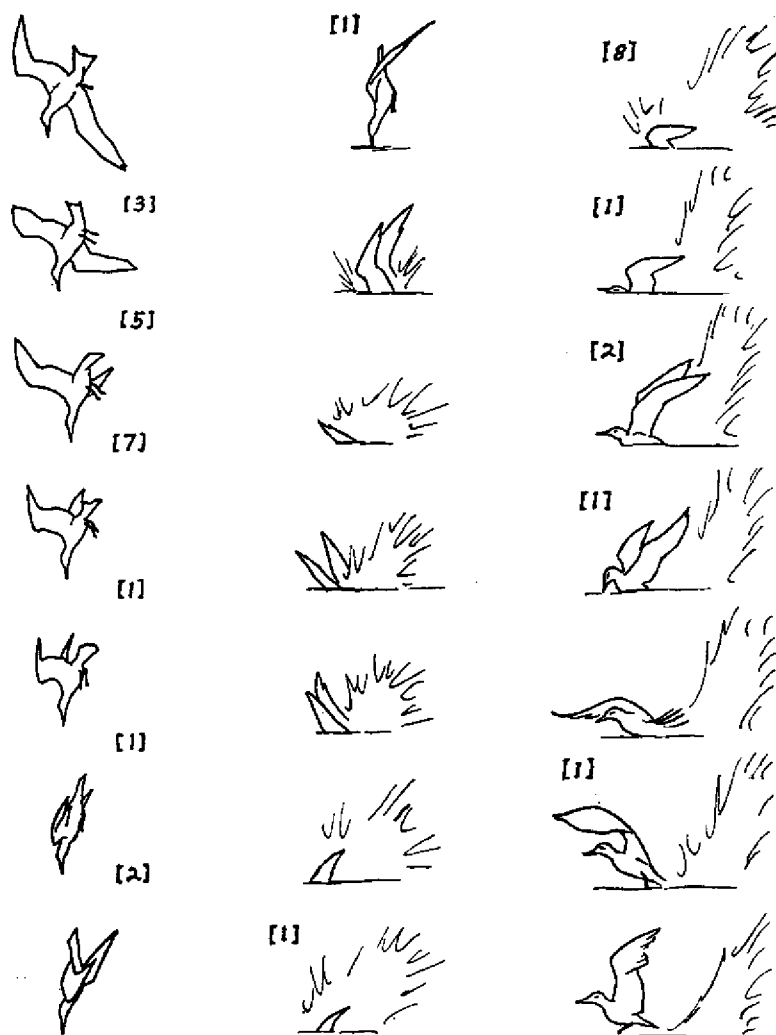


FIGURE 9. Series showing a dive of *Thalasseus maximus*. Numbers in brackets indicate number of movie frames omitted.

than two feet; indeed, this species often plunges into very shallow water from a considerable height. It is reasonable to assume that the fish is grasped almost immediately after the bird strikes the water because the bird takes careful aim before plunging, and because the surprise element is probably important for birds that plunge but

that do not pursue their prey under water. The body is no sooner submerged than it moves forward parallel to the surface of the water, apparently guided by the extended wings. How the bill, head, and neck are used in capturing fish is not known. The plunge of this tern, however, appears to be similar in pattern to the shallow dive, except that in the plunge, motion is more vertically oriented and the capture occurs under water. If this is true, then the head, with the prey grasped in the bill, is probably doubled under the body when the body changes its motion from vertical to horizontal under water. The head must then be brought forward under water to its usual position, for it appears above the surface pointed forward and somewhat raised.

The food of this species consists largely of fish and crustaceans.

#### LAUGHING GULL, *Larus atricilla*

In contrast to the preceding species, which depend chiefly on one or two feeding methods, the Laughing Gull regularly employs a variety of methods. Like other members of its genus, it quickly recognizes feeding opportunities, including many associated with the activities of man, when they arise. Here I shall discuss only those behavior patterns that I saw on the Texas coast and those that are well documented in the literature.

The Laughing Gull seldom submerges its entire body in diving. A fairly common pattern involves hovering at various heights, seldom exceeding 10 feet, dropping to the surface with wings raised, and flying up again after submerging the head and neck briefly. These gulls may barely alight on the water, or they may drop with the body tilted downward anteriorly and submerge all but the wings and tail. A group of gulls will frequently hover together, facing into the wind, each bird dropping periodically to the surface. This behavior is similar to that of fishing flocks sometimes formed by Royal Terns and is probably also initiated by the stimulus of a school of small fish near the surface. Laughing Gulls congregate in large numbers to feed upon scraps from fishing boats. In picking small food items from the water the Laughing Gull often employs a modified "swoop" similar to that of the Gull-billed Tern. The swoop is neither as steep nor as fast as that of *G. nilotica*, and the head is not raised prior to the downward nod. The bird often lowers its feet while reaching for food, and it may paddle them alternately or in unison in the water. The position at the bottom of the swoop is often one of incipient alighting with the tail spread and depressed.

Laughing Gulls frequently drop to the ground with their feet extended to pick up food with their bills. They often walk or run about, obtaining food from the beach or shallow water. They have been

observed stamping their feet alternately in shallow tidal pools, causing the water to become muddy, and apparently stirring up organisms not previously available [Saunders (1934) and Wood (1949)]. I have seen them tear pieces of flesh from large fish stranded on the beach by gripping them with the tip of the bill and pulling backward, often shaking the head at the same time. They break birds' eggs with several blows of the tip of the bill.

These gulls also take food while swimming by reaching down to grasp fish, which are then raised out of the water and swallowed. Like the Gull-billed Tern, the Laughing Gull sometimes catches flying insects on the wing.

According to the literature, the food of Laughing Gulls consists of fish, crustaceans, insects, earthworms, and other invertebrates, as well as birds' eggs, carrion, and garbage.

## Part 2

### STRUCTURAL ADAPTATIONS

#### ADAPTATIONS OF THE BILL

The remarkable bill of *Rynchops* has been described and figured many times. The account of its external features by Coues (1874:715) is especially thorough; and Wilson and Bonaparte (1878:34), Schildmacher (1931), Stresemann (1927-1934:470) and others have discussed the structure of the beak in relation to its function.

The symphysis of the lower jaw of *R. nigra* differs from that of a gull or tern in its greater length and depth, its extreme lateral compression, and the fusion of the tomia to form a single sharp edge (Figures 10, 13). The profile of the symphysis is highly streamlined for motion through water regardless of the angle at which the bill is held to the surface, and water resistance to forward motion through compression and friction may be very small, even at speeds up to 20 m.p.h. The upper jaw is also streamlined, though less so than the lower jaw. (Figures 11, 12)

Beebe (1906:236) showed that the rhamphotheca of the lower jaw of a captive Black Skimmer that had never skimmed attained a length of  $6\frac{3}{4}$  inches when the bird was 18 months old, a length considerably greater than that of an adult wild bird. He concluded that the rapidly growing bill of a wild bird is worn down to a moderate length by friction against the water during skimming. Contrary to Beebe's view, the streamlined shape and smooth surface of the rhamphotheca suggest that water resistance is slight. I have noticed that prepared specimens of *Rynchops nigra*, as well as freshly killed birds, exhibit great variation in the degree of protrusion of the lower jaw and in the shape of its tip. Some jaws have a smoothly beveled tip while others are rounded, truncate, or irregularly shaped (Figure 10). The edges of some truncate tips are sharp, but most tips are rounded and show faint abrasion marks. The rhamphotheca, which extends beyond the tip of the dentary in a fresh bird, is exceedingly thin, somewhat flexible, and easily broken. These facts suggest that the length of the lower jaw is controlled mainly through abrasion and breaking of the tip. Breakage and abrasion quite likely occur when the bill strikes mud, sand, and submerged objects.

The tomium, gonys, and apex of the lower jaw of *R. nigra* are richly supplied with blood by branches of the mental artery. Blood vessels



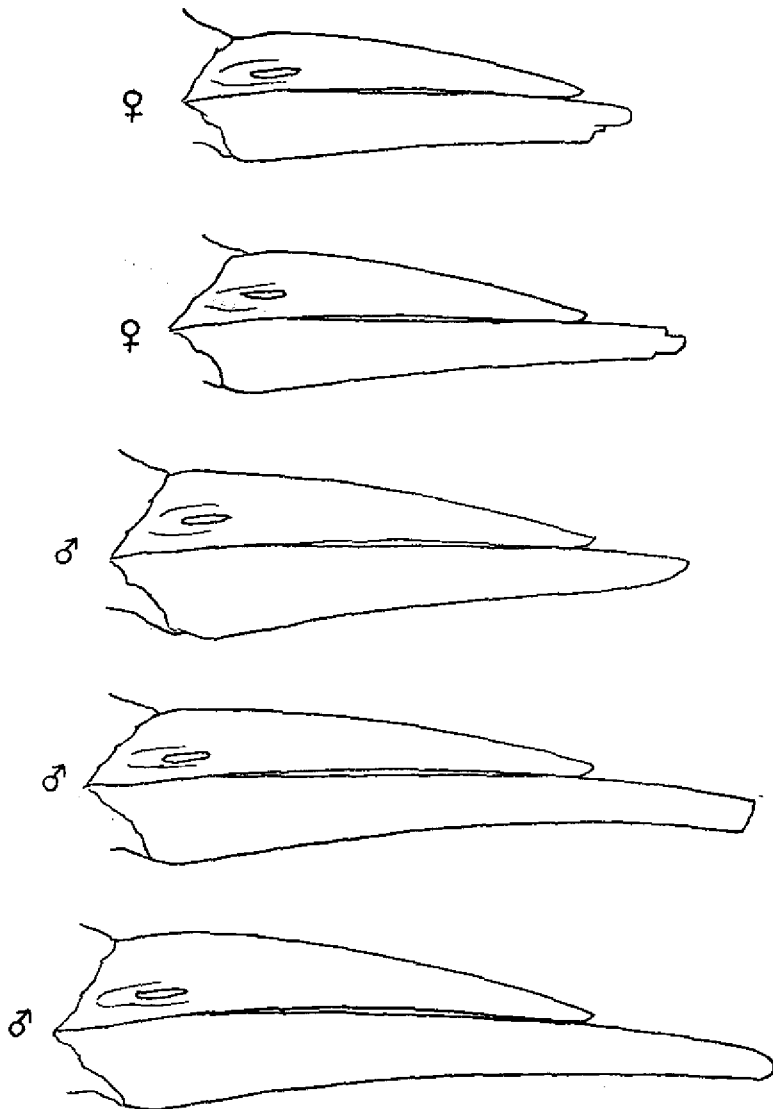


FIGURE 10. Bills of adult *Rynchops nigra* showing effects of breakage and abrasion on the rhamphotheca of the lower jaw.

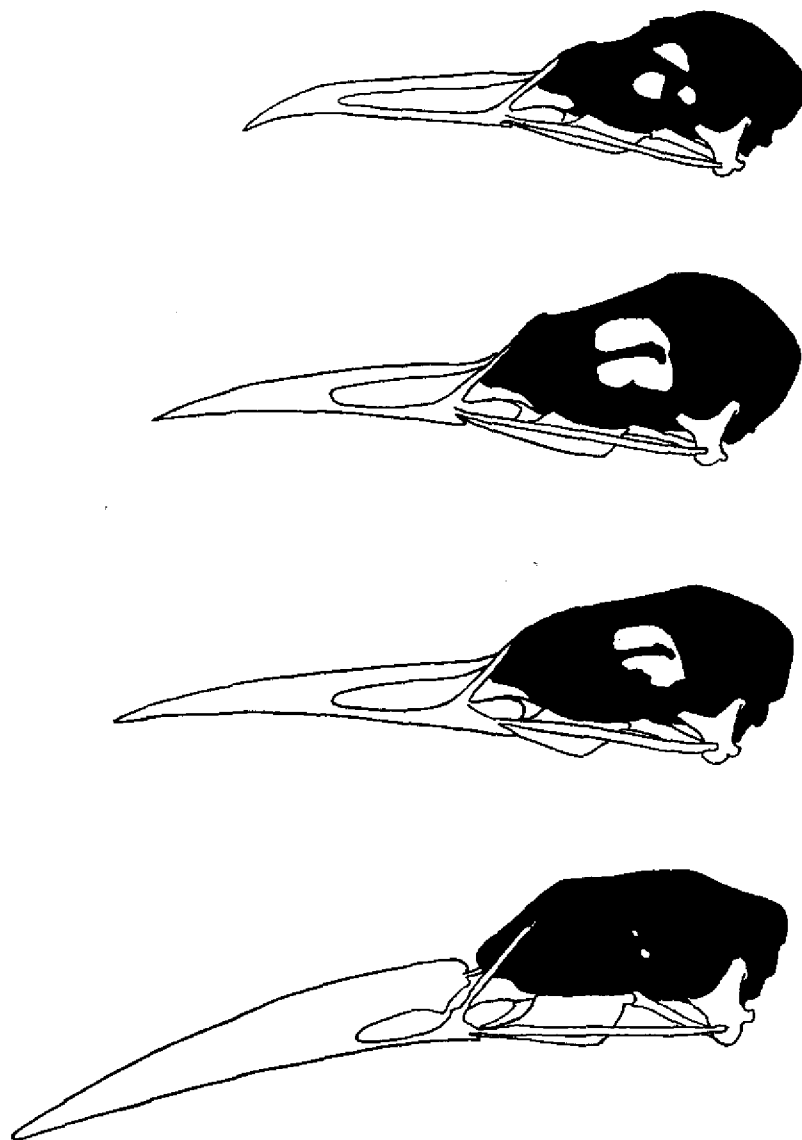


FIGURE 11. Lateral view of skull of (top to bottom) *Larus atricilla*, *Gelochelidon nilotica*, *Thalasseus maximus*, and *Rynchops nigra*, adjusted to the same body size. Oriented with basitemporal plates parallel.

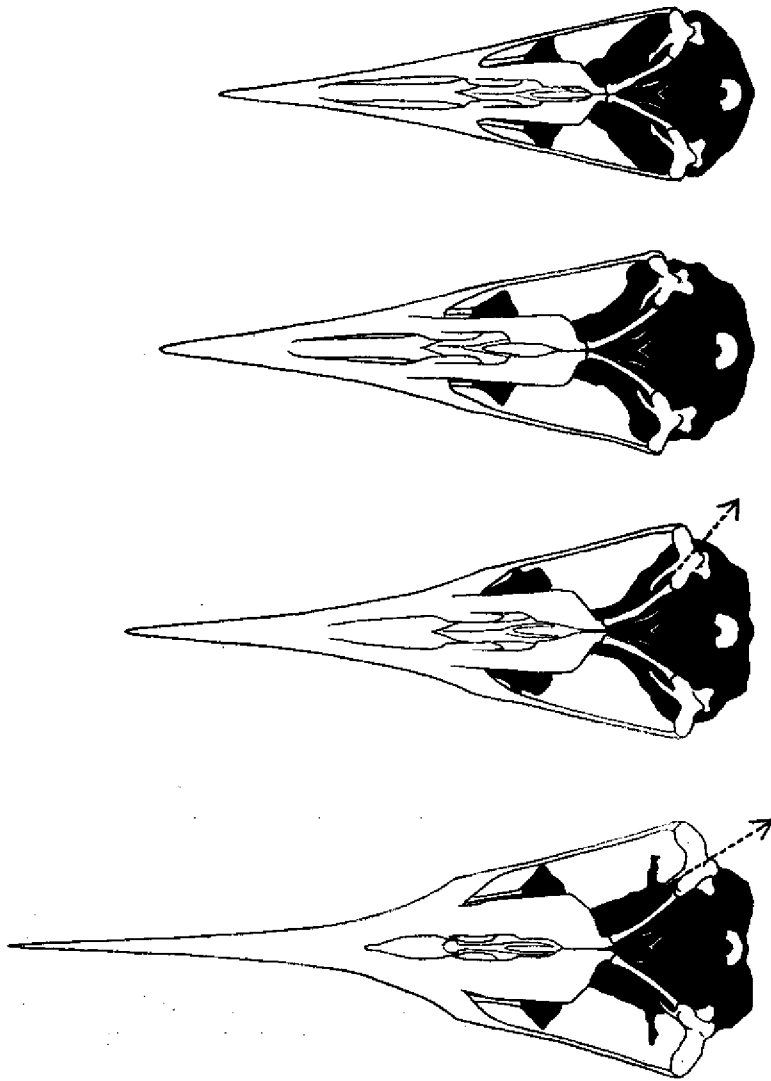


FIGURE 12. Ventral view of skull of (top to bottom) *Larus atricilla*, *Gelocheidon nilotica*, *Thalasseus maximus*, and *Rynchops nigra*, adjusted to the same body size. Dotted arrows indicate direction of motion of articular during opening of lower jaw.

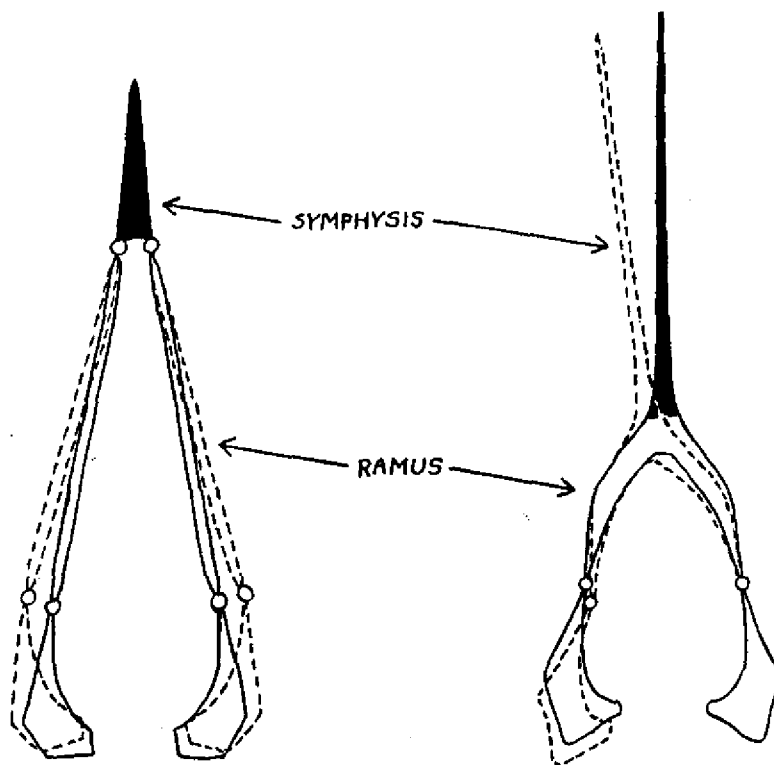


FIGURE 13. Diagram of bowing of the lower jaw of *Larus atricilla* (left), and lateral movement of the lower jaw of *Rynchops nigra* (right) from dorsal view.

extend forward from the tip of the dentary to the end of the rhamphotheca, and this region is probably the site of most rapid growth of the rhamphotheca. The Royal Tern differs from the Black Skimmer in that the mandible is less vascular, and the blood vessels do not reach the tip of the rhamphotheca although they extend a short distance beyond the dentary.

On each side of the lower jaw of *R. nigra* is a series of low, roughly parallel ridges that slope posteroventrally from near the tomium toward the gonys. Most of the ridges are unbranched and straight but some are forked anteriorly. In *Rynchops nigra* there are about 16 ridges per inch of rhamphotheca. The angle of the ridges to the long axis of the middle of the lower jaw of 20 adult specimens averaged  $43^\circ$  ( $30^\circ$ - $48^\circ$ ). The angle is larger toward the base of the rhamphotheca, and the ridges are indistinct or lacking near the tip. In chicks

they are less uniform, and slope at a smaller angle (about  $33^\circ$ ) to the tomium.

Schildmacher (1931) examined the bill ridges of *Rynchops nigra* and proposed an explanation of their significance. He postulated that the force of friction acts perpendicularly to the frontal plane of the lower jaw and that it can be divided into a vertical downward component and a horizontal drag component. The downward component acting on the anterior end of the bill, according to Schildmacher, shifts the bird's center of gravity forward and causes difficulty in flying while feeding. He stated that the ridges slope at an angle of about  $40^\circ$  to the tomium of the rhamphotheca, and that, if the jaw were held at an angle of less than  $40^\circ$  to the water surface, water pressure on the ventral surface of the ridges would result in a force directed upward and backward. The upward component would tend to restore the center of gravity to its usual position during flight.

There are two principal difficulties with Schildmacher's theory. First, there is little evidence that water pressure on the bill is sufficient to make flying difficult; and second, the birds usually skim with their bills at such an angle that the ridges would contribute to, rather than counteract, the downward force on the jaw.

Stresemann (1927-1934:470) believed that the ridges might indicate the courses of tactile papillae which would help the bird detect its prey. The ridges, however, are solid thickenings of the rhamphotheca, and no tactile corpuscles associated with them have been demonstrated. The lateral position of the ridges would seem to exclude a possible use in detecting prey since fish must be struck by the tomium in order to be grasped.

The presence of ridges on the rhamphotheca must tend to disrupt the smooth, laminar flow of water along the bill, particularly when they are at an angle to the direction of motion of the bill. Normally they are angled downward so that the water strikes their dorsal surface and is deflected upward. The ridges are probably responsible for the slight vibration of the bill that one can feel when the bill is moved rapidly through the water. I felt a vibration only when the bill was held at an angle of about  $90^\circ$  to the surface and was moved at speeds exceeding 15 m.p.h. It is possible that the ridges, by their vibration, help the birds to know when and how deeply the bill is submerged, and perhaps its angle with the surface. A means of knowing the relationship of the bill to the water other than by sight might be especially important for night feeding.

Marshall (1895:183) suspected that the tomial region of the lower jaw of *Rynchops* was well supplied with nerves that made the bird instantly aware of a collision. By comparing the bill of a Black

Skimmer with that of a Royal Tern I showed that Marshall's supposition was correct. The mandible of both birds is supplied by the right and left mandibular rami of the trigeminal nerve. In the Black Skimmer they run side by side through the symphysis and beyond the tip of the dentary. The mandibular ramus in the Black Skimmer has about twice the diameter of that of the Royal Tern. Each ramus gives off a series of branches that run anterodorsolaterad and penetrate the compact bone of the mandible through small foramina. In a Royal Tern I found eight branches from each mandibular ramus and in a Black Skimmer, ten. The branches in both species were themselves divided into smaller rami, which opened onto the lateral surface of the mandible near the tomium. The branches and their subdivisions were of greater diameter in *R. nigra* than in *Thalasseus maximus*. Unfortunately, all details of the pattern of nerve endings and the type and arrangement of sense organs in the bills of lariform birds are not yet known. Nevertheless, the rich innervation of the surface of the dentary suggests that the Black Skimmer immediately becomes aware of impacts on the lower jaw and that the bird may be sensitive to slight vibrations of the rhamphothecal ridges.

Frieling (1936) has called attention to the gap between the closed jaws of the Black Skimmer (Figure 10). He claimed that the beak, when but slightly opened, forms a trap for prey which slide up the lower jaw to become wedged between the tomia near the base of the bill. Whistler (1928), Potter (1932), and Lowther (1949) made similar suggestions. In order to test this hypothesis, Frieling pushed the head and slightly opened bill of a Black Skimmer through the water of an aquarium containing living sticklebacks. He soon caught a fish, which remained firmly held in the bill. As shown in Figure 8, however, the Black Skimmer does not feed in this manner (page 12). The gap results from curvature of the tomia of the upper jaw, and is probably valuable because of the increased ease of maintaining a grip on the prey.

The elongated jaw has been described by several authors as detrimental because it prevents the bird from picking food from the ground and because, by striking submerged objects, it tends to somersault the bird. I have never seen an adult Black Skimmer attempt to take food from the ground, although it can do so by turning the head sideways (Kenneth C. Parkes, oral communication, and Potter, 1932). The adjustments preventing somersaulting have been described.

