

Fig. 1. Alizarin-stained stapes of A, *Philepitta castanea* and B, *Neodrepanis* sp. Both are from American Museum of Natural History alcoholic specimens Nos. 2230 and 2231, respectively. Both approximately $\times 50$.

of the New World Furnariidae (including woodhewers), Formicariidae, Conopophagidae, Rhinocryptidae, Cotingidae, Pipridae, Tyrannidae, and Phytotomidae, with the Old World Eurylaimidae and Pittidae. I have recently been able to dissect the stapes from alcoholic specimens of *Philepitta castanea* and *Neodrepanis* sp. and have discovered that they both possess the derived suboscine type of stapes (Fig. 1), thus illustrating their affinity to the other groups of suboscines.

This work was supported by a grant from the University of North Carolina Research Council. Specimens of *Philepitta* and *Neodrepanis* in the collection of the American Museum of Natural History were lent through the kindness of Wesley Lanyon.—ALAN FEDUCCIA, *Department of Zoology, University of North Carolina, Chapel Hill, North Carolina 27514*. Accepted 6 Dec. 74.

Behavioral evidence on skimmers' evolutionary relationships.—The suborder Lari (Charadriiformes) is composed of the families Stercorariidae (skuas and jaegers), Rynchopidae (skimmers), and Laridae (gulls and terns). It is generally accepted that within this suborder the gulls and terns are more closely related to one another than either is to the skuas (A.O.U. 1957), but the evolutionary position of the skimmers within the suborder is less certain.

Schnell (1970a, 1970b) concluded that skimmers are more closely related to terns than to gulls or skuas, based on a phenetic study of skeletal and external characters, as did Zusi (1962, 1971) on the basis of a comparative study of anatomical and behavioral feeding adaptations. We feel that many of the anatomical similarities between skimmers and terns may be the result of convergence caused by similarities in flight and feeding behavior. Mayr (1969) suggested that any set of features arising after the invasion of a new food niche will evolve very rapidly and therefore are poor characters for basing hypotheses of evolutionary relationship.

On the basis of comparative study of courtship and agonistic displays, Wolk (1959: 69; see also Moynihan 1959) suggested that skimmers are "derived from an ancestral *Larus*-type gull independently of the terns (*Sterna*)."

Further study and reinterpretation of the behavioral evidence leads us to believe that the divergence of the skimmers from their parental evolutionary line took place at least as early as the divergence of the gulls and terns and perhaps significantly earlier. This belief is largely in agreement with the conclusions of Hudson et al. (1969), who placed the skimmers in the family Rynchopidae and the gulls, terns, and skuas in the family Laridae on the basis of a detailed study of wing and leg muscles. Also Zusi has indicated (pers. comm.) that his published works and current unpublished opinions based on functional anatomy are not in conflict with this interpretation.

Our study was conducted during the spring and summer of 1971 and 1973 on an unnamed island in Bogue Sound 0.5 miles south of Morehead City, Carteret County, North Carolina. We worked in a colony of about 20 pairs of Black Skimmers (*Rynchops niger*) and in a larger mixed colony of skimmers, Common Terns (*Sterna hirundo*), and Gull-billed Terns (*Gelochelidon nilotica*). Visual displays were photographed on super-8 movie film, and vocalizations were recorded with an Uher 4000 Report L tape recorder and M514 microphone at a tape speed of 7½ i.p.s. These recordings were spectrographically analyzed on a Kay Elemetrics Corporation Sona-Graph Model 7029 A using the wide band filter. The more common displays of the Black Skimmer are described below, and their taxonomic implications are discussed. For more complete descriptions, see Wolk (1959).

Upright oblique.—In this posture, the body and tail are horizontal, the neck is extended upward almost vertically, and the bill is pointed up at an angle between 0° and 45° above the horizontal. The wings are slightly abducted. During this display, the bird may vocalize (see bark below), and the bill may be open or closed. The upright oblique is one of the most common postures seen during aggressive encounters. This display is almost certainly homologous with the upright posture of most larids (see Tinbergen 1959, for descriptions of gull displays), but it is considerably simpler in form. Almost all gulls and the noddy terns have two forms of the upright posture, a bill-down form most often followed by attack and a bill-up form most often followed by escape. These have been termed the aggressive upright and the intimidated or anxiety upright, respectively. The black-capped terns lack the upright postures, but elements of these appear in the terns' erect display, and this lack seems to be due to loss of some components and exaggeration of others (Moynihan 1962). Skimmers, in contrast, have a simple undifferentiated upright, and the same is true of skuas (Moynihan 1962, Anderson 1971; but see Perdeck 1960, 1963).

