

Evolution of the Rails
of the South Atlantic Islands
(Aves: Rallidae)

STORRS L. OLSON

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 152

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ABSTRACT

Olson, Storrs L. Evolution of the Rails of the South Atlantic Islands (Aves: Rallidae). *Smithsonian Contributions to Zoology*, number 152, 53 pages, 8 figures, 11 plates, 1973.—Abundant remains of a medium-sized, flightless rail collected on Ascension Island are described as a new species, *Atlantisia elpenor*. The very large, extinct, flightless rail, previously described as *Aphanocrex podarces*, is also shown to be a member of the genus *Atlantisia*, the only other member of which is the diminutive, flightless, living species *A. rogersi* of Inaccessible Island in the Tristan da Cunha group. These three species are believed to be descended from a common mainland ancestor of a pro-*Rallus* stock that arrived as wind-blown vagrants to all three islands where each population independently evolved flightlessness and divergent body sizes in response to different environmental conditions. Bones of a flightless rail much smaller than *A. podarces* were also discovered on St. Helena and represent a new species, *Porzana astrictocarpus*, which, along with the flightless species "*Porzanula*" *palmeri* of Laysan Island in the Pacific, is thought to be descended from the widespread Old World species *Porzana pusilla*. The two nearly identical flightless gallinules of Tristan da Cunha (*nesiotis*) and Gough (*comeri*) Islands are considered as each having been independently derived from volant *Gallinula chloropus* and are, therefore, best treated as separate species or as subspecies of *G. chloropus* rather than one being a subspecies of the other. Two species of purple gallinules (*Porphyryla*) are regular vagrants to the South Atlantic islands yet have never established breeding populations on any of them. This genus is thought to be too specialized morphologically to adapt to insular environments. Flightlessness in rails is shown to be a neotenic condition that involves only the control of relative growth of body parts, is evolved at a rapid rate, and therefore has limited taxonomic significance. The evolutionary advantage of flightlessness is thought to be in the conservation of energy resulting from the decrease in mass of the flight muscles.

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Evolution of the Rails of the South Atlantic Islands (Aves: Rallidae)

Storrs L. Olson

INTRODUCTION

Among the families of terrestrial vertebrates, the rails (Rallidae) have one of the most comprehensive geographical distributions. Not only are they widespread in continental areas, except in regions of extreme cold or aridity, but practically no island or group of islands is too remote or inhospitable to have been discovered and inhabited by some species of rallid.

The islands of the mid-South Atlantic are among the smallest and most isolated in the world; yet as it has turned out, each harbored one or more species of rail. Ascension, St. Helena, and the Tristan da Cunha group, remote from each other as they are, have been occupied by one group of these rails which has radiated almost as if it were in an archipelago. In these solitary microcosms has unfolded an evolutionary story in its own way as fascinating as that of the Galapagos or Hawaii.

The islands with which we will be concerned are entirely volcanic and are part of the Mid-Atlantic Ridge. Ascension and Tristan lie directly on the ridge and both are geologically very young. St. Helena lies to the east of the center of the ridge and is considerably older (Baker, 1970). The map (Figure 1) demonstrates how far re-

moved these islands are from each other and from the continents.

Ascension was discovered in 1501, St. Helena in 1502, and Tristan da Cunha in 1506. St. Helena, being of good climate and rich in resources, was

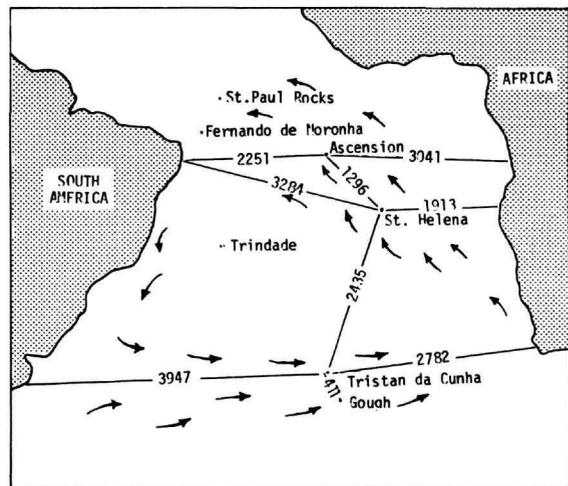


FIGURE 1.—Map of the South Atlantic Ocean showing the principal islands. Numbers represent distances in kilometers and were computed by F. C. W. Olson from coordinates obtained from the *World Port Index* (Publication 150, U.S. Navy Oceanographic Office, 1963). Arrows indicate direction of prevailing surface winds.

