

The Late Pleistocene Avifauna of La Carolina, Southwestern Ecuador

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ABSTRACT

A collection of fossils from the late Pleistocene site known as La Carolina, located on the arid Santa Elena Peninsula of southwestern Ecuador, contains 53 species of birds, representing 16 families and 42 genera, including 7 extinct species previously recorded only from the Talara Tar Seeps of northwestern Peru. New species of *Buteo* and *Oreopholus* are described. The genus *Protoconurus* Spillman is synonymized with *Aratinga*.

Seventy-two percent of the species recorded from La Carolina were also recorded from the Talara Tar Seeps. The resemblance between the two avifaunas suggests a similarity in age, habitat, and climatological conditions at the two sites at the time of deposition. Evidence suggests that during glacial periods the currently arid Santa Elena Peninsula was part of a broad, forested coastal savanna extending from central Ecuador south to northern Peru.

Introduction

While on a visit to Quito, Ecuador, in early 1970, in connection with my research on the late Pleistocene avifauna of the Talara Tar Seeps of northwestern Peru (Campbell, in press), I had the pleasure of meeting and talking with Professor Gustav Orcés V. of the Escuela Politécnica Nacional. During the course of our conversations I learned that he had in storage at the Escuela a collection of fossil birds from a site known as La Carolina, located on the Santa Elena Peninsula. The collection

was made by Dr. Robert Hoffstetter in the course of his work on the Pleistocene mammals of Ecuador (Hoffstetter, 1952). I was most graciously granted permission to take the fossil birds back to the University of Florida where I could work on them in conjunction with the Talara avifauna.

The La Carolina site is located on the north side of the Santa Elena Peninsula near the town of La Libertad (Figure 1). Hoffstetter (1952) and Edmund (1965) have described the location and geological history of this and other nearby sites. Spillman (1942) also contributed to our knowledge of the paleontology and geological history of the Santa Elena Peninsula, including descriptions of what he regarded as two extinct genera and species of birds.

I have not visited the site personally and must therefore refer the reader to the description published by Hoffstetter (1952). The fossil beds consist of fine-grained aeolian and fluvial sands that were deposited in a broad, shallow estuarine environment. Certain zones of the deposit are impregnated with pitch and some evidence suggests that this occurred subsequent to the deposition of the sands (Edmund, 1965). Preservation of the fossil material is generally excellent, indicating rapid burial with little disturbance. In addition to the specimens recorded below, there are a large number of small, delicate specimens of various species of Passeriformes that are not sufficiently prepared to include in this report.

Species distributions were taken from Chapman (1926), Marchant (1958), and Meyer de Schauensee (1966). For osteological characters of the various species the reader is referred to a pending paper on the paleoavifauna of the Talara Tar Seeps (Campbell, in press). The La Carolina specimens

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are currently uncataloged and will be returned to Professor Orcés in the near future.

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ARDEIDAE

Nycticorax nycticorax (Linnaeus)

MATERIAL.—One complete right coracoid, humeral end of 1 left coracoid, 1 complete left carpometacarpus, proximal ends of 1 right and 1 left femur.

REMARKS.—*N. nycticorax* is resident in Ecuador.

ANATIDAE

Dendrocygna autumnalis (Linnaeus)

MATERIAL.—One left scapula, 1 complete right coracoid, proximal end of 1 right ulna, distal end of 1 left tibiotarsus.

REMARKS.—*D. autumnalis* is resident in Ecuador.

Anatidae genus and species

MATERIAL.—Two complete right and 2 complete left coracoids, humeral end of 1 right coracoid, 1 complete left ulna, 1 complete left radius, 1 complete right carpometacarpus, proximal ends of 1 right and 1 left carpometacarpus.

REMARKS.—This new genus and species of Anatidae is being described as a form of Tadorninae



FIGURE 1.—Location of the La Carolina fossil site, southwestern Ecuador, relative to the Talará Tar Seeps of northwestern Peru. The dotted line marks the approximate eastward limit of the arid zone of the Santa Elena Peninsula.

from the Talará Tar Seeps of northwestern Peru (Campbell, in press). The presence of this and the other extinct species listed below indicate that paleoclimatic conditions at La Carolina were similar to those at the Talará Tar Seeps, much as similar conditions exist at the two sites today.

Anas species 1

MATERIAL.—One complete right coracoid, proximal end of 1 right radius, distal end of 1 right tibiotarsus, 1 complete left tarsometatarsus.

REMARKS.—The proximal end of the radius is not included in the description of *Anas* species 1, from the Talará Tar Seeps (Campbell, in press). The present specimen is referred to this species on the basis of size (proximal width, 4.4 mm), and because it differs from the radius being referred to *Anas* species 2 (Campbell, in press) by having: (1) ligamental prominence high, (2) ulnar depression deep, (3) scapholunar facet broad and flat.

Anas species 3

MATERIAL.—One left scapula, 1 complete left humerus (holotype), 2 complete left carpometacarpi.

REMARKS.—The complete humerus from La Carolina is being used as the holotype in the description of *Anas* species 3 (Campbell, in press), because it is in better condition than any of the material from the Talara Tar Seeps. Elements of this species not found in the Talara Tar Seeps include the scapula and carpometacarpus. The small size of these specimens indicates that they may be safely referred to *Anas* species 3. In addition to its small size, the scapula is characterized by having: (1) acromion of moderate length and width, with anteroventral corner a prominent projection; (3) attachment of Lig. furculoscapulare dorsale oval in shape, located on midline of shaft. Measurements of the scapula are: proximal height, 7.7 mm; proximal width, 2.4 mm.

