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A Revision of the Family Laridae (Aves)

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INTRODUCTION

The object of the present paper is to give a revised classification of the skuas, gulls, skimmers, and terns, with some comments on their evolution and adaptive radiation. The revision is based largely on a comparative analysis of behavior.

I have been able to study some of the behavior patterns of several Old World and North American gulls in considerable detail and have observed various species of skuas, gulls, and terns in South America and some of the Pacific islands. Other workers have studied the behavior of other larids in North America, Europe, and elsewhere.

The ethological evidence has been supplemented by a comparison of certain external morphological characters. As far as the gulls are concerned, this has meant little more than a reëvaluation of the characters discussed in the exhaustive works of Dwight (1925) and von Boetticher (1935).

I am greatly indebted to Dr. Dean Amadon of the American Museum of Natural History, Dr. J. C. Greenway, Jr., of the Museum of Comparative Zoölogy, and Dr. Herbert Friedmann of the United States National Museum for permitting me to study certain specimens in their care; and to Dr. Amadon, Dr. Ernst Mayr, and Dr. J. M. Cullen for reading and criticizing parts of this paper. My observations of the behavior of various larids in the field and in captivity were made possible by grants from the United States National Science Founda-

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PRINCIPAL DIVISIONS OF THE FAMILY

Previous workers have given the skuas, gulls, skimmers, and terns different taxonomic rank. Each group has sometimes been given separate family status. They are, however, generally similar in both morphology and behavior, and it would seem to be convenient, and more in keeping with most recent taxonomic procedure, to keep them all within the same family.

Two subfamilies may still be recognized: the Stercorariinae and the Larinae. The latter may be divided into three tribes: Larini, Rynchopini, and Sternini.

RELATIVE VALUE OF DIFFERENT ETHOLOGICAL CHARACTERS IN DETERMINATION OF RELATIONSHIPS WITHIN THE FAMILY

It is generally recognized that certain kinds of behavior patterns are more useful than others in evolutionary studies, providing more reliable evidence of relationships. Lorenz (1951–1953) has emphasized the value of certain stereotyped and species-specific “fixed motor patterns,” the ritualized “displays.”

As used here, the term “display” includes any and all behavior patterns that have become standardized or stereotyped, in any way, in order to subserve a social signal function. It thus includes all vocalizations and a great variety of postures and movements, many of which have become exaggerated in physical form.

The reliability of display characters is largely due to the fact that they are less often, or less thoroughly, affected by convergent evolution than many morphological features. Displays need not be so closely adapted to as many aspects of the external environment. A hypothetical example may help to illustrate this statement. It does not matter, within certain fairly broad limits, if a bird conveys “threat” by uttering a distinctive call, or making peculiar head movements, or stamping up and down, or flapping its wings, so long as the “meaning” of

the pattern, the signal it is designed to convey, is clear to the opponent towards which the threat is directed. Previous studies have shown that almost any type of movement or posture or call can be ritualized to convey almost any sort of signal.

A note of caution must be inserted here. Displays are very far from being absolutely independent of the external environment. They may also evolve along parallel lines. Displays produced by similar motivation in different animals are often derived from similar sources (see Moynihan, 1955a). Thus, for instance, the aggressive threat displays of many obviously unrelated species have come to include more or less similar components derived from unritualized attack behavior. The effects of this sort of parallel evolution can be discounted only by really detailed comparison of all aspects of the displays involved. The comparative significance of a display cannot be assessed by an analysis of its physical form alone. It is also absolutely necessary to consider such aspects as the function, or functions, of the display, its usual association with other patterns in different social contexts, and the actual and relative strengths of the drives responsible for its production.

Another confusing factor may be introduced by the problem of maintaining social (and especially reproductive) isolation between sympatric species (see Mayr, 1942, and Sibley, 1957). Even the most closely related species might be expected to develop very different-appearing displays when their ranges come to overlap. This does not seem to have occurred very often among larids, however. It is just those groups which include the largest number of sympatric species (e.g., the large white-headed gulls and the typical black-capped terns) which seem to have the most nearly uniform behavior. Many of the closely related sympatric larids seem to maintain their isolation primarily by selective responses to relatively small morphological distinctions, e.g., slight differences in size and flesh colors and small differences in voice.

Some displays are much more conservative and stable than others. In the case of the Laridae, the primarily sexual displays are very similar in almost all species. The primarily hostile displays are just the reverse. They differ greatly in different species and groups of species. Probably the most useful of the hostile displays, from a comparative point of view, are those that are produced by moderately strong motivation, especially the notes, postures, and movements included in the "Long Call complex" and related patterns. The lower intensity displays are much more uniform, and little is known about the highest intensity displays in most species.

SYSTEMATIC ACCOUNT

PROCEDURE

It will not be necessary to discuss particular behavior patterns at length in the following account. Some of the more widespread display postures are illustrated in figure 1. Most of the other patterns are cited merely by name, as they have been, or will be, described and analyzed elsewhere.

All the names of behavior patterns used throughout this paper are those used in Moynihan (1955b, 1956, 1958a, and 1958b) unless specifically noted otherwise. The initial letters of the names of all ritualized patterns are capitalized.

Almost all the specific names follow Peters (1934).

All the morphological and ethological characters discussed are those of adult birds, unless otherwise stated.

All the approximate ranges cited are breeding ranges.

There are lists of the species whose display behavior has been studied at the beginning of the discussions of most species groups. Those species whose display behavior has been analyzed in considerable detail are marked by an asterisk in these lists.

SKUAS: SUBFAMILY STERCORARIINAE

The characteristic morphological features of the skuas are well known (see, for instance, the summary in Witherby, Jourdain, Ticehurst, and Tucker, 1944). They are the most peculiar and distinctive of the Laridae in anatomy, but not in other respects. They can all be included in the genus *Stercorarius*, as the differences in size and proportions between the Great Skua, *S. skua*, and the lesser skuas or jaegers are not very significant.

The relationships between the various forms of the Great Skua are still obscure, but they may all be conspecific (see the discussion in Murphy, 1936). The behavior patterns of the South American form *chilensis* (Moynihan, in preparation) appear to be nearly identical with those of the typical northern subspecies (see Perry, 1948).

The Great Skua is by far the best-known species from an ethological point of view, but the few brief and incomplete published descriptions of the hostile and sexual patterns of the jaegers or lesser skuas (e.g., in Perry) suggest that they are all very similar.

In general, the whole hostile and sexual repertory of the Great Skua is surprisingly gull-like. Some of the most important hostile patterns are particularly reminiscent of those of the "primitive" hooded gulls (e.g.,

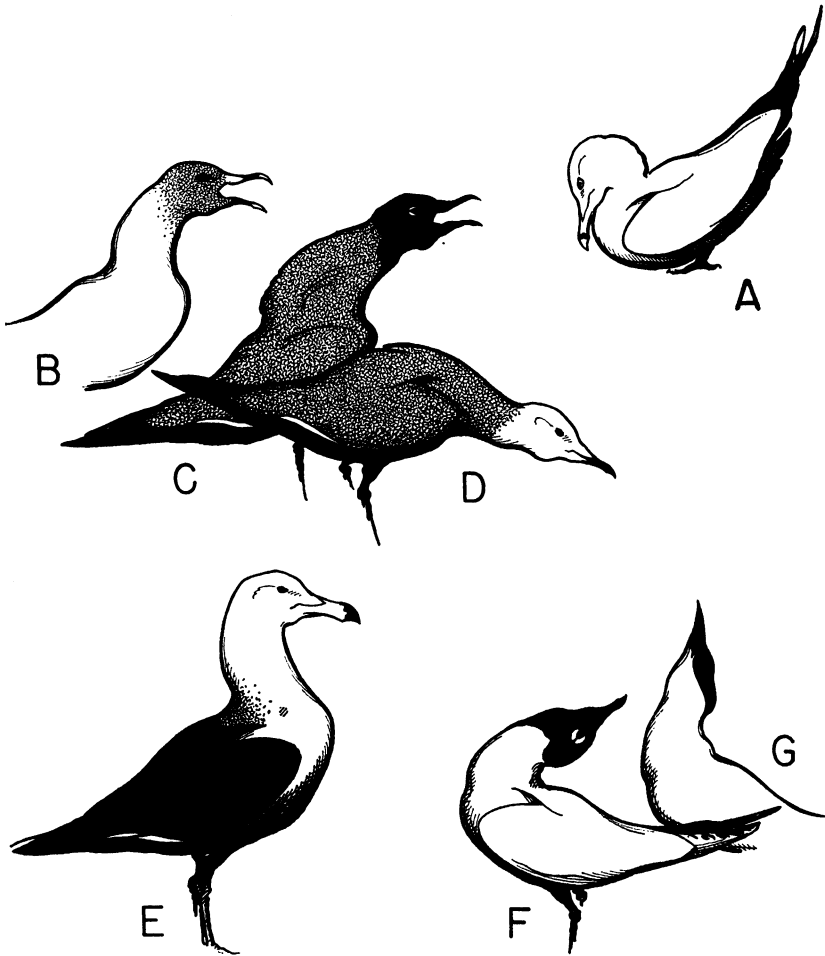


FIG. 1. Sketches of some of the more widespread display postures found in many species of the family Laridae. These are particular postures of particular species, but the homologous patterns of other species are similar in physical form. The examples shown may be taken as more or less "typical." A. The Choking Posture as it occurs during the Choking of the Ring-billed Gull. B. The semi-Oblique Posture as shown by the Swallow-tailed Gull. C. The Oblique Posture as it occurs during the Long Call of the Galapagos Dusky Gull. D. The Low Oblique Posture as it occurs during the Mew Call of the Peruvian Gray Gull. E. An Upright Posture as it occurs during the Upright Posture as shown by Belcher's Gull. F. The posture reached at the climax of a Head-tossing movement in Franklin's Gull. G. The Erect Posture as shown by the Gull-billed Tern.

the Long Call is usually accompanied by Oblique and Low Oblique Postures), but there are also resemblances to those of the large white-headed gulls (the Low Oblique may approximate the Head-down Posture, Upright Postures are relatively common, and Grass-pulling is sometimes conspicuous). The general appearance of the hostile display behavior of the skuas is relatively simple, including fewer distinct patterns than the corresponding repertoires of many gulls, a fact that may support the suggestion that the skuas are the most "primitive" of the Laridae (Fisher and Lockley, 1954).

SUBFAMILY LARINAE

GULLS: TRIBE LARINI

Previous workers have recognized several different genera of gulls. Almost everyone has separated some of the most obviously specialized forms as monotypic or very small genera. Dwight and von Boetticher also divided the remaining species into two or three larger genera.