The value of the discrepancy in jaw lengths may be explained on the assumption that the bird's chances of obtaining food are increased by elongation of the lower jaw because of greater area of coverage in water. When the upper jaw can no longer reach prey struck at the tip of the lower jaw, further elongation of the lower jaw results

in inefficiency. Abrasion and breakage keep the length of the rhamphotheca probably close to optimum efficiency (page 20). The upper jaw, usually held above the water, does not reduce the effective striking edge of the lower jaw. The longer the upper jaw, the greater the degree of protraction necessary to keep it above the water; therefore limitations of the kinetic mechanism require a relatively short upper jaw for greatest effectiveness.

Murphy (1936:1177) believed that the elongated lower jaw is detrimental to *R. nigra* in most respects and that its only practical function is to serve as a lure. He proposed that the moving black and red beak, or the surface disturbance caused by it, probably attracts fish to the surface, and that the bird returns over the skimmed route to take the fish. But he did not explicitly state how the prey is captured.

Although fish may at times be lured to the surface, there is considerable evidence that this is not the primary function of the elongated lower jaw. When feeding in large areas of open water or along the edge of an extensive beach, Black Skimmers seldom retrace their skimmed path. Furthermore, they are primarily shallow-water feeders; the submerged mandible may nearly reach the bottom, or may actually cut through the soft mud. In such cases there is no advantage in luring fish to the surface. When a Black Skimmer retraces its initial path, as it often does in more circumscribed areas, fish are taken as often during the first skim as during the second or third. It appears that a catch made during the first skim in a particular locality stimulates the bird to retrace its path several times.

The bill of a newly hatched chick of *R. nigra* is short, deep, and laterally compressed. The tips of both jaws show swellings. The swelling on the lower jaw tip projects slightly beyond that of the upper. The tomia of the lower jaw are not yet fused but lie close together, and ridges on the rhamphotheca are lacking. By the time the bird is able to fly, the tomia have fused, and irregular ridges are present, but there is as yet no marked difference in length of the jaws. The bones of the jaws have reached almost their maximum length, and further elongation of the lower jaw is due primarily to growth of the rhamphotheca. The only adaptation for skimming not well developed when the bird first skims is the marked discrepancy in the lengths of the jaws. Early equality of jaw lengths is important, since the chicks pick up food from the ground or from the adult's bill.

## ADAPTATIONS OF THE HEAD

### SKULL AND JAWS

*Forces.* When feeding, the Black Skimmer is subject to (1) some forces, acting on all species considered, which are generally of greater magnitude or duration in a skimmer, and (2) certain forces that seldom or never act on the gulls and terns studied.

(1) Water pressure on the lower jaw of a skimming bird produces a resultant force that is approximately perpendicular to the long axis of the jaw, tending to depress the jaw. As Schildmacher (1931) has pointed out, this force has a vertical downward component and a horizontal backward component. When the sagittal plane of the lower jaw parallels the direction of motion of the jaw, the force is probably slight because of the remarkable streamlining of the bill. Should the sagittal plane of the jaw deviate from the direction of motion of the jaw, however, water pressure on one side of the bill would exert a force acting posteroventrolaterally. A lateral component is thus added to the vertical and backward components, and all three must sometimes be of considerable magnitude.

Both the Black Skimmer and Royal Tern also combat lateral forces from the struggling of large fish carried crosswise in their bills, often for considerable distances. The knife-like beak of *R. nigra* must be especially susceptible to lateral displacement by these forces.

The direction of the force applied on the tomium by collision with a submerged object is not easily determined. If the collision were perfectly elastic, i.e., if the prey bounced off the jaw with no loss of kinetic energy, the force would act perpendicularly to the jaw, whereas a perfectly inelastic collision in which the prey stuck to the jaw after impact would produce a force acting opposite to the direction of motion of the bill. In ordinary collisions the direction of the force undoubtedly lies between these extremes. After the initial impact, the bird's head moves downward and backward relative to the body. If this movement is in part voluntary, then the force produced by the impact will be considerably reduced.

Diving gulls and terns are probably less subject to forces on the lower jaw than is *R. nigra*. In terns that plunge into the water, there may be considerable force on both opened jaws just before the prey is seized, but because the jaws are either closed or only slightly opened when the bill enters the water, this force must be exerted for a short time only.

Once grasped, prey exerts forces on the jaws that oppose those exerted by the jaw muscles. The Black Skimmer has only one gripping edge on each jaw in contrast to two in other lariform birds. It



must therefore exert a greater minimum pressure with its jaws in holding its prey. Fish taken by me from stomachs of skimmers usually showed deep grooves across the body caused by the birds' jaws, and smaller fish were sometimes almost severed. Royal Terns made slight grooves with their jaws, but no grooves appeared on fish that I took from other species.

(2) When the tip of the lower jaw strikes bottom, a component of the force of impact is directed backward along the jaw's axis, tending to disarticulate the jaw. Other species probably never experience backward jolts of the mandible. Gulls occasionally use the tip of the bill for pecking, but the impact is probably in large part on the upper jaw.

In addition to the lateral forces mentioned previously, downward pressure of water on a skimmer's upper jaw when it is submerged tends to oppose protraction. The gulls and terns studied seldom if ever experience strong water pressure on the protracted upper jaw, and, in contrast to the Black Skimmer, they maintain protraction for only brief moments.

*Proportions.* The Black Skimmer is a large-headed bird, resulting in part from inflation of the nasal bones and nasal portions of the premaxillae, and in part from the extraordinary breadth between the prefrontals. (See figures 14, 15, and 16 for skull terminology.) Size is due in greater part, however, to the much enlarged jaws and palatal mechanism (Figures 11, 12). If one assumes that *R. nigra* was derived from a lariform ancestor, then it is evident from Figures 11 and 12 that selection has favored elongation of the jaws, broadening of the frontonasal hinge supporting the upper jaw, increase of the interquadrate distance, increase in the size of the quadrates, and enlargement of the surface area of the palatines — all of which are adaptations to the skimming method of feeding. In addition to elongation of the ramphotheca of the lower jaw, the general hypertrophy of both jaws increases the chances of catching fish. The frontonasal hinge has been broadened and strengthened, probably to withstand unusual bending tension and lateral forces. The increased interquadrate distance and enlargement of the distal articular surfaces of the quadrates help to stabilize and support the lower jaw, particularly in response to lateral forces on the symphysis, while the enlarged palatines provide greater area for attachment of the retractor muscles of the upper jaw. Associated with these changes is the complete ossification of the interorbital septum, which provides increased support for the enlarged jaws and palate in *R. nigra*. Elongation of the facial region of the skulls of the two terns and the Black Skimmer may be associated with support of their relatively large jaws. Some differences

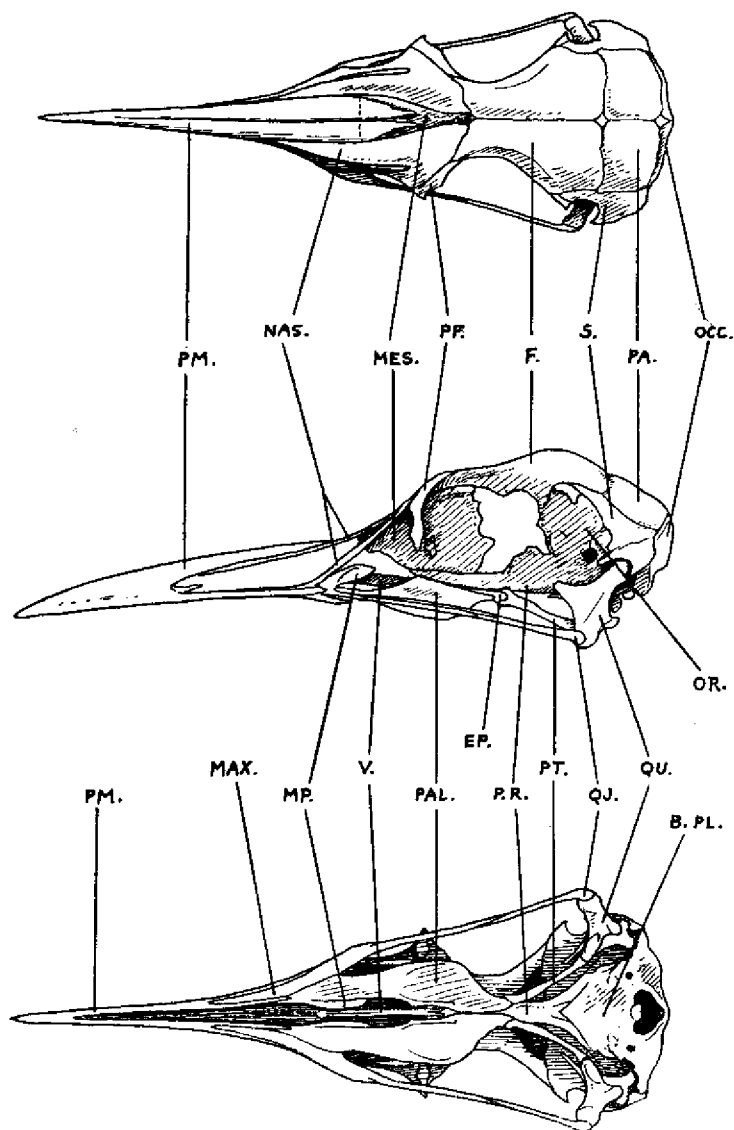


FIGURE 14. Bones of the skull of a chick of *Rynchops nigra*. Above, dorsal view. Middle, lateral view. Below, ventral view. B.PL., basitemporal plate; EP., epipterygoid; F., frontal; MAX., maxillary; MES., mesethmoid; MP., maxillopalatine; NAS., nasal; OCC., occipital; OR., orbitosphenoid; PA., parietal; PAL., palatine; PF., prefrontal; PM., premaxillary; P.R., parasphenoid rostrum; PT., pterygoid; QJ., quadratojugal; QU., quadrate; S., squamosal; V., vomer.

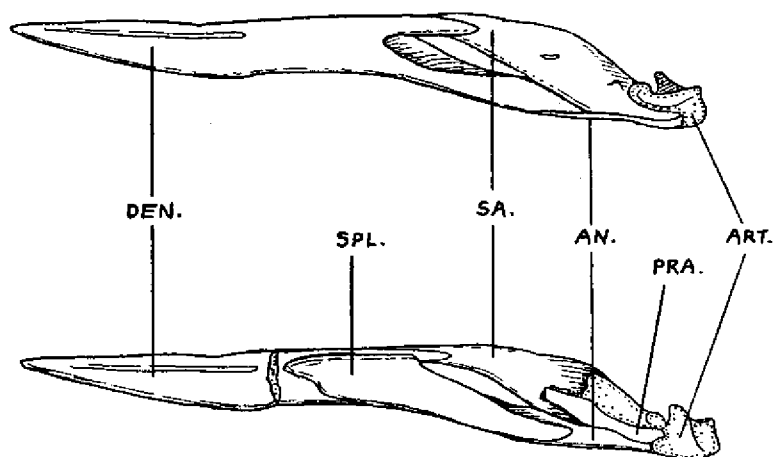


FIGURE 15. Bones of the lower jaw of a chick of *Rynchops nigra*. Above, lateral view. Below, medial view with left ramus removed. AN., angular; ART., articular; DEN., dentary; PRA., prearticular; SPL., splenial; SA., surangular.

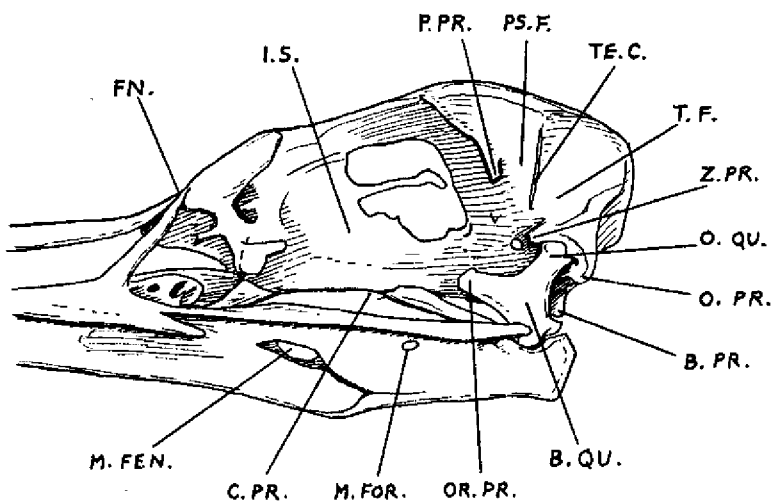


FIGURE 16. Features of the skull of *Thalasseus maximus* shown in lateral view. B. PR., basitemporal process; B. QU., body of quadrate; C. PR., coronoid process; FN., frontonasal hinge; I. S., interorbital septum; M. FEN., mandibular fenestra; M. FOR., mandibular foramen; O. PR., opisthotic process; OR. PR., orbital process of quadrate; O. QU., otic process of quadrate; P. PR., postorbital process; PS. F., pseudotemporal fossa; TE. C., temporal crest; T. F., temporal fossa; Z. PR., zygomatic process.

in proportion between the Black Skimmer and its close relatives were pointed out by Brandt as early as 1840.

*Arthrology.* Since Bock (1960a:28-29) has described and figured the quadrate-articular joint of the Black Skimmer, I shall emphasize only the important points of difference between the skimmer and the Royal Tern, which closely resembles the Gull-billed Tern and Laughing Gull.

In both of these species the three condyles (lateral, posterior, and medial) on the distal end of the quadrate are arranged as points of a triangle, enclosing a depression that receives the anterior condyle of the articular bone in the closed jaw. The posterodorsal border of the articular is notched in the Royal Tern. This notch is filled by the internal jugomandibular ligament; the anteroventral surface of the ligament lies on the posterior condyle of the articular, while its antero-dorsal surface rests on the posterior condyle of the quadrate. This ligament is lacking in the Black Skimmer, but its posterior portion is replaced by bone; thus there is no notch on the articular, in contrast to the Royal Tern. The four ligaments supporting the lower jaw of *T. maximus*, and their static functions, are as follows (Figure 17):

1. Occipitomandibular ligament. Maintains upward tension on the closed mandible keeping the articulation tight.
2. Postorbital ligament. Maintains upward tension on the closed or depressed mandible. With the help of the external jugomandibular ligament, opposes extreme posterior movement of the mandible on the quadrate. Prevents disarticulation of quadratojugal and quadrate (see also page 47). Long postorbital process in *R. nigra* allows ligament to run almost vertically (from anterior view) to lower jaw without bending sharply across quadratojugal.
3. External jugomandibular ligament. Maintains upward tension on the closed or depressed mandible. Opposes forward movement of the mandible on the quadrate.
4. Internal jugomandibular ligament. Opposes backward movement of the closed or depressed mandible. To some extent opposes medial movement of the mandible on the quadrate. Also prevents disarticulation of the quadratojugal and quadrate. A sesamoid bone, which abuts against the quadrate posteriorly between the posterior and lateral condyles, is present in this ligament. It helps to prevent the ligament from sliding forward between the quadrate and articular when the ligament is under tension.

The posterior condyle of the quadrate in *R. nigra* is more dorsally situated than in the Royal Tern. An arrow drawn tangential to the lateral surfaces of the medial and posterior condyles (Figure 12) indicates the approximate direction in which the articular slides on the

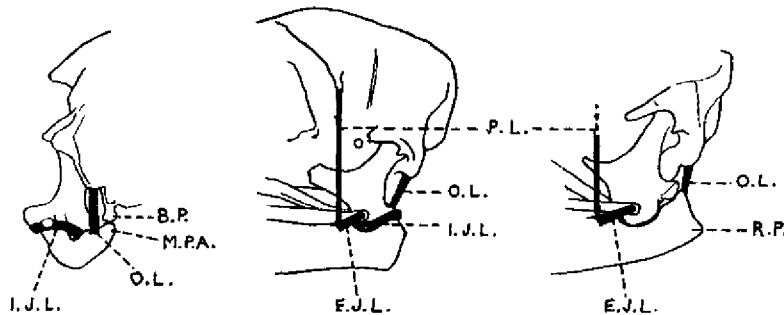


FIGURE 17. Ligaments of the jaw-quadrates articulation. Left, posterior view of *Thalasseus maximus*. Center, lateral view of same. Right, lateral view of *Eynchops nigra*. B. P., basitemporal process; E. J. L., external jugomandibular ligament; I. J. L., internal jugomandibular ligament; M. P. A., medial process of articular; O. L., occipitomandibular ligament; P. L., postorbital ligament; R. P., retroarticular process.

quadrates during depression of the lower jaw. The lateral component of this motion is considerably greater in the Royal Tern than in the Black Skimmer.

Shufeldt (1890:71) described the articulation of the medial process of the articular with a ventral process of the basitemporal plate (basitemporal process) in lariform birds (Figure 17) and pointed out that it reached its highest development in the Black Skimmer. Bock (1960a) has recently discussed the function of this "secondary jaw articulation" and surveyed its occurrence in birds. He has shown that these two processes meet as a diarthrosis with articular pads of fibrocartilage in both the Herring Gull, *Larus argentatus* Pontoppidan, and the Black Skimmer. The joint is enclosed by a loose synovial membrane.

*R. nigra* has a moderately developed retroarticular process of the articular that is lacking in *T. maximus* (Figure 17).

**Lower Jaw.** If the lower jaw of a skimming bird is to be held in a relatively constant position and not dislocated by collisions, then forces equal and opposite to those acting on the mandible must be exerted by the jaw muscles and by the jaw-quadrates articulation. Forces involved depress the lower jaw, swing it laterally in either direction, and push it directly backward along its axis. These forces tend to dislocate the jaw, although depression can cause dislocation only if the mandible is fully opened. In addition to forces exerted by the environment, the pterygoideus muscles exert a powerful forward pull on the mandible when an object is grasped.

In the species studied the dorsal tip of the internal process of the articular lies ventrolateral to the basitemporal process when the jaws are closed. As the lower jaw is depressed, the internal process moves laterally and dorsally with the articular, and comes to lie between the basitemporal process and the quadrate. In this position the jaw and quadrates are firmly braced (by contact of the internal process and basitemporal process) against lateral or medial movement.

Backward disarticulation tends to occur when the tip of the ramphotheca of the lower jaw strikes bottom during skimming. In the gull and terns studied the internal jugomandibular ligament opposes backward disarticulation, but in *R. nigra* the posterior part of this ligament is replaced by bone, and the attachment with the jugal bar is absent; there is thus no effective protection against backward disarticulation by means of ligaments in the Black Skimmer. Furthermore the basitemporal process is probably of little assistance in this regard since it lies medial to, rather than posterior to, the internal process of the opened mandible, and there is no strong ligamentous attachment (only a loose synovial membrane) connecting these processes. Bock argued that the function of these two processes in the Black Skimmer was to oppose backward disarticulation during skimming, primarily because he felt that the fibrocartilage pad between them indicated considerable pressure, and because he considered the quadrate to offer but little support to the depressed mandible.

By manipulating the jaws of freshly killed Herring Gulls, *Larus argentatus*, I found that considerable lateral displacement of the tip of the lower jaw is possible when the jaw is closed or nearly closed. As the jaw is depressed, lateral displacement is reduced, and the fully opened jaw is quite rigidly anchored against lateral movement. Similarly, the closed jaw can be displaced backward along its axis, but the depressed jaw cannot. Progressive removal of the jaw ligaments, jaw muscles, and the basitemporal processes had little effect on these relationships. The jaw ligaments and muscles (especially *M. pseudotemporalis superficialis*) serve to hold the lower jaw against the quadrate, but backward and lateral forces on the jaw are counteracted principally by the condyles themselves, which interlock to best advantage only when the jaw is depressed. The sliding of the condyles of the articular on those of the quadrate during opening of the jaws is produced by motion of the lower jaw and by forward motion of the quadrate. The posterior condyle of the quadrate comes to lie solidly in a deep depression of the articular, while the other condyles maintain contact with the articular. I cannot agree with Bock (1960a:34) that the anterior quadrate condyles lose contact with the articular and that the lower jaw thus receives the least support from the quadrate when the bill is open. The significance of the

basitemporal articulation in the Black Skimmer and other lariform birds deserves more study.

It is perhaps surprising that the jaw of the Black Skimmer is less well constructed, in terms of ligaments, to withstand backward disarticulation than are those of other lariform birds, since its method of feeding makes it unusually prone to disarticulation. The resultant force, however, does not act on the jaw alone, but also acts indirectly on the skull and neck. Because of the dorsal flexibility of the middle segment of the neck, the head is free to move upward and backward easily, greatly reducing the strain on the jaw articulation. It is possible that the force of collision between the bill, moving at 20 m.p.h., and an immovable object would tear any tight, restraining ligaments or even bony processes. The immediate shock may be absorbed by breakage of the rhamphotheca and by the passive motion of the head.

Forward motion of the jaw along its long axis is prevented in the Black Skimmer by abutment of the posterodorsal ridge of the articular against the posterior condyle of the quadrate. This brace is important in anchoring the mandible against the forward pull of the pterygoideus muscles, and against forward motion of either articular when lateral forces are exerted on the symphysis. In the Laughing Gull, Royal Tern, and Gull-billed Tern, the posterior condyle of the quadrate fits into a bony socket only when the jaw is strongly depressed.

Opposing depression of the lower jaw are the adductor muscles and to some extent the pterygoideus muscles. The adductors, acting with the depressor mandibulae, hold the lower jaw in position during skimming, and undoubtedly resist depression of the jaw when objects are struck. The adductor muscles are highly developed in the Black Skimmer, relative both to the weight of the bird and to the size of the lever system they operate.

If the skulls of a Black Skimmer, Laughing Gull, Royal Tern, and Gull-billed Tern are oriented so that the ventral surfaces of the basitemporal plates lie in the same plane, it is at once apparent that there is a pronounced downward flexure of the jaws at the level of the frontonasal hinge in *R. nigra* (Figure 11). Because of this flexure a feeding Black Skimmer achieves a greater depth of submersion of the lower jaw with a given depression of the lower jaw than would be possible in a gull or tern. Consequently, the lower jaw is seldom, if ever, maximally depressed during skimming. When objects are struck, most of the force can be absorbed by the adductor muscles before maximum depression is reached. The downward flexure of the jaws thus appears to be an adaptation preventing dislocation of the lower jaw. The downward flexure also tends to submerge the upper jaw to a greater extent, but the highly developed kinetic ability of *R. nigra* prevents submersion of the upper jaw in most actual cases.

If the mandible were a rigid unit, a lateral push on the symphysis of the closed mandible would cause one articular to move posteromedially on the quadrate. Because of the construction of the articulation, dislocation would result from such movement. The lower jaw, however, is rigid only with respect to dorsoventral forces. In gulls and terns lateral or medial bending of the rami is possible near the posterior end of the dentary and near the symphysis (Figure 13). In *R. nigra* the symphysis is long and inflexible, and the anterior third of each ramus is rigid. The middle segment of the ramus, however, is compressed laterally and is exceedingly thin. Flexibility of the rami at this point allows the articulators to slide posterolaterally on the quadrates while the lower jaw is being opened. In addition it is possible to move the symphysis laterally without exerting a strong rotational force on the jaw-quadrates articulations. If the symphysis is moved to the left, the right articulation remains in place, and the left articular bone slides posterolaterally on the quadrate (Figure 13). In the Black Skimmer, the lateral component of motion of the articular is, as we have seen, less than in the Royal Tern, and the amount of bending of the rami for a given lateral deflection of the symphysis is correspondingly reduced.

Gregory (1952:83) discussed the flexibility of the rami in certain fish-eating birds, and pointed out that it "permits outward bowing of the jaws to a greater extent than is otherwise possible without dislocation. This device allows the swallowing of much larger prey than would otherwise be possible." Flexibility of the rami of gulls and terns may well be explained in this way, but in the Black Skimmer, outward bowing of the rami is not possible because of the inflexibility of the rami just posterior to the symphysis. As shown in Figure 13, bowing of the rami requires that they be flexible between the symphysis and the point of maximum bowing. On the other hand, the shape of the mouth enclosed by the rami in the Black Skimmer enables the bird to swallow relatively large prey. Flexing of the rami in the Black Skimmer probably cushions the shock of a sudden lateral pressure on the mandible, and allows the articular to move in a direction that minimizes the possibility of dislocation.