The carpometacarpus is characterized by having: (1) process of metacarpal I moderately high and long; (2) proximal edge of metacarpal I sloping slightly proximad; (3) proximal metacarpal symphysis of moderate length, distal symphysis long; (4) internal face of external rim of carpal trochlea angular proximally; (6) area covered by external cuneiform ligament moderately convex; (7) posterior carpal fossa of moderate width for its length; (8) surface of carpal trochlea extending deep into posterior carpal fossa; (9) internal rim of carpal trochlea with posterior edge bowing externally. Measurements (in mm) of the two carpometacarpi are as follows: length, 35.0 and 35.2; height through metacarpal I, 8.1 and broken; proximal width, 3.9 and 3.9; least width of shaft, 2.5 and 2.7; length of distal fornix, 5.0 and 4.9.

The numbered characters listed above correspond to those being used in the descriptions of *Anas* species 1, and *Anas* species 2 (Campbell, in press). The absence of *Anas* species 2, from La Carolina may be a result of the small sample size, although it was more common at the Talara Tar Seeps than *Anas* species 3.

Anas bahamensis Linnaeus

MATERIAL.—Portions of 12 crania, 9 right and 4 left scapulae, 23 complete right and 27 complete left coracoids, humeral ends of 5 right and 7 left coracoids, 4 complete right and 2 complete left humeri, proximal ends of 1 right and 2 left humeri, distal ends of 1 right and 4 left humeri, 16 complete right and 18 complete left ulnae, proximal

ends of 3 right and 3 left ulnae, distal ends of 2 right and 3 left ulnae, 11 complete right and 3 complete left radii, proximal ends of 7 right and 4 left radii, distal ends of 3 right and 5 left radii, 28 complete right and 34 complete left carpometacarpi, proximal ends of 3 left carpometacarpi, 5 complete right and 8 complete left femora, proximal ends of 2 left femora, distal ends of 3 left femora, 3 complete right and 1 complete left tibiotarsus, 1 almost complete right and 1 almost complete left tibiotarsus, proximal ends of 1 right and 1 left tibiotarsus, distal ends of 4 right and 3 left tibiotarsi, 19 complete right and 24 complete left tarsometatarsi, proximal ends of 2 right and 4 left tarsometatarsi.

REMARKS.—In terms of numbers of specimens and of individuals, *A. bahamensis* is the second most abundant species in the La Carolina deposits. This species is currently found in large numbers in southwestern Ecuador when standing bodies of fresh water occur (Marchant, 1958).

I am elsewhere (Campbell, in press) expressing my belief that it was material of this species that Spillman (1942) named *Archeoquerquedula lambrechtii*. The absence of any large, extinct duck from the La Carolina deposits upholds the view that *Archeoquerquedula lambrechtii* should be synonymized with *Anas bahamensis*.

VULTURIDAE

Vulturidae genus and species indeterminate

MATERIAL.—Proximal end of 1 right tarsometatarsus.

REMARKS.—This specimen is too broken to be identified further. It represents a condor the size of a large individual of *Vultur gryphus* Linnaeus. The intercotylar prominence is very broad and low, unlike that found in either *Vultur* Linnaeus, *Gymnogyps* Lesson, or the new genus of condor being described from the Talara Tar Seeps (Campbell, in press). I am convinced the specimen represents a new genus and species, but consider the specimen too fragmentary to describe.

Coragyps cf. *atratus* (Bechstein)

MATERIAL.—Distal ends of 1 right and 1 left carpometacarpus.

REMARKS.—These specimens resemble those from the Talara Tar Seeps in differing slightly from the subspecies of *C. atratus* currently resident in southwestern Ecuador and northwestern Peru.

Cathartes aura (Linnaeus)

MATERIAL.—One right scapula, proximal end of 1 left radius, 1 complete left tarsometatarsus, distal ends of 2 left tarsometatarsi.

REMARKS.—*C. aura* is resident in southwestern Ecuador.

ACCIPITRIDAE

Accipitridae genus and species

MATERIAL.—Proximal end of 1 left femur.

REMARKS.—This extinct new genus and species of large eagle is being described from the Talara Tar Seeps (Campbell, in press). Hoffstetter (1952: 40) mentioned an enormous eagle from La Carolina. The specimens he was referring to probably belong to this species.

Geranoaetus melanoleucus (Vieillot)

MATERIAL.—Proximal end of 1 right carpometacarpus, distal end of 1 left tibiotarsus.

REMARKS.—*G. melanoleucus* is resident in western Ecuador today.

Buteo polyosoma (Quoy and Gaimard)

MATERIAL.—Proximal ends of 1 right and 1 left humerus, proximal end of 1 right radius, 1 complete left carpometacarpus, distal end of 1 right tibiotarsus, 2 complete left tarsometatarsi.

REMARKS.—*B. polyosoma* is a common resident in southwestern Ecuador.

Buteo hoffstetteri, new species

FIGURE 2

HOLOTYPE.—Right tarsometatarsus lacking medial portion of proximal end. Uncataloged.

PARATYPE.—Almost complete left tarsometatarsus.

DIAGNOSIS.—Tarsometatarsus agrees with that of

Buteo Lacépède and differs from that of all other South American genera of Accipitridae by having those characters of the genus *Buteo* as listed by Campbell (in press).

Tarsometatarsus characterized by having: (1) internal cotyla very concave (moderately concave in *B. lineatus*, very concave in *B. polyosoma*); (2) anterior metatarsal groove very deep immediately distal to intercotylar prominence and distal to tubercle for tibialis anticus (moderately deep in both areas in *B. lineatus* and *B. polyosoma*); (3) shaft narrow abruptly distal to tubercle for tibialis anticus (narrows gradually in *B. lineatus*, abruptly in *B. polyosoma*); (4) shaft with posterior metatarsal groove moderately deep (very deep in *B. lineatus*, moderately deep in *B. polyosoma*); (5) intertrochlear notches wide (narrow in *B. lineatus* and *B. polyosoma*); (6) internal trochlea with very prominent angular proximolateral projection (not as prominent in *B. lineatus*, very prominent in *B. polyosoma*); (7) external trochlea narrow, short, and projecting posterodistad at approximately 45° to axis of shaft (wide, long, and at approximately 85° to axis of shaft in *B. lineatus* and *B. polyosoma*); (8) shaft very slender (similar in *B. lineatus*, wider in *B. polyosoma*).