None of this division is, however, really necessary or justifiable. All gulls are very similar to one another in fundamental morphological features (see Wetmore, 1926). Recognition of genera such as those proposed by Dwight and von Boetticher might be convenient, but it would separate closely related species. Recognition of the monotypic genera would be much less convenient and would give a misleading impression of the main lines of evolution in the group. These genera have been erected on the basis of such characters as bill shape, tail shape, and development of the hind toe, all of which are obviously immediate or special superficial adaptations to particular modes of life, such as different feeding habits or ways of flying. Such characters should not be given more than specific valence, especially as they may differ in different subspecies of the same species, different individuals of the same subspecies, or different plumages of the same individual. Some of the more peculiar species are also connected with more generalized forms by intermediate species.

Such facts indicate that all the gulls must be included in the single genus *Larus*. This inclusion makes a very large and varied genus, but it is no more varied than some of the genera now recognized in other families of birds, such as the Anatidae (Delacour and Mayr, 1945) and the Drepanididae (Amadon, 1950).

Several subdivisions can be distinguished within this genus. Some 10 or 11 groups of species seem to be natural units, and these groups can be distributed among two or three subgenera, if such formal distinction is considered desirable.

The hooded gulls and most closely related species can be put into the subgenus *Xema*; the Ivory Gull may deserve to be separated from the hooded gulls in a subgenus *Pagophila* by itself; and the large white-headed gulls can be put in the subgenus *Larus*.

In an earlier comparative survey of what was then known of gull behavior (Moynihan, 1955b), the hooded species were called the *Hydrocoloeus* gulls, but *Xema* has considerable priority.

A. HOODED GULLS, SUBGENUS *Xema*

This subgenus includes a whole series of varied species groups. The first group, the "primitive" hooded gulls, seems to occupy a central position. All the other groups appear to be more or less closely related to the "primitive" group, but they are widely disparate in other ways. They seem to have followed independent lines of divergent evolution from a common source, which would probably be included in the first group if it were alive today.

GROUP 1: "PRIMITIVE" HOODED GULLS

SPECIES INCLUDED: (1) *Larus (Xema) atricilla* (east and Gulf coasts of North and Central America, West Indian region, Salton Sea); (2) *leucophthalmus* (Red Sea region and western Indian Ocean); (3) *hemprichi* (Red Sea region); (4) *fuliginosus* (Galapagos Islands); (5) *pipixcan* (central North America); (6) *ichthyaetus* (southern Russia and central Asia); and (7) *melanocephalus* (Mediterranean region and central Asia).

SPECIES WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: *Larus (Xema) atricilla** (Noble and Wurm, 1943; Moynihan, 1955b); *fuliginosus* (Moynihan, in preparation); *pipixcan** (Moynihan, 1956, 1958a, and 1958b).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: (See fig. 2). Size medium and build slender to moderately heavy (except in the very large *ichthyaetus*); bill slender to very heavy, usually moderately thick; bill and legs usually reddish; lighter-colored bills often with a more or less distinct subterminal band; a dark hood in nuptial plumage; this hood is black (except in *hemprichi*, in which it is brown), and "complete," extending down the nape; white "eyebrows" always present, usually in conspicuous contrast to the hood; a white band along the rear edge of the wing; primaries black in the majority of species.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: The hostile and sexual repertoires of these gulls are rather elaborate, and it may be useful to list their more important and distinct displays, in order to provide a stand-

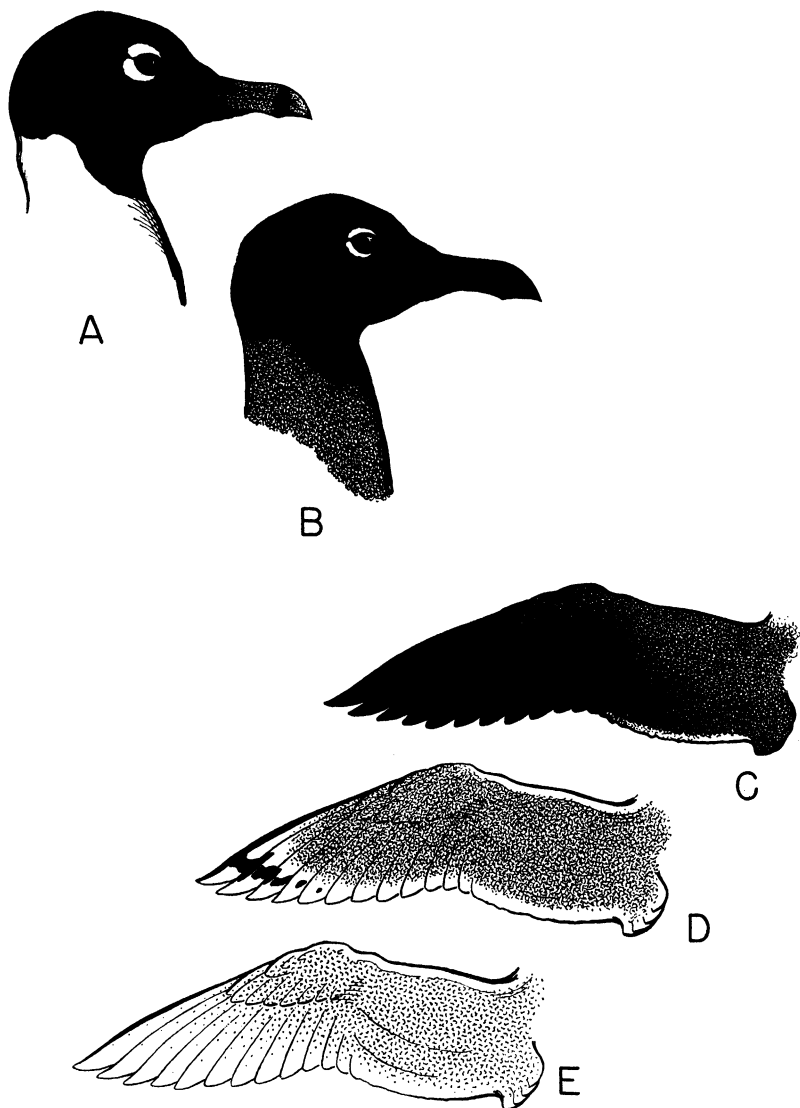


FIG. 2. Head and wing patterns of some "primitive" hooded gulls. A. Head pattern of *pipixcan*. B. Head pattern of *fuliginosus*. C. Wing pattern of *fuliginosus*. D. Wing pattern of *pipixcan*. E. Wing pattern of *melanocephalus*.

ard with which to compare the behavior patterns of other groups.

Adult *atricilla* and *pipixcan* have silent Aggressive and Anxiety Upright Postures (produced by relatively weak attack and escape drives);

Head-flagging (usually produced by weak hostile drives also); Long Call Notes, and a complete Long Call accompanied by an Oblique Posture and then a Low Oblique, followed by Head-tossing (all of which are produced by moderately strong attack and escape drives, differing slightly in each display or display component); a partly hostile and partly sexual Mew Call, which is also given from a Low Oblique Posture (essentially identical with the purely hostile Low Oblique of the Long Call in physical form); a complex Choking display (produced by relatively very strong activation of the attack and escape drives, with an added sexual component in some cases); and primarily sexual Begging (accompanied by Head-tossing like the Tossing associated with the Long Call) in pre-copulatory situations; *pipixcan* also has a conspicuous and very aggressive Gakker display.

Most of these displays are also found in other larids, in one form or another, and the "primitive" hooded gulls have no absolutely diagnostic ethological characters as such. But no other dark-hooded gulls have similar voices, always flexible and varied in tone quality, and usually melodious or "trumpeting," in combination with a Long Call from Oblique and Low Oblique Postures, followed by Head-tossing.

REMARKS: This appears to be a relatively old group. Most of the species are quite distinct from one another. (This group is the most varied of the larger groups of gulls, much more so than either the masked gulls or the typical large white-headed gulls.) None of the species has a very extensive range, and some of them have quite restricted and possibly "relict" ranges in the tropics, where other gulls are scarce or absent.

The apparently primitive or generalized characters of the group are the usual body size and proportions; the black primaries of some species (a juvenal character in many gulls of other groups); the dark head markings (also characteristic of the skuas and the black-capped terns); the quality of the voice (somewhat reminiscent of that of the skuas, the kittiwakes, the large white-headed gulls, and the skimmers); and the form of the postures and movements associated with the Long Call (also more or less strongly reminiscent of those of the skuas, the large white-headed gulls, the skimmers, the noddies, and several other groups as well).

The Laughing Gull, *atricilla*, appears to be an almost perfectly unspecialized form, in most respects, and an excellent "structural ancestor" of all the other hooded gulls.

The two tropical Old World species, *leucophthalmus* and *hemprichi*, are probably rather close to the Laughing Gull. The extensive dark

areas in their body plumage might suggest that they are intermediate between the Laughing Gull and the very dark *fuliginosus*, but dark coloration may be a purely adaptive response to tropical insolation. Dwight and von Boetticher both suggested that dark color is primitive in gulls, but it is so widespread among tropical larids that this suggestion may be doubted. All sorts of different tropical gulls, skimmers, noddies, and black-capped terns seem to have acquired dark color of plumage or skin, independently, in very different ways.

The Galapagos Dusky Gull, *fuliginosus*, is certainly closely related to the preceding species, but it may be slightly more specialized in one or two behavioral characters. Its Long Call is definitely bipartite, and its Low Oblique Posture during the Long Call is particularly exaggerated, sometimes approaching a Forward display (see below).

The remaining species of the group are rather more "progressive" in various ways.

Franklin's Gull, *pipixcan*, is very reminiscent of the Laughing Gull, and much of its display behavior is almost equally unspecialized. It is a lighter and more aerial species, however, and it has adopted very peculiar nesting habits, building floating nests on water. The Great Black-headed Gull, *ichthyaetus*, appears to be most closely related to Franklin's Gull. It has the same characteristic pattern on the primary feathers—white tips with black subterminal patches. Its heavy bill and lighter flesh colors are probably strictly correlated with its larger size.

The Mediterranean Black-headed Gull, *melanocephalus*, is rather more isolated. Its primary pattern is distinctive, but not unlike the corresponding pattern of the masked gulls. It may be related to both the typical "primitive" hooded gulls and the masked gulls, but its complete hood, the white stripe along the rear edge of its wing, and the few published descriptions of its voice (e.g., in Hartert, 1912–1921) all suggest that it is closer to the former than the latter. It may be retained in the "primitive" hooded gull group, at least until its behavior has been studied more thoroughly.