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settled not long after its discovery. Because of its barren nature, Ascension was not permanently inhabited until 1815. The Tristan group, composed of the main island of Tristan da Cunha, the two smaller adjacent islands of Inaccessible and Nightingale, and Gough Island considerably to the south, was not settled permanently until 1810, and then only the main island of Tristan was occupied; the rest to this day remain uninhabited. As a consequence of man's interference, a number of species of birds from these islands have become extinct and, of these, most are known only from bones. In search of fossil bird remains, I made collections on Ascension Island (12 June–15 July 1970, 1 June–4 June, and 19 July–31 July 1971) and on St. Helena (5 June–17 July 1971). These collections include, in addition to thousands of specimens of seabirds and a few other landbirds, three species of rails, two of which are described here as new. The bulk of this paper will concern itself with the origins, relationships, descriptions, ecology, and adaptations of the living and fossil rails of the South Atlantic Islands. The most striking modification of most of these species is their flightlessness. This is a condition that appears often in insular rails, yet one that has received little analysis. The origins, advantages, and significance of flightlessness in the Rallidae are also treated here.

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My first two years of research were undertaken while holding scholarships as a graduate student in the Department of Pathobiology, Johns Hopkins University, School of Hygiene and Public Health. I am most grateful to Frederik B. Bang for providing this opportunity and for his considerable personal and administrative support. Barreda Howell continually and patiently helped me through administrative crises, large and small, during my tenure at Hopkins. My last year of graduate study was financed by a visiting research fellowship from the Office of Academic Studies of the Smithsonian Institution, during which period Gretchen Gayle and Hazel Fermino helped with a multitude of details.

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Sheila Ford generously executed Plates 1c, 7d, and 8i. The patience, care, and dispatch exercised by Victor E. Krantz in taking and printing the photographs is very much appreciated. N. Drahos and I. Ikehara kindly supplied me with specimens of the Guam rail. The late James A. Peters assisted in making calculations on time-share com-

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RAILS OF ASCENSION ISLAND

History of the Endemic Ascension Rail

The 7th June anno 1656. Att evening wee arrived att Ascention and anchored on the NW. side of the iland. On our rightt hand was a faire sandy bay and on our leftt were multi[tu]de of rarreg [ragged], craggy, sharpe pointed hard rocks for many miles along the shoare, and up toward the land, appearing white with the dung of sea foule, of which were innumerable of severall kinds. The most desolate, barren [land] (and like a land thatt God had cursed) thatt ever my eies beheld (worse then Kerne Ky, etts. in Cornewall). I co[n]ceave the whole world affoards nott such another peece of ground: most part of the collour of burnt bricke, reddish, the substance stones, somwhatt like pumice stones; the rest like cinders and burnt earth. The hills, of which there are many, were meere heapes of the same. It may bee supposed thatt the fire in former ages hath consumed the substance therof, hath made it incapable of producing any vegetalls. Only the topps of the high mountaines in the middle appeared somwhatt greene, there beeing a kind of rushes and spicy [spiky] grasse. Some of our company went up and broughtt downe six or seven goates, doubtlesse att first left there by the Portugalls: allsoe halfe a dozen of a strange kind of fowle, much bigger then our sterlings ore stares: collour gray or dappled, white and blacke feathers intermixed, eies red like rubies, wings very imperfitt, such as wherewith they cannot raise themselves from the ground. They were taken running, in which they are exceeding swift, helping themselves a little with their wings (as it is said of the estridge), shortt billed, cloven footed, thatt can neither fly nor swymme. It was more then ordinary dainety meatt, relishing like a roasting pigge (Peter Mundy, in Temple and Anstey, ed., 1936:82-83).