Measurements (in mm) of the holotype and paratype (in parentheses) are as follows: length, 74.6 (76.3); proximal width, broken (11.1 ± 1.0); distal width, 10.7 (12.2 ± 0.5); least width of shaft, 4.0 (4.2).

REFERRED MATERIAL.—Distal end of 1 left and 1 right tibiotarsus.

CHARACTERS.—Tibiotarsus characterized by having: (1) shaft only slightly concave at postero-proximal end of internal condyle (moderately to deeply concave in *B. lineatus* and *B. polyosoma*); (2) internal condyle short (long in *B. lineatus*, of moderate length in *B. polyosoma*); (3) external condyle merging gradually with shaft antero-proximally, not forming a lip (merges abruptly, forming a lip in *B. lineatus* and *B. polyosoma*). The only measurement that can be taken is the distal width (10.6 mm) of one specimen.

ETYMOLOGY.—This species is named for Dr. Robert Hoffstetter of the Muséum National d'Histoire Naturelle, Paris, France, in recognition of his paleontological work in Ecuador and his role in the preservation of the La Carolina fossils.

REMARKS.—Although *Buteo lineatus* does not oc-



FIGURE 2.—Holotype right tarsometatarsus of *Buteo hoffstetteri*, new species (uncataloged), in anterior, external, and posterior view, $\times 1$.

cur in South America, it was used in the diagnosis because its tarsometatarsus resembles that of *B. hoffstetteri* in being long and slender rather than short and stout. While the tarsometatarsus of *B. polyosoma* is the same length as that of *B. lineatus*, it is much more robust. In all other species of *Buteo* with tarsometatarsi of similar length, the bone is even more robust than in *B. polyosoma* and these species must therefore also differ from *B. hoffstetteri*.

Circus cinereus Vieillot

MATERIAL.—Proximal end of 1 left carpometacarpus, 1 complete right femur, distal end of 1 left tibiotarsus.

REMARKS.—*C. cinereus* is resident in western Ecuador, but has not been recorded from the Santa Elena Peninsula.

FALCONIDAE

Falco peregrinus Tunstall

MATERIAL.—Two left scapulae, sternal end of 1 right coracoid, proximal end of 2 left humeri, distal end of 1 right humerus, 1 complete left ulna,

proximal end of 1 right ulna, distal ends of 2 left ulnae, proximal end of 1 right radius, 2 complete right carpometacarpi, proximal ends of 1 right and 1 left carpometacarpus, distal end of 1 right carpometacarpus, 1 complete left femur, distal end of 1 right tibiotarsus, 1 complete right tarsometatarsus, proximal ends of 2 left tarsometatarsi.

REMARKS.—*F. peregrinus* occurs in Ecuador both as a northern and a southern migrant.

Falco femoralis Temminck

MATERIAL.—One complete left coracoid, proximal end of 1 left tibiotarsus.

REMARKS.—*F. femoralis* is resident in western Ecuador.

Polyborus plancus (Miller)

MATERIAL.—Five right and 4 left scapulae, 2 complete right and 2 complete left coracoids, humeral ends of 4 right and 1 left coracoid, proximal ends of 3 right and 1 left humerus, distal ends of 1 right and 1 left humerus, 1 complete right ulna, proximal ends of 2 left ulnae, distal ends of 3 right and 2 left ulnae, 1 complete right and 3 complete left carpometacarpi, proximal ends of 2 left carpometacarpi, proximal ends of 2 left femora, distal end of 1 right femur, distal ends of 2 right and 1 left tibiotarsus, proximal end of 1 left tarsometatarsus, distal ends of 3 right and 4 left tarsometatarsi.

REMARKS.—These specimens differ from the subspecies presently found in southwestern Ecuador and northwestern Peru in the same way as do the specimens from the Talara Tar Seeps. The complete right carpometacarpus is considerably lighter in build than the rest of the carpometacarpi from this site as well as those from the Talara Tar Seeps and is perhaps sufficiently different to warrant consideration as a distinct species. However, the great variation found in *Polyborus* makes it unwise to describe a new species without a larger sample. *P. plancus* is common in southwestern Ecuador.

Milvago species

MATERIAL.—Two left scapulae, 1 complete left carpometacarpus.

REMARKS.—This species is being described from

the Talara Tar Seeps (Campbell, in press). No species of *Milvago* presently occurs west of the Andes Mountains in Peru or Ecuador.

CHARADRIIDAE

Pluvialis dominica (Statius Müller)

MATERIAL.—One complete right and 3 complete left coracoids, 8 complete right and 4 complete left humeri, distal ends of 1 right and 2 left humeri, 5 complete right and 5 complete left carpometacarpi, 2 complete left femora, proximal ends of 2 right tibiotarsi, distal ends of 3 right and 1 left tibiotarsus, 1 complete right and 5 complete left tarsometatarsi, proximal ends of 1 right and 1 left tarsometatarsus, distal ends of 2 right tarsometatarsi.

REMARKS.—As North American migrants, *P. dominica* and the following 3 species of plovers occur as seasonal visitors or residents along the coast of Ecuador.

Pluvialis squatarola (Linnaeus)

MATERIAL.—Proximal end of 1 right humerus.

Charadrius vociferus Linnaeus

MATERIAL.—Proximal end of 1 left tibiotarsus.