*Upper jaw and palate.* One of the characteristics of the avian skull is its system of hinges and movable struts permitting the upper jaw to be raised (protracted) or lowered (retracted) by contraction of the appropriate muscles. Most holorhinal birds have a single frontonasal hinge, and the upper jaw pivots about the axis of that hinge. (A bony "hinge" is a restricted, flattened portion of a bone or bones where flexibility is greatly increased.) The principal resistance to movement, in the skeleton at least, is offered by five bony hinges at the base of the upper jaw — one frontonasal hinge, two jugal hinges, and two



palatal hinges. The situation is more complicated in most schizorhinal birds in that the dorsal hinges of the nasal struts, which in holorhinal birds form the lateral extremes of the frontonasal hinge, are displaced dorsocaudally. This means that the nasal struts are no longer integral parts of the upper jaw, but that they swing about their own pivots, and tend to change the shape of the upper jaw during protraction or retraction (see Hofer, 1945 and 1954 for further discussion).

If we assume that the upper jaw is flexible along its length, or at localized hinges (C, D, Figure 18), then it is clear that the presence of two pivots A and B in the frontonasal region will cause the tip of the jaw to be bent upward during protraction because C follows an arc of radius BC, and D an arc of radius AD. The Laughing Gull, Royal Tern, and Gull-billed Tern, however, have almost no flexibility

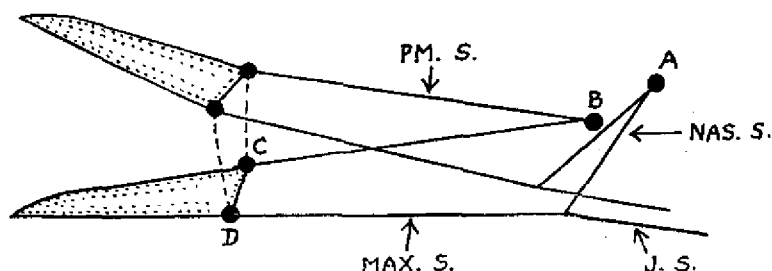


FIGURE 18. Diagram of strut and hinge system of upper jaw of a typical schizorhinal bird. Note upbending of symphysis in protracted state. J. S., jugal strut; MAX. S., maxillary strut; NAS. S., nasal strut; PM. S., premaxillary strut; A-D represent bony hinges.

at C and D, although some dorsoventral bending of the maxillary strut is possible. During protraction the jaw rotates about the two centers, A and B (Figure 19). It is impossible for points C and D to follow their respective arcs, with the result that tension is produced in the premaxillary strut and compression in the maxillary struts. Forces also tend to reduce the angle between the nasal and maxillary struts. The magnitude of these forces is relatively small because hinges A and B are not widely separated in the gull and terns studied; consequently there is relatively little divergence between the arcs of radii AD and BC within the range of protraction (about 25°) of these birds. Apparently the flexibility of the nasal and maxillary struts is sufficient to effect the change in bill shape required by the double frontonasal hinge during protraction. Bending of these struts, however, produces forces that oppose protraction.

In the bill of *Rynchops nigra* hinges C and D are absent, and the maxillary strut is dorsoventrally flattened and moderately flexible.

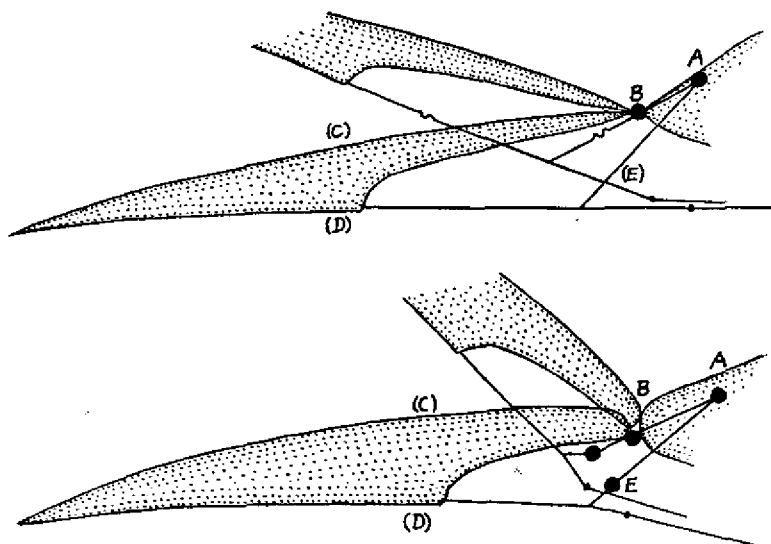


FIGURE 19. Diagram of protraction of upper jaw in *Thalasseus maximus* (above) and *Rynchops nigra* (below). A-E represent positions of bony hinges, but brackets indicate that no hinge is present.

The conditions that oppose protraction in the Laughing Gull, Royal Tern, and Gull-billed Tern have been virtually eliminated in the Black Skimmer, despite a greater distance between A and B, by the presence of a hinge at E, which allows reduction of angle AED during protraction (Figure 19). This reduction permits point D to move along the arc of radius BD, rather than that of radius AD. In addition, the flexibility of the maxillary strut allows point E to follow the arc of the radius AE, rather than the slightly different arc of radius BE which it would otherwise follow. These modifications of the lariform bill have reduced opposition to protraction in the Black Skimmer, and the bill is functionally similar to that of holorhinal birds in that there is little change in its shape during protraction.

The Black Skimmer differs from the other species studied in its ability to protract the upper jaw to a greater degree, and in its habit of maintaining protraction for longer periods of time, sometimes against the resistance of water pressure.

Other things being equal, the following adaptations increase the degree of protraction possible in the avian skull:

1. A longer quadrate (otic articulation to jaw articulation).
2. A quadrate (otic articulation to pterygoid articulation) which

- at rest is more nearly perpendicular to the parasphenoid rostrum along which the palatines slide (from lateral view).
3. A pterygoid, which at rest is as nearly perpendicular as possible to the parasphenoid rostrum (from lateral view).
  4. A reduction of the vertical distance from the frontonasal hinge to the hinges of the palatines and of the jugal bars.
  5. Reduction of protraction stops. (When one bone abuts on another, preventing further protraction, I have referred to the two bones as a protraction "stop". For other examples of bony stops, see Fisher, 1955.)

By comparing *R. nigra* with *L. atricilla*, *G. nilotica*, and *T. maximus* (Figure 11), we see that in 1, 2, 3, and 5 above, *R. nigra* is better adapted for a greater degree of protraction than are the other three species. In 4, the vertical distance from the frontonasal hinge to the ventral hinges in the Black Skimmer is only slightly greater than that in *G. nilotica* and *L. atricilla* and is similar to *T. maximus* when distances are adjusted to body size.

Protraction in the Laughing Gull, Royal Tern, and Gull-billed Tern is stopped when the tip of the orbital process of the quadrate touches a swelling of the orbitosphenoid. In *R. nigra* the orbital process of the quadrate is considerably reduced in size and does not serve as a protraction stop (Figure 11). On the other hand, *R. nigra* possesses a stop not found in the gull and terns studied, formed by inflation of the premaxillae and of the nasal bones in the region of the frontonasal hinge. Protraction ceases when these inflated bones touch each other. This stop may be of value to the Black Skimmer in preventing excessive protraction through collision, which might dislocate the palatal struts. I found that protraction in a cleaned skull of *Rynchops nigra* was stopped by these bones at 45°, while protraction of a cleaned skull of *Thalasseus maximus* was stopped by the orbital process of the quadrate at 25°.

Several other features of the Black Skimmer's skull may be explained in terms of its increased kinetic abilities, i.e., its ability to raise its upper jaw almost twice as far as other lariform birds. The parasphenoid rostrum curves upward anteriorly to a greater degree in this species than in the gull and terns studied. This curvature allows the palatines to maintain maximum contact with the rostrum as they slide forward and upward during protraction. A straight rostrum would necessitate separation of the palatines from the rostrum; if this in turn were prevented, protraction would not be possible.

The vomer is completely fused to the palatines in the adult Black Skimmer. In the Laughing Gull, Royal Tern, and Gull-billed Tern the vomer is closely applied to the palatines but is not fused with these

bones. One function of the vomer is to hold the palatines close together anteriorly, preventing these bones from sliding upward along the lateral surfaces of the rostrum during protraction, and from separating due to the pull of the pterygoideus muscles during retraction. The pterygoids perform a similar function at the posterior end of the palatines. Fusion of the palatines with the vomer in the Black Skimmer may be an adaptation to the unusual protraction and retraction stresses in this species.

The function of the jugal struts in birds deserves further study. Gadow and Selenka (1891:37) spoke of the stabilization and guidance of the movable upper jaw afforded by the jugal and palatal struts. This function is probably important to all birds, but the stabilization and direction afforded the quadrate by the jugal struts is perhaps especially important. Moller (1931:143) and Kripp (1933:490) stated that the jugal struts were important in transmitting the forward rotational force of the quadrate to the base of the upper jaw, while Marinelli (1928:143) believed that the pterygoids and palatines performed this function and that the jugal struts served as tension struts.

In lariform birds the jugal strut is slender, laterally compressed, and evidently not structurally suited to withstand strong compression. As a tension member, however, the jugal strut undoubtedly serves to coordinate movements of the quadrate and the upper jaw so that a sudden upward force on the latter, or a backward force on the former, will not cause disarticulation of the anterior and posterior articulations of the pterygoid. The palatal strut system cannot, by itself, withstand severe tension.

There is some evidence that the jugal strut in lariform birds helps to hold the palatines against the parasphenoid rostrum. During protraction, increasing pressure is applied to the pterygoid and palatine, and the angle between these struts approaches  $180^\circ$ . I have demonstrated on a cleaned skull of the Royal Tern, after disarticulating the jugal struts, that during extreme protraction the palatal struts will suddenly lose contact with the rostrum, and form an angle greater than  $180^\circ$  ventrally. This is prevented by articulation of the jugal struts, which, as tension members, maintain the normal geometric relationships of the bones of the palate. This function of the jugal struts must be of particular importance to *R. nigra*, which maintains strong protraction for long periods. The perpendicular distance from the articulation between palatine and pterygoid to the jugal strut from lateral view is greater in the Black Skimmer than in the other species studied (Figure 11), permitting greater protraction without an increased tendency for separation of the palatines from the rostrum.

## JAW MUSCULATURE

Relatively few published descriptions of the jaw musculature of lariform birds exist. In 1857 Giebel described briefly the jaw musculature of the Great Black-backed Gull, *Larus marinus* Linnaeus, and gave comparative notes on other gulls. The figures of jaw muscles, erroneously labeled *Sterna hirundo* in Gadow and Selenka (1891, Pl. 27) are properly referred to *Larus* in the text, pages 321, 322. Frieling (1936) has described briefly some of the superficial jaw muscles of *Rynchops nigra*.

In the following discussion I shall describe the Royal Tern in some detail, and the Gull-billed Tern, Laughing Gull, and Black Skimmer only in so far as they differ significantly from the Royal Tern. This procedure will emphasize and isolate the structural modifications of the Black Skimmer. Each muscle is classified on the basis of the relationship of its fibers to the tendons or aponeuroses of origin and insertion. In muscles that lack aponeuroses, the fibers run in the direction of pull of the belly. These muscles are termed "parallel." By contrast, in the "pennate" muscles the fibers attach on aponeuroses and run obliquely to the pull of the belly. Pennate muscles may be classified as follows: unipennate — fibers run obliquely from the aponeurosis or bone of origin to the aponeurosis or bone of insertion; bipennate — fibers converge from either side onto a central aponeurosis; multipennate — fibers from several aponeuroses converge on intervening aponeuroses; circumpennate — fibers converge from all sides on a central aponeurosis. I have further classified some of the pennate muscles as weakly pennate. These muscles have aponeuroses at one or both of their attachments, but the bulk of the belly is of the parallel type.

If more than one aponeurosis is present in a muscle, each is designated by a letter. Aponeuroses of origin are lettered A, B, C, et cetera; those of insertion are lettered M, N, O, et cetera. Where both attachments of a muscle are freely movable, the letters A, B, C, et cetera, are arbitrarily assigned to the aponeuroses of one attachment, and M, N, O, et cetera to those of the other. A synonymy of the muscles and their parts is given in Table 2.

TABLE 2  
JAW MUSCLE SYNONYMY

Zusi	Beecher (1951)	Lakjer (1926)	Hofer (1950)	Starck & Barnikol (1954)
<i>L. atricilla</i> , <i>T. maximus</i> , <i>G. nilotica</i> , <i>E. nigra</i>	<i>Moluthrus ater</i> and other Icteridae	<i>Cephus grylle</i>	Various species	Various species
Adductor mandibulae externus	+	+	+	+
Part A	superficialis (part) & medialis	superficialis (I) & medialis (II)	superficialis (part) & medius	Aponeurosis 2 portion
Part B	profundus	profundus (III), caudal part	profundus	Aponeurosis 3 portion
Part M	superficialis (part)	profundus (III), rostral part	superficialis (part)	Aponeurosis 1 portion
Adductor mandibulae posterior	+	+	+	+
Pseudotemporalis profundus	+	+	Quadratmandibularis	+
Pseudotemporalis superficialis	+	+	Pseudotemporalis	+
Protractor quadrati	+	protractor quadrati & protractor pterygoidei	protractor quadrati & protractor pterygoidei	protractor quadrati & protractor pterygoidei
Depressor mandibulae	+	—	+	—

TABLE 2 (Cont.)

				Bock (1960b) #
				Various passeriform species
Pterygoideus	+	+	+	+
Part M	ventralis anterior	dorsalis lateralis & ventralis lateralis	dorsalis lateralis	dorsalis lateralis & ventralis lateralis (part ?)
Part N	ventralis posterior	ventralis medialis	ventralis	ventralis lateralis (part ?) & ventralis medialis
Part O	dorsalis anterior & dorsalis posterior	dorsalis medialis & dorsalis 1	dorsalis medialis	dorsalis medialis

+ same as Zusi.

- not included.

# refers only to the pterygoideus.

## M. DEPRESSOR MANDIBULAE (Figures 20, 21)

*Thalasseus maximus*

*Origin.* Fleshy fibers arise from the posterolateral surface of the squamosal and the adjoining ventrolateral ridge of the exoccipital. More extensive than the bony origin is that from aponeuroses, dorsally from aponeurosis A and ventrally from aponeurosis B, which is closely associated with the aponeurotic surface of the rectus capitis lateralis. The medial portion of aponeurosis B attaches to the articular as a stout ligament (occipitomandibular ligament) which also provides origin for this muscle.

*Insertion.* Fleshy fibers insert on the posterior surface of the articular and on aponeurosis M, which attaches to the ventral edge of the articular.

*Structure.* Unipennate. In general, the posterior fibers of this muscle are the longest, the more anterior fibers becoming progressively shorter. The belly is somewhat thinner laterally than medially.

*Comparison*

Weakly unipennate in *L. atricilla*. Aponeurosis M is very small, and the other aponeuroses are rather weakly developed.

In *G. nilotica*, aponeurosis A is reduced, but M is well developed.

*R. nigra.* The origin is similar, but the anterolateral edge of aponeurosis B is well developed and aponeurosis B is closely associated with M. complexus. Fibers insert on the posterolateral surface of the articular in addition to its posterior surface. The muscle is consequently more nearly divided into an anterolateral portion and a posteromedial portion than in the other species. The occipitomandibular ligament attaches further ventrally on the posterior surface of the articular.

*Action*

This muscle depresses the mandible. Its action on the lower jaw approximates a first-class lever in which the jaw-quadrates articulation is the fulcrum, the portion of the jaw posterior to the fulcrum is the power arm, and the part anterior to the fulcrum is the work arm. The fulcrum in this case is actually not a simple pivot, but a sliding articulation. The power arm is somewhat longer in *R. nigra*, giving the muscle a greater mechanical advantage in opposing the pull of the adductor muscles. To maintain the jaw in a partially depressed position during skimming, the adductor muscles (especially *M. pseudotemporalis superficialis*) and *M. depressor mandibulae* probably act together. The increased mechanical advantage of the depressor mandibulae in *R. nigra* undoubtedly affords greater ease of control in this prolonged interplay between opposed muscle masses. As Frieling



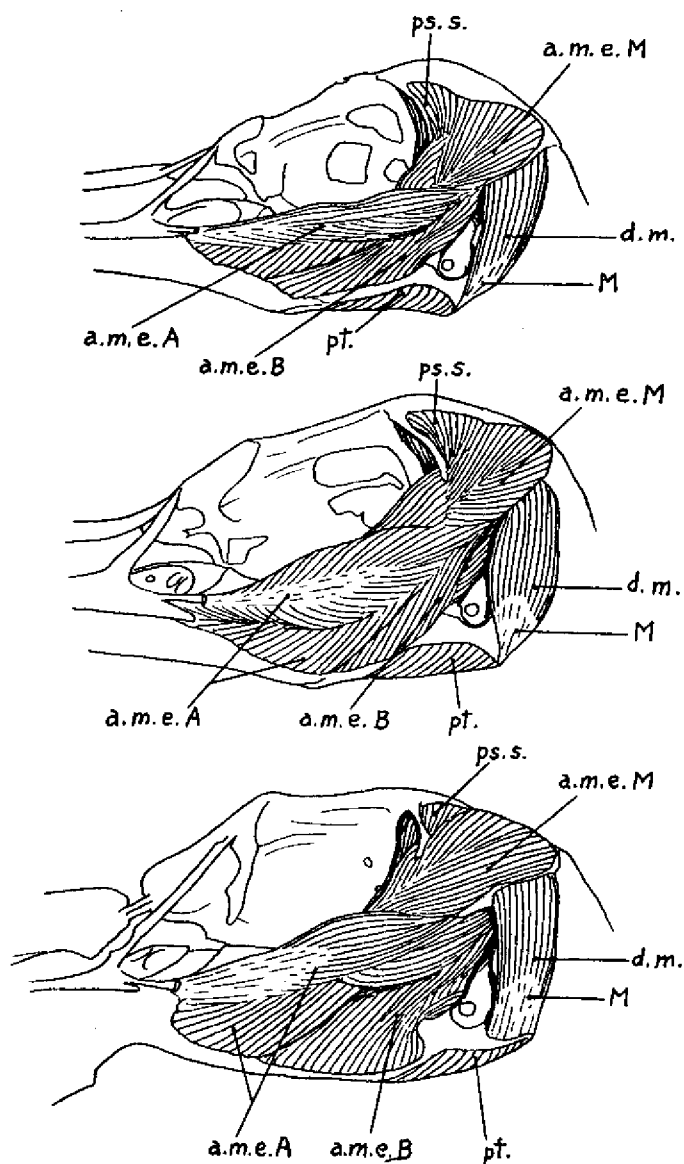


FIGURE 20. Lateral view of superficial jaw muscles. Above, *Larus atricilla*. Middle, *Thalasseus maximus*. Below, *Rynchops nigra*. All are adjusted to the same body size. a. m. e., adductor mandibulae externus (A, B, and M mean part A, part B, and part M); d. m., depressor mandibulae (M = aponeurosis M); ps. s., pseudotemporalis superficialis; pt., pterygoideus.

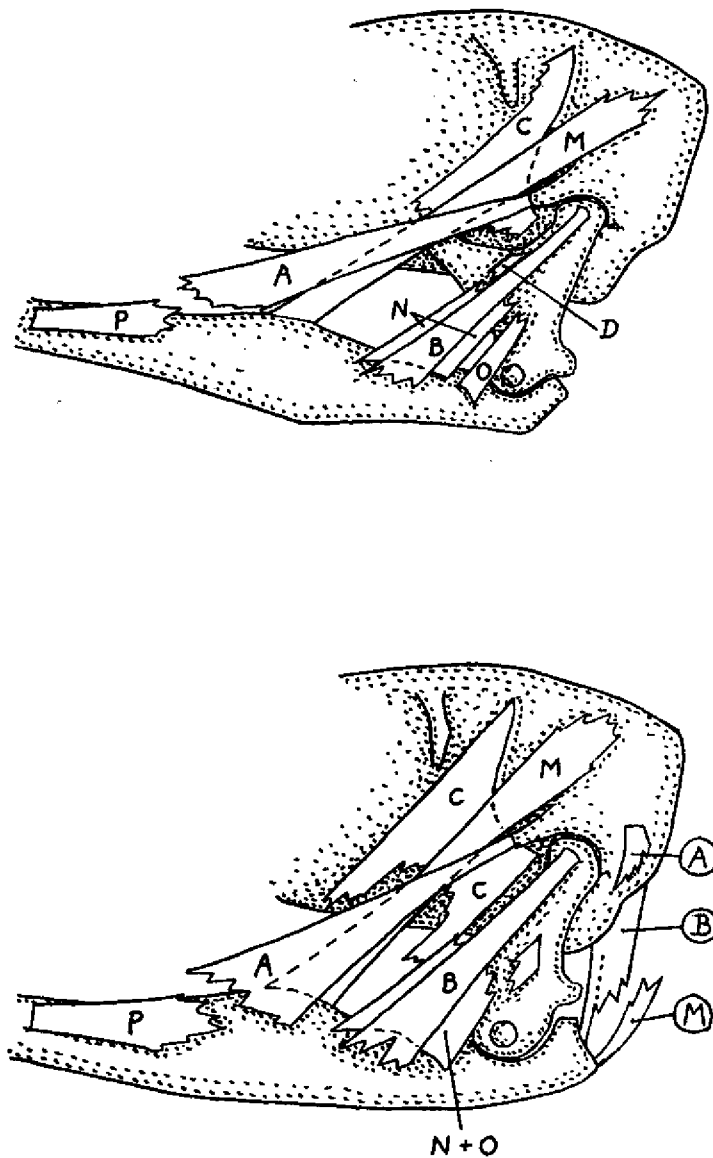


FIGURE 21. Diagram of lateral view of the aponeuroses of the adductor mandibulae externus and depressor mandibulae. Above, *Thalasseus maximus*. Below, *Rynchops nigra*. A-D, aponeuroses of origin. M-P, aponeuroses of insertion. Encircled letters indicate aponeuroses of the depressor mandibulae.

(1936:438) has pointed out, a small mechanical advantage is adequate for terns (and gulls), which open the beak rapidly and momentarily in seizing food.

The depressor mandibulae (especially the lateral mass) pulls forward at an angle to the axis of the quadrate in the Black Skimmer, while in the other species it pulls approximately parallel to the axis. In the Black Skimmer the anteriorly directed component of the force of this muscle acts through the mandible to rock the quadrate forward, thus protracting the upper jaw, and the muscle probably aids *M. protractor quadrati* in maintaining protraction during skimming. Since *M. adductor mandibulae externus* acts in part to retract the upper jaw, which would nullify the protraction effect of the depressor mandibulae, it is likely that *M. pseudotemporalis superficialis*, which exerts no backward force on the mandible, is used to oppose the depressor mandibulae during skimming.

The depressor mandibulae may also assist in protraction of the upper jaw indirectly through the postorbital ligament. Contraction of this muscle tends to rotate the mandibular attachment of the ligament downward and backward. The ligament is not elastic, however, and the jaw can therefore be depressed only if the quadrate rocks forward and upward, relieving the tension in the postorbital ligament. This mechanism probably operates in all four species. Its importance for skimming is not yet known.

The occipitomandibular ligament (Figure 17) attaches farther ventrally on the articular of *R. nigra*, preventing this point of attachment from moving anterior to the center of rotation during strong depression of the mandible. If such a shift occurred, tension in this ligament would tend to adduct the mandible rather than to depress it.

#### *M. PROTRACTOR QUADRATI* (Figure 22)

##### *Thalasseus maximus*

**Origin.** Fleshy, from the posterolateral walls of the parasphenoid and the adjacent ventral portion of the orbitosphenoid.

**Insertion.** Fibers attach on the anteromedial surface of the body of the quadrate and on the base of the orbital process of the quadrate. Fibers also insert on the posteromedial tip of the pterygoid and on a superficial aponeurosis which attaches to the posterodorsal crest of the pterygoid.

