ONTOGENETIC EVIDENCE FOR RELATIONSHIPS WITHIN THE LARIDAE

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ABSTRACT.—Comparative growth patterns of selected cranial and postcranial skeletal characters are used to test hypotheses of phylogenetic relationships between the major groups within the family Laridae. The development of the bill in skimmers and terns is characterized by highly nonlinear size-dependent allometries in contrast to the relatively constant, linear allometric relationship found in gulls. These comparative ontogenetic trajectories thus support the hypothesis that skimmers and terns are more closely related to one another than either is to the gulls. The linear size-dependent allometry found throughout development in gulls is similar to that found early in the ontogeny of all larids. In contrast, the highly nonlinear allometry which characterizes the later stages of development in terns and skimmers suggests additional complexity in the genetic control of bill development. The more parsimonious phylogenetic hypothesis is that the shape of the bill in gulls and skuas is the more primitive character state. The bill shape in skimmers relative to terns may reflect the heterochronic extension of the ontogenetic trajectory characteristic of the later stages of development in terns. Ontogenetic transformations found among postcranial characters are consistent with the hypothesis of relationships based on bill ontogenies. However, because of similar nonlinear characteristics in both gull and tern growth trajectories, phylogenetic inferences drawn from the relative ontogenies of postcranial dimensions are considered less compelling. *Received 22 January 1993, accepted 27 March 1993.*

A NUMBER of hypotheses of phylogenetic relationships among the major groups of birds comprising the Laridae (skuas, gulls, terns, and skimmers) have been suggested (for historical summary, see Sibley and Ahlquist 1990). These can be summarized in three phylogenetic trees (Fig. 1). The first hypothesis (Fig. 1A), which suggests that the terns and gulls are more closely related than either is to the skuas (Stercorariinae) and skimmers (*Rynchops*), reflects the traditional classification used by Peters (1934) and Wetmore (1960), and is supported by evidence from protein electrophoresis (Hackett 1989) and DNA-DNA hybridization (Sibley and Ahlquist 1990). Behavioral analyses (Moynihan 1959; see also Burger and Gochfeld 1990) support a similar relationship. In contrast, a closer relationship between the skuas and gulls and between the skimmers and terns (Figs. 1B and 1C) has been suggested by comparative parasitology (Timmermann 1957) and an analysis of skeletal morphology (Strauch 1978).

Based on a morphometric analysis of skeletal characters, Schnell (1970b) felt that, phenetically, skimmers showed similarities to terns, with skimmers and terns being differentiated from gulls and skuas primarily by characters of the bill. Here I describe the ontogenetic transformations underlying these bill-shape differences and examine their phylogenetic implications. Gulls and terns also can be differentiated morphometrically by several postcranial characters; consequently, the phylogenetic inferences that can be derived from differences in the underlying postcranial developmental trajectories are explored.

MATERIALS AND METHODS

Specimens in development series.—During the 1988, 1989, and 1990 breeding seasons, 31 Common Tern (*Sterna hirundo*) embryos ranging in age from 10 days of incubation to 22 days (pipping), and 58 young from 1 to 57 days posthatching, were collected or salvaged on Great Gull Island (GGI). The island, which lies at the eastern end of Long Island Sound (72°07′W, 41°12′N), Suffolk Co., New York, is the site of a long-term study of reproductive success in the Common Tern (Hays and Riseborough 1972). Each year a team checks the island daily, numbering new nests and eggs. When chicks hatch they are banded and the nest association recorded. Consequently, the age of chicks later recovered is known to within 24 h.

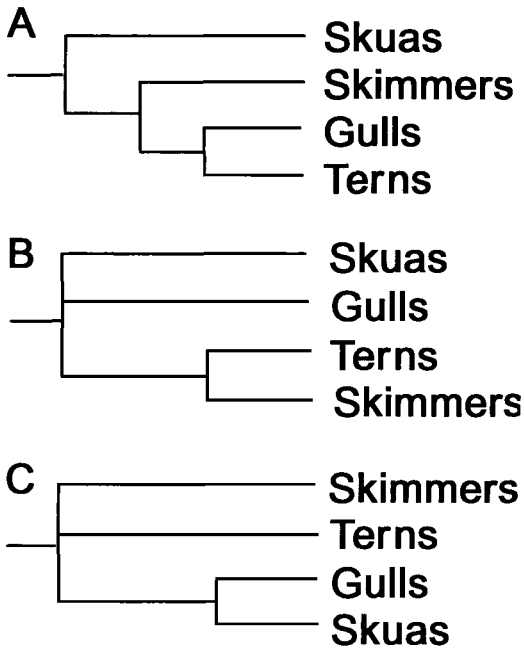For other taxa, developmental specimens consisting of 10 Herring Gull (*Larus argentatus*) and two Great