Charadrius semipalmatus Bonaparte

MATERIAL.—One complete left humerus, distal end of 1 left tibiotarsus.

Oreopholus orcesi, new species

FIGURE 3

HOLOTYPE.—Complete left femur. Uncataloged.

DIAGNOSIS.—Femur agrees with that of *Oreopholus* and differs from that of all other genera of South American plovers (with possible exception of *Zonibyx* Reichenbach, *Pluvianellus* Gray, and *Phegornis* Gray, which were not available for comparison) by having: (1) head disc-shaped, projecting mediad, perpendicular to shaft, without protruding dorsad above level of flat iliac facet; (2)

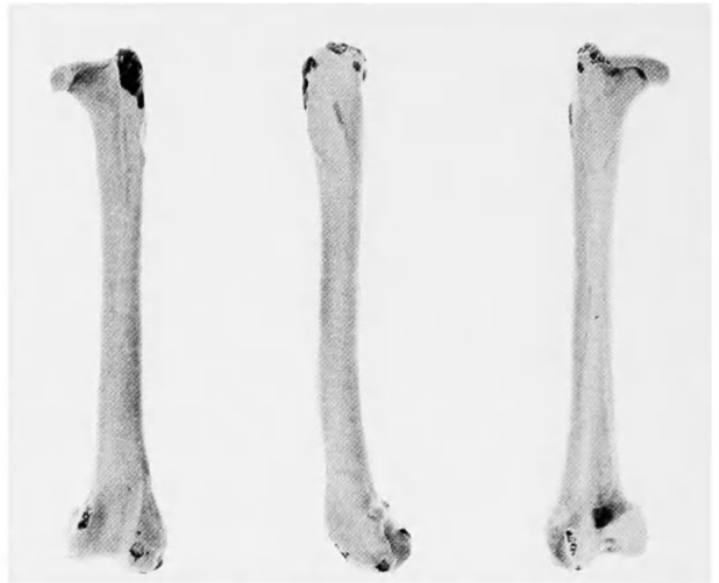


FIGURE 3.—Holotype left femur of *Oreopholus orcesi*, new species (uncataloged), in anterior, external, and posterior views, $\times 2$.

attachment of *M. flexor ischiofemorialis* elevated along anterior edge; (3) shaft with proximal two-thirds straight, and marked anteroposterior flexure in distal third, in lateral view; (4) shaft with distal end turned sharply mediad posterior to anteroproximal termination of internal condyle, in anterior view; (5) internal condyle with posteroproximal corner projecting proximad more than external condyle; (6) shaft very wide immediately proximal to condyles.

Femur differs from that of *Oreopholus ruficollis* (Wagler) by having: (1) head much smaller; (2) attachment of *M. iliacus* marked by sharp, high ridge along corner of shaft (ridge absent and attachment much larger in area in *O. ruficollis*); (3) shaft with greater anteroposterior flexure; (4) shaft with marked concavity at point of flexure medial to internal condyle, resulting in internal condyle terminating proximally in high, narrow ridge (not as excavated in *O. ruficollis*, but with internal condyle more rounded); (5) internal condyle deeper anteroposteriad, with posterior articular surface flat (convexity present on surface in *O. ruficollis*); (6) external condyle projecting less proximad, and at a greater angle to axis of shaft, in posterior view; (7) attachment of *M. gastrocnemius*, pars externa, smaller in area, more elevated, and positioned more posteriad; (8) rotular groove narrower and deeper.

Measurements (in mm) of the holotype, with

those of one specimen of *O. ruficollis* (in parentheses), are as follows: length from external condyle to iliac facet, 29.7 (30.0); width of proximal end, 5.9 (6.2); width of distal end, 6.0 (6.1); least width of shaft, 2.5 (2.4).

ETYMOLOGY.—This species is named for Professor Gustav Orcés V., of the Escuela Politécnica Nacional, Quito, Ecuador, for his pioneering work in the natural history of Ecuador.

REMARKS.—Although only one specimen of *O. ruficollis* was available for comparison, the majority of the characters cited above are considered unlikely to vary with a larger sample. The species of *Zonibyx*, *Pluvianellus*, and *Phegornis* are all much smaller than *O. orcesi*. In the event that the species described here does not belong in *Oreopholus*, but in one of the three genera listed above, it would still represent a new species, if based solely on size.

SCOLOPACIDAE

Tringa solitaria Wilson

MATERIAL.—Proximal end of 1 left tibiotarsus, proximal end of 1 left tarsometatarsus, distal end of 1 left tarsometatarsus.

REMARKS.—As North American migrants, *T. solitaria* and the following 12 species of the family Scolopacidae occur as seasonal visitors or residents along the coast of Ecuador.

Totanus flavipes (Gmelin)

MATERIAL.—One complete right coracoid, 1 complete right and 2 complete left humeri, 1 complete right and 1 complete left carpometacarpus, shaft and proximal end of 1 right femur, distal ends of 3 right and 1 left tarsometatarsus.

REMARKS.—I consider the osteological differences between *Tringa* and *Totanus* as sufficient to separate them at the generic level.

Totanus melanoleucus (Gmelin)

MATERIAL.—Humeral end of 1 right coracoid, 1 complete left humerus, proximal end of 1 right humerus, distal end of 1 left humerus, 1 complete left carpometacarpus.

Catoptrophorus semipalmatus (Gmelin)

MATERIAL.—Distal ends of 2 right and 1 left humerus, 3 complete right and 3 complete left carpometacarpi, proximal end of 1 left carpometacarpus, shaft and proximal end of 1 right femur, distal end of 1 right tibiotarsus, proximal end of 1 right tarsometatarsus.