**Structure.** Weakly unipennate. The fibers run posteroventrally and laterally to their insertion. The bulk of the belly attaches distally on the quadrate. The anterior fibers, inserting on the pterygoid and on the aponeurosis, may represent *M. protractor pterygoideus*, but these fibers are not clearly separable from the rest of the belly.

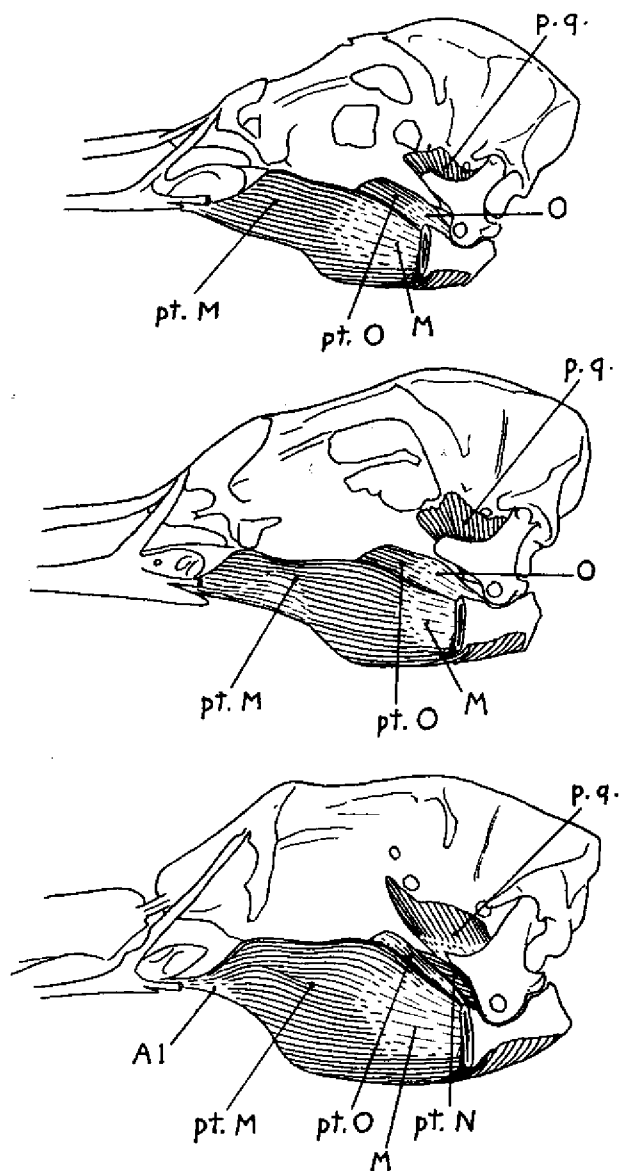


FIGURE 22. Lateral view of deep protractors and retractors of upper jaw. Above, *Larus atricilla*. Middle, *Thalasseus maximus*. Below, *Rynchops nigra*. Most of lower mandible and jugal strut removed. All are adjusted to the same body size. p. q., protractor quadrati; pt. M, pt. N, and pt. O mean part M, part N, and part O of the pterygoideus muscle. Al, M, and O indicate aponeuroses.

### Comparison

Similar in *G. nilotica* and *L. atricilla*.

Similar in *R. nigra*, but the muscle is relatively larger (longer). The fibers, however, are similar in length to those of *T. maximus*. The aponeurosis from the pterygoid is relatively longer, and additional area for insertion is provided by a superficial aponeurosis that attaches along the dorsal edge of the orbital process of the quadrate.

### Action

The sole function of this muscle seems to be the initiation and maintenance of protraction of the upper jaw. The muscle rotates the quadrate anterodorsomedially about its articulations with the skull and pulls the posterior end of the pterygoid in the same direction. The resulting forward movement of the jugal and palatal struts causes protraction of the upper jaw. Although this is not a large or powerfully constructed muscle, the bulk of its fibers attach distally on the quadrate, thereby increasing the force arm of the quadrate lever. As protraction increases, the angle of the fibers to the quadrate approaches 90°, i.e., maximum efficiency.

This muscle is more powerful in the Black Skimmer than in the other species because of the more extensive area of insertion provided by aponeuroses, but the differences between the species are not as striking as one might expect in view of the unusual kinetic abilities of the Black Skimmer. However, as we have already seen, *M. depressor mandibulae* aids this muscle in protracting the upper jaw in *R. nigra*, and the bony mechanism is modified for greater ease of protraction.

### M. ADDUCTOR MANDIBULAE EXTERNUS (Figures 20, 21, 23)

This complex muscle has been considered by Lakjer (1926), Hofer (1950), and others, to consist of three parts (superficialis, medialis, profundus), which have been variously subdivided. Edgeworth (1935) treated the muscle as a single unit, while Starek and Barnikol (1954) analyzed the muscle complex in terms of three major aponeuroses. The synonymy charts given by Starek and Barnikol reveal that the parts "superficialis," "medialis," and "profundus" of some authors correspond to the portions of this muscle associated with aponeuroses 1, 2, and 3, respectively, while those of other authors do not. Confusion has arisen because names have been applied to superficial variations in the parts of this muscle; Starek and Barnikol, however, have shown that most or all variations of this muscle are built on the basic pattern of three major aponeuroses. For this reason, I have chosen to analyze the muscle in terms of its aponeuroses of origin (A-D) and insertion (M-P). In his detailed study of the jaw muscles of *Podiceps*

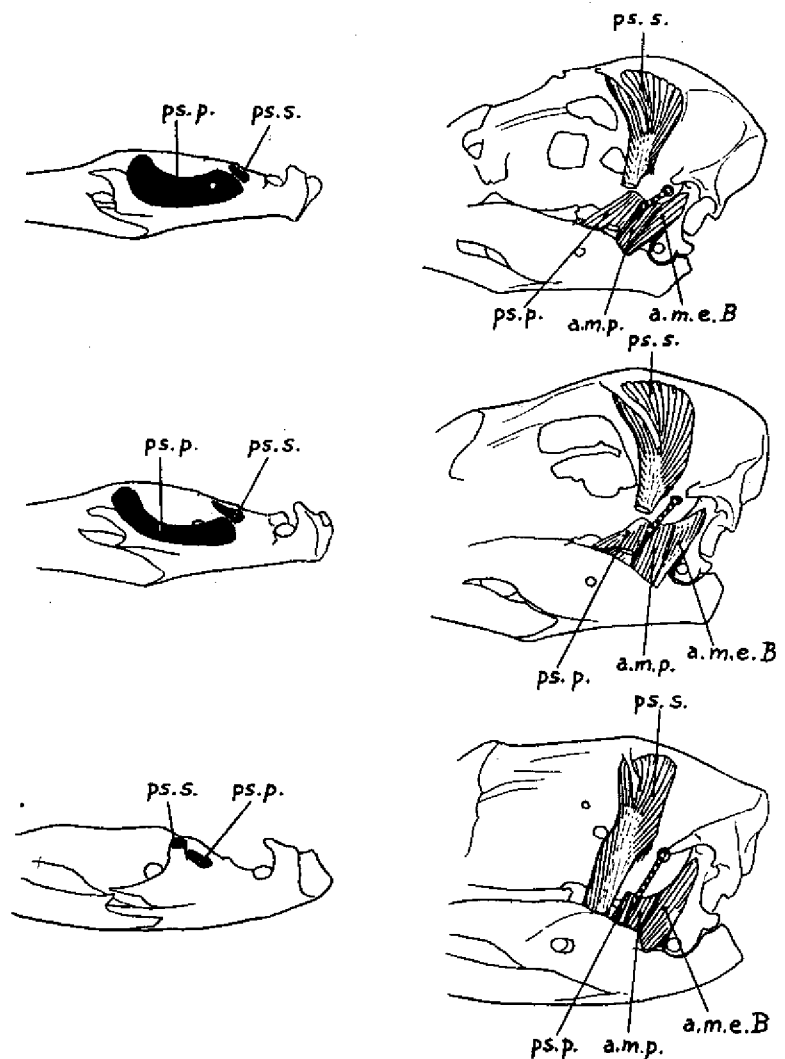


FIGURE 23. Right, lateral view of deep jaw adductors. Left, medial view of jaw showing insertions. Above, *Larus atricilla*. Middle, *Thalasseus maximus*. Below, *Rynchops nigra*. Part of *M. pseudotemporalis superficialis* removed in *Larus atricilla* and *Thalasseus maximus*. All are adjusted to the same body size. a. m. e., adductor mandibulae externus; a. m. p., adductor mandibulae posterior; ps. p., pseudotemporalis profundus; ps. s., pseudotemporalis superficialis. Ramus pterygoideus of trigeminal nerve cross-hatched.

*cristatus*, Bams numbered the aponeuroses consecutively. The following synonymy appears to be valid: aponeurosis A (Zusi) = aponeurosis XII (Bams, 1956), B = XIV, C = X, M = III, N and O = VII, P = IX (?). There are no aponeuroses in *R. nigra*, *T. maximus*, *G. nilotica* or *L. atricilla* corresponding to IV, V, or VIII of Bams.

*Thalasseus maximus*

*Origin.* The fibers of part M arise from the entire temporal fossa and from the superficial fascia covering the temporal portion of the muscle; from an aponeurosis (Ap. C) that runs anteroventrally from the temporal crest overlying part of *M. pseudotemporalis superficialis*; and from the anterior portion of the postorbital process and the postorbital ligament.

Fibers of part A originate from a large aponeurosis (Ap. A) which attaches to the tip of the zygomatic process and runs anteroventrally.

In part B, fibers originate from an aponeurosis (B) which attaches to a tubercle on the dorsolateral surface of the otic process of the quadrate. Fibers also originate from the anteroventral surface of the zygomatic process, from the anterolateral surface of the otic process, and from the dorsolateral surface of the base of the orbital process and aponeurosis D.

*Insertion.* The fibers of part M from the temporal fossa, from the superficial temporal fascia, from aponeurosis C, from the postorbital process and ligament, and some fibers from the medial surface of aponeurosis A, insert on a strong aponeurosis (Ap. M), which attaches to the dorsal crest of the surangular (coronoid process), and runs posterodorsally to the region of the temporal fossa.

Fibers of part A originating from the medial surface of aponeurosis A insert on the posterolateral surface of the dentary and on the surangular laterally, as well as on the anterior surface of aponeurosis N. From the lateral surface of aponeurosis A fibers run to the medial surface of aponeurosis P.

In part B fibers from the zygomatic process, the quadrate, aponeurosis B, and the ventral portion of C, insert on aponeurosis N and on the posterolateral surface of the surangular. Fibers from the quadrate and aponeurosis D insert on aponeurosis O and on the posterodorsal surface of the surangular.

*Structure.* Multipennate. Although this muscle complex is a large one, the muscle fibers are relatively short. The aponeurotic attachments of muscle fibers exceed in area the bony attachments, and the former are consequently more significant for functional analysis than the latter. In general the more distal and superficial aponeuroses pull at a smaller angle to the axis of the mandible than the proximal

and deep ones. Aponeuroses A and D of this muscle and aponeurosis M of the pseudotemporalis superficialis run approximately tangential to the surface of the eye.

It is impossible to make a clear separation between the bellies of parts M, A, and B of this muscle complex because the medial fibers of one part are in fact the lateral fibers of another. The structure of the muscle, however, becomes clear when the relationships of the aponeuroses are understood.

#### Comparison

Basically similar in *G. nilotica* but aponeurosis O and the dorsal portion of C are reduced, and aponeurosis D is absent. The fibers of part B are not clearly distinguishable from those of M. adductor posterior.

In *L. atricilla*, part B is enlarged at the expense of part A. The above description for *G. nilotica* also applies to *L. atricilla*.

*R. nigra* differs in that aponeuroses N and O are continuous with one another. Aponeurosis D is lacking, but an additional aponeurosis is present on the body of the quadrate. Part B is relatively large as in *Larus*. Fibers from the lateral surface of aponeurosis C insert on the medial surface of M and on the inner surface of the surangular, anterior to the prearticular.

#### Action

The primary action of this muscle is to raise the lower jaw. The mechanical advantage of part A is greater than that of part M; on the other hand, the efficiency of the latter exceeds that of the former because aponeurosis M pulls at a greater angle to the mandible than does aponeurosis A. It is likely that the proximal portions are important in initiating rapid closing of the beak, while the distal portions serve chiefly to apply steady pressure in grasping.

Because the angle of pull is not perpendicular to the jaw, a force component acts posteriorly along the long axis of the mandible. As Lakjer (1926:97) has pointed out, this component tends to rotate the quadrate posteriorly, thereby retracting the upper jaw. The adductor mandibulae and the pterygoideus are important synergists, together providing most of the biting power of the bill, and the backward force component of the adductor mandibulae (part A) may be important in anchoring the jaw against the forward pull of the pterygoideus.

The adductor mass is best developed, both in bulk and in extent of aponeuroses, in the Black Skimmer. This species is thus well adapted to effect a powerful grasp while carrying fish in its knife-like bill, and to counteract the depression forces on the mandible when objects are struck during skimming.



In the Herring Gull this muscle acts passively to bow out the lower jaw as it is lowered by the depressor mandibulae. By manipulation of freshly killed birds I found that, in the absence of the adductor mandibulae, the lower jaw is bowed inward during depression. The muscle is thus an important part of the adaptive complex for swallowing large prey in the Herring Gull. In the Black Skimmer its lateral force component probably serves only to counteract medial components of synergists, such as the pterygoideus.

M. ADDUCTOR MANDIBULAE POSTERIOR (Figure 23)

*Thalasseus maximus*

*Origin.* Fleishy, from the lateral and ventral surfaces of the orbital process of the quadrate. The anteriormost fibers attach deep to the attachment of M. pseudotemporalis superficialis. A few fibers attach on the anteromedial tip of the orbital process.

*Insertion.* Fleishy fibers attach on the posterodorsal surface of the lower jaw between the insertions of M. pseudotemporalis superficialis and part O of M. pterygoideus, and on a small superficial aponeurosis. Some of the deeper fibers attach on the aponeurotic surface of M. pterygoideus posterior near its insertion on the lower jaw.

*Structure.* Parallel. The lateral fibers run anteroventrally to the jaw while the deeper fibers run posteroventrally. This muscle is separated from M. pseudotemporalis profundus anteriorly by ramus pterygoideus of the trigeminal nerve.

*Comparison*

Similar in *G. nilotica*.

Similar in *L. atricilla*, but the aponeurosis is lacking.

In *R. nigra* the muscle is somewhat reduced. It attaches on the lower jaw between the pseudotemporalis profundus and the quadrate.

*Action*

Because of the poor mechanical advantage, the small size, and the parallel construction of this muscle, it probably has little effect in closing the jaws. However, the muscle undoubtedly contributes to the support of the lower jaw on the quadrate. A relatively slight force acting to keep the condyles of the jaw-quadrate articulation in their respective depressions enables these bony clasps to counteract stronger forces on the mandible.

M. PSEUDOTEMPORALIS PROFUNDUS (Figure 23)

*Thalasseus maximus*

*Origin.* Fibers of this muscle attach on the anterolateral surface of the orbital process of the quadrate, and on an aponeurosis that

attaches to the anterior edge of the orbital process. The primarily superficial aponeurosis extends anteroventrally for about one-half the length of the muscle. Most of the fleshy fibers attach to the posterior side of the aponeurosis, but a small portion of the belly springs from its anteroventral surface.

*Insertion.* Fleshy, on the medial surface of the lower jaw, principally in the trough between the prearticular and the surangular, but also on the adjacent surfaces of these bones.

*Structure.* Unipennate. A stout, triangular muscle. The anterior fibers run anteroventrally to the mandible, while the posterior fibers run primarily ventrally.

#### *Comparison*

Similar in *G. nilotica* and *L. atricilla*.

Much reduced in *R. nigra*. No aponeurosis is present, and the muscle is of the parallel type. The insertion is posterior to that of *M. pseudotemporalis superficialis* rather than anterior to it.

#### *Action*

This muscle depresses the upper jaw, at the same time elevating the lower jaw. It would therefore appear to be useful in coördinating the closing of both jaws. The marked reduction of this muscle and its more posterior attachment on the mandible in the Black Skimmer may be merely a by-product of reduction of the orbital process of the quadrate, and thus of no direct adaptive value.

#### *M. PSEUDOTEMPORALIS SUPERFICIALIS* (Figures 20, 23, 24)

##### *Thalasseus maximus*

*Origin.* Fibers originate from the pseudotemporal fossa and from a large area on the posterior wall of the orbit. Two aponeuroses (A and B) attaching to tubercles on the posterior wall of the orbit also serve as origin for fleshy fibers. Aponeurosis A is superficial and it extends ventrally from its attachment on the orbitosphenoid, parallel with the main portion of aponeurosis M. The short aponeurosis, B, is surrounded by fleshy fibers throughout its length.

*Insertion.* Most of the fibers insert on aponeurosis M, one branch of which supplies the orbital portion of the muscle and another branch the pseudotemporal portion. These branches unite beneath the postorbital process to form a single aponeurosis, which attaches to a tubercle on the medial surface of the jaw at the posterior end of the groove between the surangular and the prearticular. Fibers from aponeurosis A insert on a concavity in the main part of M and on the surangular anterior to aponeurosis M.

*Structure.* Bipennate. The relatively short fibers are concentrated dorsally, while ventrally the muscle becomes narrow and essentially tendinous.

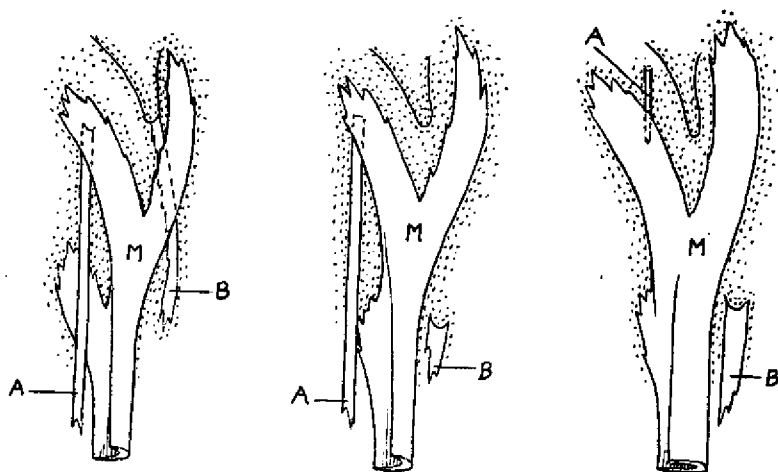


FIGURE 24. Diagram of aponeuroses of *M. pseudotemporalis superficialis* in anterotlateral view. Left, *Larus atricilla*. Center, *Thalasseus maximus*. Right, *Rynchops nigra*. A and B, aponeuroses of origin; M, aponeurosis of insertion.

#### Comparison

Similar in *G. nilotica*.

Essentially similar in *L. atricilla*, except for the greater development of a third branch of aponeurosis M, which extends dorsomedially and passes posterior to aponeurosis A. Fibers from the medial portion of the orbitosphenoid insert on this branch. Aponeurosis B attaches along a crest that extends from the postorbital process ventrad to the tubercle.

In *R. nigra*, aponeurosis M divides into two major portions dorsally as in the terns. Aponeurosis A, however, is reduced to a tiny and virtually functionless strip and is buried in the musculature from the dorsal portion of the orbitosphenoid. Aponeurosis B is better developed than in the other species. Aponeurosis M inserts on a dorsal projection of the articular.

#### Action

The principal action of this muscle is adduction of the lower jaw. It is powerfully constructed but its mechanical advantage is poor; contraction therefore causes rapid closing of the jaw. The combined actions of *M. depressor mandibulae* and this muscle hold the lower jaw in position during skimming and keep the lower jaw firmly against the quadrates.

The mechanical advantage of this muscle is greater in the Black Skimmer because of its relatively more distal attachment on the jaw. This muscle is also more efficient when the jaw is open in *R. nigra* than in the other species because the angle of pull on the depressed mandible is somewhat closer to 90°. These features may be adaptations for stabilization of the mandible during skimming.

M. PTERYGOIDEUS (Figures 20, 22, 25)

Because of the complexity of this muscle and its superficial variability within the class Aves, the terminology of the pterygoideus group is almost as varied and confusing as that of the adductor mandibulae externus complex. Lakjer (1926:65) proposed to divide the muscle mass into a pterygoideus dorsalis and a pterygoideus ventralis, each of which was divided into lateral and medial parts in some species. This terminology has been followed, with certain variations, by Hofer (1950), Starek and Barnikol (1954), and Boek (1960b). Moller (1930) and Beecher (1951), however, have included a major portion of the pterygoideus dorsalis of Lakjer in their pterygoideus ventralis (anterior part). Unfortunately, this muscle has

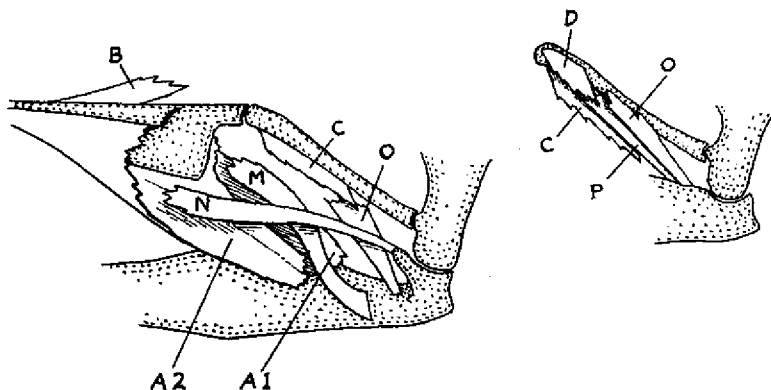


FIGURE 25. Diagram of aponeuroses of the pterygoideus complex. Left, *Thalasseus maximus*, medial view. Right, lateral view of part O of *Rynchops nigra*. A-D, aponeuroses of origin. M-P, aponeuroses of insertion.

seldom been studied in terms of its major aponeuroses, and the variability of its basic structure in birds is not known. I have considered the pterygoideus of the species studied here to consist of three major parts, M, N, and O, which are readily separable in terms of aponeuroses, although the fibers of different parts merge in several places. Both attachments of this muscle are movable, but I shall follow the example of other authors in considering the attachment on the lower jaw as the insertion.

Bams (1956) has published a partial description of the pterygoideus complex of *Podiceps cristatus* in which the aponeuroses are analyzed in detail. The following incomplete synonymy can be offered at present: A2 (Zusi) = XX (Bams), A1 = XXII, M = XIX, N = XXI + XXIII + XXV (?).

*Thalasseus maximus*

*Origin.* Fibers of part M attach on the entire dorsolateral surface of the palatine except for its anterior and posteromedial portions; and on the dorsal surface of an aponeurosis (A<sub>1</sub>), which extends laterally and posteriorly from its attachment along the lateral and posterolateral edges of the palatine. Fibers also originate from the ventral surface of aponeurosis B, which attaches to the palatine anterodorsally. Some fibers attach along the anteroventral surface of the pterygoid.

Origin for part N is provided by the concavity on the ventral surface of the palatine, the dorsal surface of an aponeurosis (A<sub>2</sub>), which attaches on the medial crest of the palatine, and the anteroventral surface of the palatine. Aponeurosis A<sub>2</sub> extends posteriorly beyond the palatine and fuses with aponeurosis A<sub>1</sub> near the latter's attachment to the lateral surface of the palatine.

Fibers of part O spring from the posterior extremity of the palatine, from the dorsolateral and ventromedial surfaces of the pterygoid, and from an aponeurosis (C) attaching along the ventrolateral edge of the pterygoid.

*Insertion.* Fibers of part M from the dorsal surface of the palatine and from aponeuroses A<sub>1</sub> and B insert on both sides of aponeurosis M and on the posteroventral and ventrolateral surfaces of the posterior portion of the lower jaw. Aponeurosis M attaches along a roughened line on the medial surface of the mandible immediately anterior to the attachment of part O of this muscle. Fibers from the anteroventral surface of the pterygoid insert on the dorsomedial surface of aponeurosis N.