Fig. 1.   Three cladograms summarizing alternative hypotheses of phylogenetic relationships within the Laridae.
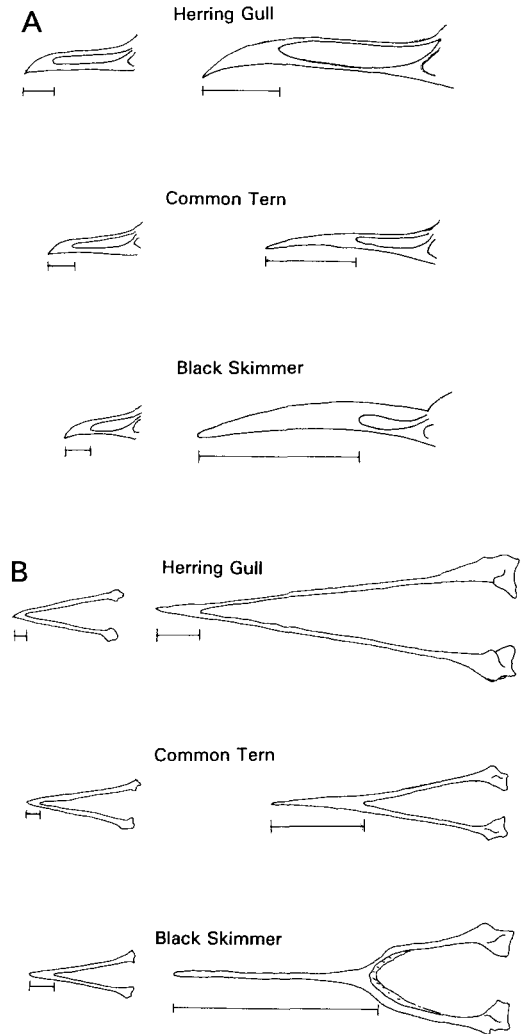

Fig. 2.   Bill measurements used. Bill shapes at about time of hatching shown on left, and adults on right. Drawings are not to scale. (A) Upper bills with bars representing the PRENAR (see Appendix 2). (B) Mandibles with SYMLEN measure indicated.

Black-backed Gull (*Larus marinus*) embryos and young were collected near or on Great Gull Island. The Black Skimmer (*Rynchops niger*) developmental material was obtained from six embryos and juvenile specimens housed in the anatomical collection of the American Museum of Natural History (AMNH).

For freshly collected material, embryos were removed from the egg and, after removal of the extraembryonic membrane, placed immediately into 10% buffered formalin. Larger specimens were injected intraperitoneally with the fixative. After 24 to 48 h (depending on size), embryos were transferred to 70% isopropanol. Posthatching specimens were skinned before being placed in formalin for several days to one week. The few specimens that showed abnormal osteological development (e.g. cranial deformities or abnormal numbers of digits) have been excluded from the analysis.

Specimens were cleared and stained using a modification of the Alcian Blue/Trypsin/Alizarin Red S technique (Wasserzug 1976, Dingerkus and Uhler 1977) in which cartilage is rendered blue and calcified bone red. After staining, specimens were stored in glycerin with thymol crystals added to inhibit contamination.

Adult specimens.—Adult skeletal measurements were obtained from material housed in the anatomical collections of the AMNH, U.S. National Museum, and Carnegie Museum. For taxa other than the Common

Tern, one or two specimens were measured (Appendix 1). The adult Common Tern data represents the averages of 28 male and 38 female specimens.

Measurements.—The bill and postcranial measures used are similar to those described by Schnell (1970a; see my Appendix 2 and Fig. 2). The measurements for the development series encompass both the ossified and cartilaginous portions of all elements. All measurements were made using digital calipers under a binocular 0.7 to 4.2× dissecting microscope equipped with 10× W.F. eyepieces. Smaller embryos were measured using a Bausch and Lomb 7.5× ocular micrometer calibrated with a steel rule.