Peter Mundy was a traveler of exceptional perception who several times in the 17th century sailed from England to India and made stops at Ascension and St. Helena while keeping a detailed journal of his observations. With his entry (above)

on Ascension Island he included a small sketch of his "strange kind of fowle" (Figure 2) which, although historically interesting, is hardly diagnostic. It shows a bird with a medium-sized bill and reduced wings, but whether the flecks on the body represent dappled plumage, as Ashmole (1963a) conjectured, or whether they are simply indications of feathers, is speculative. Kinnear (1935), in commenting on the fauna mentioned in Mundy's journal, came to the conclusion that the Ascension bird was an extinct flightless rail; a decision that was concurred in by other ornithologists



FIGURE 2.—Peter Mundy's sketch of the Ascension rail, with a sample of his script for scale. (From Temple and Anstey, ed., 1936:83.)



(Murphy, 1936:154; Hagen, 1952:230). However, as no such bird exists on Ascension today, Stonehouse (1962) felt that Mundy's description might apply to juvenile Sooty Terns (*Sterna fuscata*) despite the fact that their eyes are brown, their feet webbed, and their locomotion hardly "exceeding swift." It is certain now that this was not the case.

No further information relating to this bird on Ascension Island was forthcoming until the British Ornithologists' Union (BOU) sent an expedition to Ascension in 1957-1959 to study its seabird colonies. In order to gain some knowledge of the past seabird fauna, the expedition searched for avian remains in several sites on the island. Included among the bones they discovered was the skull of a small rail taken from a deep fumarole north of Sisters Peak, and a ralline tarsometatarsus from phosphate deposits south of South Gannet Hill. These were reported on by Ashmole (1963a), who thought them to be unlike any living rail, but he refrained from naming the bird in the hope of being able to obtain more material at a later date. He provisionally considered the species a member of the genus *Rallus* while pointing out that the skull was proportionately very similar to *Atlantisia rogersi* of Inaccessible Island in the Tristan da Cunha group. The late James Fisher (Fisher and Peterson, 1964: 241, 273) referred to the Ascension rail as "*Creocopsis* sp.," and it is listed as such in the Red Data Book (Vincent, 1966). Fisher informed me (letter of 22 January 1970) that he had done this solely on the basis of Mundy's description, but on examining the skull he had later decided to refer it to *Rallus*. *Creocopsis egregia* is an African rail which is dappled and has a red eye but which is probably not directly related to the Ascension rail.

Armed with these tantalizing scraps of information, it was my purpose in visiting Ascension to attempt to obtain additional remains of the rail. On arriving at the island in 1970, I went directly

FIGURE 3.—The collecting locality for the Ascension rail: *a*, The barren volcanic landscape around the fumaroles where the rail remains were found. Arrow indicates the large fumarole, the smaller one is almost hidden to the right. The large cinder cone is Sisters Peak. Note the white patches of old guano on the leeward side of the rocks. *b*, The precipitous descent into chamber B of the large fumarole. The floor of the chamber is about 7-8 meters below the opening visible here. It should be self-evident why flightless rails became entrapped within. (Photographs taken 14 July 1970 by Douglas S. Rogers.)

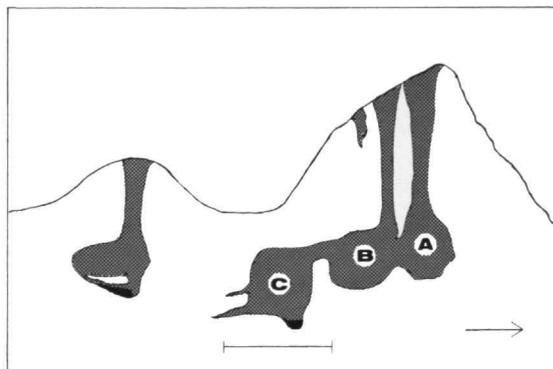


FIGURE 4.—Diagram of a cross-section through the interior of the fumaroles shown in Figure 3. The blackened areas show where most of the rail bones were found. Scale=approx. 5 m. Arrow points north.