Fibers of part N from the ventral surface of the palatine insert on the dorsal surface of aponeurosis N and on the medial surface of the internal process of the lower jaw. From the dorsal surface of aponeurosis A<sub>2</sub> fibers run to the ventral surface of aponeurosis N and to the ventral surface of the internal process of the mandible. Aponeurosis N attaches on the posterodorsal edge of the internal process of the mandible.

Fibers of part O from the lateral and medial surfaces of the pterygoid and from aponeurosis C insert on aponeurosis O and on the posteromedial surface of the lower jaw anterior to the internal process. Aponeurosis O attaches on the posterodorsal surface of the

lower jaw immediately anterior to the jaw-quadrangle articulating surfaces.

*Structure.* Multipennate. As in the adductor mandibulae complex, the fibers of this large muscle are relatively short and the aponeurotic areas of attachment exceed the bony ones. The anterior portion of aponeurosis N reaches into the space enclosed by the palatine and aponeurosis A<sub>2</sub> where the fibers are arranged in circumpennate fashion. The extension of aponeuroses A<sub>1</sub> and A<sub>2</sub> posterior to the palatine wing is  $\perp$ -shaped in cross section.

#### *Comparison*

Similar in *G. nilotica*.

Basically similar in *L. atricilla*, but aponeurosis B is lacking, and all aponeuroses are relatively less developed.

*R. nigra* is similar in basic pattern, but the musculature is hypertrophied and the aponeuroses are more extensive than in the other species. The dorsomedial part of aponeurosis M curves around to form a cone, all surfaces of which serve for the attachment of fibers. The posterior portion of aponeurosis B extends into this cone and the fibers converge on it in circumpennate fashion. In addition to aponeuroses O and C, two others are present; one (D) attaches on the anterodorsal tubercle of the pterygoid and runs posteroventrally. The other (P) is deep and runs between the two aponeuroses of origin. Part O is therefore multipennate in *R. nigra* but unipennate in the other species.

#### *Action*

The pterygoideus is perplexing in that both its origin and insertion are movable and are interconnected by a strut system such that the pull on the origin tends to depress the upper jaw while the pull on the insertion tends to do just the opposite (as well as adducting the lower jaw). Despite this apparent contradiction, the muscle, in fact, depresses the upper jaw. If we represent the muscle and strut system diagrammatically (Figure 26) and assume for simplicity that the pterygoideus (P) inserts on the distal tip (C) of the quadrate (QU), we may focus our attention on the junction (B) of the palatine (PAL) and the pterygoid (PT). If a resultant force moves B anteriorly along the axis (AX) of the parasphenoid rostrum, the upper jaw is protracted; if B moves posteriorly, it is retracted. A given contraction of P causes equal and opposite forces ( $f$  and  $f_1$ ) at its origin and insertion. The components of these forces acting along the palatine and pterygoid produce a resultant force ( $r$ ) at B. This force may be replaced by two components— $s$  acting perpendicular to AX, and  $t$  directed posteriorly along AX. Force  $t$  draws the palate backward and retracts the upper jaw while component  $s$

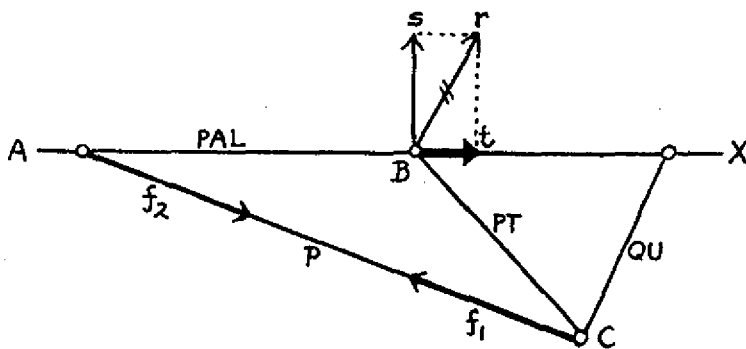


FIGURE 26. Force diagram of *M. pterygoideus*. Above, relationships of muscle and skull. Below, forces during contraction of muscle. For explanation see text, page 58. AX, axis of parasphenoid rostrum; B, junction of palatine and pterygoid; C, insertion *M. pterygoideus*; P, *M. pterygoideus*; PAL, palatine; PT, pterygoid; QU, quadrate; f, r, s, t, forces or force components.

serves to hold the sliding palatal mechanism in place on the parasphenoid rostrum against the downward pull of the pterygoideus. Figure 26 also represents a ventral view of the palate, in which case component *s* acts to hold the posterior ends of the palatines together. The insertion of the pterygoideus is, of course, on the lower jaw rather than on the quadrate, and the jaw-quadrates articulation is a sliding one in which the jaw slides backward during depression and forward during adduction. Force *f*<sub>1</sub>, then, not only acts on the palatal mechanism but it adducts the lower jaw and slides it forward as well. The power of the pterygoideus is thus potentially available for three actions and is not necessarily used solely for the retraction of the palate. In view of the close proximity of the tendons of insertion to the point of rotation of the jaw, however, it would appear that its chief function in the species studied is lowering of the upper jaw.

Part *O* apparently acts principally to hold the lower jaw firmly against the quadrate and to prevent backward disarticulation of the jaw, although it also aids slightly in adducting and protracting the lower jaw. Its more powerful construction in the Black Skimmer may be an adaptation to prevent backward dislocation of the mandible during skimming. The hypertrophy of muscle mass and area of aponeuroses of the pterygoideus complex in the Black Skimmer complements that of the adductor mandibulae complex, and enables this species to maintain a powerful grasp on its prey.

#### DISCUSSION

The jaw musculature of *R. nigra* shows little difference in basic pattern from that of the terns and gull studied. The pseudotemporalis profundus, however, is greatly reduced, and its insertion is shifted posteriorly. All other jaw muscles of the Black Skimmer, except perhaps the adductor mandibulae posterior, are relatively larger and more powerfully constructed, or have greater mechanical advantage, than in the other three species. Frieling (1936) mentioned the enlargement of the temporal portion of *M. adductor mandibulae externus* (= part *M*) and of *M. pseudotemporalis superficialis* in the Black Skimmer relative to those of the Large-billed Tern, *Phaetusa simplex* (Gmelin). The Royal Tern provides perhaps a more meaningful comparison in this case because of its larger jaws. Frieling may have been mistaken, however, in stating that the pterygoideus muscles and the remaining portion of *M. adductor mandibulae externus* (= parts *A* and *B*) showed only unimportant differences.



Frieling related the hypertrophy of the jaw adductors in *R. nigra* to the forces on the lower jaw that it must overcome during skimming. I have already suggested that the pseudotemporalis superficialis may be the chief adductor acting to stabilize the mandible during skimming. The greater development of the adductor mandibulae externus and of the pterygoideus is probably also related to the hypertrophy of the jaws in the Black Skimmer and to the powerful grip necessary to hold a fish while pulling it out of the water or carrying it for considerable distances.

Bock (1960b) emphasized the importance both of the lateral parts of the pterygoideus found in passerine birds for raising the lower jaw, and of the medial parts for lowering the upper jaw. The anatomical and functional division of the pterygoideus is much less pronounced in lariform birds, where the pterygoideus is primarily a retractor of the upper jaw while the adductor mandibulae is primarily an adductor of the mandible. In a kinetic skull the force of the bite is no stronger than that of the weaker jaw; thus in lariform birds hypertrophy of one muscle mass is accompanied by hypertrophy of the complementary mass—a condition well illustrated by the Black Skimmer.

The primary and secondary actions of the jaw muscles of the four species studied are presented in Table 3. Each of the jaw muscles may affect the motion of both jaws, if only to a slight degree. Contraction of the protractor quadrati causes the quadrate to rock forward, raising the upper jaw, but the motion of the quadrate combined with the restraining actions of the occipitomandibular ligament and postorbital ligament also causes a weak depression of the lower jaw. Similarly, a weak retraction of the upper jaw can be effected through ligaments when the lower jaw is raised by the pseudotemporalis superficialis. Even if we ignore these incidental actions (which have been omitted in Table 3), four of the six major jaw muscles may still act strongly on both jaws when contracting in isolation. The actions are always complementary, producing opposite motions of the two jaws. A muscle that raised or lowered both jaws would, of course, be ill-adapted either for opening or for closing the bill. Although both of the possible actions of each muscle do not necessarily occur during synergistic contraction, the evolutionary potential of the jaw muscles for assuming new functional roles through shifts in their origins and insertions is considerable. In the Black Skimmer, only the depressor mandibulae has adopted a new role, and the extent of its modification is much less than in some other birds (see Zusi, 1959b). Adaptations for skimming have thus been achieved with only moderate change in the pattern of jaw muscles characteristic of gulls and terns.

TABLE 3  
JAW MUSCLE ACTIONS OF *T. maximus*, *G. nilotica*, *L. atricilla*,  
and *R. nigra*

Muscle	Open Mouth		Close Mouth	
	Protract Maxilla	Depress Mandible	Retract Maxilla	Adduct Mandible
Protractor quadrati	++			
Depressor mandibulae	+*	++		
Adductor mandibulae			+	++
Pseudotemporalis superficialis				++
Pseudotemporalis profundus			++	++
Pterygoideus			++	+

++ primary action.

+ secondary action.

\* *R. nigra* only.

## ADAPTATIONS OF THE NECK

### VERTEBRAE

*Forces.* Environmental forces acting on the lower jaw of a feeding Black Skimmer (page 28) are transmitted to the skull and neck in varying degrees, depending upon the stability of the mandible and skull and the lever systems through which the forces are transferred. Frieling (1936) has discussed the levers by which a force tending to depress the mandible is augmented at the level of the dorsal neck muscles in the Black Skimmer. His conclusions will be discussed along with the neck muscles.

Figure 31 shows the position of the jaws, skull, and neck vertebrae of a feeding skimmer. Forces tend to cause downward and backward rotation of the head on the neck, and down-bending of the entire neck. Such forces are strong when the head is bent under the body and when it is drawn forward against water pressure. The weight of the head with its hypertrophied jaw muscles, and of fish carried in the bill, constitute further downward forces on the neck and head. Other forces acting posteriorly along the long axis of the jaw tend to bend upward the anterior and middle portions of the neck. Finally, lateral pressure of water on the bill tends to turn the head and neck to either side.

Although the manner in which the Royal Tern uses its head and neck underwater is not known, I have assumed that the head is doubled under the body and brought forward to its normal position under water. Thus water pressure may exert a strong backward and downward force on the head and neck. In addition the neck must support the weight of large fish carried in the bill.

There appear to be no unusually strong forces acting frequently on the neck in the Gull-billed Tern or the Laughing Gull. These species are versatile in the use of the neck, however, and they may at times be subject to forces similar to those described for the Black Skimmer and the Royal Tern.

*Proportions.* Figures 27 and 28 illustrate the cervical vertebrae of the Laughing Gull, Gull-billed Tern, Royal Tern, and Black Skimmer, adjusted to the same body size. The neck of the Black Skimmer is relatively longer and more massive than those of the other species. The increase in length is due to elongation of the more anterior vertebrae (especially the second and third, but not the atlas). The transverse distances between the prezygapophyses and between the postzygapophyses of the first 10 vertebrae are much greater in the Black Skimmer. The neural spines of vertebrae 2-4 and 8-14 are enlarged in height and surface area, and the anapophyses

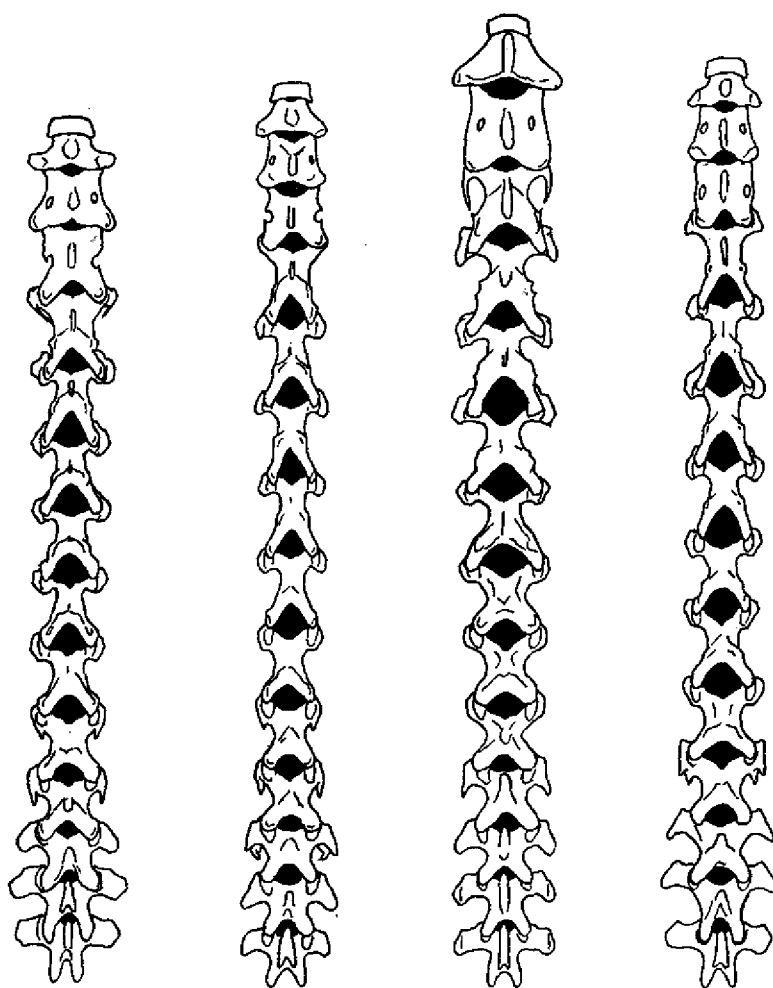


FIGURE 27. Dorsal view of cervical vertebrae. Left to right, *Thalasseus maximus*, *Gelochelidon nilotica*, *Rynchops nigra*, *Larus atricilla*. All are adjusted to the same body size.

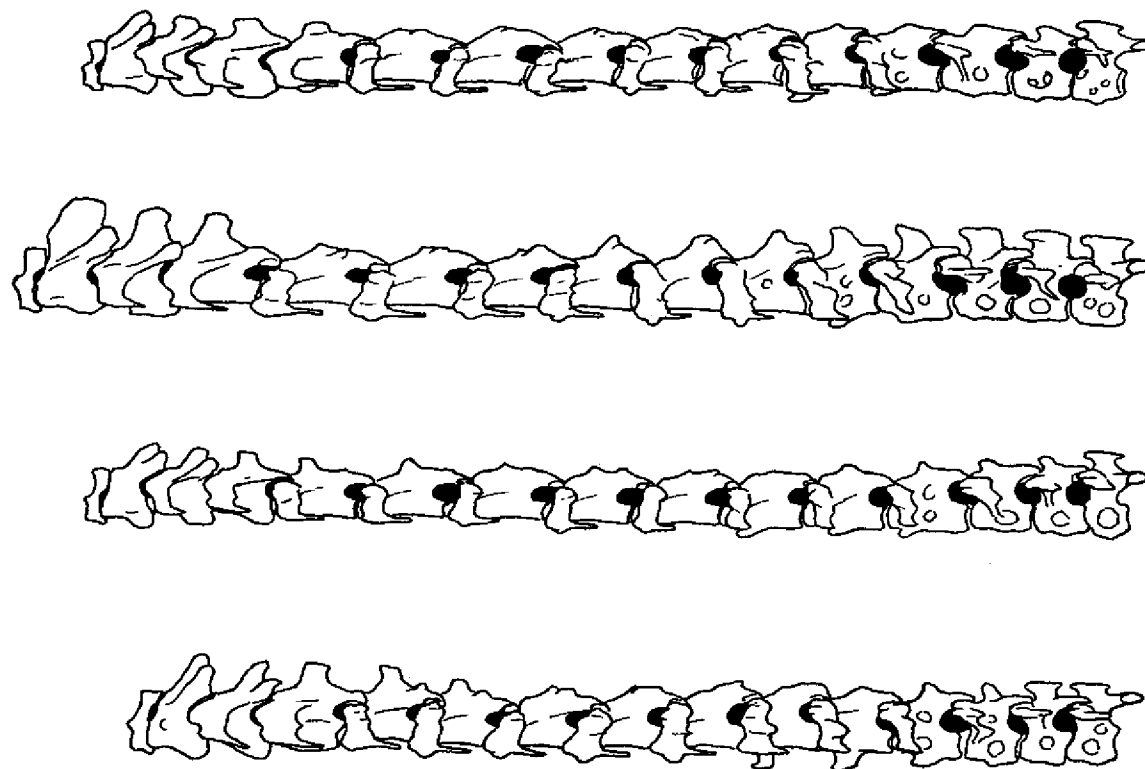


FIGURE 28. Lateral view of cervical vertebrae. Top to bottom, *Larus atricilla*, *Rynchops nigra*, *Gelochelidon nilotica*, *Thalasseus maximus*. All are adjusted to the same body size.

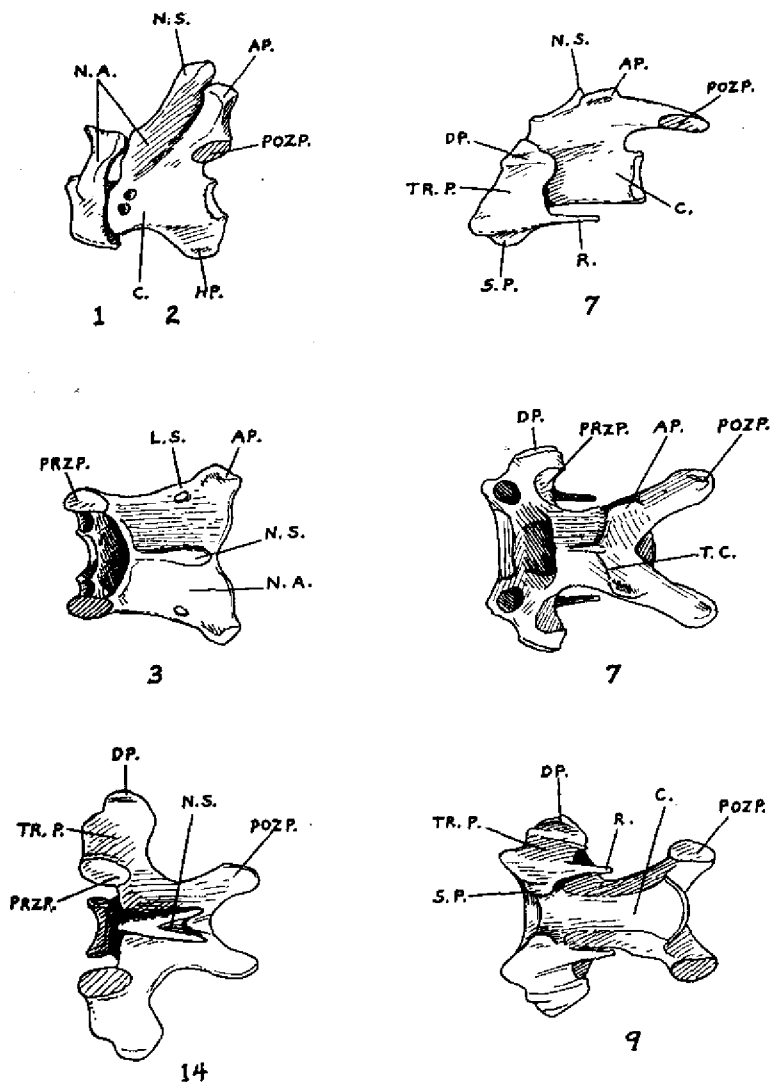


FIGURE 29. Cervical vertebrae of *Thalasseus maximus* with processes labeled. Numbers identify vertebrae. Above, lateral view. Middle, dorsal view. Below, dorsal (left) and ventral (right) views. AP., anapophysis; C., centrum; DP., diapophysis; HP., hypapophysis; L. S., lateral strut; N. A., neural arch; N. S., neural spine; POZP., postzygapophysis; PRZP., prezygapophysis; R., rib; S. P., sublateral process; T. C., transverse-oblique crest; TR. P., transverse process.

are well developed, but there is no corresponding increase in the hypapophyses. (See Figure 29 for parts of vertebrae.)

These differences of proportion in the vertebrae of the Black Skimmer reflect the hypertrophy of some of the neck muscles, and they also represent adaptations to counteract forces that act primarily during skimming. The enlarged neural spines provide greater surface of origin for the splenius and spinalis muscles, and allow for greater efficiency with respect to the direction of pull of these muscles, which counteract downward forces on the head and neck. The increased transverse distances between the zygapophyses in effect increase the force arms of the lateral neck muscles (*intertransversarii*), thereby providing greater stability against lateral bending of the neck. Elongation of the neck will be discussed later.

Rockwell *et al.* (1938:104) have pointed out that in vertebrates when the neck is flexed downward, the neural arches of the cervical vertebrae transmit tension stresses, and the vertebral centra resist compression stresses. When the neck is not flexed downward, tension stresses are transmitted through the dorsal neck muscles. The centra, however, must resist compression at all times except when the neck is flexed upward maximally, at which time the neural arches resist compression while the centra transmit tension stresses. The nature of the vertebral articulations is such that all of the cervical vertebrae may be maximally flexed downward during the normal activities of a bird, but only the more posterior and anterior vertebrae are likely to be maximally flexed upward. The forces on the vertebrae of lariform birds are summarized in Table 4.

TABLE 4

FORCES EXERTED ON THE NECK OF LARIFORM BIRDS  
(See text for explanation.)

Condition	Tension	Compression
Neck or segment maximally flexed downward	Neural arches	Centra
Neck or segment maximally flexed upward	Centra	Neural arches of anterior and posterior vertebrae only
Neck or segment in intermediate position	Dorsal neck musculature	Centra

Downward forces acting on the neck of the Black Skimmer during maximal downward or upward flexion of parts of the neck are greater and more prolonged than in the other species studied. While skimming, the bird must hold its neck in the position shown in Figure 31, with the posterior and middle segments of the neck flexed downward and the anterior segment bent upward against the middle portion. Under these conditions, compression stresses are present in the neural arches of the anterior vertebrae and in the centra of the middle and posterior vertebrae. In response to increased stresses, the centra, neural arches, and dorsal neck muscles are unusually well developed in *R. nigra*.

*Neck Segments.* Boas (1929) noted that the neck of birds consists of three functionally and morphologically distinct segments. I have diagrammed these segments in Figure 30. Boas discussed only the "true" cervical vertebrae, that is, those that either have fused ribs or that lack ribs. In this paper I shall use the term "cervical vertebrae" to mean the true cervicals and the cervicodorsal vertebrae as well. The two cervicodorsal vertebrae support movable ribs that have no contact with the sternum. Unlike the dorsal vertebrae they are not tightly bound together and for functional analysis they are best considered a part of the neck. In Figure 30 the vertebrae are represented as hinged at either end of the centrum, and the spaces between the vertebrae above or below the hinges indicate the potential for dorsoventral bending.

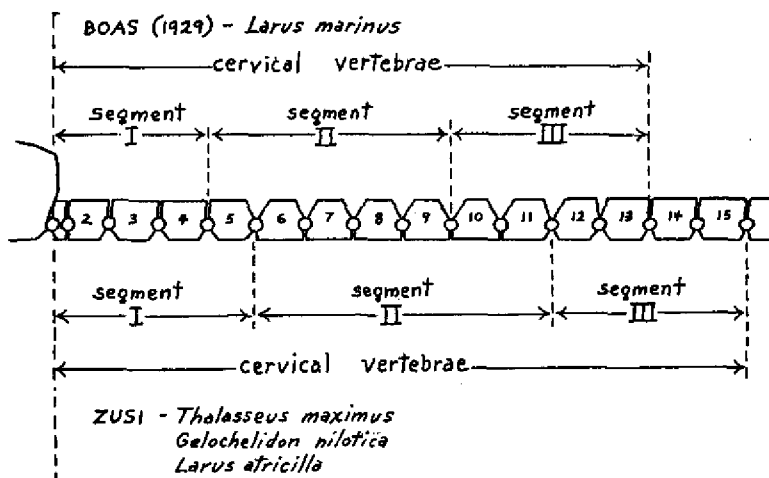


FIGURE 30. Diagram of segments of the neck in lateral view, as interpreted by Boas above, and by Zusi below.