TABLE 1. Three principal components extracted from covariance matrix of postcranial skeletal characters (see Appendix 2) for adult larids (taxa in Appendix 1).

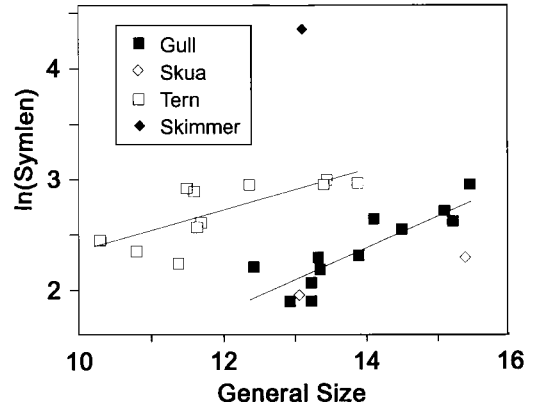| Variable	P1	P2	P3
COR	0.26	0.15	−0.24
SCP	0.24	0.16	−0.30
ILM	0.26	0.21	0.01
ISH	0.28	0.10	0.04
SAC	0.16	0.44	0.05
FEM	0.29	0.09	−0.07
TBT	0.32	−0.17	0.15
TMT	0.36	−0.52	0.58
TOE	0.33	−0.51	−0.67
HUM	0.29	0.07	0.09
RAD	0.28	0.19	0.17
CMC	0.26	0.09	0.04
PRX	0.21	0.29	0.05
Eigenvalue	1.815	0.046	0.018
Percent trace	95.9	2.5	1.0

Fig. 3. Logarithm of length of mandibular symphysis relative to general size (see text) for gulls, skuas, terns, and skimmers. Solid lines are least-squares fits of data for terns and gulls.

Various models for the use of size- or age-dependent allometric transformations in phylogenetic analysis have been proposed (Alberch et al. 1979, Kluge and Strauss 1985, Kluge 1988). Here the analysis focuses on size-dependent static (adult) and ontogenetic allometries of individual elements relative to general growth or size. I have defined the "general size" of an individual specimen to be equal to the sum of the logarithmically transformed values of 13 postcranial measures for that specimen multiplied by 0.277 (the square root of the inverse of the number of variables). The resultant value is then comparable to that which would be derived from principal-components analysis in the case of purely isometric growth. In such analyses, the general size of a specimen is often considered equivalent to the score of the specimen on the first principal component (PC1). In the case of isometric growth, PC1, when standardized to unit length, would have all variable coefficients equal to $p^{(-0.5)}$ where p is the number of variables (see Pimentel 1979:58+). Standarization of the components to unit length has the convenient mathematical property that the angle between vectors can be calculated by simple vector multiplication.

Ontogenetic trajectories of individual elements relative to such a general-size measure would resemble those relative to other size surrogates such as the cube root of body mass. For the adult larids included in my study, the correlation between this general-size vector and body mass (data from Dunning 1992) is 0.994. However, because of the high degree of individual variation in body masses, especially in younger specimens, the use of body mass as a size measure would serve only to obscure relative growth patterns.

Multivariate analyses were carried out using NTSYS version 1.5 (Rohlf 1988). Note that the components shown in Table 1 have been standardized to unit length. Allometric coefficients (b) for the equation $\ln(Y) = a + b \ln(\text{general size})$ were obtained from bootstrap estimates of the reduced major axes fits of the data using a FORTRAN program.

RESULTS

Schnell (1970a) found the primary variables discriminating between terns and gulls to be the length of the os premaxillae rostral to the anterior edge of the nasal opening (PRENAR) and the length of the dentary symphysis of the mandible (SYMLEN; see Appendix 2). The extent to which these measures vary across the Laridae can be seen in Figure 2. Relative to total bill size, these measures in terns and skimmers are quite large, while in gulls and skuas they are relatively small. Figure 3 shows the interspecific allometric relationships between SYMLEN and general size among the Laridae. The adult larid taxa included in this analysis are listed in Appendix 1. Interspecific allometry appears linear for both gulls and terns. Although the skimmer is quite distant from both of these groups, this could represent either a primitive or derived condition, such an array of interspecific allometries in adults thus offering little insight into evolutionary relationships.