Calidris canutus (Linnaeus)

MATERIAL.—One complete left coracoid, 6 complete right and 6 complete left humeri, 5 almost complete right and 5 almost complete left humeri, proximal ends of 2 right and 3 left humeri, distal ends of 4 right and 5 left humeri, 5 complete right and 3 complete left carpometacarpi, proximal ends of 2 right carpometacarpi, distal ends of 7 right and 3 left tibiotarsi.

Erolia melanotos (Vieillot)

MATERIAL.—Three complete right and 8 complete left humeri, 1 almost complete right humerus, proximal ends of 1 right and 1 left humerus, distal end of 1 left humerus, 1 complete right and 2 complete left carpometacarpi, 1 complete right femur, distal end of 1 left femur, distal end of 1 right tibiotarsus, 1 complete left tarsometatarsus.

REMARKS.—I consider the osteological differences between *Calidris*, *Erolia*, and *Ereunetes* as sufficient to separate them as three distinct genera.

Ereunetes pusillus (Linnaeus)

MATERIAL.—One complete right and 1 complete left humerus, distal end of 1 right humerus.

Ereunetes mauri (Cabanis)

MATERIAL.—Two complete right and 4 complete left humeri, distal ends of 1 right and 3 left humeri.

Micropalama himantopus (Bonaparte)

MATERIAL.—One complete right femur.

Bartramia longicauda (Bechstein)

MATERIAL.—One complete right humerus, distal

end of 1 right humerus, 1 complete right and 1 complete left carpometacarpus, distal ends of 2 left tibiotarsi, proximal end of 1 left tarsometatarsus, distal end of 1 left tarsometatarsus.

***Numenius phaeopus* (Linnaeus)**

MATERIAL.—Two complete left coracoids, 1 complete right carpometacarpus, distal end of 1 left tibiotarsus.

***Limosa fedoa* (Linnaeus)**

MATERIAL.—One complete right and 1 fragmentary left carpometacarpus.

***Arenaria interpres* (Linnaeus)**

MATERIAL.—Two complete left and 1 complete right coracoid, humeral end of 1 right coracoid, proximal end of 1 left carpometacarpus, 1 complete left femur, 1 complete left tarsometatarsus.

Scolopacidae genus and species

MATERIAL.—One complete left coracoid, 1 complete right femur.

REMARKS.—A new genus and species of Scolopacidae is being described from the Talara Tar Seeps (Campbell, in press) on the basis of a coracoid and a tarsometatarsus. The coracoid from La Carolina agrees in all characters with the holotype coracoid, differing only in being more robust. Measurements (in mm) of the La Carolina coracoid are as follows: length, 17.3; head to scapular facet, 6.7; depth of proximal end, 4.9; least width of shaft, 2.4; length of sternal facet, 5.8.

The above femur agrees with the other elements assigned to the new genus in superficially resembling *Limnodromus* more than any other genus of scolopacid. The femur differs from that of *L. griseus* by having: (1) neck longer and much more constricted; (2) head directed more anteriorly; (3) shaft flexed anteriorly at level of attachment of M. iliacus, in lateral view (straight in *L. griseus*); (4) shaft curved gradually posteriorly in distal half, in lateral view (curvature more localized in *L. griseus*); (5) attachment of M. gastrocnemius, pars externa, more elevated, facing more posteriorly, but

lying more on corner of shaft, farther from base of external condyle; (6) external condyle more distinctly set off at base posteriorly. The internal condyle is too broken to yield any characters.

Measurements (in mm) of the femur are as follows: length from iliac facet to external condyle, 28.9; width of proximal end, 5.3; width of distal end, 4.8; least width of shaft, 2.2; depth of proximal end, 4.0.

RECURVIROSTRIDAE

***Himantopus mexicanus* (Statius Müller)**

MATERIAL.—One complete right coracoid.

REMARKS.—*H. mexicanus* is generally distributed along the coast of Ecuador.

PHALAROPODIDAE

***Phalaropus fulicarius* (Linnaeus)**

MATERIAL.—One complete right humerus, shaft and distal ends of 2 right humeri, 2 complete left carpometacarpi.

REMARKS.—As North American migrants, *P. fulicarius* and the following two species of phalaropes occur in western Ecuador as seasonal visitors or residents.

***Lobipes lobatus* (Linnaeus)**

MATERIAL.—Two complete right and 6 complete left humeri, 1 almost complete left humerus, 1 complete right and 4 complete left coracoids, proximal ends of 1 right and 1 left humerus, distal ends of 1 right and 2 left humeri, 2 complete right and 2 complete left carpometacarpi, proximal end of 1 right carpometacarpus, 1 complete right and 3 complete left tarsometatarsi.

***Steganopus tricolor* Vieillot**

MATERIAL.—Five complete right and 4 complete left coracoids, 19 complete right and 20 complete left humeri, 3 almost complete right and 2 almost complete left humeri, proximal ends of 1 right and 2 left humeri, distal ends of 3 right and 7 left humeri, 5 complete right and 9 complete left carpo-

metacarpi, 2 complete right and 2 complete left femora, distal ends of 6 right and 5 left tibiotarsi, 2 complete right tarsometatarsi, 1 almost complete right and 1 almost complete left tarsometatarsus, proximal ends of 1 right and 1 left tarsometatarsus, distal end of 1 right tarsometatarsus.

***Steganopus* species**

MATERIAL.—One complete right and 1 complete left humerus, distal end of 1 left humerus, 1 complete right tarsometatarsus.

REMARKS.—This species is being described from the Talara Tar Seeps on the basis of a complete femur (Campbell, in press). As the above elements differ significantly from *S. tricolor* they are here referred to the new species.