In the gull and terns studied, segment I includes the first five vertebrae. Segment II is composed of vertebrae 6-11, and segment III comprises vertebrae 12-15. Vertebra 5 is intermediate morphologically and functionally between those of segments I and II, and it is arbitrarily included in segment I. Similarly vertebra 12 is intermediate between those of II and III, and is included in segment II.

In describing the dorsoventral or lateral motion of the neck segments, I shall use the term "flex" to indicate bending away from a straight position of two or more vertebrae, and "straighten" to indicate bending toward a straight position. Segment I can be flexed only downward and segment II can be flexed only upward, while segment III can be flexed downward, and in its anterior portion, upward as well. The skull is functionally comparable to an additional vertebra of segment I in that it can be flexed downward only. The neck is ordinarily held in an S-shaped curve with all segments somewhat flexed.

Since Boas has described in detail the morphology and relation to function of the vertebrae of each segment, I shall restrict my comments primarily to features of the four species that appear to be adapted to feeding behavior.

*Segment I.* The dorsal border of the foramen magnum is connected with the neural arch of the atlas by a broad, tough ligament that limits downward flexure of the head on the neck. Upward movement of the head is stopped when the dorsal border of the foramen magnum abuts against the neural arches of the atlas and axis. The total downward flexure possible in preserved specimens from which I removed all the muscles was 73° in a Laughing Gull and a Royal Tern, 74° in a Gull-billed Tern, and 80° in a Black Skimmer.

*E. nigra* differs from the other species studied in having only four vertebrae in the first segment, vertebra 4 being intermediate in structure between those of the first and second segments. The presence of lateral struts (although incomplete) suggests that this vertebra is homologous with vertebra 4 in gulls and terns and that it has been secondarily modified in the Black Skimmer. The adaptive nature of this change in the segments is best understood in terms of the action of *M. complexus*, which will be fully described later. Through reduction in number of vertebrae in the first segment a larger percentage of the bulk of the complexus is effective in flexing that segment upward on Segment II, and the efficiency of the muscle is also considerably increased.

Total downward flexure of the first segment of the Black Skimmer is reduced because of the reduction in number of vertebrae, but this reduction is accompanied by increased downward mobility of the head. The maximum flexure of the head and neck segments

together is thus similar in the four species. Lateral flexion of the head on the atlas is considerable in all of these birds, and lateral bending is possible between successive vertebrae of the first segment.

*Segment II.* This segment is capable of pronounced dorsal flexion in the four species. As I have already mentioned, much of the upward and backward force exerted when the lower jaw of the Black Skimmer strikes bottom is probably absorbed through dorsal flexion of this segment.

Lateral flexion of the vertebrae is limited when this segment is in a dorsoventrally straightened position, but it is appreciable in conjunction with flexion or straightening of the segment. The posterior vertebrae bend laterally more freely than the others.

With the transfer of a vertebra from segment I to segment II the second segment is lengthened. If one considers the angle at which this segment is held during skimming (Figure 31), it is evident that *R. nigra* can maintain a greater distance between its body and the water surface than could a gull or tern under comparable

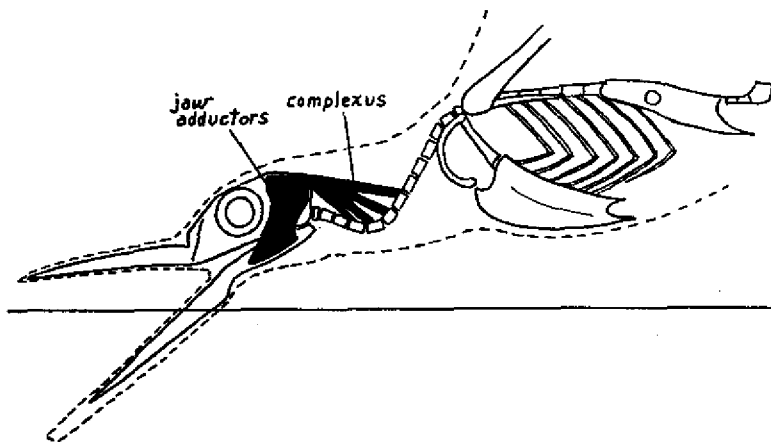


FIGURE 31. Diagram of position of skeleton and key muscles of *Rynchops nigra* during skimming.

conditions. When the vertebral column of a Laughing Gull and that of a Black Skimmer are held in a position similar to that of a skimming bird with the first segments at the same level, the dorsal vertebrae of the Black Skimmer are about  $\frac{1}{2}$  inch above those of the gull. Whether or not an increase of this magnitude in the height of the body over the water is of adaptive value is difficult to say, but it may at times be important in permitting the wings to be flapped through a greater arc without touching the water.

*Segment III.* This segment is anatomically and functionally similar in the four species. It is capable of considerable lateral bending, slight dorsal flexion anteriorly, and pronounced ventral flexion.

#### NECK MUSCULATURE

Boas (1929) wrote an excellent account of the neck musculature of the Great Black-backed Gull, *Larus marinus*. I have used his terminology without alteration. The work of Palmgren (1949) on the neck muscles of certain oscines supplements that of Boas. In his brief functional-anatomical study, Frieling (1936) compared several superficial neck muscles of the Black Skimmer with those of the Large-billed Tern, but there appears to be no detailed description in the literature of the neck musculature of a tern.

The musculature of the thoracic vertebrae will not be included except where it has a direct bearing on the functioning of the neck. Because of the segmentation of the vertebral column, a muscle may have many bellies or slips arranged in segmental fashion. These will appear as diagrams, an example set by Boas.

The origin of each muscle or slip is considered its posterior attachment, and the insertion its anterior attachment. Throughout the descriptions, numbers refer to vertebrae. Starting with the atlas, the cervical vertebrae are numbered 1-15, higher numbers referring to the thoracic vertebrae. In comparing the other species with *Thalasseus maximus* the term "similar" always refers back to *T. maximus*.

I shall discuss the actions of those neck muscles showing adaptations for feeding. For the other muscles reference can be made to Table 5, which summarizes individual actions of each muscle. Although other functions are possible through synergistic contraction, these are not included in the table. Three muscles (rectus capitis superior, flexor colli brevis, rectus capitis ventralis) cross the vertebral pivot points either dorsoventrally or ventrodorsally. Their contraction causes upbending of the segment at the origin and downbending at the insertion, or vice versa, but only the action at the insertion is shown in Table 5. The other action is presumably very weak because of the poor mechanical advantage of the muscles near their origin.

#### M. COMPLEXUS (Figures 32, 33, 34, 35)

##### *Thalasseus maximus*

*Origin.* Fleshy fibers arise from the diapophyses of 5 and 6 and from aponeuroses running forward from these diapophyses. The main slip arises by a broad aponeurosis from the diapophysis of 7. Fleshy fibers arise from the lateral surface of this aponeurosis opposite diapophysis 6. The medial surfaces of the aponeuroses of origin receive fibers from the *ascendentes cervicis*.

TABLE 5  
NECK MUSCLE ACTIONS OF *T. maximus*, *G. nilotica*, *L. atricilla*, and *R. nigra*

Muscle	Head			Segment I					Segment II					Segment III			Depressors	Elevators
	Tilt upward	Turn laterally	Tilt downward	Straighten	Raise on II	Bend laterally	Flex downward	Lower on II	Straighten	Lower on III	Bend laterally	Flex upward	Raise on III	Straighten	Bend laterally	Flex downward		
Splenius capitis	+	+																
Rectus capitis lateralis*	+	+				+												
Complexus	+	+		+	+													
Biventer cervicis	+			+	+													
Splenius colli				+	+													
Interspinales				+	+													
Spinalis cervicis				+	+													
Intercistales				+	+													
Ascendentes cervicis				+	+													
Intertransversarii						+												
Inclusi superior																		
Dorsales pygmaei																		
Rectus capitis superior			+															
Rectus capitis ventralis		+				+												
Flexor colli brevis							+											
Flexor colli profundus							+											
Longus colli ventralis							+											
Inclusi inferior								+										

\* also rotates the head about its axis.

*Insertion.* Fibers attach on the thickened dorsal edge of the occipital bones and on a short superficial aponeurosis. The medial fibers insert on a median raphe extending posteriorly from the mid-dorsal occipital region. The insertion extends laterally to the origin of the depressor mandibulae.

*Structure.* Weakly unipennate. The belly is broad and flat, and consists of three slips posteriorly, of which the dorsal slip originating from 7 is the largest. The belly is also divided into four segments by three tendinous intersections.

#### *Comparison*

*G. nilotica.* Originates from diapophyses of 6 and 5, and from the lateral strut of 4. Insertion similar.

*L. atricilla.* Originates by four slips as follows: by a flat tendon from diapophysis 6, from the diapophysis of 5, the lateral side of the transverse process of 4, and the anapophysis of 3. The anterior slip is weak, and the belly is relatively thinner than in *T. maximus*. The muscle consists of only three segments.

*R. nigra.* Originates as in *T. maximus*, with the addition of a fourth slip from diapophysis 4. The muscle is very well developed, and the aponeuroses are relatively more extensive. The area of insertion is increased by an extensive superficial aponeurosis on the anterior end of the muscle. The muscle is divided into four segments.

#### *Action*

Despite the obvious importance of this muscle for feeding in the Black Skimmer, the importance of its individual actions is difficult to assess. The complexus tilts the head upward about its pivot on the atlas. When the head abuts against the neural arches of the atlas and axis, further contraction serves to straighten segment I, and part of the muscle also swings segment I upward with respect to II. The latter part may also flex the anterior vertebrae of segment II upward. Finally, unilateral contraction causes turning of the head and segment I sideways. The work of raising the head and segment I is left to the slips originating on segment II; in *R. nigra* three strong slips originate on segment II in contrast to two in *T. maximus* and only one in *G. nilotica* and *L. atricilla*.

Since the head and neck of a skimming bird are held in a constant relationship by various neck muscles, including the anterior slips of the complexus, we may consider that those slips of the complexus originating on the second segment serve to prevent downward pivoting of a unit comprising the jaws, cranium, and first neck segment. This unit (represented by ABC in Figure 34) pivots at the articulation of the centra of vertebrae 4 and 5 in *R. nigra* and of vertebrae 5 and 6 in the Laughing Gull, Royal Tern, and Gull-billed

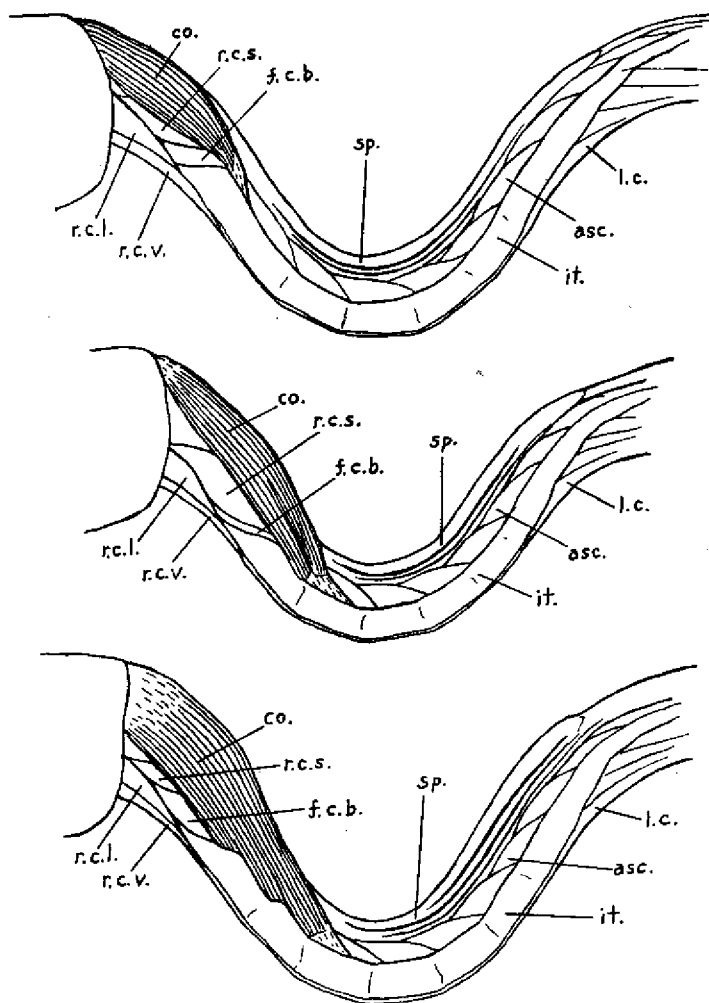


FIGURE 32. Lateral view of superficial neck muscles. Above, *Larus atricilla*. Middle, *Thalasseus maximus*. Below, *Rynchops nigra*. All are adjusted to the same body size. M. complexus shaded for emphasis. asc., ascendentes cervicis; co., complexus; f. c. b., flexor colli brevis; it., intertransversarii; l. c., longus colli ventralis; r. c. l., rectus capitis lateralis; r. c. s., rectus capitis superior; r. c. v., rectus capitis ventralis; sp., spinalis cervicis.

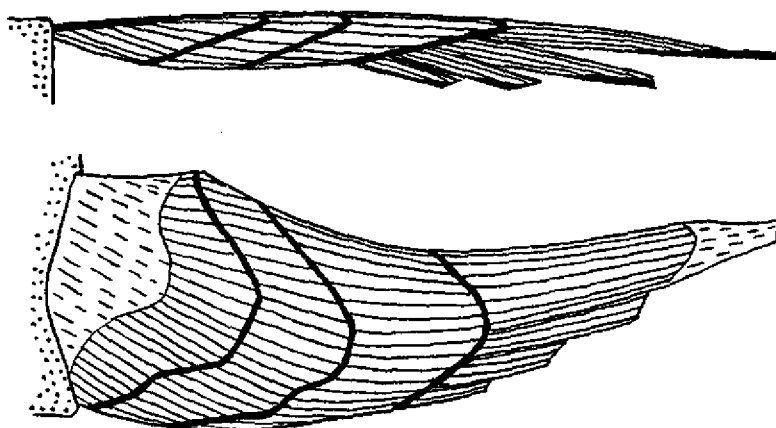


FIGURE 33. Diagram of structure of *M. complexus* of *Rynchops nigra*. Above, left lateral view. Below, dorsal view of left muscle. Heavy lines indicate tendinous intersections.

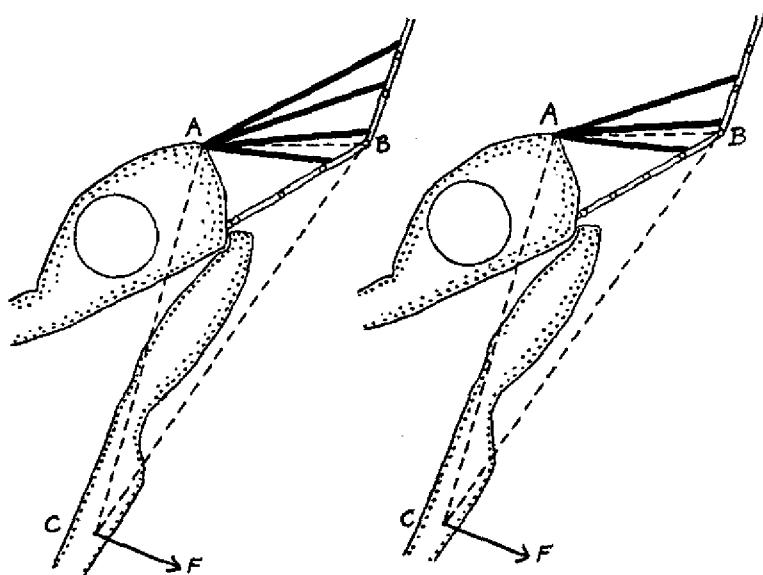


FIGURE 34. Left, diagram of *M. complexus* in *Rynchops nigra* during skimming. Right, the same with the complexus and neck of *Thalasseus maximus* substituted for those of *R. nigra*. Heavy lines represent *M. complexus*. F means environmental force. A B C represents unit pivoting at B. For explanation see text, page 73.

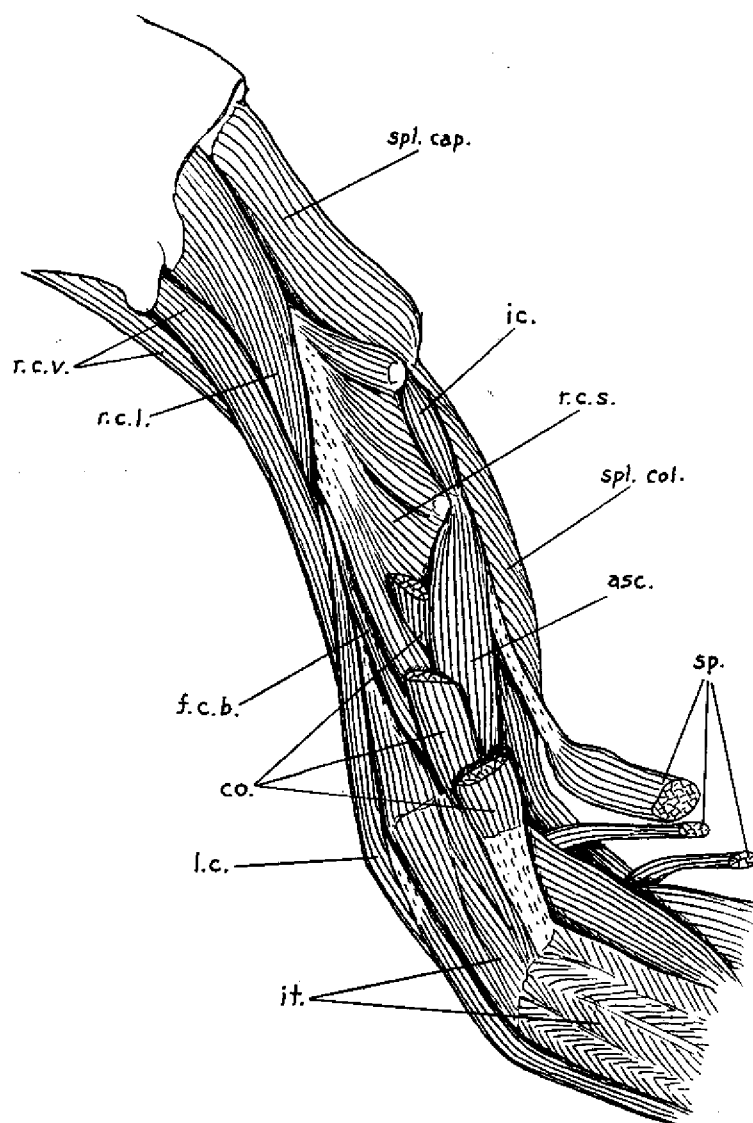


FIGURE 35. Lateral view of anterior neck muscles of *Thalasseus marinus*. Complexus, biventer cervicis, and spinalis cervicis removed. asc., ascendentes cervicis; co., complexus; f. c. b., flexor colli brevis; ic., intercristalis; it., intertransversarii; l. c., longus colli ventralis; r. c. l., rectus capitis lateralis; r. c. s., rectus capitis superior; r. c. v., rectus capitis ventralis; sp., spinalis cervicis; spl. cap., splenius capitis; spl. col., splenius colli.



Tern. The angle of pull of the complexus (Figure 34) is consequently such that the force component countering downward rotation of the head and first segment is considerably greater in *R. nigra*, and a given force exerted by the complexus in *R. nigra* counteracts a greater force on the lower jaw than in the other species studied.

Although it is possible to demonstrate on a wooden model, using elastic bands for muscles, that the complexus alone could maintain the skimming position of the head and neck against downward forces such as gravity and water pressure, it is likely that various synergists cooperate to increase the effectiveness of action of the complexus. Ventral flexors of the head may act with the splenius capitis and complexus to hold the head in position relative to the first neck segment. The splenius colli serves to keep the first segment straight, while the slips of the longus colli ventralis inserting on the anterior vertebrae of segment II prevent flexion of these vertebrae by the complexus. The primary action of the complexus then would be to raise the head and segment I with respect to segment II, a function for which the complexus and the neck segments are well adapted in *R. nigra*.

The complexus of the Royal Tern is more highly developed in bulk (relative to body weight) and extent of origin than that of the Gull-billed Tern. The latter experiences no unusual downward forces on the head during feeding, while the former probably draws its head forward and upward against water pressure, and also carries relatively heavy fish in its bill. The adaptive modification of the complexus in *T. maximus* approaches that of *R. nigra*.

#### M. BIVENTER CERVICIS (Figure 36)

##### *Thalasseus maximus*

**Origin.** Fibers arise from the dorsomedial portion of the flat aponeurosis of origin of *M. spinalis cervicis* at the level of 12. The portion of this tendon from which the muscle originates attaches on the neural spines of 16 and 17.

**Insertion.** By a short, broad, and flat tendon on the dorsomedial edge of the occipital bones immediately deep to *M. complexus* and dorsal to *M. splenius capitis*.

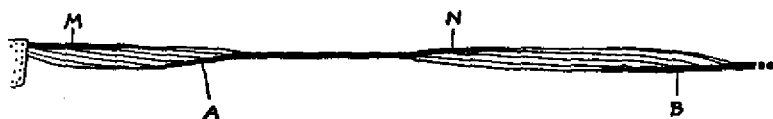


FIGURE 36. Diagram of structure of the biventer cervicis of *Thalasseus maximus*, left lateral view. A and B, aponeuroses of origin. M and N, aponeuroses of insertion.

*Structure.* Weakly unipennate. From its origin the fibers form a rather long, flat belly which gives way to a stout tendon at about the level of 6 or 7. This tendon runs forward just lateral to the mid-line and becomes fleshy again at 3, continuing forward as a flat belly to its insertion.

*Comparison*

Similar in *G. nilotica*, *L. atricilla*, and *R. nigra*. The muscle is well developed in *T. maximus* and *R. nigra*.

*Action*

This muscle tilts the depressed head upward around the pivot formed by the atlas and the occipital condyle. In addition it acts to straighten segment I, to flex segment II upward, and to straighten segment III, at the same time swinging each segment upward. Contraction of this muscle produces all of these effects simultaneously unless one or more of the effects is blocked by other muscles or by environmental forces. The relatively greater development of this muscle in *R. nigra* and *T. maximus* may be directly related to the exceptional downward forces acting on the head and neck of these species.

M. SPINALIS CERVICIS (Figures 32, 35, 41)

*Thalasseus maximus*

*Origin.* Fleshy fibers originate as a series of more or less distinct slips from the ventral surface of a broad, flat aponeurosis attaching to the dorsal ridge of the neural spines of 15, 16, 17, and 18. Aponeuroses from more posterior vertebrae, which fuse with the aponeuroses of this muscle, are associated with the posterior continuation of this muscle, the spinalis thoracis.

*Insertion.* The most anterodorsomedial slip attaches by a long, strong tendon on the anapophysis of 2. This tendon serves also for the attachment of M. splenius colli. The remaining slips insert on the anapophyses of 5 through 14.

*Structure.* Weakly unipennate. The anterior slips are longest, the posterior ones becoming shorter, broader, and less distinctly separable. The slips to 5, 6, 7, and 8 attach on tendons running superficially along the bellies of the ascendentes cervicis which also insert on the anapophyses of these vertebrae. The medial portions of the broad slips to 9 and 10 have fleshy insertion on the anapophyses in close association with the dorsales pygmaei. The broad, short slips to 11, 12, and 13 insert directly on the anapophyses medial to the corresponding ascendens slips. The last slip is very short, and represents a transition between the distinct slips of M. spinalis

cervicis and the fused slips of *M. spinalis thoracis* which are continuous with this muscle.