GROUP 2: WHITE-HOODED GULLS

SPECIES INCLUDED: (1) *Larus (Xema) modestus* (Humboldt Current region of Peru and northern Chile); (2) *heermanni* (California Current region of Mexico and Baja California).

SPECIES WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: *Larus (Xema) modestus** (Moynihan, in preparation).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Very similar to the more typical "primitive" hooded gulls in most features, but there is a white

hood in nuptial plumage, sharply contrasting with the dark neck and body.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: The display behavior of the Peruvian Gray Gull, *modestus*, is very reminiscent of that of the Laughing Gull and Franklin's Gull and is at least as unspecialized in most respects. Its Long Call is bipartite (in somewhat the same way as in the Galapagos Dusky Gull) and accompanied by Oblique and Low Oblique Postures and followed by Head-tossing.

REMARKS: These species are very close to the "primitive" hooded gulls, especially to *fuliginosus*, but they may deserve to be put in a separate group because of their specialized nuptial plumage, which is just the reverse or "negative" of that of the other hooded gulls (and most other larids).

The almost incredible nesting and incubation habits of the Gray Gull, nesting in the barest and hottest inland desert regions and leaving the eggs exposed to the sun during the daytime, are certainly the most remarkable in the whole family (see Goodall, Philippi, and Johnson, 1945).

GROUP 3: KITTIWAKES

SPECIES INCLUDED: (1) *Larus (Xema) tridactylus* (northern Holarctic); and (2) *brevirostris* (some of the North Pacific islands).

SPECIES WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: DR. Esther Cullen has conducted a thorough study of the Atlantic Black-legged Kittiwake, *t. tridactylus* (1957, and personal communication).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Size medium, with short legs and long wings; bill plain yellow; legs and feet red or black; hallux reduced or vestigial; no hood in nuptial plumage; white stripe along rear edge of wing; primaries abruptly black-tipped.

REMARKS: I do not want to say much about kittiwake behavior before Cullen publishes the complete results of her investigation, but it should be mentioned that the voice of the Atlantic Kittiwake is flexible and melodious, and that its Long Call is bipartite (the actual "kitti-wake") and given from a rather variable semi-Oblique Posture. Some of its other displays are more distinctive in physical appearance, but they can be homologized with some of the displays of the "primitive" hooded gulls (and many other gulls as well). This correspondence in behavior, plus the evidence of the juvenal plumage, indicate that the kittiwakes are quite closely related to the hooded gulls, in spite of the fact that they have lost the hood itself in the course of evolution. Cullen has already pointed out that many of the ethological peculiari-

ties of the kittiwakes are strictly correlated with their cliff-nesting habits, which is probably also true of their most distinctive morphological features. Such characters do not justify the creation of a separate genus, *Rissa*, for the kittiwakes alone. They are not more specialized or isolated than some of the other hooded gulls.

GROUP 4: SAUNDERS' GULL, *saundersi*

This distinctive species from eastern Asia presents the same problem as the Mediterranean Black-headed Gull in a more acute form. It also resembles the masked gulls in the pattern of its primaries, and the typical "primitive" hooded gulls in having a white stripe along the rear edge of the wing. Its hood is black, but the actual shape of the hood is difficult to determine in prepared skins. Some of its other characters, i.e., the shape of its bill, its relatively long legs, and the deeply incised webs of its feet, are even more peculiar. It may have adopted less aquatic and more aerial and terrestrial habits than most gulls (apparently confirmed by the few observations of its activities in winter in Japan; N. Kuroda, personal communication). Its display behavior is unfortunately completely unknown, so the best provisional course may be to keep it in a separate group.

GROUP 5: MASKED GULLS

SPECIES INCLUDED: (1) *Larus (Xema) philadelphia* (subarctic north-western North America); (2) *ridibundus*, including *brunnicephalus* and *maculipennis* (widely distributed in the temperate Palearctic, the high plateau of Tibet, southern Chile, Argentina, and the Falkland Islands); (3) *serranus* (high Andean lakes); (4) *genei* (Mediterranean region); (5) *cirrocephalus* (probably widely distributed in warm temperate South America and east Africa); (6) *novae-hollandiae* (Australia, New Zealand, New Caledonia, and South Africa); and (7) *bulleri* (New Zealand).

SPECIES WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: *Larus (Xema) philadelphia* (Moynihan, 1955b, 1956); *ridibundus** (Moynihan, 1955b; and in preparation); *serranus* (Moynihan, in preparation); *cirrocephalus* (Moynihan, in preparation); and *novae-hollandiae* (Moynihan, 1955b; Tinbergen and Broekhuysen, 1954).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: (See fig. 3). Size medium to small; build slender to moderately heavy (*serranus*); bill red, brown, or blackish, without bars or spots; legs reddish or brownish; most species with a dark hood in nuptial plumage, but there is a general tendency in the group for the hood to become paler, brown or pale gray,

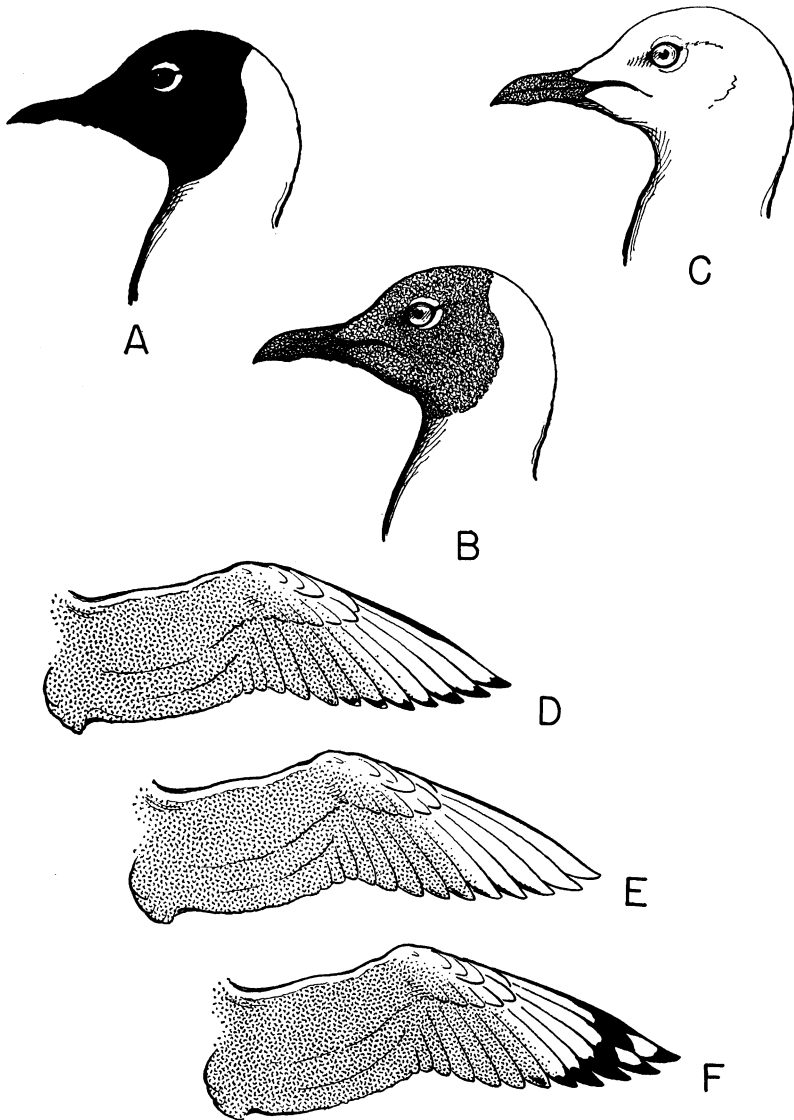


FIG. 3. Head and wing patterns of some masked gulls. A. Head pattern of *philadelphia*. B. Head pattern of *cirrocephalus*. C. Head pattern of *novae-hollandiae*. D. Wing pattern of *r. ridibundus*. E. Wing pattern of *r. maculipennis*. F. Wing pattern of *cirrocephalus*.

and three species (*genei*, *novae-hollandiae*, and *bulleri*) have lost the hood completely; the hood, if present, "mask-shaped," cut out in the back to leave the nape white; white eyebrows more or less conspicuous

in the nuptial plumage of the hooded forms; no white stripe along the rear edge of the wing; primary pattern on the upper surface of the wing variable, but always including a white triangle along the leading edge, bounded or interrupted by more or less black towards the tips of the feathers; underneath side of the forewings usually almost entirely suffused with blackish.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: Display behavior not very unlike that of the "primitive" hooded gulls, but voice much less flexible, rasping or screeching; Long Call given from Oblique and Forward Postures; Oblique much less vertical than in most gulls; aerial hostile displays relatively common and elaborate, including pursuit flights with Swoops and Soars, but no Glides; Head-bobbing by males before copulation.

REMARKS: Dwight suggested that the Tibetan Brown-headed Gull, *brunnicephalus*, the Andean Gull, *serranus*, the Gray-headed (or Gray-hooded) Gull, *cirrocephalus*, and the Silver Gull, *novae-hollandiae*, were only distantly related to the other forms. His opinion was based on their primary patterns and relatively thicker bills. Later evidence has shown that this view is incorrect. The behavior of all the species is very similar. The primary pattern of the Andean Gull is really intermediate between that of a species such as the Gray-headed Gull and that of such forms as the Northern "Black-headed" or Brown-headed Gull (typical *ridibundus*). And Stegmann (1935) has shown that the Tibetan and Northern Brown-headed Gulls interbreed where their ranges meet.

Most of the forms in this group, in fact, might almost be included in a single species. The three brown-headed forms are almost certainly conspecific. The Patagonian Brown-headed Gull, *maculipennis*, is geographically widely separated from the other two forms, but its behavior is nearly or completely identical with that of typical *ridibundus* in all details (personal observation), and it is more nearly similar to typical *ridibundus* in plumage pattern and bill shape than is the Tibetan *brunnicephalus* which interbreeds with typical *ridibundus*. Hellmayr (1932) concluded that *maculipennis* and *ridibundus* were conspecific from a consideration of their morphological features alone. The intervening forms, Bonaparte's Gull (*philadelphia*) and the Andean Gull, are very similar, but they are slightly divergent (in different ways) in behavior. It may be better to retain them as separate species, probably in the same superspecies. The Slender-billed Gull, *genei*, may be another member of the same superspecies. The reports that its breeding range overlaps that of the Northern Brown-headed Gull

would seem to deserve further investigation and confirmation. The Gray-headed and Silver Gulls are still more distinct and obviously closely related to each other. They both, for instance, have a characteristic form of the Oblique Posture, in which the head and bill are kept horizontal or even pointed slightly downward. They might be put in a separate superspecies of their own. It would be interesting to know if they interbreed, with any appreciable frequency, where their ranges approach or overlap in Africa. The New Zealand Black-billed Gull, *bulleri*, is probably closely related to the Silver Gull.