to the locality where Ashmole collected the rail skull, this site being the larger of two fumaroles situated on an elevated plain a few hundred meters north of the base of Sisters Peak. A more inhospitable place is hardly to be imagined (Figure 3a). The plain, which lies at about the 550 foot contour, consists of volcanic ash and cinders interspersed with mounds of lava. Looming some 300 meters above is the summit of Sisters Peak, a large cone entirely composed of cinders. Aside from a few lichens and wisps of dry grass, the area is barren of life. In the midst of this "lunar" landscape project two fumaroles, or driblet cones, made up of blobs of red lava, remnants of the most recent volcanic activity on the island. The largest is about 8 meters high and is penetrated by two chimney-like openings that descend for a depth of about 10-12 meters (Figure 3b). These open into three large interconnecting chambers (Figure 4). For historical geology and further descriptions of this area see Daly (1925) and Stonehouse (1960).

From both fumaroles the BOU party collected bird remains, among which Ashmole (1963a) identified bones of Masked Booby (*Sula dactylatra*), Fairy Tern (*Gygis alba*), and Sooty Tern (*Sterna fuscata*). In chamber B of the large fumarole, I found remains of *Sterna fuscata*, *Sula dactylatra*, and Red-footed Booby (*Sula sula*), and, in addition, a single femur of a rail lying by itself on top of a pile of recently dislodged debris. No other rallid remains were found in this chamber and it is possible that

this one bone was accidentally dropped there by one of the BOU party or other subsequent visitors to the fumarole. A narrow crevice near the ceiling of the south wall of chamber B led into a third chamber (c). Access into (and egress out of) this room was made difficult by a sheer drop of about 3 meters at the end of the crevice. In the east corner of this totally dark chamber, in a depression about 1.5 × 2 meters, lay a myriad of small bones, all of rails. Amongst them were shell fragments of a single land crab (*Gecarcinus lagostoma*), a species which is now common on the southeastern vegetated part of the island and on Green Mountain, but is seldom met with elsewhere on Ascension. In five descents into the large fumarole, accompanied by D. S. Rogers or J. M. Couch, I picked up with forceps all the large bones I could reach, and with the aid of a camel's hair brush and a spoon, removed a quantity of the smaller bones and associated debris. From chamber c ran several tunnels too narrow to permit passage but into which a rail might easily have slipped. From the largest of these, which Rogers with much difficulty was able to enter a short way, were extracted bones of two rails and a single *Gygis alba*, the latter the only seabird found in chamber c. Rogers saw other skeletons in this tunnel which he could not reach but which he thought were railid.

On analyzing the bones collected in this fumarole, I can account for the presence of about 35 individual rails—doubtless more remain secreted in inaccessible crannies. Some of the bones are friable and chalky and variously eroded, but others are in an excellent state of preservation with very delicate processes still intact. None is mineralized. A few appear somewhat yellowish as if they might retain some grease, while the proximal end of one tibiotarsus still has a few shreds of tendon adherent. Most of the bones are of adult birds but a few show the spongy articulations characteristic of immaturity.

A few meters south of the large fumarole is the rather wide opening of a smaller fumarole that rises 2–3 meters above the plain. I did not explore it until 1971, but previously Ashmole (1963a) had reported no rail remains from this fumarole and Stonehouse (1960:181) had said that he had taken from it "all the skulls and fragments of long bones." In three trips, however, I removed from this site hundreds of additional bones of *Sterna*

fuscata from not less than 146 individuals, remains of several *Gygis* and *Sula* and more importantly, nearly 200 bones or fragments from at least 17 individual rails, and surprisingly, a few bones of a single small heron (Olson, in prep. (a)).

Conditions in the small fumarole were somewhat different than in the large one. The main part of the floor lay about 6 meters below the rim and off to one side was a pocket about 1.5 meters deeper which contained nearly all the bones discovered at this site except for those of a few *Sula*. The bottom of this pocket, about 1 × 3 meters in area, was filled with a loose, dry deposit of dust, cinders, and the organic debris resulting from the decomposition of hundreds of bird carcasses, to a depth of 60 cm, or more, in places. Bones lay jumbled on the surface and throughout the powdery matrix, those from the deeper layers being stained dark brown while those on the surface were white. This was in contrast to the large fumarole where the bones were lying on bare rock.