The ontogenetic trajectories underlying the differences in PRENAR and SYMLEN across the Laridae are shown in Figure 4. Throughout embryonic and early posthatching development, gulls, terns, and skimmers show a similar size-

Fig. 5. Scores of adult larid taxa on first two components extracted from covariance matrix of logarithmically transformed postcranial characters. PC1 approximates general size (see text). Letters indicate: (L) gull, (C) skua, (K) kittiwake, (S) tern, and (R) skimmer.
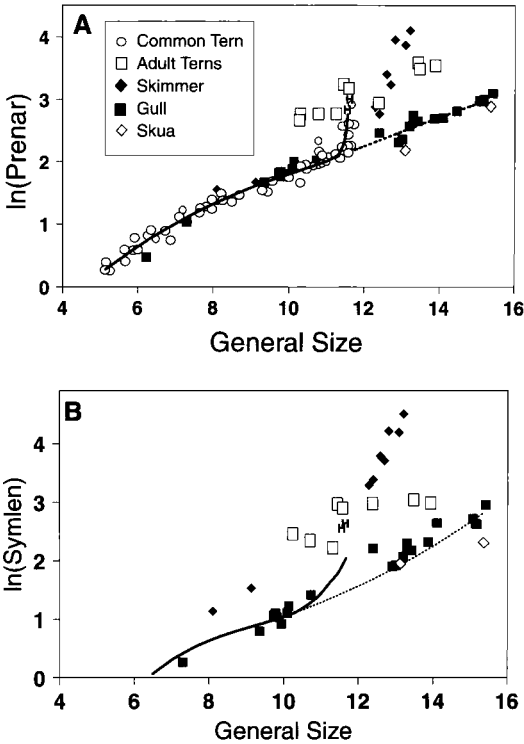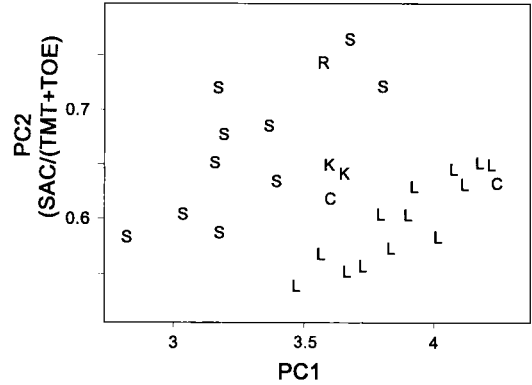
Fig. 4. (A) Developmental trajectories for rostral end of premaxilla (PRENAR) relative to general size. Solid line is approximate polynomial fit of ontogenetic trajectory defined by 89 Common Tern specimens. H represents adult Common Terns. Dashed line is developmental trajectory in Herring Gulls and Great Black-backed Gulls with adults of these species represented at end of gull trajectory. Other adult gulls arrayed along this trajectory. Gulls having a general size less than 12 reflect values for embryos and early posthatching specimens of Herring Gulls and Great Black-backed Gulls. (B) Ontogeny of the mandibular symphysis (SYMLEN) relative to general size. Ontogenetic trajectory for Common Tern represented by solid curve, which reflects polynomial least-squares fit ($r^2 = 0.85$).

dependent allometric growth pattern in the rostral end of the bill. However, in the Common Tern at about three weeks posthatching, although general body growth is essentially complete, bill growth as represented by PRENAR and SYMLEN, continues. Consequently, a marked shift occurs in the allometric growth of PRENAR (Fig. 4A) and SYMLEN (Fig. 4B) relative to body size. A similar shift in developmental allometries is found in the skimmer, although the final development phase in skimmers, especially in SYMLEN, extends be-

yond that in terns, which, if a derived condition (see Discussion), would suggest hypermorphosis (sensu Alberch et al. 1979; Fig. 4). For gulls, no such shift occurs. Rather, throughout posthatching development the growth of the rostral end of the premaxilla (Fig. 4A) and of the dentary symphysis (Fig. 4B) relative to overall growth continues along the same trajectory seen early in development; change in rostral bill form is primarily a change in size that parallels general growth with little or no change in shape.