GROUP 6: THE LITTLE GULL AND (PROBABLY) THE ROSY GULL

SPECIES INCLUDED: (1) *Larus (Xema) minutus* (northern Palearctic); (2) (?) *roseus* (the delta of the Kolyma River in Siberia, with one record of breeding in Greenland).

SPECIES WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: *Larus (Xema) minutus* (Moynihan, 1955b).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Size small to very small; small-headed, rather pigeon-shaped; bill small and black; legs red; one species (*minutus*) with a complete black hood, without white eyebrows, in nuptial plumage; the other species without a hood, retaining only a black collar; white stripe along rear edge of wing; primaries otherwise unpatterned.

REMARKS: These two species are very distinct, but they show enough similarities in size, proportions, and plumage pattern (including juvenile plumage) to suggest that they are more closely related to each other than either is to any of the other hooded gulls.

The Little Gull, *minutus*, is the only one of the two species whose behavior has been really studied, and its display patterns are rather specialized. Its voice is peculiar, generally melodious and varied in tone, like that of the "primitive" hooded gulls and the kittiwakes, but most of its Long Call Notes are bisyllabic. Its Long Call is given from Oblique and Vertical Postures. Its elaborate aerial patterns are relatively very common and quite distinct in physical form, including complex pursuit flights, sometimes involving three or more birds, with aerial Vertical Postures and Glides, but no Swoops or Soars.

The only published description of one or two display patterns of the Rosy or Ross' Gull, *roseus* (Buturlin, 1906), is very brief and difficult to interpret. The Rosy Gull may deserve to be put in a separate group, but this question cannot be decided on the available evidence now.

GROUP 7: FORK-TAILED GULLS

SPECIES INCLUDED: (1) *Larus (Xema) furcatus* (Galapagos Islands); and (2) (?) *sabini* (Holarctic, in the far north).

SPECIES WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: *Larus (Xema) furcatus* (Moynihan, in preparation).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Size large to small; build slender; bill black, with light tip; a gray, complete hood in nuptial plumage, without white eyebrows (*furcatus* has white spots and patches around the base of the bill); wing with a white triangle along rear edge (much expanded in *furcatus*), and more or less black along the leading edge of the primaries; tail forked.

REMARKS: The Swallow-tailed Gull, *furcatus*, is quite remarkably specialized. It has been observed only very briefly, but its displays seem to be more aberrant than those of any other gull studied. Its voice is very peculiar, including a variety of strange peeping, whistling, and rattling noises. It seems to lack most of the exaggerated display movements and postures of other gulls. The homologue of the Long Call is usually given from a simple semi-Oblique Posture (possibly a paedomorphic character, as it is typical of the chicks and juvenile birds of several other species; personal observation). The homologue of the Long Call itself is completely bipartite, really two distinct new calls, partly independent of each other. The first of these new calls is strongly reminiscent, in sound, of the first part of the less-specialized Long Call of the other Galapagos gull, *fuliginosus*.

This latter fact may be significant in connection with the difficult problem of the relationship between the Swallow-tailed Gull and Sabine's Gull, *sabini*. It might suggest that the two Galapagos species are derived from a common ancestral stock, which became isolated in the islands and then split up *in situ*. This, in turn, might suggest that the physical similarities between the Swallow-tailed Gull and Sabine's Gull are largely due to convergence. It is also possible, however, that the Swallow-tail has been derived from an isolated population of some ancestor of *sabini* which lost the tendency to migrate. Part of the Pacific population of *sabini* migrates down the coast of North and Central America to Peruvian waters. The physical similarities between the Swallow-tail and Sabine's Gull are certainly so many and so varied, involving features of bill, wings, and tail, that it is difficult to believe that the two species are not more closely related to each other than either is to most of the other gulls.

The behavior of Sabine's Gull is still almost completely unknown,

but I have seen a short film of some of its hostile patterns (for which I am indebted to Mr. Tom Barry of the Department of Conservation of Cornell University). This film must be interpreted with extreme caution, but it suggests that the hostile repertory of Sabine's Gull is less peculiar and specialized than that of *furcatus*. It shows, for instance, that Sabine's Gull has an Alarm Call like that of most of the other hooded gulls, a call that appears to be completely absent in the Swallow-tail. Further research may eventually indicate, therefore, that *sabini* and *furcatus* should be placed in separate groups, even if the existence of a special relationship between them should be definitely confirmed.

B. IVORY GULL, SUBGENUS *Pagophila*

GROUP 8: THE IVORY GULL

The Ivory Gull, *eburneus*, is still another distinctive arctic species whose social behavior remains unknown, and whose systematic position is even more difficult to assess. Von Boetticher has cited a number of morphological features in which it agrees with the "primitive" hooded gulls and the white-hooded gulls, and they may well be its closest relatives, but its ecology is so specialized and its plumage pattern is so peculiar (unique among gulls) that it may be left in a separate subgenus for the time being, as a matter of convenience.

C. LARGE WHITE-HEADED GULLS, SUBGENUS *Larus*

These gulls are not particularly aberrant (they are much less specialized than some of the hooded gulls), but they seem to have followed a rather distinct line of evolution, becoming adapted to a rather different way of life (see below).

GROUP 9: THE DOLPHIN GULL, *scoresbii*

RANGE: Magellanic region of South America.

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: (See fig. 4). Size medium; build moderately heavy; bill red and rather thick for the size of the bird; legs red; no distinct hood, but the head is whitish or very pale gray in nuptial plumage, blending into the darker gray suffused over the neck and under parts; white stripe along rear edge of wing; primaries black.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: (Moynihan, in preparation). Voice flexible and melodious; Alarm Call relatively short (as in most hooded gulls); Long Call accompanied by a preliminary Oblique Posture, a Head-down Posture (an exaggerated form of the Low Ob-

lique), and a second (and slightly different) Oblique Posture, in that order, followed by Head-tossing; independent Head-tossing relatively common in many purely hostile situations; Upright Postures relatively very rare (as rare as in many hooded gulls).

REMARKS: The comparatively dark Dolphin Gull is the most distinct of the large white-headed gulls, but it is certainly closely related to the other species. Its nearest relative is probably *belcheri*. The juvenal plumages of *scoresbii* and *belcheri* are almost identical, and *belcheri* has a trace of dark color on the neck in adult plumage.

The display behavior of the Dolphin Gull is generally elaborate and rather peculiar in certain respects, but some of its displays are particularly reminiscent of those of the skuas and "primitive" hooded gulls on the one hand and of the more typical, large white-headed gulls on the other. Its Long Call display complex is almost exactly intermediate in form, and must be very close to the ancestral version from which the Long Call displays of all the other large white-headed gulls have been derived.

GROUP 10: TYPICAL LARGE WHITE-HEADED GULLS

FORMS WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: *Larus* (*Larus*) *belcheri* (Moynihan, in preparation); *delawarensis** (Moynihan, 1956, 1958a, and 1958b); *canus** (Weidmann, 1955); *californicus* Moynihan, 1958a); *argentatus** (Tinbergen, 1953; Moynihan, 1955b); *fuscus* (Tinbergen, 1953); *dominicanus* (Moynihan, in preparation); *marinus* (Broekhuysen, 1937); and *hyperboreus* (Steinbacher, 1952).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: (See fig. 4). Size medium to very large, large on the average; build usually heavy; bill thick, usually yellow with black and/or red subterminal or terminal spots or bars; legs usually light-colored, greenish, yellow, or flesh-colored; no hood in nuptial plumage; white stripe along rear edge of wing; primaries black, or black-tipped with one or more white subterminal "mirrors" (see Dwight), becoming paler or even completely white in some forms.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: Voice flexible and usually melodious; Long Call usually accompanied by a preliminary Oblique Posture, a Head-down Posture, and a second Oblique Posture (the first Oblique seems to be absent in some forms); Alarm Calls relatively long in most species, including more notes than the corresponding calls of hooded gulls or *scoresbii*; Upright Postures relatively very common; relatively frequent and elaborate redirection of aggression upon

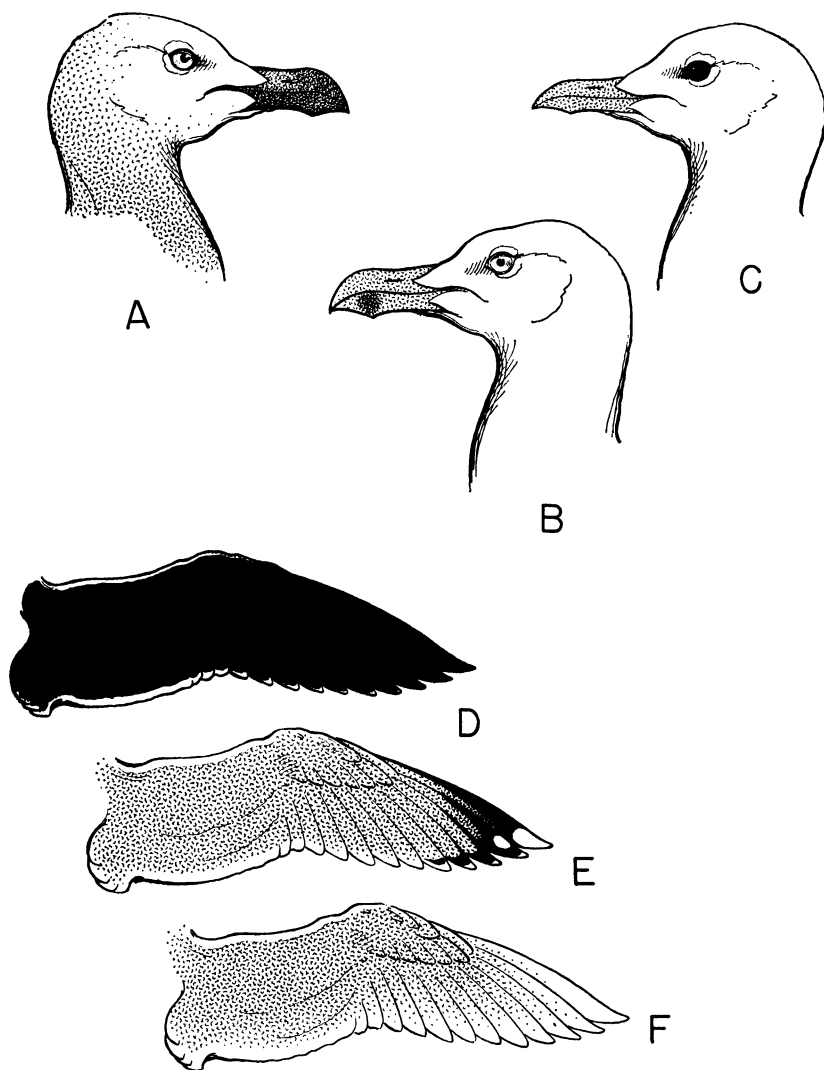


FIG. 4. Head and wing patterns of some large white-headed gulls. A. Head pattern of *scoresbii*. B. Head pattern of *a. argentatus*. C. Head pattern of *c. canus*. D. Wing pattern of *belcheri*. E. Wing pattern of *delawarensis*. F. Wing pattern of *hyperboreus*.

inanimate objects (e.g., the "Grass-pulling" of the Herring Gull); aerial hostile patterns rare and comparatively simple.