The humerus of the new *Steganopus* differs from that of *S. tricolor* by having: (1) median crest larger, less excavated; (2) internal tuberosity larger, more rounded, directed less dorsad, and projecting less anconally; (3) head not undercut by capital shaft groove; (4) attachment of *M. proscapulohumeralis* positioned closer to base of median crest; (5) attachment of *M. triceps*, external head, larger dorsoventrad and bordered ventrally by distinct lip of bicipital crest, resulting in a larger bicipital crest; (6) deltoid crest longer, thicker, and higher; (7) impression of *M. brachialis anticus* shallower, not as deeply inset at the edges; (8) attachment of anterior articular ligament shorter and higher; (9) attachment of *M. pronator brevis* positioned more distad; (10) internal and external condyles longer; (11) shaft much larger.

The tarsometatarsus of the new species differs from that of *S. tricolor* by having: (1) internal trochlea larger, but projecting less posteriad; (2) internal trochlea less excavated adjacent to middle trochlea; (3) middle trochlea more rounded posteriad in medial view; (4) internal trochlea positioned close to, and directed more toward, midline of shaft. The proximal ends of the tarsometatarsi of *Steganopus* apparently do not ossify completely except in older individuals. Although the present specimen showed only a slight indication of pitting, no reliable characters could be obtained from the proximal end.

For measurements of the humerus and tarso-

metatarsus of the two species of *Steganopus*, see Table 1.

BURHINIDAE

***Burhinus superciliaris* (Tschudi)**

MATERIAL.—Proximal end of 1 left humerus, distal ends of 1 right and 3 left humeri, 1 complete right and 3 complete left coracoids, proximal end of 1 left coracoid, distal end of 1 right scapula, distal end of 1 right ulna, 1 complete right and 2

TABLE 1.—Measurements (mm) of the humerus and tarsometatarsus of *Steganopus* (OR = Observed range, M = Mean, N = Number of specimens)

Character and measurement	<i>Steganopus</i> species	<i>Steganopus tricolor</i> Recent	<i>Steganopus tricolor</i> La Carolina
HUMERUS			
Length			
OR	31.6–32.5	32.1–38	31.6–37.1
M	32	34.6	34.3
N	2	8	35
Width of proximal end			
OR	7.1–7.4	6.9–8.2	6.8–8
M	7.3	7.4	7.3
N	2	8	35
Width of distal end			
OR	5–5.1	4.5–5.6	4.7–5.6
M	5.1	4.9	5.1
N	2	8	35
Least width of shaft			
OR	2.4	2–2.3	2–2.6
M	2.4	2.2	2.3
N	2	8	35
TARSOMETATARSUS			
Length			
OR	30.6	31–34.7	32.8–34.5
M	–	32.2	33.6
N	1	8	2
Width of proximal end			
OR	3.5	3.2–3.7	3.5–3.8
M	–	3.4	3.6
N	1	8	4
Width of distal end			
OR	3.2	3–3.3	3.3–3.5
M	–	3.2	3.4
N	1	8	2
Least width of shaft			
OR	1.2	1.2–1.3	1.3
M	–	1.2	1.3
N	1	8	4

complete left carpometacarpi, 1 complete left femur, distal end of 1 left tibiotarsus, distal end of 1 right tarsometatarsus.

REMARKS.—*B. superciliaris* is common in the semi-arid region of Ecuador.

THINOCORIDAE

Thinocorus rumicivorus Eschscholtz

MATERIAL.—One complete right and 1 complete left humerus, 1 complete right and 1 complete left carpometacarpus.

REMARKS.—*T. rumicivorus* is resident in the arid regions of Ecuador.

LARIDAE

Larus pipixcan Wagler

MATERIAL.—One complete right carpometacarpus, proximal end of 1 right carpometacarpus.

REMARKS.—A North American migrant, *L. pipixcan* is a seasonal resident of Ecuador.

Larosterna inca (Lesson)

MATERIAL.—Humeral end of 1 left coracoid.

REMARKS.—A small, shallow attachment of Lig. humerocoracoideum anterius superius, located on the anteroventral corner of the head of the coracoid, is characteristic of *Larosterna*. This is the first fossil record of the genus. *L. inca* is found along the coast of southern Ecuador.

COLUMBIDAE

Zenaida auriculata (Des Murs)

MATERIAL.—Two right and 2 left scapulae, 1 complete right and 8 complete left coracoids, humeral ends of 1 right and 1 left coracoid, 1 complete right and 6 complete left humeri, proximal ends of 2 right and 3 left humeri, distal ends of 1 right and 1 left humerus, 4 complete right and 5 complete left ulnae, 2 complete right and 2 complete left radii, 5 complete right and 6 complete left carpometacarpi, 1 complete right and 1 complete left femur, 1 complete right and 1 complete left tibio-

tarsus, distal end of 1 right tibiotarsus, 4 complete right and 1 complete left tarsometatarsus, shaft and proximal end of 1 left tarsometatarsus.

REMARKS.—*Z. auriculata* is resident in western Ecuador.

Zenaida asiatica (Linnaeus)

MATERIAL.—Proximal end of 1 left carpometacarpus.

REMARKS.—*Z. asiatica* is resident in southwestern Ecuador.

Columbina cruziana (Knip and Prevost)

MATERIAL.—One complete right humerus.

REMARKS.—*C. cruziana* is common in southwestern Ecuador.

PSITTACIDAE

Aratinga roosevelti (Spillman)

MATERIAL.—Portions of 11 crania, 12 premaxillaries, 14 mandibles, 24 right and 17 left scapulae, 35 complete right and 46 complete left coracoids, humeral ends of 2 left coracoids, 25 complete right and 24 complete left humeri, proximal end of 1 right humerus, distal ends of 3 left humeri, 55 complete right and 56 complete left ulnae, proximal ends of 1 right and 1 left ulna, distal end of 1 left ulna, 30 complete right and 28 complete left radii, proximal ends of 5 right and 1 left radius, distal ends of 2 right and 2 left radii, 85 complete right and 71 complete left carpometacarpi, proximal ends of 3 right and 2 left carpometacarpi, shafts of 2 left carpometacarpi, 29 complete right and 22 complete left femora, distal ends of 1 right and 1 left femur, 36 complete right and 24 complete left tibiotarsi, proximal ends of 1 right and 1 left tibiotarsus, distal ends of 4 right and 1 left tibiotarsus, 21 complete right and 19 complete left tarsometatarsi, proximal ends of 2 left tarsometatarsi, distal ends of 3 left tarsometatarsi.