In skimmers the rostral end of the mandible projects beyond the rostral tip of the premaxilla. The limited data suggest that this, in part, may be due to either relatively rapid growth very early in embryonic development or larger initial mesenchymal condensations in the mandibular anlage. Either would result in the positive displacement in the developmental trajectory of the mandibular symphysis suggested by the current data set (Fig. 4B). If confirmed by further data, such a displacement would seem unique to skimmers and, thus, of little use in the elucidation of phylogenetic affinities.

Comparative postcranial ontogenies.—Discrimination among terns, skimmers, gulls, and skuas also can be achieved using only postcranial skeletal characters. Table 1 shows the results of a principal-components analysis of 13 postcranial skeletal characters for 28 larid taxa (Appendix 2). The first component (PC1) is similar

TABLE 2. Ratio to body mass[a] of three postcranial measures comprising major sources of interspecific variation among larids as indicated by principal-components analysis (see Table 1).

Taxon	No. species measured	Ratio to body mass of		
		SAC	TMT	TOE
Terns	10	2.6	4.4	1.7
Skimmers	1	2.6	5.2	1.3
Gulls	15	2.0	6.5	2.3
Skuas	2	2.4	7.3	2.4

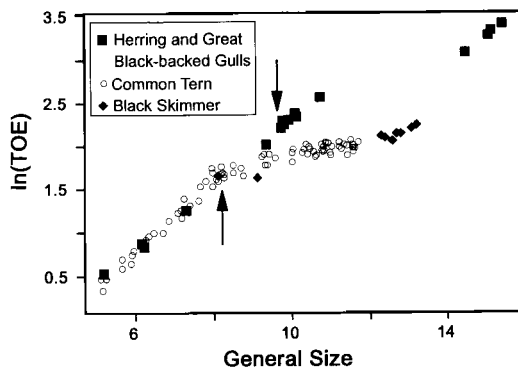[a] Masses from Dunning (1992). Ratios to cube roots of body mass.

Fig. 6. Ontogenetic trajectory for development of TOE. Upward- and downward-facing arrows indicate time of hatching in Common Terns and Herring Gulls, respectively. All trajectories terminate with adult taxa. The four gulls in upper-right corner are two adult Herring Gulls and two adult Great Black-backed Gulls.

to a general-size vector that would have all co-efficients equal to 0.277 (the angle between such a theoretical vector and PC1 is 10.6°). The second component (PC2) contrasts synsacral width (SAC) with distal hindlimb elements (TMT and TOE). Figure 5 shows the score of the individual taxa on these major axes of postcranial variation. I interpret PC2 to reflect the major axis of interspecific postcranial "shape" variation.

In comparison to gulls and skuas (for a given general size), skimmers and terns have a relatively larger ratio of synsacral widths (SAC) to distal hindlimb lengths (see Table 2). This is a consequence of quite different allometric growth patterns in several skeletal elements relative to overall growth. During prehatching development in terns, and apparently also in skimmers, the growth allometry of SAC relative to overall growth appears to be significantly more positive than that in gulls. The prehatching allometric coefficient, b, for the allometric equation

$$\ln(SAC) = a + b \ln(\text{general size})$$

for the Common Tern is

$$b = 0.272 \pm 0.012,$$

$n = 27$, while in the Herring Gull

$$b = 0.216 \pm 0.016,$$

$n = 7$. During posthatching development, gulls, terns and skimmers all appear to exhibit similar allometric growth (Common Tern, $b = 0.217 \pm 0.006$, $n = 58$; Herring Gull, $b = 0.198 \pm 0.050$, $n = 5$). Tarsometatarsal (TMT) growth in terns and skimmers slows during the posthatching period, although some reacceleration is seen in the final stages of growth. A similar TMT developmental trajectory is seen in gulls, although posthatching growth deceleration appears to be somewhat less than in terns and

skimmers (data not shown). The most noticeable difference in postcranial ontogenetic trajectories is found for TOE (Fig. 6). In terns and skimmers, there is an abrupt slowing of growth after hatching. In gulls, a similar but less marked slowing occurs during posthatching development.