REMARKS: This is the largest, most widespread, and most successful

group of gulls. Its general limits are clear, as are the general inter-relationships of most of the forms within it, but the precise status of some of the forms and the exact number of distinct species that should be recognized have long been matters of dispute and are still debatable.

The group as a whole may be conveniently, if rather artificially, divided into two subgroups: first, a series of forms with a few primitive and/or aberrant characters; and, second, the remaining forms, the Herring Gull and its closest relatives.

The classification of the first subgroup is relatively easy. It certainly includes the following forms (the specific distinctness of which has never been seriously questioned): (1) *belcheri* (Humboldt Current region of Peru and northern Chile); (2) *crassirostris* (eastern Asia); (3) *pacificus* (southern Australia); (4) *audouini* (Mediterranean region); (5) *delawarensis* (eastern and central temperate North America); and (6) *canus* (temperate Palearctic and northwestern North America).

Larus (Larus) belcheri and *crassirostris* may be somewhat primitive in having completely black primaries, banded tails, and comparatively extensive areas of red or red and black on the bill as adults, as these are characters of juvenile birds of other species or adult "primitive" hooded gulls. The display behavior of *belcheri* is, however, generally quite "progressive" or specialized. Most of its displays are similar to those of the Herring Gull; only its Alarm Call is the same as that of the hooded gulls and of the Dolphin Gull.

The Australian *pacificus* may be most closely related to *belcheri* and *crassirostris*, as it is rather similar to one or both of them in general proportions, bill colors, and primary pattern. Peters (1934) included *pacificus* with *scoresbii* in a separate genus, *Gabianus*. He seems to have based his opinion on the fact that both species have relatively thick bills, but *pacificus* is much closer to the other typical large white-headed gulls in all other morphological features. (See also the comments in Murphy, 1936.)

Larus (Larus) audouini and the Ring-billed Gull, *delawarensis*, are intermediate between the preceding species and the species of the Herring Gull subgroup in several respects, and they may be rather closely related to each other (the distinctive flesh colors of *audouini* are approached by the most highly colored *delawarensis* males). The display behavior of the Ring-bill is also very reminiscent of that of the Herring Gull (including a comparatively long Alarm Call), but it is rather more elaborate. Its Long Call complex includes a modified Head-tossing element which is apparently homologous with the Long Call Tossing of the "primitive" hooded gulls and *scoresbii*.

The Mew Gull, *canus*, is obviously related to the Ring-bill, but this relationship may be less close than some workers have thought (e.g., Fisher and Lockley, 1954). The Mew Gull's plain yellow bill, and its Low Oblique instead of a Head-down Posture during the Long Call, are unique among the large white-headed gulls.

The remaining forms, the Herring Gull, the Black-backed Gulls, the Glaucous Gull, and similar forms are also linked to the Ring-bill (*californicus* is an almost perfectly transitional form), and they are all very closely related to one another. The known display patterns of all the forms that have been studied seem to be nearly identical.

The numerous forms of this Herring Gull subgroup have proved difficult to classify satisfactorily. The difficulty has been due to several factors. Some forms that are very similar morphologically have been shown to behave as distinct species in some regions where their ranges overlap, even though they may be connected by "intermediate" forms in other regions; while too little is known about the exact nature of some of the possible social and reproductive contacts between other forms whose breeding ranges may also overlap or approach one another very closely (especially some of the arctic, central Asian, and Mediterranean forms).

The following forms have usually been recognized as distinct species in most recent publications: (1) *californicus* (inland, western and central North America); (2) *argentatus* (widespread in much of the temperate and northern Holarctic); (3) *glaucoides* (Greenland and part of eastern arctic North America); (4) *fuscus* (widespread in Palearctic); (5) *dominicanus* (pan-antarctic and Humboldt Current region of western South America); (6) *occidentalis* (west coast of North America); (7) *schistisagus* (northeastern Asia); (8) *marinus* (North Atlantic region); (9) *glaucescens* (northwest coast of North America); and (10) *hyperboreus* (Holarctic, in far north).

Some of these are certainly quite valid species, but others (e.g., *dominicanus*) have been reduced to subspecific rank by some authors, and it is also possible that some forms that have usually been considered subspecies (e.g., the form that has been called *argentatus thayeri*) may eventually be proved to be additional full species.

There is no point in discussing such controversial problems here, as they cannot be solved until the actual reactions of the dubious forms have been studied more thoroughly in the field under natural conditions. It should only be noted that the existence of such problems serves to emphasize the essential homogeneity of the whole subgroup.

GENERAL COMMENT, GULLS

The above arrangement of the gulls is roughly similar to the classifications of Dwight and von Boetticher insofar as the hooded gulls and the large white-headed gulls are recognized as major divisions, but the grouping of the various species within the hooded gull division, and the allocation of the more or less dark species (von Boetticher's *Adelarus* and associated forms) between the two divisions, are rather different from anything proposed heretofore.

SKIMMERS: TRIBE RYNCHOPINI

The distinctive morphological characters of the skimmers are numerous. Their shape is tern-like, and their plumage pattern is reminiscent of that of such terns as *Sterna fuscata* and *anaethetus*. Other characters, such as bill and eye structure, are absolutely unique in the whole family. Previous investigators have had to rely on such evidence, and they have usually concluded that the skimmers are highly specialized terns.

This conclusion must be modified in the light of recent studies of the behavior of the North American Black Skimmer (R. G. Wolk, personal communication). The display repertory of this form is quite remarkably similar to that of the "primitive" hooded gulls. The tone quality of its voice is rather reminiscent of that of these gulls, and it has Long Call Notes and a sort of Long Call which are given from Oblique Postures. Its whole hostile behavior is relatively simple and quite different from the complex and elaborate hostility of most terns. Many components of the hostile behavior of terns are also homologous with patterns of gulls (see below), but they are organized in a very different way. This behavior suggests that the terns and skimmers have both been derived, quite independently, from some primitive gull and that the special physical similarities between them are the result of parallel or convergent evolution—similar adaptations to somewhat similar methods of flying and feeding.

The skimmers are a very closely knit group of allopatric forms, and it is rather difficult to decide how many species should be recognized. Most recent authors have recognized three: *nigra* for all the American forms, and *flavirostris* and *albicollis* for the African and Asiatic forms. This arrangement may well be correct. It is probable, however, that the African and Asiatic forms with light-tipped bills are more closely related to each other than either is to any of the American forms with black-tipped bills. Bill colors are important sign stimuli in many

groups of larids, and it is possible, therefore, that the African and Asiatic skimmers may eventually be shown to be conspecific.

TERNs: TRIBE STERNINI

The terns represent the climax of larid evolution in several ways. They are certainly more varied than any of the other tribes, and they can be divided into three genera: *Anoüs*, *Larosterna*, and *Sterna*.

A. NODDIES, *Anoüs*

The three main types of noddy are fairly distinct, but the genus as a whole is so small that there is no need for the recognition of formal subgenera.

GROUP 1: DARK NODDIES

SPECIES INCLUDED: (1) *Anoüs stolidus*; and (2) *tenuirostris*, including *minutus*. Both species are world wide in tropical and subtropical oceans and extend to the sub-antarctic in some areas.

The display patterns of the Brown Noddy ("the Noddy Tern" of the Check-list, American Ornithologists' Union, 1957), *stolidus*, have been observed and analyzed in detail (Watson, 1908; Warham, 1956; Moynihan, in preparation), and some of the patterns of the Black Noddy, *tenuirostris*, have been studied very briefly (Warham, 1956; Moynihan, in preparation; and J. M. Cullen, personal communication).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Bill and legs blackish; culmen curved; white cap contrasting with the rest of the dark plumage; black and white spots around eye; tail distinctive, partly wedge-shaped and only slightly forked.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: The hostile and sexual behavior patterns of the dark noddies are more thoroughly gull-like than those of any other terns. Among their display patterns are Upright Postures, Bill-down Postures, Oblique Postures, Low Oblique Postures, Gaping, Food-begging by the female, and regurgitation by the male, all of which are more or less strictly homologous with the corresponding patterns of gulls and usually very similar in physical form. They also have several Cawing vocal patterns which are partly or completely homologous with the Long Call Notes and Long Calls of gulls. All the lower-intensity, non-aerial hostile displays, the Uprights, Bill-downs, Erect Postures, Obliques, Low Obliques, and Gaping, may be grouped together in a complex, variable, and silent "Nodding" performance. The principal aerial display is a High Flight, including

a Butterfly Flight. The most distinctive of all the display patterns is Mutual Preening before copulation, a pattern that seems to be absolutely confined to the noddies, and quite different from the Begging pre-copulatory patterns of all other Laridae.

REMARKS: These two species are very closely related to each other. They seem to be among the most primitive terns, in so far as they are particularly gull-like, and they are certainly the most primitive of the noddies.

There is no reason to recognize more than one species of Black Noddy, as all the forms are allopatric and very similar in all morphological features. It is difficult to understand why such authors as Peters (1934) and Murphy (1936) retained the old separation between *tenuirostris* and *minutus*. The differences between these two groups of forms are hardly greater than the differences between the various geographical races which are usually included in *minutus* without question.

GROUP 2: INTERMEDIATE NODDIES

There are two species of these terns according to Murphy (1936): (1) *ceruleus* (tropical islands of the Pacific); and (2) *albivittus* (southern subtropical islands of the Pacific).