#### Comparison

*G. nilotica* and *L. atricilla* similar, but the second slip attaches on 6 rather than 5.

*R. nigra* similar. The slender tendons of the anterior slips are longer than in *T. maximus*.

#### Action (Table 5)

#### MM. ASCENDENTES CERVICIS (Figures 32, 35, 37)

##### *Thalasseus maximus*

**Origin.** Fibers arise from the diapophyses of vertebrae 18 through 5 and from superficial aponeuroses on the lateral and medial surfaces of the bellies. Fibers also arise from the lateral strut of 4.



FIGURE 37. Diagram of slips of the ascendentes cervicis of *Thalasseus maximus*, dorsal view. Slips from vertebrae 8, 9, 11, 12, 15, 16, and 17 omitted. Heavy and fine lines used for clarity.

**Insertion.** Vertebrae 15 through 3; on the anapophyses and on superficial aponeuroses attaching to the anapophyses of the second and third vertebrae anterior to the vertebra of origin of each muscle. Fibers from 4 insert on the anapophysis of 3.

**Structure.** Weakly pennate. The bellies of these muscles are thick and roughly fusiform, and they form a rather uniform overlapping series. Each muscle consists of two or more closely associated slips — a superficial one from each vertebra to the third vertebra anterior, and a deeper one to the second vertebra anterior. Additional slips connecting adjacent members of the superficial series are present posteriorly, and the superficial slip from 7 sends a slip to 3. Variations in the pattern of slips at the anterior and posterior ends of the series are best shown in diagrammatic fashion (Figure 37). The relationship of *M. spinalis* to this muscle is discussed under the spinalis. This series of muscles continues posteriorly onto the thoracic vertebrae as MM. ascendentes thoracis. The dividing line between cervicis and thoracis was considered to be behind the most posterior slip which attaches on the last cervical vertebra (15). Boas (1929) considered 13 to be the last cervical vertebra, and consequently he divided the series differently.

### Comparison

Similar in *G. nilotica* and *L. atricilla*. The superficial slip from 7 to 3 is lacking in *R. nigra*. The bellies and aponeuroses of this muscle are relatively well developed in *R. nigra*.

### Action (Table 5)

#### MM. DORSALES PYGMAEI (Figure 38)

##### *Thalasseus maximus*

**Origin.** By slender tendons from the neural spines of 14 and 13, fleshy from the neural spine of 12, and fleshy from the medial portions of the neural arches of 11, 10, 9, and 8.

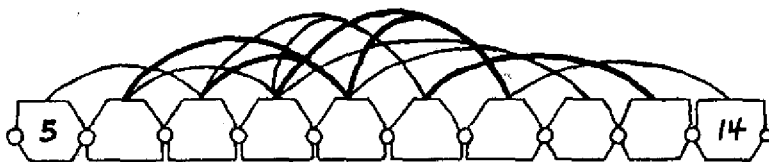


FIGURE 38. Diagram of slips of M.M. dorsales pygmaei, lateral view, based on *T. maximus*, *G. nilotica*, *L. atricilla*, and *R. nigra*.

**Insertion.** Fleshy, on the medial portions of the transverse-oblique crests of 11, 10, 9, 8, 7, and 6.

**Structure.** Weakly unipennate or parallel. Some of the rather thin, cylindrical bellies of these muscles divide into two or three slips, the relationships of which are best shown diagrammatically.

### Comparison

The pattern of slips shown in Figure 38 is applicable to all four species, although minor variations in the number and arrangement of slips occur. The bellies are best developed in *R. nigra*.

### Action (Table 5)

Although the spinalis cervicis, ascendentes cervicis, and dorsales pygmaei muscles show a relative increase in size or development of aponeuroses in the Black Skimmer, assessment of the importance of these modifications is difficult. Since their actions supplement those of more highly adapted muscles that oppose downward or lateral forces, the increased strength of each muscle probably represents an adaptation for feeding by skimming.

#### MM. INTERCRISTALES (Figures 35, 39)

##### *Thalasseus maximus*

**Origin.** Fleshy from the anterior surfaces of the neural spines of 14 and 13, and from the transverse-oblique crests of 12 through 3.

Fibers also originate from the anapophysis of 3 and from much of the dorsal surfaces of the neural arches and the post-zygapophyses of 3 and 4, and from the ventrolateral surface of the neural spines of 3 and 4.



FIGURE 39. Diagram of action of the intereristales. Left, segment I, and right, segment II of *Thalasseus maximus*, lateral view. Heavy line represents muscle.

*Insertion.* Fleishy on the neural spine of 13 and on the transverse-oblique crests of 12 through 2. The muscles form a series, each belly of which connects two adjacent vertebrae. The lateral fibers from 5 insert on the posterodorsal portion of the neural arch of 4; medial fibers from 5 insert on an aponeurosis which attaches on the anapophysis of 3. Fibers from 4 insert on the posterodorsal portion of the neural arch of 3. Fibers from 3 insert on the anapophysis and the neural arch of 2.

*Structure.* Parallel. The bellies are flat and straplike, those of the anterior vertebrae particularly broad and well developed. The belly connecting 13 and 14 resembles *M. interspinales*.

#### *Comparison*

Similar in *G. nilotica*, but the most posterior origin is from 15. The muscle between 15 and 14 connects the neural spines.

*L. atricilla* similar, but posteriormost origin is from 15.

*R. nigra* similar.

#### *Action* (Table 5)

### MM. INTERSPINALES

#### *Thalasseus maximus*

*Origin.* Fleishy, from the anterior surface of the neural spines of 5, 4, and 3.

*Insertion.* Fleishy, on the posterior surfaces of the neural spines of 4, 3, and 2.

*Structure.* Parallel. These flat bands of muscle interconnect the neural spines of the first neck segment.

#### *Comparison*

Similar in *G. nilotica* and *L. atricilla*. The neural spine of 5 is

very small in *R. nigra*; the muscle consequently originates from near the middorsal line of neural arch 5.

*Action* (Table 5)

MM. INTERTRANSVERSARI (Figures 32, 35)

*Thalasseus maximus*

*Origin.* From the anterolateral surfaces of the transverse processes of 12 through 6, the anterodorsal and ventrolateral edges of the transverse process of 5, the anterior surface of the transverse process of 4, and the sublateral process of 3. Posterior to 13 the muscle consists only of a dorsal slip which becomes very small and is replaced by calcified tendons on the thoracic vertebrae. More extensive than the attachments on bone described above are those from aponeuroses, several of which attach on the transverse process of each vertebra and extend forward.

*Insertion.* The bellies of this series of muscles interconnect successive vertebrae. Insertions are on the centra and the posterolateral sides of the transverse processes of 11 through 4; on the centrum, the transverse process, and the medial surface of the rib of 3 and by a tendon to the tip of the rib of 3; and on the lateral surface of the centrum of 2. The belly connecting 12 and 13 consists of a dorsal slip from the transverse process of 13, and a ventral slip from the rib of 13. Posterior to this, the muscle consists only of small dorsal slips connecting the transverse processes. Most of the fibers attach on aponeuroses which extend back from the transverse process of each vertebra and interdigitate with the aponeuroses of origin.

*Structure.* Multipennate. These are mostly very powerful muscles. The typical belly is rectangular, with interdigitating aponeuroses of origin and insertion. The fibers are short and numerous, and the amount of area for fiber attachment is very large relative to the bulk of the belly.

*Comparison*

Similar in *G. nilotica* except that the belly connecting 13 and 12 is less distinctly two-parted, and it originates entirely from the transverse process.

Similar in *L. atricilla*.

Similar in *R. nigra*. The anterior slips are more extensive; strong superficial aponeuroses provide additional surface of origin for the first slip and additional area of insertion for the second slip.

*Action*

These muscles produce the following movements of the neck: (1) by unilateral contraction they bend the neck to either side; (2) through bilateral contraction of the anterior slips they straighten

segment I; (3) contraction of the middle bellies flexes segment II; and (4) the posterior bellies straighten segment III. These actions may be independently or simultaneously produced. A further function is that of absorbing tension forces on the neck and resisting dislocation of the articulations of the pre- and postzygapophyses. The muscles have greater mechanical advantage in the Black Skimmer because of the enlarged transverse processes, and they are undoubtedly important in stabilizing the neck against lateral forces that act on the lower jaw during skimming. The special adaptations of *M. splenius capitis* for counteracting lateral forces on the head depend on synergistic action of these muscles for their effect.

#### MM. INCLUSI

##### *Thalasseus maximus*

These muscles are closely associated with the intertransversarii. They consist of two series of bellies which are separated by the vertebral artery and vein. The dorsal series are the MM. inclusi superior, the ventral series the MM. inclusi inferior. Each belly extends from its origin on a given vertebra to its insertion on the adjacent anterior vertebra.

*M. inclusi superior (origin)*. Fibers attach on the anterodorsal surfaces of the transverse processes and on superficial aponeuroses attaching on the transverse processes of vertebrae 11 through 6.

*M. inclusi superior (insertion)*. Fleshy, on the posterolateral surfaces of neural arches 10 through 6, and on the lateral surface of the centrum and neural arch of 5.

*M. inclusi inferior (origin)*. Fibers arise from the anteroventral surfaces of the transverse processes and from aponeuroses attaching on the transverse processes of vertebrae 11 through 6.

*M. inclusi inferior (insertion)*. Fleshy, on the lateral surface of centra 10 through 5.

*Structure*. The fibers of the rather thick bellies of both inclusi superior and inclusi inferior fan out as they run anteromedially to their insertions. The posterior bellies of both series are much reduced in size.

##### *Comparison*

Similar in *G. nilotica*, but an additional belly of inclusi inferior connects 11 and 12.

Similar in *L. atricilla*.

Similar in *R. nigra*, but the muscle is better developed, even the posterior bellies being quite large.

*Action* (Table 5)

## M. SPLENIUS CAPITIS (Figures 35, 40, 41)

*Thalasseus maximus*

*Origin.* Fibers originate from the dorsal and lateral surfaces of the neural spine of 2 and from aponeuroses A and B originating on the spine.

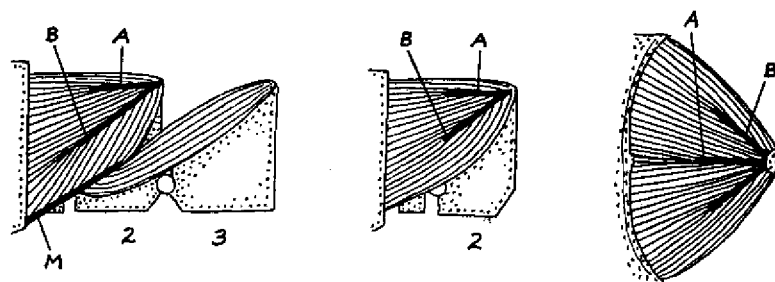


FIGURE 40. Diagram of structure of the splenius capitis. Left, *Rynchops nigra*, left lateral view. Middle, *Thalasseus maximus*, left lateral view. Right, *T. maximus*, dorsal view of right and left muscles. A and B, aponeuroses of origin. M, aponeurosis of insertion.

*Insertion.* Fleshy, on the dorsal and lateral portions of the posterior wall of the skull beneath the biventer cervicis and the complexus, and medial to the origin of the rectus capitis lateralis. Ventrally the fibers insert on an aponeurosis which attaches along the ventral part of the posterior wall of the skull from the opisthotic process to the foramen magnum.

*Structure.* Bipennate. The right and left muscles are closely connected along the median line and they share the median aponeurosis, A.

*Comparison*

Similar in *G. nilotica* and *L. atricilla*.

The muscle as described for *T. maximus* represents only a portion of this muscle as it appears in *R. nigra*, where additional fibers originate on the lateral surfaces of the neural spines of 2 and 3 and insert on the lateral surface of a strong aponeurosis on the ventrolateral surface of the main belly. This aponeurosis attaches on the lateral crest of the exoccipital. The muscle may be considered multipennate in *R. nigra*.

*Action*

This muscle tilts the depressed head upward, and upon unilateral contraction it turns the head to one side at the same time. The slip



from the neural spine of vertebra 3, found only in *R. nigra*, functions chiefly in turning the head to the side or in counteracting lateral forces on the lower jaw. The muscle is thus adapted for stabilizing the head during skimming in conjunction with its important synergists, the MM. intertransversarii.

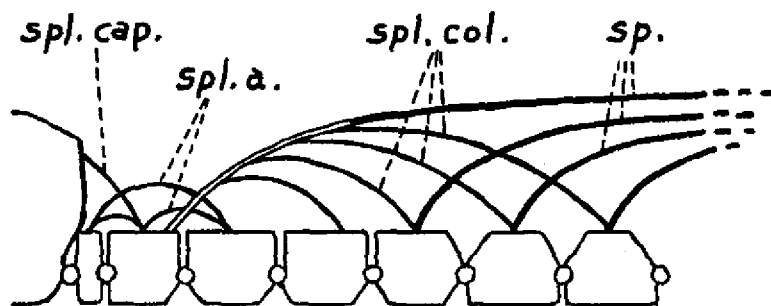


FIGURE 41. Diagram of slips of splenius and spinalis muscles of *Thalasseus maximus*, lateral view. sp., spinalis cervicis; spl. a., splenius anticus; spl. cap., splenius capitis; spl. col., splenius colli.

#### M. SPLENIUS COLLI (Figures 35, 41)

##### *Thalasseus maximus*

**Origin.** Fleishy from the lateral surface of the neural spines of 7, 6, 5, 4, and 3. Some fibers also attach on the neural arch of 2.

**Insertion.** The slips from 7, 6, 5, and 4 insert in the same sequence on the tendon of M. spinalis cervicis. Fibers from the neural spine of 3 and from a small aponeurosis attaching to it insert on the neural arch of 2 and on an aponeurosis which narrows to a tendon and attaches to the anapophysis of 1. Fibers from the neural arch of 2 also insert on this tendon and on the transverse-oblique crest of 1.

**Structure.** Unipennate. The slips originating from 4, 5, 6, and 7 are thick and straplike. They run anteriorly to their insertion. The posterior slip attaches on the ventral surface of the tendon of M. spinalis cervicis while the other slips curve around the medial side of the tendon to insert on it dorsally. The portion of this muscle associated with 1, 2, and 3 corresponds to M. splenius anticus (Boas, 1929:165).

##### Comparison

Similar in *G. nilotica* and *L. atricilla*.

In *R. nigra* slips from 7 and 6 are absent; stout slips from the neural spines of 5, 4, and 3 insert on the medial surface of the

rather broad and flat tendon of the spinalis cervicis. *M. splenius anticus* is similar.

#### *Action*

In the gull and terns studied this muscle may serve to straighten segment I, to raise segment I against segment II, to flex the anterior vertebrae of segment II, and to bend segment I laterally. The two posterior slips of this muscle are absent in *R. nigra* (although the total bulk of the muscle is not correspondingly reduced) and its action in this species is primarily to straighten segment I. This effects a division of labor by which the full force of the complexus can act in raising the head and segment I against segment II in the Black Skimmer.

#### *M. RECTUS CAPITIS LATERALIS* (Figures 32, 35)

##### *Thalasseus maximus*

*Origin.* Fibers attach on aponeuroses from the hypapophyses of 5, 4, 3, and 2 (hypapophyses small in 4 and 5).

*Insertion.* Fibers insert on an aponeurosis which attaches to the lateral crest of the exoccipital between the depressor mandibulae and the splenius capitis and between the lateral portion of *M. complexus* and the opisthotic process.

*Structure.* Unipennate. The belly is broad and straplike. The fibers originating posteriorly are somewhat longer than those from the anterior vertebrae.

#### *Comparison*

Similar in *G. nilotica* and *L. atricilla*.

In *R. nigra* originates by aponeuroses from the hypapophyses of 2 and 3. Insertion similar.

#### *Action* (Table 5)

#### *M. RECTUS CAPITIS SUPERIOR* (Figures 32, 35)

##### *Thalasseus maximus*

*Origin.* Fleshy, from the transverse process of 5: from the lateral strut and the ventral edge of prezygapophysis 4; from bone and aponeurosis between the anterolateral surface of the anapophysis and the ventral edge of the prezygapophysis of 3; from the anterior surface of the anapophysis and from the lateral surface of the neural arch of 2; also fleshy from the lateral surface of neural arch 1.

*Insertion.* Fibers from the extensive origin converge on a broad aponeurosis which divides into a lateral and medial part. Both of these attach on a transverse ridge of the basitemporal plate. Some fibers attach on the plate just posterior to the lateral aponeurosis.

*Structure.* Unipennate. This muscle is fan-shaped.

*Comparison*

Similar in *G. nilotica* and *L. atricilla* but less well developed.

Similar in *R. nigra*, but no origin from 5, and the slip from 4 is reduced.

*Action* (Table 5)

M. FLEXOR COLLI BREVIS (Figure 32, 35)

*Thalasseus maximus*

*Origin.* From the transverse process of 5 and an aponeurosis extending anteroventrally from the transverse process; from the transverse process and lateral strut of 4 (ventral to the origin of rectus capitis superior); the sublateral process and the lateral surface of the rib of 3; and from the lateral surface of a superficial aponeurosis of the intertransversarii which attaches to sublateral process 3.

*Insertion.* By a stout tendon on the ventral tuberosities of the centrum of the atlas.

*Structure.* Unipennate. A flat muscle, the fibers of which converge on the tendon of insertion. This muscle resembles the rectus capitis superior and lies immediately deep to it.

*Comparison*

Similar in *G. nilotica* and *L. atricilla* but less well developed.

In *R. nigra*, additional fibers originate from the transverse process of 6. The posterior portion is relatively large.

*Action* (Table 5)

M. RECTUS CAPITIS VENTRALIS (Figures 32, 35)

*Thalasseus maximus*

*Origin.* Fibers arise from a short aponeurosis on the sublateral process of 6 and from the aponeurosis of origin of M. rectus capitis lateralis which attaches on the hypapophyses of 5, 4, 3, and 2; also from the ventral mid-line of centrum 1.

*Insertion.* The fibers tend to form two bellies (pars lateralis and medialis) which are separated by the intervening dorsal carotid arteries. Pars lateralis inserts on a flat aponeurosis which attaches on the lateral surface of the basitemporal plate (anteromedial to the basitemporal process) and on adjacent areas. Pars medialis has a fleshy insertion on the entire surface of the basitemporal plate anterior to the aponeurosis of the rectus capitis superior and to the pars lateralis.

*Structure.* Weakly unipennate. In ventral view, the fibers of medialis fan out gradually from a long, narrow origin to a broad, flat insertion while those of lateralis converge on the aponeurosis of insertion. The fibers of medialis originate anterior to the more posterior fibers of lateralis and consequently most of them are shorter.

*Comparison*

Similar in *G. nilotica* and *L. atricilla*.

Basically similar in *R. nigra*, but originates by short aponeuroses from the sublateral processes of 6 and 5, and from the mid-ventral line of the centrum or the hypapophyses of 4, 3, 2, and 1.

*Action* (Table 5)

M. FLEXOR COLLI PROFUNDUS (Figure 42)

*Thalasseus maximus*

*Origin.* Fibers originate from a tendon on the sublateral process of 6; from the ventral surface of the transverse process and from the hypapophysis of 5; from the ventral surface of the transverse process of 4; and from the hypapophysis of 3.

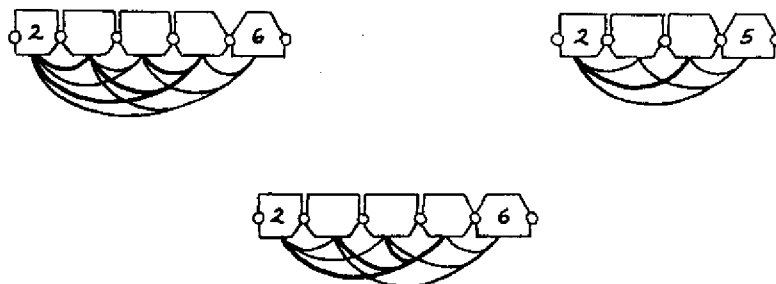


FIGURE 42. Diagram of slips of the flexor colli profundus in lateral view. Left, *Thalasseus maximus*. Center, *Larus atricilla*. Right, *Rynchops nigra*. Heavy and fine lines used for clarity.

*Insertion.* Slips from the sublateral process of 6 run forward to the hypapophyses of 4, 3, and 2, as well as to the ventral surface of the centrum of 5; slips from the hypapophysis of 5 run forward to the hypapophyses of 2 and 3; slips from the transverse process of 5 attach on the centrum of 4 and the hypapophysis of 3; fibers from the transverse process of 4 insert on the centrum of 3 and on hypapophysis 2; fibers from 3 insert on hypapophysis 2.

*Structure.* Pennate. The muscle is composed of a series of slender slips, some of which are in close association with MM. intertransversarii.

### Comparison

Similar in *G. nilotica*.

The pattern of slips in *L. atricilla* and *R. nigra* is shown in Figure 43. Although the number of slips is reduced in *R. nigra*, the total bulk of the muscle is not relatively smaller. The lack of slips from 6 is associated with shortening of the first segment.

Action (Table 5)

M. LONGUS COLLI VENTRALIS (Figures 32, 35, 43, 44)

*Thalasseus maximus*

**Origin.** Fleshy from the sublateral processes, from the hypapophyses, and from the anteroventral portions of the centra of vertebrae 18 through 6.

**Insertion.** Fibers attach on long tendons which extend anteriorly from the slips to attach on the posterior tips of ribs 13 through 3.

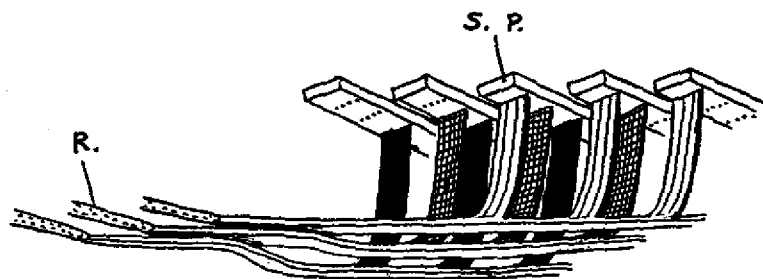


FIGURE 43. Diagram of structure of a portion of *M. longus colli ventralis*, ventromedial view, based on *T. maximus*, *G. nilotica*, *L. atricilla*, and *R. nigra*. R., rib; S. P., sublateral process.

**Structure.** Unipennate. In general, the slips of this muscle are arranged in a definite sequence within the belly, the tendons of those slips originating medially and posteriorly being dorsal to the tendons of those originating laterally and anteriorly (Figure 43). One may regard each division of this muscle as all of the slips originating from a given vertebra and the tendons associated with those slips, or as the tendon which inserts on a given vertebra and all of the muscle slips (originating from different vertebrae) associated with that tendon. The latter point of view is probably the more significant in terms of function. Most of the fleshy slips originate from the posterior vertebrae of segment II and the anterior vertebrae of segment III.