DISCUSSION

In the rostral development of the bill, the differences in the ontogenetic trajectories seen for terns and skimmers versus gulls (and apparently skuas; Fig. 4) are not due to a simple size- or age-dependent transposition; rather, there are two fundamentally different growth patterns. One is common throughout development in gulls and skuas, and in early developmental stages in skimmers and terns, while the other is seen only in the late stages of development of skimmers and terns. Similarly, as demonstrated by SAC and TOE (Fig. 6), the ontogenetic trajectories for postcranial growth in terns more closely resemble those found in skimmers rather than the trajectories found in gulls. However, in these postcranial characters there are qualitative similarities in all larid growth trajectories: although SAC developmental allometry is more positive in terns and skimmers during the prehatching period, gulls as well as terns and skimmers exhibit a shift to less positive SAC allometry during posthatching development; the ontogenetic trajectory for

TOE (Fig. 6) seen in terns and skimmers is different from that seen in gulls, but the gulls examined here (as well as terns and skimmers) show a similar slowing of growth in the post-hatching period. The difference is one of degree and perhaps in the timing of this transformation during posthatching development (the limited data here suggest that the transformation to slower TOE growth in gulls takes place somewhat later in the posthatching period).

Although the qualitative similarities in the trajectories for all larid taxa examined here limit the phylogenetic inferences that can be drawn from the postcranial evidence, the relative ontogenies of hindlimb and especially bill characters suggest a phylogenetic hypothesis that reflects a closer relationship between terns and skimmers and between gulls and skuas (Figs. 1B and 1C). Which hypothesis is to be favored depends on decisions regarding character polarity (i.e. whether the condition found in gulls and skuas is more primitive [Fig. 1B], or more derived [Fig. 1C] relative to the condition in the terns and skimmers).

Theoretical arguments for the use of comparative ontogenies in determining character polarity (e.g. see critique in Wheeler 1990) would seem to support the hypothesis that the condition of the bill in gulls and skuas is the phylogenetically more primitive character state (Fig. 1B). Workers (e.g. Hennig 1966, Fink 1982, Patterson 1983) have argued that phylogenetically more primitive character states often precede more derived ones during ontogeny. Others (Patterson 1983, de Queiroz 1984) have noted that ontogenetic transformations themselves are the shared-derived characters sought in phylogenetic analyses. Empirical evidence (e.g. Kraus 1988) generally supports ontogenetic-polarity arguments (but see also Mabee 1989). Such criteria depend on the modification of ontogenies through terminal additions; nonterminal additions (e.g. see Kluge and Strauss 1985, Mabee 1989) and paedomorphosis can confound the use of ontogeny in the determination of character polarity. With this caveat, it can be argued (Crowson 1970, Nelson 1978) that, when immature stages of one taxon (terns and skimmers here) show resemblance to adults of another (gulls, skuas), this is evidence that the first taxon has descended from ancestors resembling the second. The reverse would imply neoteny (or the gain and subsequent loss of a terminal

character state) and, although possible, is less probable on the basis of parsimony (see below).

I argue that evidence for character polarity also can be derived from the relative complexity of the ontogenetic transformations leading to the diversity of larid bill shapes. Consider the relative growth patterns found in two taxa, A and B. Taxon A has highly nonlinear size-dependent allometric growth, while no such shift in relative growth patterns is found in taxon B. The ontogenetic trajectory in A, involving not only simple size changes during development but also age-dependent shape changes, is more complex than the development pattern seen in taxon B (most likely reflecting greater complexity in genetic control of development). This greater developmental complexity would suggest a more derived state. Such an interpretation would be further supported if, along with having less complexity, the allometric growth pattern present throughout development in taxon B is the same as that occurring at an earlier stage of development of A. This common ontogenetic allometry would be assumed to be the more primitive or ancestral growth trajectory.

The marked shifts in relative growth of the bill seen late in development in the skimmers and terns would suggest the existence in these taxa of more localized controls (here resulting in age-dependent shape changes) added to a basic larid development pattern. In contrast, the relative simplicity of size-dependent allometry in gulls, as well as its occurrence in the early stages of development in all larids, suggests that the bill shape and underlying ontogenetic trajectory found in gulls (as well as in skuas) is the more primitive condition, thus favoring the hypothesis reflected in Figure 1B. To argue the reverse (i.e. that the common ancestor of larids had a bill ontogeny similar to that of skimmers and terns; Fig. 1C) would imply neoteny in gulls, or the gain and subsequent loss of complexity in relative growth patterns, which would be less parsimonious. Such a hypothesis would require the introduction of an extra step in the evolution of the group: first the evolution of the tern/skimmer bill ontogenetic trajectory from an ancestor that had only the prehatching developmental pattern; and then the loss of the tern/skimmer posthatching growth pattern in gulls and skuas.