Low oblique.—In this posture, the head and neck are lowered so that the entire body is almost parallel to the ground, with the bill pointing slightly below and the tail slightly above the line of the body. As in the upright oblique, the wings are held quite close to the body, and frequently a short bark (see below) is uttered. This is also a common posture in aggressive encounters, but it is seen more often after an attack whereas the upright oblique occurs more often before an attack. The commonly occurring sequence of vocal upright oblique followed by vocal low oblique is very similar to the common larid oblique-cum-long call display. It seems very likely that these two sequences are homologous and thus that the skimmer low oblique is homologous with the larid oblique posture. The oblique

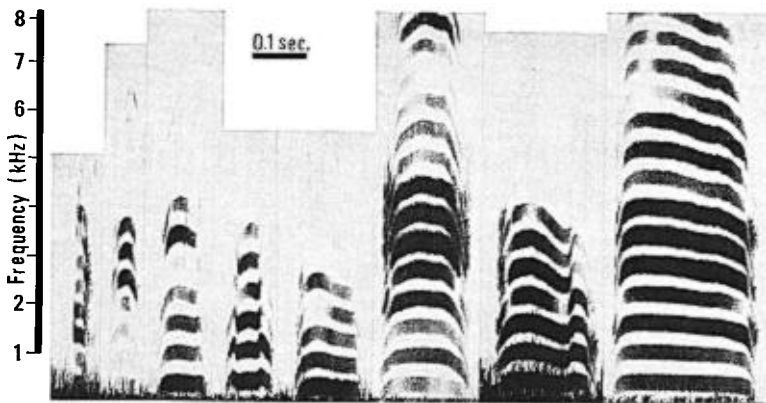


Fig. 1. Spectrograms of eight selected barks of the Black Skimmer showing variation in duration and in form.

is also present in skuas (Perdeck 1960, Moynihan 1962, Anderson 1971) and in most gulls, the noddy terns, and the Inca Tern (*Larosterna inca*) (Moynihan 1962). It is not present and thus has presumably been lost in the black-capped terns.

Bark.—This common note of the skimmer varies in form from a short bark, which is a soft but sharp “out,” to a long bark, which is a longer cawing sound. Wolk (1959) seems to suggest that the bark occurs in two discrete forms, the long bark and the short bark; but our observations suggest that the duration of this note may form a continuum (Fig. 1). The bark occurs during aggressive encounters and during courtship, the long forms being more commonly delivered during flight and the short forms being more commonly uttered on the ground. The bark is probably homologous with the common larid long call. As indicated above, it accompanies the skimmer’s homologue of the larid oblique-cum-long call display. In its simplicity it is more similar to the long call of the skuas and gulls than to the more complex calls of the terns.

Bill high.—In this posture, the head and tail are pointed vertically upwards, giving the skimmer a U-shaped appearance. It is usually performed in a sitting position, and often the bird will scrape sand backwards with its feet. The wings are drooped and abducted slightly. This posture is involved in pair formation and maintenance of the pair bond. It does not seem to be homologous with any display of the other members of the Lari.

Draw.—This display is a simple movement of the bill down and under the sitting bird and then back to a nearly horizontal position. It occurs in the same situations as the bill high and in high intensity territorial encounters.

These two postures, the bill high and the draw, often occur together; and the situations in which they occur are those in which choking is performed in gulls. We see no justification for hypothesizing a homology between them as Wolk (1959) does, because the forms of the displays are completely dissimilar. Choking is a bill-down display performed standing and with none of the scraping or drawing movements of the bill high and draw. On the other hand, the bill high and draw are similar to the kicking and drawing movements of functional nest building in the skimmer, and we suspect the displays have been ritualized from this source.

Choking in gulls may be derived from nest-building behavior and it is possible that evolutionary changes in choking have paralleled changes in nest-building movements. The exaggerated movements of choking, bill high, and draw are presumably ritualized and emancipated from their original motivations, and there would seem to be no adaptive value in the displays evolving to resemble nesting behavior; indeed, further divergence from nest building seems more likely than convergence. It thus appears that skimmers do not have the choking posture, nor do skuas, whereas most gulls and the noddy terns do. It is not present and has presumably been lost in the black-capped terns. We feel that this is an important conclusion, because Wolk seems to consider the hypothesized homology between the skimmer bill high and draw and the gull choking to be strong evidence for a close skimmer-gull relationship.

Food begging.—In the skimmer begging consists of simple pecking by the female at the bill of the male, her head held lower than his. This display occurs during pair formation. Food begging is a very common display, occurring in every family of the suborder, but it is very simple in form in the skimmers. There is no call or head tossing movement, either or both of which are associated with food begging in the gulls and the black-capped terns. The noddy terns also have a simple form of food begging, as do skuas (Moynihan 1962, but see Stonehouse 1956 and Perdeck 1960).