The deposits of bones in both fumaroles bear evidence of having accumulated over some period of time but the latest specimens, to judge from their appearance, can hardly be older than a few hundred years. Unfortunately, in spite of the dry conditions, no mummification appears to have taken place and no feathers or other soft parts remain. However, all the elements of the skeleton are represented, including such rarely preserved items as the lacrimals, pterygoids, and even the ossified portions of cricoid cartilages. None of the rail specimens from either fumarole shows any pathological condition although in my experience in such a large series (at least 52 individuals) it would not be unexpected to find a few bones that had been broken and subsequently mended.

The remarkably reduced wing elements and carina of the sternum disclosed at first glance that these remains were from an absolutely flightless bird. As there were no other landbirds on the island, there can be little doubt that these bones are from the species described by Mundy. Being unable to fly, the birds that ventured up the sides of the fumaroles and tumbled into the steep vents would not have been able to effect their escape. Thus trapped, they must have wandered about the interior until they dropped into the farthest recesses where they succumbed to lack of water and food.

On comparing the exceptionally fine series of bones of the Ascension rail with skeletons of other Rallidae (see Appendix 1 for species compared), one species emerged as being inescapably similar in proportions and most details of structure, this being the diminutive, flightless, *Atlantisia rogersi* Lowe from Inaccessible Island, until now considered a monotypic genus. More surprisingly, the very large, extinct rail, *Aphanocrex podarces* Wetmore, of St. Helena, also agrees closely in morphology with the Ascension bird and with *A. rogersi*. For these and other reasons discussed further on, I consider these three forms as congeners. The characters of the expanded genus *Atlantisia* are discussed in Appendix 2.

Atlantisia elpenor, new species

HOLOTYPE.—Complete left tarsometatarsus, fully ossified (Plate 5*e,f,g*). Vertebrate paleontological collections of the National Museum of Natural History (USNM 170129). Collected in depression on the east side of the southernmost chamber of the largest fumarole located about 260 meters true north of the summit of Sisters Peak, Ascension Island, South Atlantic Ocean (approximately 7°55'25"S; 14°22'15"W), on 17 June 1970, by Storrs L. Olson and Jesse M. Couch. Directly associated with the type were right and left humeri, ulnae, radii, carpometacarpi, coracoids, scapulae, fibulae, left femur, sternum, furcula, mandible, left quadrate, 13 ribs, 18 vertebrae, and 15 pedal phalanges which have been cataloged under the same number, as I am confident that they are all from the same individual. As this specimen was well exposed and in an excellent state of preservation and had the mandible present but the rest of the skull lacking, it is possible that the skull (Ashmole No. F21) picked up by Ashmole and now in the British Museum (Natural History) may be from the same individual. However, lest there possibly be any confusion, and since there were so many other rail remains in the area, I designate only the tarsometatarsus as the holotype. The associated elements may be considered as especially significant paratypes in the large series of paratypical material from the two fumaroles.

The type tarsus is 38.0 mm in total length; transverse breadth across head 5.5 mm; transverse breadth across center of shaft 2.5 mm; transverse

breadth across trochleae 5.7 mm. It is near the maximum length and stoutness for the species and is yellowish white in color. There being so much more material of tarsi and other skeletal elements, I will not further belabor the description of the actual type.

PARATYPES.—All of the various elements of rallid material from the two fumaroles included in the series USNM 169773–170128, 170130–170272, and 175803–175853 may be considered paratypes.

RANGE.—Ascension Island, South Atlantic Ocean.

STATUS.—Extinct; exterminated sometime after 1656.

ETYMOLOGY.—Elpenor was one of Odysseus' crew members, who, while stranded on Circe's island, fell from the roof of her palace, was killed, and descended straight to Hades. Odysseus later encountered Elpenor's shade during his journey through the Underworld. The Ascension rail was also stranded on an island and upon falling off the lip of the fumarole, descended straight to the bowels of the earth and was not known again until its shades were stirred up by inquiring mortals invading its underworld tomb. The specific name stands in apposition to that of the genus and is in the nominative case.