For postcranial characters, while there are differences in size-dependent growth trajectories

that suggest affinities between terns and skimmers relative to gulls (and skuas), qualitatively the shapes of the trajectories underlying postcranial differentiation are similar across the larids examined. Consequently, while the greater degree of nonlinearity in the ontogenetic trajectories in terns and skimmers for characters such as SAC or TOE may indicate a more derived condition, polarity arguments based on the relative complexity of postcranial developmental trajectories must be considered more equivocal.

Although Zusi (1962) felt his osteological and myological data were inconclusive, he tentatively suggested that the skimmers are a highly specialized offshoot of the terns. The ontogenetic evidence presented here would support such a hypothesis. The relatively less complex ontogenetic trajectories for the bill suggest that skuas and gulls lie closer to the ancestral root of the Laridae. These characteristics of bill ontogeny, as well as the differing patterns of development in distal hindlimb elements, indicate that terns and skimmers are more closely related to each other than either is to the gulls or skuas, with skimmers being the more highly derived taxon.

ACKNOWLEDGMENTS

LITERATURE CITED

ALBERCH, P. S., S. J. GOULD, G. F. OSTER, AND D. B. WAKE. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296–317.

BAUMEL, J. J., A. S. KING, A. M. LUCAS, J. E. BREAZILE, AND H. E. EVANS (Eds.). 1979. Nomina Anatomica Avium. Academic Press, London.

BURGER, J., AND M. GOCHFELD. 1990. The Black Skimmer. Social dynamics of a colonial species. Columbia Univ. Press, New York.

CROWSON, R. A. 1970. Classification and biology. Atherton Press, New York.

DE QUEIROZ, K. 1984. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. Syst. Zool. 34:280–299.

DINGERKUS, G., AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol. 52:229–232.

DUNNING, J. B., JR. 1992. CRC handbook of avian body masses. CRC Press, Boca Raton, Florida.

FINK, W. L. 1982. The conceptual relationship between ontogeny and phylogeny. Paleobiology 8:254–264.

HACKETT, S. J. 1989. Effects of varied electrophoretic conditions on detection of evolutionary patterns in the Laridae. Condor 92:73–90.

HAYS, H., AND R. W. RISEBOROUGH. 1972. Pollutant concentrations in abnormal young terns from Long Island Sound. Auk 89:19–35.

HENNIG, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana.

KLUGE, A. G. 1988. The characterization of ontogeny. Pages 57–81 *in* Ontogeny and systematics (C. J. Humphries, Ed.). Columbia Univ. Press, New York.

KLUGE, A. G., AND R. E. STRAUSS. 1985. Ontogeny and systematics. Annu. Rev. Ecol. Syst. 16:247–268.

KRAUS, F. 1988. An empirical evaluation of the use of the ontogeny polarization criterion in phylogenetic inference. Syst. Zool. 37:106–141.

MABEE, P. 1989. An empirical rejection of the ontogenetic polarization criterion in phylogenetic inference. Cladistics 5:409–416.

MOYNIHAN, M. 1959. A revision of the family Laridae (Aves). Am. Mus. Novit. 1928.

NELSON, G. 1978. Ontogeny, phylogeny, paleontology and the biogenetic law. Syst. Zool. 27:324–345.

PATTERSON, C. 1983. How does phylogeny differ from ontogeny? Pages 1–31 *in* Development and evolution (B. C. Goodwin, N. Holder, and C. C. Wylie, Eds.). Cambridge Univ. Press, Cambridge.

PETERS, J. L. 1934. Check-list of birds of the world, vol. 2. Harvard Univ. Press, Cambridge, Massachusetts.

PIMENTEL, R. A. 1979. Morphometrics. Kendall/Hunt, Dubuque, Iowa.

ROHLF, F. J. 1988. NTSYS-PC, Numerical taxonomy and multivariate analysis system, version 1.5. Exeter Publishing, Setauket, New York.