The Blue Noddy, *ceruleus*, and the Gray Noddy, *albivittus* (or "ternlets" as they are often called), have been placed in a genus *Procelsterna* by themselves, but they seem to be a link between the dark noddies, on the one hand, and the White Noddy, on the other, and too similar to both the other groups to justify the generic distinction. Their behavior is unknown, but they are more or less perfectly intermediate in various morphological features. The general color of the plumage of the Blue Noddy is more like that of the dark noddies, while the color of the Gray Noddy is much paler, almost like that of the white species. Neither the Blue nor Gray Noddy has a well-marked light cap in nuptial plumage, but some specimens of the gray species in the Museum of Comparative Zoölogy at Harvard College, presumably young birds, have white caps contrasting with dark cheeks in much the same way as in adult dark noddies. The bills of both the Blue and Gray Noddies are reminiscent of the bill of the Black Noddy, while their tails are more like the tail of the White Noddy in shape.

GROUP 3: THE WHITE NODDY, *albus*

RANGE: Tropical and southern subtropical islands of the Pacific Indian, and South Atlantic oceans.

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Bill black or blue and black; culmen nearly straight; legs dark; skin under feathers black; plumage almost completely white; a ring of black feathers around eye; tail simply forked.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: (Moynihan, in preparation). Hostile behavior greatly simplified; very few display postures; Cawing rather like that of dark noddies; no real High Flight; Mutual Preening before copulation.

REMARKS: The White Noddy ("White Tern" or "Fairy Tern") is among the most specialized of all terns, and the simplification of its behavior is almost certainly secondary. It seems unnecessary, however, to recognize a separate genus *Gygis*, as *albus* is similar to the dark noddies in several significant displays, as well as being connected with them by the Blue and Gray Noddies. Its nesting habits are also peculiar, but they are only an exaggeration of the arboreal habits of such species as the Black Noddy.

All the forms of the White Noddy may be included in a single species (see Baker, 1951).

B. THE INCA TERN, *Larosterna inca*

This species is probably peculiar enough to merit a genus of its own, although its behavior is somewhat reminiscent of the black-capped *Sterna* terns (Moynihan, in preparation).

RANGE: Humboldt Current region of Peru and northern Chile.

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Bill and legs crimson; yellow wattle at the gape; bill shape rather like that of the Brown Noddy; wings broad for a tern; general color of the plumage dark, blackest on crown and lighter on chin; ornamental white plumes on the side of the head; white stripe along rear edge of wing; tail slightly forked.

REMARKS: The hostile and sexual behavior of the Inca Tern is somewhat simpler than that of the dark noddies. Many of its hostile reactions are homologous with those of noddies, but they are arranged or combined in a manner which is more reminiscent of those of the black-capped terns. The place of Nodding is taken by two groups of patterns: (1) silent Uprights and Erects and Bill-downs; and (2) a Rapid Call from Oblique and Low Oblique Postures (often alternating). The aerial display behavior of the Inca Tern is somewhat more distinctive, being simplified and probably "degenerate" (although less so than that of the White Noddy). It seems to lack both High Flights and Fish

Flights. Its Butterfly Flight remains as an independent pattern, and it has developed a characteristic Moth Flight which is very common.

C. BLACK-CAPPED TERNS, *Sterna*

This genus is almost as large as *Larus*, but it is much more homogeneous. The range of variation in the black-capped terns (if *Larosterna* is kept apart) is less than in gulls, or the noddies for that matter. All the black-capped terns are relatively very similar in both plumage and behavior. Several groups of species can be recognized fairly easily, and most of these have been segregated in separate genera by some of the previous workers, but such genera seem to be even less justifiable than the genera proposed for the more specialized gulls. They are also based on very superficial and special adaptive characters, and most of them are also connected by intermediate species.

It would seem to be most convenient, therefore, to recognize about six species groups, without bothering with subgenera.

The display behavior of the black-capped terns is almost as well known as that of gulls. Many of the European species have been studied very intensively. The most recent and extensive comparative survey is that of J. M. Cullen (MS).

GROUP 1: GULL-BILLED TERN, *nilotica*

RANGE: Widely but irregularly distributed in the tropical and warm temperate zones of both the Old World and New World, with the apparent exception of Africa.

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: The plumage pattern of the Gull-billed Tern is much the same as that of most species of the genus, with a black cap in nuptial plumage, contrasting with white cheeks and neck, and generally light plumage of body, wings, and tail. The peculiar features of this species are its relatively heavy black bill, long legs, and slightly forked tail.

REMARKS: The Gull-billed Tern appears to be the most isolated and distinctive of the black-capped terns, as its build and general proportions are relatively gull-like. It is particularly unfortunate, therefore, that its display behavior is almost completely unknown. The few patterns that have been seen (Bent, 1947; Jensen, 1946; and personal observation) suggest that its hostile and sexual patterns are at least roughly similar to those of the other *Sterna* terns. Its voice is perhaps more like that of the "primitive" hooded gulls than is usual in the genus (personal observation). The comparative significance of the various special similarities between the Gull-billed Tern and the gulls

is difficult to assess, however, as many of them may be due to convergent evolution, following the initial divergence of the original black-capped tern stock. The Gull-billed Tern feeds in much the same way as do many of the more lightly built hooded gulls.

GROUP 2: CRESTED TERNS

FORMS WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: *Sterna caspia** (Bergman, 1953); *maxima* (Wolk, personal communication); *bergii* (Tinbergen and Broekhuysen, 1954); and *sandvicensis** (van den Assem, 1954; J. M. Cullen, MS).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Size medium to very large; build fairly heavy; bill usually red, orange, or orange-yellow, sometimes greenish yellow or with extensive black; feet black; a black cap in nuptial plumage, extending into a crest at the nape; most individuals of most forms retaining some white on the forehead even in complete nuptial plumage; tail slightly to moderately forked.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: Behavior generally like that of the typical black-capped terns, including much the same range of displays (see below). Among the few relatively minor peculiarities of the crested terns (according to J. M. Cullen) are a distinctive form of the Stretch Posture; an elaborate Gakking Display (like that of Franklin's Gull); Begging behavior like that of gulls; a very poor development of Tilting; and a peculiar Up-down Posture instead of the Bent Posture (in *s. sandvicensis*). The nesting habits of these forms are also very characteristic (i.e., relatively very crowded colonies, frequent changes of colony sites, and early departure of the young from the nest area).

REMARKS: This group presents some of the same problems as the typical, large, white-headed gulls. The general limits of the group are fairly clear (see also the remarks in the discussion of the typical black-capped terns below), but the number of species that should be recognized is more debatable.

One species, the Caspian Tern (*caspia*), is certainly quite distinct, and is sometimes generically separated from the other crested terns. It is probably less closely related to the other crested terns than the latter are to one another, but all these forms seem to be very similar in behavior, and the few distinctive morphological features of the Caspian Tern (larger size, heavier bill, and shorter crest) are not very significant.

The remaining forms have been split into six or seven species at various times, but this number may prove to be excessive.

They can certainly be split into two groups on the basis of size. The

first group, including the forms that are only slightly smaller than the Caspian Tern, is usually divided into two species: *maxima* and *bergii*. The second group, including the smallest crested terns, has often been divided into the following species: (1) *sandvicensis*; (2) *eurygnatha*; (3) *elegans*; (4) *zimmermanni*; and (5) *bengalensis*. These are the species that were recognized by Peters (1934).

Both groups are almost world wide, along tropical and subtropical coasts. The forms within each group are almost strictly allopatric and differ from one another primarily in color (and sometimes size and proportions) of the bill.

The bill color differences between many of these forms are greater than those separating undoubtedly distinct species in some other groups of larids (e.g., the typical black-capped terns), but Junge and Voous (1955) have shown that two crested terns with very differently colored bills, *sandvicensis acufavidus* and *eurygnatha*, interbreed where their ranges meet or overlap. This fact indicates that bill color may be a poor specific character in crested terns (unlike most of the other groups of larids), which in turn suggests that some of the currently recognized species may eventually have to be reduced to subspecific rank. It is even conceivable that further studies of these forms in the field may show that all the crested terns, except *caspia*, should be included in one or the other of two world-wide polytypic species, equivalent to the two groups cited above, which would then be called *maxima* and *sandvicensis*.

GROUP 3: TYPICAL BLACK-CAPPED TERNS

SPECIES INCLUDED: (1) (?) *Sterna dougallii* (widely but irregularly distributed around the world, with the apparent exception of South America and Africa); (2) (?) *sumatrana* (islands of southwest Pacific and Indian Ocean); (3) *hirundo* (widespread throughout the Northern Hemisphere); (4) *hirundinacea* (temperate South America and Humboldt Current region); (5) *vittata* (pan-antarctic); (6) *virgata* (Kerguelen Islands); (7) *paradisaea* (Holarctic, generally north of the range of *hirundo*); (8) *aleutica* (islands of North Pacific); (9) *striata* (Tasmania, New Zealand, and adjacent islands); (10) *forsteri* (central North America, extending to east coast); (11) *trudeaui* (temperate South America); (12) *repressa* (southern Red Sea and western Indian Ocean); (13) *balaenarum* (coast of west Africa); (14) *lunata* (Oceania); (15) *anaethetus* (pan-tropical, on islands); (16) *fuscata* (pan-tropical, on islands); (17) *melanogaster* (rivers of India, Burma, and western Indo-China);

(18) *aurantia* (much the same range as the preceding species); and (19) *albistriata* (New Zealand).

SPECIES WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: *Sterna dougallii**, *hirundo**, *paradisaea**, *striata*, and *fuscata*. J. M. Cullen has studied the first three species and summarizes previous work on all five.

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Size small to medium; bill usually slender, usually red or orange-red, sometimes with more or less black towards the tip; legs usually red; usually a complete black cap in nuptial plumage (a few species retain some white on forehead in nuptial plumage, and *trudeaui* breeds in a plumage like the winter plumage of the other species); no definite crest, although the feathers of the back of the nape may be slightly lengthened; tail usually long and more or less deeply forked.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: The non-aerial hostile and sexual repertoires of the Common Tern, *hirundo*, and the Arctic Tern, *paradisaea*, include the following postures and movements, among others: the Erect Posture, Tilting, the Approach Posture, the Slant, Bowing, the Bent Posture, the Crouch, and Begging (without Head-tossing) in both the Hunched Posture and a somewhat taller, more erect, posture.

This terminology is that of J. M. Cullen, and it may be useful to list the probable homologies of some of these patterns with the displays of other larids to which I have given other names in the preceding pages. The Erect Posture is essentially identical with the Erect Postures of the dark noddies and the Inca Tern, and all these patterns are obviously related to the Anxiety Upright Postures of almost all other larids, of which they seem to be an exaggeration or further development. The Approach Posture is similar to the Aggressive Upright Postures of other larids. The Slant is probably homologous with the Oblique Postures accompanying the Long Calls of other larids. The posture assumed during the low phase of Bowing is apparently homologous with the purely hostile Low Obliques of many other larids, and the whole Bowing performance thus appears to be largely homologous with the complete Long Call performances of the skuas and most of the typical large white-headed gulls, most of the complete Long Call performances of the "primitive" hooded gulls, the white-hooded gulls, the Dolphin Gull, and the Ring-billed Gull, the alternation of Upright Obliques and Low Obliques of the Black Skimmer, and the Rapid Call performance of the Inca Tern. The Bent Posture seems to be related to the

Low Oblique Postures that almost all other larids assume in some partly hostile and partly sexual situations. The Crouch may be partly homologous with the posture assumed by gulls and dark noddies in the Choking display.