REMARKS.—Spillman (1942) reported a large collection of parrot fossils from a site on the Santa Elena Peninsula near La Carolina. He placed this material in a new genus and species, *Protoconurus roosevelti*. From his descriptions and illustrations

it is reasonably certain that the present material belongs to the same species. I could not detect sufficient differences between this fossil material and Recent specimens of the genus *Aratinga* to warrant the placement of the former in a different genus. Therefore, I suggest that *Protoconurus* be synonymized with *Aratinga*.

It is not possible at this time to say whether the fossil material represents an extinct species, as Spillman believed, or an extant species. This cannot be determined until a satisfactory series of comparative material is available. The fossil material is slightly larger than the one available specimen of *A. erythrognys* from southwestern Ecuador and differs from that species in many ways.

One coracoid of those listed above is significantly smaller than the others and may represent a different species.

Aratinga species

MATERIAL.—One complete left coracoid, distal end of 1 right humerus.

REMARKS.—These two specimens appear to represent a species of *Aratinga*, but may possibly represent another genus, as not all genera of Ecuadorian parrots were available for comparison. They are considerably larger than the corresponding elements of *A. erythrognys*.

TYTONIDAE

Tyto alba (Scopoli)

MATERIAL.—One complete right coracoid.

REMARKS.—*T. alba* is resident in western Ecuador.

STRIGIDAE

Speotyto cunicularia Gloger

MATERIAL.—One complete right and 1 complete left carpometacarpus, distal ends of 2 right tibiotarsi, distal end of 1 left tarsometatarsus.

REMARKS.—*S. cunicularia* is resident in western Ecuador.

Discussion

ECOLOGICAL CONSIDERATIONS.—La Carolina is located in the most arid region of Ecuador. Vegetation is very sparse, except in the larger dry river valleys. Ecological and climatological conditions at the site are very similar to those found at the Talara Tar Seeps, except that La Carolina is much closer to the coastline and receives slightly more rainfall. The major difference between the arid region of Ecuador and that of coastal Peru is in the greater area of the latter. Whereas the Peruvian coastal desert is thousands of kilometers long, the Ecuadorian desert is essentially limited to the Santa Elena Peninsula (Figure 1). The transition from barren desert to heavy forest is very abrupt, in some places occurring over only a few kilometers.

The principal references concerning the modern avifauna of southwestern Ecuador are the works of Chapman (1926) and Marchant (1958, 1959, 1960). A point stressed by both authors is the rapidity with which the arid and semi-arid regions are colonized by birds from the adjacent forests following the rare periods of rainfall. Marchant also documents how large numbers of birds are attracted to standing bodies of fresh water on the peninsula, such as an artificial lake.

The importance of the La Carolina avifauna in interpreting the paleoecology of southwestern Ecuador is difficult to assess. This is because the desert region is so small, the transition to forest so sharp, and the speed of colonization under the proper conditions so rapid, that only a few years of heavy rainfall are needed to change the desert into a lush savanna with seasonally flowing rivers. Such rivers would in turn form wide deltas in the low-lying, flat coastal zone. This type of environment undoubtedly attracts birds from the surrounding areas and provides excellent stop-over points for the North American migrants that make up over 43 percent of the paleoavifauna.

A climatological phenomenon known as El Niño (Chapman, 1926; Murphy, 1926) periodically brings heavy rains to southwestern Ecuador and northern coastal Peru. This supposedly occurs every seven years, but in reality the phenomenon may take place in any year. When rains do come to southwestern Ecuador they occur during the northern hemisphere winter. This increases the probability of migrant species encountering favor-

able conditions during passage to and from their wintering grounds.

If the avifauna of the Talara Tar Seeps were not known, one would probably interpret the avifauna of La Carolina, and possibly the mammalian fauna as well, as having been deposited during El Niño years. However, the Talara avifauna strongly suggests that the entire climatological regime of northern coastal Peru, and thus by inference that of southwestern Ecuador, was quite different from that found today. Instead of desert, the area was probably a lush savanna or, in the case of the Santa Elena Peninsula, more probably a tropical dry deciduous forest. Archeological work on the Santa Elena Peninsula also indicates a moister climatic regime in the past (Meggers, Evans, and Estrada, 1965; Richardson, 1973). The causes of the present dry climate, as opposed to the wetter climate present during glacial periods, are the subject of another paper currently in preparation.

COMPARISON WITH THE AVIFAUNA OF THE TALARA TAR SEEPS.—Of the 53 species from La Carolina, 38 (72%) were also found at the Talara Tar Seeps (Table 2). This includes 7 extinct species common to both sites that were first recorded from the Talara Tar Seeps. The high degree of similarity between the paleoavifaunas of the two localities, as well as that between the modern avifaunas, confirms that there must have been a great deal of interchange between coastal Ecuador and coastal Peru. A similar situation is observed between the mammalian faunas of the two sites (Lemon and Churcher, 1961).

The straight line distance between La Carolina and the Talara Tar Seeps is approximately 273 kilometers. At the present time the Gulf of Guayaquil separates the arid region of Ecuador from that of northern Peru. During glacial periods, however, the lowered sea level exposed as dry land the area currently covered by the Gulf of Guayaquil, allowing easy movement between the two areas. The formation of the Gulf of Guayaquil at the end of the Pleistocene resulted in the isolation of the avifauna of the arid Santa Elena Peninsula from that of coastal Peru. Consequently, a great deal of subspeciation has occurred between the two areas (Chapman, 1926).