DIAGNOSIS.—A medium-sized flightless rail, roughly the size of a Virginia Rail (*Rallus limicola*) but with much reduced pectoral girdle and wings, and stouter hind limbs. It is very similar in most respects to *Atlantisia rogersi* but much larger, the major bones averaging 25 to 35 percent longer. On the other hand, *A. elpenor* is but half the size of *A. podarces* (Table 2).

DESCRIPTION.—The skull of *A. elpenor* (Plate 1*b*) is represented by several nearly complete crania and cranial fragments, fragments of bill, and one specimen that is nearly complete, with bill, palatal bones, and cranium intact. In this specimen (USNM 170131) the interorbital bridge had been corroded away and when first collected the bill and palate were connected to the cranium by only a thread of the parasphenoid rostrum which with subsequent handling parted. The specimen is superior to the skull collected by Ashmole (1963a, pl. 10), which I have not examined, in that the anterior portions including the palatines, vomer, maxillopalatines, portions of the jugal bar, etc., remain attached. By approximating the two portions of the specimen, I got an overall measure-

ment of 51.6 mm length, which is essentially identical to the 51 mm Ashmole estimated for the British Museum specimen. The interorbital bridge is quite narrow; 7 specimens range from 2.70 mm to 3.25 mm (average 2.97) in width at the narrowest point. The bill is like that of *A. rogersi* (Plate 1a). The nasal bar is narrow and twisted dorsally in *A. elpenor* and is broader and flat in *A. rogersi*. The palate is essentially like that of *A. rogersi* save that the posterior portions of the palatines are slightly more expanded and squared. The scars for the attachment of *M. pseudotemporalis superficialis* and *M. adductor mandibulae* are larger and deeper in *A. elpenor*, indicating a greater development of the jaw muscles than in *A. rogersi*.

The lacrimal in rails is a small delicate bone and is not fused to the skull. Lowe (1928:123) drew attention to the very distinctive nature of the lacrimal of *A. rogersi* and I therefore felt myself most fortunate to obtain three lacrimals of *A. elpenor* for comparison. These in no way resemble *A. rogersi* but are more like the typical rallid form (Plate 2e). In *A. rogersi* the descending process is long, slender, and twisted, the head of the bone is reduced to a pointed, anteriorly projecting spur, and the horizontal process is a short hook. In contrast, in *A. elpenor* there is a broad square head with a deep depression on the medial surface and a well-developed area for the attachment to the nasal; the descending process is fairly short and the horizontal process is long, strong, and tapering. Lowe (1928:124) considered the peculiar lacrimal of *A. rogersi* to represent a remarkable degree of "generalization"; however, I cannot agree with this determination. The condition of the lacrimal of *A. rogersi* is much more likely some sort of specialization. It is not a retention of a generalized embryonic condition in the Rallidae, as none of the embryos or chicks of rails I have seen possess such a lacrimal. The lacrimal does not provide attachment for muscles, but numerous ligaments do attach to it and in rails it may provide a brace for the jugal bar and protection for the anterior orbital region (Cracraft, 1968). This bone in rails is quite variable in shape as I have previously noted (Olson, 1970), but the adaptative significance of such variations is unknown.

The mandible of *A. elpenor* (Plate 2c,d) is very

like that of *A. rogersi*, although in the latter the symphysis seems slightly wider and more trough-like.

The furcula (Plate 3h) is slender and in the shape of a narrow U, with the epicleideum represented by only a slight swelling.

The coracoid (Plate 3f,g) like all of the pectoral elements, is reduced in size. The shaft is proportionately wider than in *A. rogersi*, not thickened and bent as in *A. podarces*. As in *A. rogersi*, the brachial tuberosity is in line with the shaft. The sterno-coracoidal impression is considerably shallower than in *A. rogersi* and the scapular facet is also shallow.

In the scapula of *A. elpenor* (Plate 3i) the tubercle for the attachment of the dorsal branch of the tendon of *M. expansor secundariorum* is completely lacking, whereas in *A. rogersi* a reduced but distinct tubercle is still present.