The aerial display patterns of the Common and Arctic Terns include a High Flight (very similar to that of the dark noddies, but without the Butterfly Flight component); a Fish Flight; and V-flying, which may be homologous with the Moth Flight of the Inca Tern.

The calls of all the black-capped terns, and particularly those of this group, are less easy to homologize with the corresponding patterns of other larids. This does not mean that they are not roughly homologous, but it is usually difficult to trace "one-to-one" correlations with particular calls of species of other genera. The whole vocal repertory of the black-capped terns appears to have been "recast" or almost totally reorganized. (It is easy to see how this change could be achieved, as all the calls of all adult larids seem to develop, ontogenetically, from one or two "Distress Calls" of newly hatched chicks; personal observation.) The black-capped terns seem to have a much more varied vocal repertory, a greater number of morphologically distinct calls, than other larids. Most species have relatively shrill, screeching, rasping, or buzzing voices.

The peculiar ethological features of the Common and Arctic Terns, which serve to distinguish them from the *Sterna* terns of other groups, include a form of ground "advertisement" (in addition to the Fish Flight) used by males to attract females, conspicuous Tilting, an unusually rapid Begging Call, Begging from a relatively tall posture, and the comparatively slight development of Gakkerling.

REMARKS: This is the largest group of black-capped terns, and its limits are less easy to define than those of some of the smaller groups. Part of the difficulty is due to the existence of intermediate species, but two other complicating factors are also important. Ethological studies have been practically confined to a few European and North American forms, while the display patterns of the more problematical species of the Old World tropics and Australasian region remain unknown. Some of the sympatric species are so similar morphologically that it is almost impossible to assess the comparative significance of the slight morphological differences between some of the allopatric forms.

The position of the Roseate Tern, *dougallii*, is clear, however. It is almost exactly intermediate between such species as the Arctic and Common Terns and the crested terns. This position is shown by some

of its morphological characters, such as the downy and juvenal plumages, and even more clearly by its behavior, its nesting habits, and its hostile displays. It might equally well be included in either group. I have kept it with the typical black-capped terns in order to retain the more traditional arrangement.

Sterna sumatrana may be another link between the crested terns and the typical black-capped species. Its display behavior is unknown, and it lacks a crest, but some of its morphological features, such as the white forehead in nuptial plumage, the black bill with yellow tip, and the black legs and feet, are reminiscent of those of *sandvicensis*. *Sterna sumatrana* and *dougallii* are also rather similar in proportions and juvenal plumage, and they associate with each other when they occur together in the same region (Robinson and Chasen, 1936).

The really typical black-capped terns are those that are numbered 3 through 11 in the above list. They are all very similar to the Common and Arctic Terns in morphology. Possibly some of them should be lumped together in the same species (e.g., *vittata* may be no more than a subspecies of *paradisaea*; see Murphy, 1936; Kullenberg, 1947; and Clay, 1948), but such action would be premature until the behavior of more forms has been studied in greater detail.

The two small tropical African species, *repressa* and *balaenarum*, are very similar to the preceding species, but they may conceivably be related to the little terns as well.

The three dark-backed tropical species, *lunata*, *anaethetus*, and *fusca*, are obviously very closely related to one another, and the little that is known of the display behavior of the last-named suggests that it is essentially identical with that of the Common and Arctic Terns.

The remaining three species are rather divergent, but they are all suggestive of the marsh terns in one way or another. *Sterna melanogaster* is small and very dark underneath; *aurantia* shares one of the parasites of the typical marsh terns (Clay, 1948); and *albistriata* has the webs of its feet deeply incised, and a relatively slightly forked tail, in addition to a plumage pattern like that of *hybrida* (see below). Such characters may indicate a real relationship, but they may also be the results of similar feeding habits in similar environments. *Sterna albistriata* is the most puzzling case. It has sometimes been put in the separate genus *Chlidonias* with the marsh terns (see Peters, 1934; and Oliver, 1955), but its nesting habits (Stead, 1932) and its non-nuptial plumage are more like those of some of the typical black-capped terns.

GROUP 4: MARSH TERNS

SPECIES INCLUDED: (1) *Sterna hybrida* (southwest Palearctic, south and east Africa, Madagascar, New Guinea, Australia); (2) *leucoptera* (southeastern Europe and central Asia); and (3) *nigra* (western pale-arctic and North America).

SPECIES WHOSE DISPLAY BEHAVIOR HAS BEEN STUDIED: *Sterna nigra** (Baggerman, Baerends, Heikens, and Mook, 1956).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Size small; webs of feet incised; bill small and slender in *leucoptera* and *nigra*, somewhat heavier in *hybrida*; bill red in *hybrida*, largely black in the other two species; *hybrida* with complete black cap in nuptial plumage, white cheeks, and dark gray under parts; the other two species with extensive blackish all over head, neck, and under parts; tail slightly forked in all three species.

DIAGNOSTIC CHARACTERS, ETHOLOGICAL: The display behavior of the European Black Tern, *n. nigra*, seems to be rather simpler than that of the typical black-capped terns. The homologue of the Bent and partly sexual Low Oblique Postures of other larids is particularly exaggerated (Baggerman and her co-authors call it "Stooping") and may include a nest-building component, but the probable homologue of the Oblique and Slant is comparatively slightly developed, and there seems to be little or nothing in the way of an Aggressive Upright, Tilting, Bowing, or a purely hostile Low Oblique. The Black Tern does have High Flights and Fish Flights, but their usual chronological sequence during pairing appears to be the reverse of that of the corresponding flights of the typical black-capped terns (J. M. Cullen, MS). All three marsh terns build more or less floating nests over water.

REMARKS: *Sterna hybrida* is at least partly intermediate between the typical black-capped terns and the other two marsh terns, and there seems to be little justification for the separate genus *Chlidonias*.

GROUP 5: LITTLE TERNS

SPECIES INCLUDED: (1) *Sterna albigrons*, possibly including *superciliaris* (widely distributed in warm and temperate regions around the world, including the great river basins of eastern South America); (2) *lorata* (desert coast of the Humboldt Current region of South America); and (3) *nereis* (southern Australia, New Caledonia, and New Zealand).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Size small; bill and legs largely or completely yellow or yellow-orange; bill moderately heavy

for the size of the bird; a white forehead and partial black cap in nuptial plumage; tail slightly forked.

REMARKS: The little terns lack conspicuous morphological peculiarities such as those that led to the erection of separate genera for some of the other groups of black-capped terns, but the little that is known of the display behavior of the European and North American forms of the Least Tern, *albifrons* (Wolk, MS; and Rooth, personal communication), suggests that they may be quite as distinct as the other groups.

The four principal types of little tern are very similar in morphology, and they all seem to be strictly allopatric. They might almost be included in a single species, and Hellmayr (1929) may be correct in putting *superciliaris* with *albifrons*, but the other two forms are somewhat more isolated. *Sterna lorata* seems to have a characteristically different voice (Murphy, 1936), and *nereis* has a differently shaped white forehead patch in nuptial plumage. It may be better to recognize the two latter forms as separate species, for the time being, putting them in the same superspecies as *albifrons*.

GROUP 6: THE LARGE-BILLED TERN, *simplex*

RANGE: Great river basins of tropical and warm temperate South America).

DIAGNOSTIC CHARACTERS, MORPHOLOGICAL: Size large; build heavy; bill large and heavy, yellowish; legs and feet yellowish or olive; a complete black cap in nuptial plumage; tail slightly forked and relatively very short.

REMARKS: The display behavior of this species is unknown, but it resembles the little terns in various morphological characters, such as proportion, flesh colors, and juvenal plumage.

GENERAL COMMENT, TERNS

This survey may be completed by a few comments about the genus *Sterna* as a whole and its probable relationship to the other terns.

The six groups of black-capped terns are rather different from the comparable groups of gulls and noddies insofar as they all seem to have reached a roughly similar level of evolutionary development. It would be difficult to pick out any particular group of *Sterna* terns (with the possible exception of the Gull-billed Tern) as notably more or less specialized than any other group.

The monophyletic origin of the Sternini has seldom or never been questioned, but it is not, perhaps, absolutely indisputable.

The Inca Tern resembles the black-capped terns in having a dark cap contrasting with white cheeks (i.e., the ornamental plumes) and several of the same displays (of which the Bowing with the Rapid Call and the pre-copulatory Begging would seem to be the most significant). The noddies are very different, however, with their complex silent Nodding (in the two dark species) and pre-copulatory Mutual Preening. Many of the characters that the noddies share with the other terns are widespread throughout the Laridae, and others may have developed independently as convergent adaptations to similar feeding habits (see below). Several of the more specialized gulls with somewhat tern-like habits have developed analogous characters quite independently, and the skimmers have also evolved along parallel lines, becoming exaggeratedly tern-like in several features.

Such facts might suggest that the association of the noddies with the other terns is artificial, but they fail to account for the most distinctive of all tern displays: the High Flight. It is most unlikely that such a complex series of actions and reactions would be developed independently, in almost exactly the same form, in very distantly related species. Certain characters of the Inca Tern, i.e., its dark body plumage, the quality of its voice, and its Butterfly Flight, may also be significant in this connection, as they also tend to link the dark noddies with the black-capped terns. These characters seem to prove that the noddies and the other terns are descended from a common ancestor which had already diverged from the other Laridae. The separation of the noddies is profound and probably ancient, but the terns do seem to be a natural group.

It is generally accepted that the original tern stock was itself derived from a gull or gull-like form, and the purely hostile Low Oblique patterns of the dark noddies, the Inca Tern, and the typical black-capped terns suggest that this ancestral form was most similar to the "primitive" hooded gulls.

SOME ASPECTS OF THE ADAPTIVE RADIATION OF THE LARIDAE

The Laridae are widespread throughout the world, in a great variety of environments, and their success may be largely due to their adaptability in acquiring new feeding and nesting habits.

They appear to have developed from the shore birds, or Charadrii (in the broad sense), and the few known fossil larids from the early or

middle Tertiary seem to be more scolopacid-like than any living forms (Miller and Sibley, 1941).