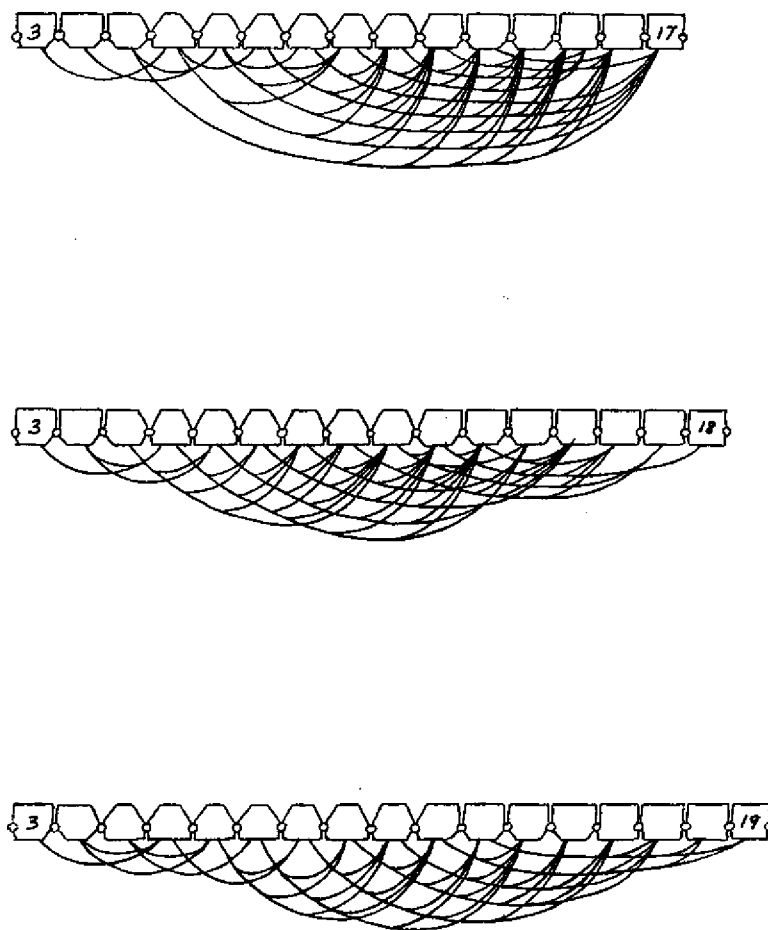


FIGURE 44. Diagram of slips of the longus colli ventralis in lateral view. Above, *Larus atricilla*. Middle, *Thalasseus maximus*. Below, *Rynchops nigra*.

### Comparison

Similar in *G. nilotica*.

*L. atricilla* differs in that most of the fleshy slips originate from the third segment and the anterior thoracic vertebrae.

*R. nigra* similar in general pattern. The posterior slips originate from a strong superficial aponeurosis which attaches to the centra of 19, 18, and 17, as well as from the centra of the vertebrae.

### Action

Contraction of this muscle causes a downward rotation of all cervical vertebrae except the atlas and axis, thereby flexing segments I and III and straightening segment II. Each slip of this complicated muscle affects all vertebrae from the origin to the insertion of that slip. In the gull and terns studied, downbending of segment I can be brought about by short slips that are independent of the more posterior portions of the muscle. These slips supplement the action of the flexor colli profundus. In *R. nigra*, vertebrae 3, 4, 5, and 6 are operated by short slips, and the first two vertebrae of segment II, as well as the first segment, are not affected by contraction of the longer posterior slips. This adaptation allows synergistic action of the anterior slips with *M. complexus* (see discussion of that muscle) without at the same time exerting downward forces on the posterior half of the neck, which, in a skimming bird, is already bent downward by environmental forces.

### DISCUSSION

The Royal Tern and Black Skimmer show hypertrophy of certain neck muscles and of the anterior cervical vertebrae when compared with the Gull-billed Tern and Laughing Gull. *R. nigra* shows the greatest development of vertebral processes, especially neural spines and transverse processes. These provide greater attachment surface and leverage for the muscles opposing downward and lateral forces on the head and neck. In each case a series of muscle synergists serves to maintain the skimming position — *M. splenius capitis* raises the head while *M. splenius colli* straightens the first neck segment, and *M. complexus* raises the head and first segment with respect to the rest of the neck. Downward forces on other parts of the neck are absorbed primarily by the vertebrae and their ligaments. The *splenius capitis* and *rectus capitis lateralis* muscles provide lateral stability for the head, while the *intertransversarii* and other muscles stabilize the neck. The muscles most directly involved in the feeding process — those associated with the head and first segment — show marked adaptations in the Black Skimmer and Royal Tern.

Frieling (1936:438-439) discussed the lever systems that augment downward forces on the bill of a skimming bird at the insertions of

the dorsal neck muscles. He claimed that all head levators in the Black Skimmer were relatively larger than those of the Large-billed Tern, *Phaetusa simplex*, but he stressed the biventer cervicis, which he described as very broad and massive, and lying almost entirely superficially in *R. nigra*. By contrast he found the small biventer of *P. simplex* deep to the complexus. In all specimens of the Black Skimmer that I examined, however, the biventer cervicis was largely covered by the complexus and the complexus was the more strikingly modified muscle.

I believe that Frieling's discussion of forces contains several inaccuracies. He used the same letter (H) to represent two different points, the cranio-cervical articulation in one figure (Abb. 1), and the cranial insertion of the dorsal neck muscles in another (Abb. 2). Force m, which should act at the articulation, was transferred to the point of insertion. Further, he neglected the pivot point between the first and second neck segments, a fulcrum of great importance in determining forces on the insertions of the biventer and complexus muscles.

For most efficient functioning of a particular neck segment it is important that muscles moving that segment not have undesirable secondary effects on other segments from which they originate. Muscles used exclusively to move the head or first segment may originate in part from the more anterior vertebrae of the second segment. With the reduction in number of vertebrae of segment I in *R. nigra* there has been a corresponding forward shift in the origins of these muscles and a consequent reduction in their undesirable effects on segment II. Modification of the splenius colli, rectus capitis lateralis, and rectus capitis superior in the Black Skimmer may be explained in this way. In the summary of neck muscle actions presented in Table 5, I have omitted such incidental effects on a few vertebrae of a segment.

Differences between the neck muscles of the Black Skimmer and the other species studied appear to represent adaptations for feeding or by-products of such adaptations. Adaptive differences between *G. nilotica* and *T. maximus* are also evident. The fundamental structural plan of the cervical vertebrae and musculature, like the structure of the skull and jaw musculature, is nevertheless similar in the four species.



## CONCLUSIONS

The Black Skimmer exhibits many structural adaptations of the head and neck that can be correlated with its feeding method. Each of these adaptations is associated with a particular aspect or several aspects of feeding behavior; streamlining of the lower jaw, for example, facilitates movement through the water, but it makes the bill less efficient for grasping and holding prey. Adaptations of the skull and jaw muscles in turn counteract this disadvantage. Elongation of the lower jaw increases the bird's chance of obtaining food, but full use of this adaptation would not be possible without increased kinetic ability. The many adaptations of the head are of survival value only in combination with modifications of the neck segments and muscles. Adaptations for lateral stability of the lower jaw require both stability of the head, provided by additional lateral slips of *M. splenius capitis* in *Rynchops nigra*, and stability of the neck, achieved through increased leverage of the powerful intertransversarii muscles. The numerous adaptations are clearly interdependent and should be regarded in their totality as an adaptive complex highly coordinated for feeding by skimming. The components of the adaptive complex may be summarized as follows:

### A. Hydrodynamic adaptations:

1. Elongation of symphysis of mandible.
2. Streamlining of upper and lower jaws.

### B. Adaptations for awareness of bill position:

1. Ridges on rhamphotheca of mandible.
2. Rich innervation of mandible.

### C. Adaptations for stabilization of jaws and head:

1. Broad frontonasal hinge.
2. Bony stop formed by inflation of premaxillary and nasal bones.
3. Stout rami of the lower jaw, each flexible at only one point.
4. Broad quadrate condyles and increased distance between quadrates.
5. Dorsal shift of posterior condyle of quadrate.
6. Condyles of jaw-quadrates articulation arranged to reduce lateral sliding of jaw during depression.
7. Downward flexure of jaws.
8. Increased contact of internal process of mandible with basitemporal process.
9. Elongation of facial region.
10. Ossification of interorbital septum.

11. Greater mechanical advantage of *M. depressor mandibulae*.
  12. Greater mechanical advantage and more efficient angle of pull of *M. pseudotemporalis superficialis*.
  13. Enlarged neural arches and centra of cervical vertebrae.
  14. Shorter first neck segment.
  15. Longer second neck segment.
  16. Increased size of belly and/or greater mechanical advantage of the complexus, splenius capitis, intertransversarii, and other neck muscles.
  17. Forward shift of splenius colli and backward shift of long slips of longus colli ventralis.
- D. Adaptations for increasing the chance of striking prey:
1. Hypertrophy of both jaws.
  2. Elongation of rhamphotheca of lower jaw.
  3. Increased kinetic ability.
    - a. Presence of ventral hinge on nasal strut.
    - b. Longer quadrate.
    - c. Quadrate more nearly perpendicular to rostrum.
    - d. Pterygoid more nearly perpendicular to rostrum.
    - e. Greater curvature of rostrum.
    - f. Reduction of orbital process.
    - g. Vomer fused to palatines.
    - h. *M. depressor mandibulae* angles forward with respect to long axis of quadrate.
    - i. *M. protractor quadrati* enlarged.
    - j. *M. pseudotemporalis profundus* reduced.
- E. Adaptations for detecting prey:
1. Rich innervation of mandible.
- F. Adaptations for holding prey:
1. Curved tomia of upper jaw.
  2. Enlargement of palatines.
  3. Hypertrophy and more powerful construction of the adductor mandibulae complex and the pterygoideus complex.
- G. Adaptation for renewal of broken or worn parts:
1. Greater blood supply to tip and edges of lower jaw.
- H. Adaptation in the chick for obtaining food:
1. Jaws of nearly the same length.

I have deduced the preceding adaptations by comparing the Black Skimmer with the Royal Tern, Gull-billed Tern, and Laughing Gull on the assumption that terns and gulls are close relatives of the Rynchopidae. Nitzsch showed that the pterylosis of *Rynchops* closely resembles that of *Sterna* (terns) and small gulls of the genus *Larus*

(Selater, 1867: 141-43). Gadow and Selenka (1891), Fürbringer (1888), Beddard (1898), and others, by utilizing a variety of anatomical characters, have also established the relationship of *Rynchops* with other lariform birds. The present paper provides further evidence in support of this view. Although some of the structural features of the head and neck of the Black Skimmer have no counterparts in the gull or terns studied (bill ridges, frontonasal hinge stop, ventral hinge of nasal strut, posterior belly of splenius capitis), most of the differences represent alterations in the shape or relative development of structures that are represented by homologues in these birds. Furthermore, almost all of the differences that tend to set the Black Skimmer apart appear to be adaptations for feeding by skimming, or by-products of such adaptations.

Some of the characters that I have considered adaptations cannot *a priori* be considered to reflect genetic differences. For example, if the hypertrophy of the jaw and neck muscles described for the Black Skimmer were merely an individual response to special environmental circumstances — the “exogenous” adaptations of Waddington — the character could not be used as an indication of phylogenetic relationships. If, on the other hand, they were “pseudo-exogenous” adaptations, those in which “the animal exhibits characteristics similar to effects which can be called forth as direct exogenous adaptations, but which on investigation are shown to be hereditary, and independent of any particular environmental influence” (Waddington, 1953:134), they should be recognized in an evaluation of affinities. A male chick of the Black Skimmer, too young to fly, showed some hypertrophy of the adductor mandibulae externus, the pterygoideus, and the complexus when I compared it with an adult Laughing Gull, indicating the pseudo-exogenous nature of the muscle adaptations. Most of the skeletal adaptations are also clearly in evidence before the birds fly, although marked elongation of the ramphotheca of the lower jaw and development of a frontonasal hinge stop appear somewhat later.

*Gelochelidon nilotica* and *Thalasseus maximus* are intermediate between *Larus atricilla* and *Rynchops nigra* with respect to certain characters shown to be adapted to the feeding method of the Black Skimmer. In each of the following characters the Laughing Gull showed the least development and the Black Skimmer the greatest: (1) hypertrophy of both jaws; (2) relative elongation and lateral compression of the mandibular symphysis; (3) broadening of the condyles of the quadrate and increase in the distance between quadrates; (4) development of the retroarticular process of the mandible; (5) elongation of the facial region (terns equal skimmers in this character); (6) enlargement of the palatines; (7) downward flexure of the jaws; and (8) increase in relative size of M. complexus. It is thus

tempting to visualise the Rynchopidae as a specialized offshoot from the terns, a group already preadapted for skimming in various respects. This hypothesis must remain highly tentative, however, until structural variability of the gulls and terns (also skuas and jaegers) is better known. Furthermore the characters in which the terns approach *Rynchops* are primarily by-products of an increase in size and stability of the jaws — features that could have developed from gull-like birds as well. The size of the complexus is probably of little taxonomic value in view of its variability within the terns.

*R. nigra* resembles the two terns in the shape of aponeurosis M of the pseudotemporalis superficialis (Figure 24) and in the pattern of slips of the longus colli ventralis (Figure 44), but it resembles the Laughing Gull in having part B of the adductor mandibulae externus enlarged at the expense of part A (Figure 20). In other respects the skimmer either agrees essentially with the gull and two terns or differs from all three. The principal difficulty for the taxonomist in classifying *Rynchops* lies in finding clear-cut differences as a basis for differentiating the other lariform birds.

On the basis of comparative behavior studies, Moynihan (1959) has substantiated the close relationship of the groups of lariform birds, and he postulates independent origins from a primitive gull for both terns and skimmers. Similarities in shape and plumage pattern between certain terns and the skimmers are regarded as "the result of parallel or convergent evolution — similar adaptations to somewhat similar methods of flying and feeding" (page 22).

The skimmers seem to embody a mixture of gull-like and tern-like characteristics, on which is superimposed a highly developed adaptive complex associated with feeding. This complex involves anatomy and behavior. It is probable that many morphological features of the entire body have been altered during the evolution of the unique feeding method, and that many of the behavior patterns, other than skimming, have been secondarily affected.

# LITERATURE CITED

AMADON, DEAN

1943. Bird weights as an aid in taxonomy. *Wilson Bull.*, 55(3): 164-77.

ARCHER, G., AND E. M. GODMAN

1937. The birds of British Somaliland and the Gulf of Aden. Volume 2. Gurney and Jackson, London.

ARTHUR, STANLEY C.

1921. The feeding habits of the Black Skimmer. *Auk*, 38(4): 566-74.

AUDUBON, JOHN J.

1835. Ornithological biography. Volume 3. Adam and Charles Black, Edinburgh.  
1838. Ornithological biography. Volume 4. Adam and Charles Black, Edinburgh.  
1839. Ornithological biography. Volume 5. Adam and Charles Black, Edinburgh.

AZARA, F. DE.

1802. Apuntamientos para la historia natural de los paxaros del Paraguäy y Rio de la Plata. Tomo 5. Madrid: La Imprenta de la Vinda de Ibarra. Reimpresion exacta de la obra por la Biblioteca Americana, Buenos Aires, 1942.

BAMS, R. A.

1956. On the relation between the attachment of jaw muscles and the surface of the skull in *Podiceps cristatus* L., with some notes on the mechanical properties of this part of the head. *Proc. Koninkl. Nederl. Akad. van Wetenschappen — Amsterdam, Series C*, 59(1 and 2): 82-101, 248-262.

BANNERMAN, DAVID A.

1931. The birds of tropical West Africa. Volume 2. The Crown Agents for the Colonies, London.

BEDDARD, F. E.

1898. The structure and classification of birds. Longmans, Green, and Co., London.

BEEBE, CHARLES W.

1906. The bird. Henry Holt and Co., New York.

BEECHER, WILLIAM J.

1951. Adaptations for food-getting in the American blackbirds. *Auk*, 68(4): 411-40.

BENT, ARTHUR CLEVELAND

1921. Life histories of North American gulls and terns. *Bull. U. S. Natl. Mus.*, 113, Washington.

BOAS, J. E. V.

1929. Biologisch-anatomische Studien über den Hals der Vögel. *Kongl. Danske Vidensk. Selsk. Skrifter, Naturv. Math., Ser. 9*, 1: 102-222.

BOOK, WALTER J.

- 1960a. Secondary articulation of the avian mandible. *Auk*, 77(1): 19-55.  
1960b. The palatine process of the premaxilla in the passerines. *Bull. Mus. Comp. Zool.*, 122(8): 361-488.

BRANDT, J. F.

1840. Über den Skeletbau der Scherenschnäbel (*Rhynchops*) im vergleich mit den Möven (*Larus*), den Raubmöven (*Lestris*) und den Seeschwalben (*Sterna*). Mém. Acad. St. Pétersb., 6th series, Volume 5, (Pt. 2, Sci. nat.), Volume 3: 218-29.

COUES, ELLIOTT

1874. Birds of the Northwest. U. S. Govt. Printing Office, Dept. of Int. Misc. Publ. no. 3, Washington.

DARWIN, CHARLES R.

1888. Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world, under the command of Captain Fitz Roy, R.N. T. Nelson and Sons, London.

DAVIS, L. IRBY

1951. Fishing efficiency of the Black Skimmer. Condor, 53(5): 259.

EDGEWORTH, F. H.

1935. The cranial muscles of vertebrates. Cambridge Univ. Press, Cambridge, England.

ENGELS, WILLIAM L.

1940. Structural adaptations in thrashers (Mimidae: Genus *Toxostoma*) with comments on interspecific relationships. Univ. Calif. Publ. Zool., 42(7): 341-400.

FISHER, HARVEY I.

1955. Some aspects of the kinetics in the jaws of birds. Wilson Bull., 67(3): 175-88.

FRIELING, H.

1936. Funktionell-anatomische Untersuchungen am Scherenschnäbel (*Rhynchops nigra intercedens* Saunders). Journ. f. Ornith., 84: 434-41.

FÜRBRINGER, M.

1888. Untersuchungen zur Morphologie und Systematik der Vögel. Volume 2. T. J. van Holkema, Amsterdam.

GADOW, H., AND E. SELENKA

1891. Vögel, in Bronn's Klassen und Ordnungen des Thier-Reichs. Leipzig.

GIEBEL, C. G. A.

1857. Beiträge zur Anatomie d. Möven. Zeitschr. gesamte Naturwiss., 10: 20-32.

GREGORY, J. T.

1952. The jaws of the Cretaceous toothed birds, Ichthyornis and Hesperornis. Condor, 54(2): 73-88.

HOFER, H.

1945. Untersuchungen über den Bau des Vogelschädels, besonders über den der Spechte und Steisshühner. Zool. Jahrb., 69(1): 1-158.

1950. Zur Morphologie der Kiefermuskulatur der Vögel. Zool. Jahrb., 70(4): 427-556.

1954. Neue Untersuchungen zur Kopfmorphologie der Vögel. Acta XI Congressus Internationalis Ornithologici, Birkhäuser Verlag, 104-37, Basel.

HOUSSE, P. R.

1945. Las aves de Chile en su clasificación moderna, su vida y costumbres. Universidad de Chile.

- KOENIG, A.  
1932. Die Schwimmvögel (*Natatores*) Aegyptens. Journ. f. Ornith., 80: 3-191.
- KRIFF, D. VON  
1933. Der Oberschnabel-mechanismus der Vögel. (Nach den Methoden der graphischen Statik bearbeitet.) Morphol. Jahrb., 71(4): 469-544.
- LAKJER, T.  
1926. Studien über die trigeminus-versorgte Kaumuskulatur der Sauropsiden. C. A. Reitzel, Kopenhagen.
- LEAVITT, BENJAMIN B.  
1957. Food of the Black Skimmer (*Rynchops nigra*). Auk, 74(3): 394.
- LESSON, R. P.  
1828. Manuel d'ornithologie ou description des genres et des principales espèces d'oiseaux. Tome 2. Roret, Libraire, Rue Hautefeuille, Paris.
- LONGSTREET, RUPERT J.  
1930. Notes on speed of flight of certain water birds. Auk, 47(3): 428-29.
- LOWTHER, E. H. N.  
1949. A bird photographer in India. Oxford University Press, London.
- MARINELLI, W.  
1928. Über den Schädel der Schnepfe. Palaeobiologica, 1: 135-60.
- MARSHALL, W.  
1895. Der Bau der Vögel. Verlag von J. J. Weber, Leipzig.
- MOLLER, W.  
1930. Über die Schnabel-und Zungenmechanik blütenbesuchender Vögel. I. Biol. Gen., 6(4): 651-726.  
1931. Über die Schnabel-und Zungenmechanik blütenbesuchender Vögel. II. Biol. Gen., 7(1): 99-154.
- MOYNIHAN, M.  
1959. A revision of the family Laridae (Aves). Amer. Mus. Novit., no. 1928.
- MURPHY, ROBERT C.  
1936. Oceanic birds of South America. Volume 2. The American Museum of Natural History, New York.
- NICHOLSON, DONALD J.  
1948. Nocturnal fresh-water wandering of the Black Skimmer. Auk, 65(2): 299-300.
- PALMGREN, P.  
1949. Zur biologischen Anatomie der Halsmuskulatur der Singvögel. In Ornithologie als Biologische Wissenschaft. Carl Winter, 192-203, Heidelberg.
- PETTINGILL, OLIN S., JR.  
1937. Behavior of Black Skimmers at Cardwell Island, Virginia. Auk, 54(3): 237-44.
- POTTER, JULIAN K.  
1932. Fishing ability of the Black Skimmer (*Rynchops nigra nigra*). Auk, 49(4): 477.
- PRIEST, C. D.  
1934. The birds of Southern Rhodesia. Volume 2. William Clowes and Sons, Ltd., London and Beccles.

## ROBERTS, AUSTIN

1940. The birds of South Africa. H. F. and G. Witherby, Ltd., London.  
 ROCKWELL, H., F. G. EVANS, AND H. C. PHEASANT

1938. The comparative morphology of the vertebrate spinal column. *Journ. Morphology*, **63**: 87-117.

## ROOSEVELT, THEODORE

1916. The bird refuges of Louisiana. *Scribner's Mag.*, **59**(3): 261-80.

## SAUNDERS, ARETAS A.

1934. A curious habit of gulls. *Auk*, **51**(2): 234.

## SCHILDMACHER, H.

1931. Ueber das "Wasserphlügen" der Scherenschnäbel (*Rynchops*). *Ornith. Monatsberichte*, **39**(2): 37-41.

## SCLATER, P. L.

1867. Nitzsch's pterylography. Published for the Ray Society by Robert Hardwicke, London.

## SHUFELDT, R. W.

1890. Contributions to the comparative osteology of Arctic and sub-Arctic water-birds. Part 8. *Journ. Anat. and Physiol.*, **25**: 60-77.

## SIMPSON, G. G.

1957. Australian fossil penguins, with remarks on penguin evolution and distribution. *Rec. S. Aust. Mus.*, **13**(1): 51-70.

## STARCK, D., AND A. BARNIKOL

1954. Beiträge zur Morphologie der Trigemini-muskulatur der Vögel. *Morphol. Jahrb.*, **94**(1 and 2): 1-64.

## STORER, ROBERT W.

1952. A comparison of variation, behavior and evolution in the sea bird genera *Uria* and *Cepphus*. *Univ. Calif. Publ. Zool.*, **52**(2): 121-222.

## STRESEMANN, ERWIN

1927. Aves, in *Handbuch der Zoologie* by Kükenthal. Volume 7, Part 2.

1934. Walter de Gruyter, Berlin.

## TOMKINS, IVAN R.

1933. Ways of the Black Skimmer. *Wilson Bull.*, **45**(4): 147-51.

1951. Method of feeding of the Black Skimmer, *Rynchops nigra*. *Auk*, **68**(2): 236-39.

## WADDINGTON, C. H.

1953. The evolution of adaptations. *Endeavor*, **12**(47): 134-39.

## WETMORE, ALEXANDER

1926. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. *Bull. U. S. Natl. Mus.*, **133**, Washington.

## WHISTLER, HUGH

1928. Popular Handbook of Indian birds. Gurney and Jackson, London.

## WILSON, ALEXANDER, AND C. L. BONAPARTE

1878. American ornithology. Volume III. Porter and Coates, Philadelphia.

## WOOD, HAROLD B.

1949. Laughing Gulls tread out their food. *Bird-Banding*, **20**(2): 103.

## YOUNG, CHARLES G.

1928. A contribution to the ornithology of the coastland of British Guiana. *Ibis*, **4**: 748-81.



ZUSI, RICHARD L.

- 1959a. Fishing rates in the Black Skimmer. *Condor*, 61(4): 298.
- 1959b. The function of the depressor mandibulae muscle in certain passerine birds. *Auk*, 76(4): 537-39.
- 1959c. Feeding adaptations in the Black Skimmer (*Rynchops nigra*). PhD. Thesis. Univ. of Michigan (L. C. Card No. Mic. 59-3970) Univ. Microfilms Inc., 313 N. First St., Ann Arbor, Michigan.