Distraction display.—The skimmer half flies and half runs along the sand, at times stumbling forward, the wings hitting the bird's feet and trailing in the sand. The tail is spread and the bird is silent. This is commonly performed at the approach of a potential predator (e.g. man). The distraction display is common throughout the Charadrii (Armstrong 1954, Simmons 1955), is performed by at least some of the skuas (Williamson 1949, Armstrong 1954, Anderson 1971), and thus is probably primitive in the skimmer. Gulls and terns rarely perform this display, their most common strategy of nest defense being colonial nesting and direct attack on predators. Sabine's Gull (*Xema sabini*) does perform a simple distraction display (Brown et al. 1967), which may represent an independently derived condition associated with the species' extremely dispersed nesting habits; and the Black-headed Gull (*Larus ridibundus*) performs a distraction display (Kruuk 1964: 90), but with an extremely low frequency. It is very unusual for birds nesting in dense colonies to have a conspicuous distraction display; indeed skimmers may be unique in this respect.

The only behavioral feature skimmers have in common with terns is the lack of the use of the wings in fighting and the related absence of the raised-wing aggressive display. This feature is also shared by the skuas and so provides no evidence for a close skimmer-tern relationship. Similarly, characters common to skimmers and gulls include the oblique posture, a simple long call, and the lack of complex aerial courtship behavior. These are also shared by the skuas and thus provide no evidence for a close skimmer-gull relationship. The remaining behaviors are either shared only with the skuas (undifferentiated upright posture, simple food begging, distraction display, and lack of choking) or are found only in the skimmers (bill high and draw). All of these features suggest that the skimmers diverged from the ancestral line of the Lari at least as early as the divergence of the gulls and terns and possibly as early as or before the divergence of the skuas.

We thank J. A. Feduccia, G. D. Schnell, R. H. Wiley, and R. L. Zusi for comments on the manuscript. One of us (H.F.S.) also acknowledges with thanks a grant from the Frank M. Chapman Fund of the American Museum of Natural History.

LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, fifth ed. Baltimore, Amer. Ornithol. Union.
- ANDERSON, M. 1971. Breeding behaviour of the Long-tailed Skua *Stercorarius longicaudus* (Vieillot). *Ornis Scandinavica* 2: 35-54.
- ARMSTRONG, E. A. 1954. The ecology of distraction display. *Brit. J. Anim. Behav.* 2: 121-135.
- BROWN, R. G. B., N. G. BLURTON-JONES, AND D. J. T. HUSSELL. 1967. The breeding behavior of Sabine's gull, *Xema sabini*. *Behaviour* 28: 110-140.
- HUDSON, G. E., K. M. HOFF, J. VANDEN BERGE, AND E. C. TRIVETTE. 1969. A numerical study of the wing and leg muscles of Lari and Alcae. *Ibis* 111: 459-524.
- KRUUK, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull. *Behav. Suppl.* 11: 1-29.
- MAYR, E. 1969. Principles of systematic zoology. New York, McGraw-Hill.
- MOYNIHAN, M. 1959. A revision of the family Laridae (Aves). *Amer. Mus. Novitates* No. 1928.
- MOYNIHAN, M. 1962. Hostile and sexual behavior patterns of South American and Pacific Laridae. *Behav. Suppl.* 8:1-365.
- PERDECK, A. C. 1960. Observations on the reproductive behaviour of the Great Skua or Bonxie, *Stercorarius skua skua* (Brünn), in Shetland. *Ardea* 48: 111-136.
- PERDECK, A. C. 1963. The early reproductive behaviour of the Arctic Skua, *Stercorarius parasiticus* (L.). *Ardea* 51: 1-15.
- SCHNELL, G. D. 1970a. A phenetic study of the suborder Lari (Aves). 1. Methods and results of principal components analysis. *Syst. Zool.* 19: 35-57.
- SCHNELL, G. D. 1970b. A phenetic study of the suborder Lari (Aves). 2. Phenograms, discussion, and conclusions. *Syst. Zool.* 19: 264-302.
- SIMMONS, K. E. L. 1955. The nature of the predator-reactions of waders toward humans; with special reference to the role of the aggressive-escape-brooding drives. *Behaviour* 8: 130-173.
- STONEHOUSE, B. 1956. The Brown Skua *Catharacta skua lönnbergi* (Mathews) of south Georgia. *Falkland Islands Dependencies Surv., Sci. Rept.* No. 14.
- TINBERGEN, N. 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour* 15: 1-70.
- WILLIAMSON, K. 1949. The distraction behavior of the Arctic Skua. *Ibis* 91: 307-313.
- WOLK, R. G. 1959. Some reproductive behavior patterns of the Black Skimmer, *Rynchops nigra nigra* Linnaeus. Unpublished Ph.D. dissertation, Ithaca, New York, Cornell Univ.
- ZUST, R. L. 1962. Structural adaptations of the head and neck in the Black Skimmer, *Rynchops nigra*, L. *Publ. Nuttall Ornithol. Club* No. 3.
- ZUST, R. L. 1971. Functional anatomy in systematics. *Taxon* 20: 75-84.

HAROLD F. SEARS, LYNN J. MOSELEY, and HELMUT C. MUELLER, *Department of Zoology, University of North Carolina, Chapel Hill, North Carolina 27514. Present address of first author: University of South Carolina, Union, South Carolina 29379.* Accepted 9 Dec. 74.