Some of the living gulls, such as the Peruvian Gray Gull, are still very reminiscent of the shore birds in some of their habits, usually feeding on foot along the shoreline and picking up all sorts of small animals and bits of organic debris. Most of these gulls are more or less strictly coastal.

The ancestral larid was probably relatively "terrestrial" in much the same way, and probably coastal as well, but most of its descendants have adopted rather different ways of life.

Most larids have become much more "aerial." This is true of many gulls, e.g., Franklin's Gull, most of the more specialized groups of hooded gulls, and the Ivory Gull, all of which seem to have developed their relatively more aerial habits independently. Some of these gulls have also become oceanic or pelagic, flying over the surface of the water and picking up food by swoops and shallow dives. Other species have adopted similar feeding habits over inland bodies of fresh water. Some of the inland gulls may also hawk for insects in the air. Many gulls combine the advantages of both courses, feeding over fresh water during the breeding season and becoming more or less pelagic for the rest of the year.

The usual feeding methods of the terns, and even the skimmers, seem to be a further development of the same tendencies.

The Ivory Gull is rather different from most of the other aerial larids in being more of a scavenger. The skuas are equally aerial but even more distinctive in being largely predatory or parasitic.

The large white-headed gulls and (probably) the Great Black-headed Gull are the only larids that have not become much more aerial. They have become predators and scavengers, but they have remained relatively terrestrial.

The nesting habits of the Laridae are even more varied than their feeding methods. The original larids probably nested on more or less flat, open ground near water. Many of their descendants still do so, but others may select sites on cliffs (e.g., the kittiwakes, the Swallow-tailed Gull, and the Brown Noddy) or in trees (e.g., Bonaparte's Gull and the White Noddy), or even build floating nests on the water itself (e.g., Franklin's Gull and the marsh terns). The most specialized larids in this respect seem to be the Inca Tern, which nests in crevices or burrows which it may excavate for itself, and the Gray Gull, which nests in the hottest and most extremely arid tropical desert far from water.

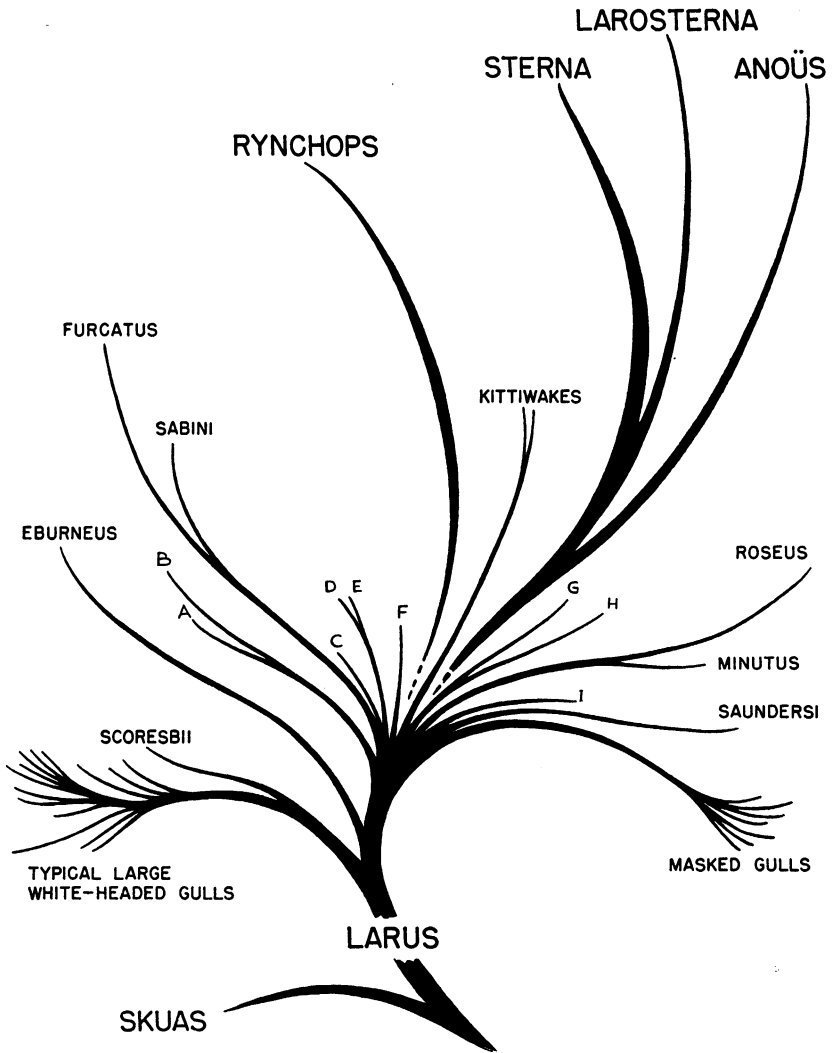


FIG. 5. A rough family tree, or dendrogram, of the Laridae, which attempts to show the interrelationships between the various groups of gulls of the genus *Larus* and the relations between this genus and the other genera of the family. The more "primitive" hooded and white-hooded gulls are indicated as follows: A, *heermanni*; B, *modestus*; C, *fuliginosus*; D, *hemprichi*; E, *leucophthalmus*; F, *atricilla*; G, *ichthyaetus*; H, *pipixcan*; I, *melanocephalus*.

Feeding and nesting habits are always correlated, at least in so far as feeding habits, both the choice of food and the method of getting it, tend to control the choice of possible nest sites, directly or indirectly.

It is also evident that feeding and nesting habits (and their consequences) are correlated with most of the morphological and ethological characters that have been used to diagnose the various groups within the family. The relationships between feeding habits and bill shape and size, relative length of wings, shape of tail, and so on, are obvious, but both feeding and nesting habits may also influence social and display characters in many ways both obvious and subtle. These, in turn, are closely correlated with such characters as plumage pattern and flesh colors. The varied primary patterns of gulls, for instance, probably subserve a species-recognition function, especially in feeding, while the contrasting light and dark areas of the head plumage and conspicuous colors of the bill and eye of most larids play an important role in many social and reproductive activities.

All these characters have evolved together, but they seem to have evolved at rather different rates in many cases. Many species have become very specialized in some ways, while remaining relatively primitive in others. The clearest examples of this in the Laridae are provided by the Gray Gull, with its relatively primitive feeding habits, shape, and display behavior, its rather specialized plumage pattern, and its remarkably specialized nesting habits; and by the Black Skimmer, with its very specialized shape and feeding behavior, moderately specialized plumage, and probably primitive display and nesting habits.

It will be noted that both of these species also illustrate the previously mentioned general rule that display patterns are usually conservative.

CONCLUSION

The apparent course of evolution in the family Laridae as a whole is shown in figure 5. This is an attempt to show both the probable origin of all the major groups and their approximate degree of divergence from one another in the form of a roughly diagrammatic family tree or dendrogram.

SUMMARY

The family Laridae can be divided into two subfamilies, the Stercorariinae and the Larinae. The latter can be divided into three tribes: the Larini, the Rynchopini, and the Sternini. Some of these major divisions can also be split into smaller units as distinctive species or groups of species. This classification can be summarized as follows:

SUBFAMILY STERCORARIINAE

Genus *Stercorarius*, probably including four species (*skua*, *pomarinus*, *parasiticus*, and *longicaudus*)

SUBFAMILY LARINAE

TRIBE LARINI

Genus *Larus*, including approximately 40 species

Group 1: "Primitive" hooded gulls, including *atricilla*, *leucoptthalmus*, *hemprichi*, *fuliginosus*, *pipixcan*, *ichthyaetus*, and *melanocephalus*

Group 2: White-hooded gulls, *modestus* and *heermanni*

Group 3: Kittiwakes, *tridactylus* and *brevirostris*

Group 4: Saunders' Gull, *saundersi*

Group 5: Masked Gulls, including *philadelphia*, *ridibundus*, *serranus*, *genei*, *cirrocephalus*, *novae-hollandiae*, and *bulleri*

Group 6: The Little Gull and (probably) the Rosy Gull, *minutus* and *roseus*

Group 7: Fork-tailed gulls, *furcatus* and (possibly) *sabini*

Group 8: The Ivory Gull, *eburneus*

Group 9: The Dolphin Gull, *scoresbii*

Group 10: Typical large white-headed gulls, including *belcheri*, *crassirostris*, *pacificus*, *audouini*, *delawarensis*, *canus*, and all the species that are very similar to the Herring Gull and the Black-backed Gulls, *californicus*, *argentatus*, *marinus*, *hyperboreus*, and others

TRIBE RHYCHOPINI

Genus *Rynchops*, probably including two or three species (*nigra*, *flavirostris*, and possibly *albicollis*)

TRIBE STERNINI

Genus *Anous*, probably including five species, the noddies

Group 1: Dark noddies, *stolidus* and *tenuirostris*

Group 2: Intermediate noddies, *ceruleus* and *albirostris*

Group 3: The White Noddy, *albus*

Genus *Larosterna* (only one species, *inca*), the Inca Tern

Genus *Sterna* (approximately 30 to 35 species), black-capped terns

Group 1: The Gull-billed Tern, *nilotica*

Group 2: Crested terns, *caspia*, and such forms as *maxima*, *bergii*, *sandwicensis*, *eurygnatha*, *elegans*, *zimmermanni*, and *bengalensis*

Group 3: Typical black-capped terns, including *dougallii* and *sumatrana* (both of which seem to be partly intermediate between the crested terns and the other typical black-capped species), *hirundo*, *hirundinacea*, *vittata*, *virgata*, *paradisaea*, *aleutica*, *striata*, *forsteri*, *trudeaui*, *repressa*, *balaenarum*, *lunata*, *anaethetus*, *fuscata*, *melanogaster*, *aurantia*, and possibly *albistriata*

Group 4: Marsh terns, *hybrida*, *leucoptera*, and *nigra*

Group 5: Little terns, *albifrons* (possibly including *superciliaris*) *lorata*, and *nereis*

Group 6: The Large-billed Tern, *simplex*

The above arrangement has entailed the suppression of many well-known genera, among them the following genera recognized by Peters (1934):

Catharacta (merged with *Stercorarius*)
Gabianus (merged with *Larus*)
Pagophila (merged with *Larus*)
Rhodostethia (merged with *Larus*)
Rissa (merged with *Larus*)
Creagrus (merged with *Larus*)
Xema (merged with *Larus*)
Procelsterna (merged with *Anoüs*)
Gygis (merged with *Anoüs*)
Chlidonias (merged with *Sterna*)
Phaetusa (merged with *Sterna*)
Gelochelidon (merged with *Sterna*)
Hydroprogne (merged with *Sterna*)
Thalasseus (merged with *Sterna*)

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