SCHNELL, G. D. 1970a. A phenetic study of the suborder Lari (Aves). I. Methods and results of principal components analyses. Syst. Zool. 19:35–57.

SCHNELL, G. D. 1970b. A phenetic study of the suborder Lari (Aves). II. Phenograms, discussion, and conclusions. Syst. Zool. 19:264–302.

SIBLEY, C. G., AND J. E. AHLQUIST. 1990. Phylogeny and classification of birds. Yale Univ. Press, New Haven, Connecticut.

STRAUCH, J. G., JR. 1978. The phylogeny of the Charadriiformes (Aves): A new estimate using the method of character compatibility analysis. Trans. Zool. Soc. Lond. 34:263–345.

TIMMERMANN, G. 1957. Studien zu einer vergleichenden Parasitologie der Charadriiformes oder Regenpfeifervögel. Tiel I: Mallophaga. Parasitologische Schriftenreihe. Heft. 8. Gustav Fischer, Jena.

WASSERZUG, R. J. 1976. A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. Stain Technol. 51:131–134.

WETMORE, A. 1960. A classification for the birds of the world. Smithson. Misc. Coll. 139(11):1–37.

WHEELER, Q. D. 1990. Ontogeny and character phylogeny. Cladistics 6:225–268.

ZUSI, R. L. 1962. Structural adaptations of the head and neck in the Black Skimmer. Publ. Nuttall Ornithol. Club no. 9.

APPENDIX 1

Adult taxa (and number measured) used in analysis of interspecific bill allometries and principal-components analysis of postcranial characters. When both sexes measured, averages of pooled male and female measurements used in analyses.

Skuas: *Catharacta skua* (1), *Stercorarius longicaudus* (1). **Gulls:** *Larus heermanni* (1), *L. delawarensis* (2), *L. canus* (2), *L. argentatus* (2), *L. fuscus* (1), *L. californicus* (2), *L. occidentalis* (1), *L. marinus* (2), *L. glaucescens* (2), *L. hyperboreus* (1), *L. atricilla* (2), *L. pipixcan* (1), *L. philadelphia* (1), *Rissa tridactyla* (2), *R. brevirostris* (2). **Terns:** *Chlidonias niger* (2), *Gelochelidon nilotica* (1), *Sterna caspia* (1), *S. hirundo* (66), *S. dougallii* (2), *S. albifrons* (2), *S. maxima* (2), *Larosterna inca* (1), *Anous minutus* (1), *Gygis alba* (1). **Skimmers:** *Rynchops niger* (3).

APPENDIX 2

Description of measurements used. Terminology follows Baumel et al. (1979); see also Schnell (1970a).

Cranial measures

PRENAR. Rostrocaudal length from anterior end of nasal opening to rostral tip of os premaxillare (Schnell's SK2). **SYMLEN.** Rostrocaudal length of symphysis mandibularis (Schnell's SK13).

Postcranial measures

COR. Length of coracoideum from most distal edge of Processus acrocoracoideus to ventral edge of processus lateralis. **SCP.** Maximum length of scapula from cranial edge of acromion to extremitas caudalis. **ILM.** Length of ilium from cranial end to midpoint of margo caudalis. **ISH.** Length of ishium from caudal edge of foramen acetabuli to caudal end of processus terminalis ischii. **SAC.** Transversely, maximum width of synsacrum between medial margins of alae ilii. **FEM.** Maximum length of femur from proximal edge of crista trochanteris to distal edge of condylus lateralis. **TBT.** Maximum length of tibotarsus from proximal edge of crista cnemialis lateralis to distal end of epicondylus lateralis. **TMT.** Maximum length of tarsometatarsus from proximal surface to distal end of trochlea metatarsi tertii. **TOE.** length of phalanx proximalis of digitus tertius of pedis. **HUM.** Maximum length of humerus from proximal surface of caput humeri to distal edge of condylus ventralis. **RAD.** Maximum length of radius from proximal surface of caput radii to distal surface of facies articularis radiocarpalis. **CMC.** Length of carpometacarpus between proximal edge of Trochlea carpalis and Facies articularis digitalis major. **PRX.** Length of phalanx proximalis digiti majoris from proximal surface of facies articularis metacarpalis to Facies articularis phalangealis.