The differences observed in the composition of the two paleoavifaunas can be attributed to two major causes—the means of entrapment and the

location relative to the coastline. The active tar seeps at Talara attracted large numbers of scavenger species that came to feed upon other animals, including large mammals, trapped in the tar. The drawing power of La Carolina in this regard must have been weak. As the Talara site is located approximately 32 kilometers inland, it has a higher percentage of terrestrial species and fewer strictly marine species that do not venture inland. The opposite is true of La Carolina which was on, or very near, the coastline.

The similarities between the avian and mammalian faunas of La Carolina and the Talara Tar Seeps, particularly in the extinct species, suggest that material was being deposited at the two sites contemporaneously. The Talara site has been dated at c. 13,900 B.P. (Churcher, 1966). If the age of La Carolina differs significantly from that of the Talara Tar Seeps, I believe it will prove to be younger rather than older, for climatological reasons to be discussed in a later publication.

ENTRAPMENT OF THE BIRDS AT LA CAROLINA.—How birds became trapped, or their remains concentrated, at La Carolina is not clear. The undisturbed matrix available with the collection was extremely rich in avian specimens, and contained only a few fragmentary mammalian bones. At other nearby sites, however, Edmund (pers. comm.) found only mammalian and no avian material.

None of the fossil material I studied shows any large concentration of pitch, although there are some indications of its presence in the matrix surrounding some specimens. The absence of heavy pitch concentrations on the bones indicates that the birds were not trapped in active tar seeps, as at the Talara Tar Seeps and Rancho La Brea. It is quite possible, however, that oil seeps may have coated the water with a surface layer of oil and that upon landing in this the feathers of the birds would become oil-soaked, preventing further flight and resulting in their drowning. As the bodies decomposed, the bones would be freed from the oil and drop to settle in the soft mud. Such a film of oil would also help to explain the lack of mammalian specimens in the concentration of avian remains. Mammals are better able to sense and avoid oil-covered water than are birds alighting from flight. For larger mammals, passage through oil covered water would be no more than an unpleasant inconvenience.

TABLE 2.—Fifty-three nonpasserine species from La Carolina, Ecuador

Species	No. of Specimens	Minimum No. of Individuals	Species	No. of Specimens	Minimum No. of Individuals
* <i>Nycticorax nycticorax</i>	5	1	* <i>Erolia melanotos</i>	22	9
* <i>Dendrocygna autumnalis</i>	4	1	<i>Ereunetes pusillus</i>	3	2
ANATIDAE genus and species	10	3	* <i>Ereunetes mauri</i>	10	7
* <i>Anas</i> species 1	4	1	* <i>Micropalama himantopus</i>	1	1
* <i>Anas</i> species 3	4	2	<i>Bartramia longicauda</i>	8	2
* <i>Anas bahamensis</i>	326	37	<i>Numenius phaeopus</i>	4	2
VULTURIDAE gen. et sp. indet.	1	1	<i>Limosa fedoa</i>	2	1
* <i>Coragyps cf. atratus</i>	2	1	* <i>Arenaria interpres</i>	7	2
* <i>Cathartes aura</i>	5	3	*SCOLOPACIDAE genus and species ...	2	1
*ACCIPITRIDAE genus and species ...	1	1	<i>Himantopus mexicanus</i>	1	1
* <i>Geranoaetus melanoleucus</i>	2	1	<i>Phalaropus fulicarius</i>	5	3
* <i>Buteo polyosoma</i>	7	2	* <i>Lobipes lobatus</i>	28	8
<i>Buteo hoffstetteri</i> , new species	4	1	* <i>Steganopus</i> species	4	2
<i>Circus cinereus</i>	3	1	<i>Steganopus tricolor</i>	102	29
* <i>Falco peregrinus</i>	22	3	* <i>Burhinus superciliaris</i>	18	4
* <i>Falco femoralis</i>	2	1	* <i>Thinocorus rumicivorus</i>	4	1
* <i>Polyborus plancus</i>	52	6	* <i>Larus pipixcan</i>	2	1
* <i>Milvago</i> species	3	2	<i>Larosterna inca</i>	1	1
* <i>Pluvialis dominica</i>	47	9	* <i>Zenaida asiatica</i>	1	1
* <i>Pluvialis squatarola</i>	1	1	* <i>Zenaida auriculata</i>	64	9
* <i>Charadrius vociferus</i>	1	1	* <i>Columbina cruziana</i>	1	1
* <i>Charadrius semipalmatus</i>	2	1	<i>Aratinga roosevelti</i>	724	88
<i>Oreopholus orcesi</i> , new species	1	1	<i>Aratinga</i> species	2	1
* <i>Tringa solitaria</i>	3	1	* <i>Tyto alba</i>	1	1
* <i>Totanus flavipes</i>	11	3	* <i>Speotyto cunicularia</i>	5	2
* <i>Totanus melanoleucus</i>	5	2	—	—	—
* <i>Catoptrophorus semipalmatus</i>	5	2	Total	1611	284
<i>Calidris canutus</i>	57	15			

* Also recorded from the Talara Tar Seeps, Peru.

Perhaps the most remarkable aspect of the avifauna from La Carolina is the tremendous number of specimens of parrots, making up approximately 44 percent of the entire collection. Parrots must have been attracted to the site in large flocks, perhaps for water, and subsequently trapped by the oil. From such large flocks of parrots one could

reason either that water was scarce and La Carolina was the only watering site available, the parrots thus having to travel long distances to reach it, or water may have been abundant and La Carolina close to the roosting or feeding areas of the parrots. If the latter were true, it would indicate the presence of forest on the presently barren peninsula.

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