The sternum of *A. elpenor* differs greatly from that of *A. rogersi* (Plate 4). In *A. elpenor* it is broad and flat, the carina being reduced to a thickened ridge about 1.5 mm at its greatest depth. Thus, literally speaking, the species barely qualifies as a "carinate" bird and was without question flightless. The carina of *A. rogersi*, in contrast, is elevated posteriorly. In *A. rogersi* there is a deep, rounded notch widely separating the coracoidal sulci and completely obliterating the spina externa. This notch is much shallower in *A. elpenor* although there is still no trace of the spina externa. The sterno-coracoidal processes of *A. elpenor* are fairly broad and short as in typical rails, not tenuous and elongate as seen in *A. rogersi* and also in the large, flightless Weka (*Gallirallus*) of New Zealand. In *A. elpenor*, the posterior lateral processes are short, scarcely extending beyond the xiphium, and the sternal notches are correspondingly reduced, being confined to the posterior fourth or less of the sternum. The xiphium of *A. elpenor* is notched, unlike *A. rogersi* but like *Gallirallus*. From the anterior end of the carina of *A. elpenor*, two well-defined ridges extend forward to the internal margin of the ventral lip of the coracoidal sulci, but in *A. rogersi* the anterior half of the sternum is much more conspicuously flattened. Overall, the sternum of *A. elpenor* is quite similar to that of *Gallirallus*, except that the latter has slender, elongate sterno-coracoidal processes like *A. rogersi*. This similarity is purely convergent as the

sterna of flightless rails assume a number of shapes that are not necessarily correlated with phylogenetic affinity (see below).

The humerus (Plate 3*a,b*) is not as robust as that of *A. podarces*. The bicipital crest is better developed and shaft slightly more curved than in *A. rogersi*. The ectepicondylar prominence and external tuberosity are further reduced than in either *A. rogersi* or *A. podarces*.

In the ulna (Plate 3*c*) the external condyle is slightly better developed than in *A. rogersi*. A distinct depression just proximal to the internal face of the external condyle of *A. elpenor* is not apparent in the other two species of *Atlantisia*.

Compared to *A. rogersi*, the carpometacarpus of *A. elpenor* (Plate 3*d,e*) has the proximal metacarpal symphysis somewhat longer and narrower, the distal portion of metacarpal III not as thin, and the external side of metacarpal II slightly narrower and flatter.

In dorsal view of the pelvis (Plate 2*a,b*) the portion of the posterior iliac crest above the antitrochanter flares rather abruptly outward, giving the area between the crests a squared appearance in *A. elpenor*. These crests in *A. rogersi* are less prominent and spread apart gradually and farther behind the antitrochanters, which gives the area between the crests a triangular shape. The anteriormost part of the ilium of *A. elpenor* forms a sharp, laterally directed point which is less developed and rounder in *A. rogersi*.

Except for size, the hind limb elements of the three species of *Atlantisia* are quite similar (Plate 10). The shaft of the femur (Plate 5*c,d*) of *A. elpenor*, in lateral view, is more curved than in *A. rogersi*. Proportionately, the shaft of the tibia (Plate 5*a,b*) is narrower and the fibular crest is shorter in *A. elpenor* than in *A. podarces*. The fibula (Plate 5*a,b*) of *A. elpenor* is a long slender splint with the head less stout than *A. podarces*. None of the 50 appropriate specimens of tarsometatarsus (Plate 5*e,f,g*) of *A. elpenor* has the ossified tendinal loop for the tendon of *M. extensor digitorum longus* on the proximal anterior face. In *A. rogersi* this loop is mostly cartilaginous and the same may be assumed for *A. elpenor*; however, this loop is fully ossified in *A. podarces*. The scar for the hallux is deep in *A. elpenor* and is longer than that of *A. podarces*. The internal trochlea of

A. elpenor is noticeably less flared medially than in *A. podarces*.

The toes of *A. elpenor*, as far as can be determined from assembling the disarticulated phalanges, are of about the same proportions as *A. rogersi*. The claws are not nearly as long and well developed as those of *A. podarces*.

In plotting the lengths of the humerus, femur, tibia, and tarsus on a graph, no bimodality is apparent except possibly in the tarsal measurements, so it cannot be conclusively demonstrated that *A. elpenor* was sexually dimorphic in size. The amount of variation in size (Table 1), may nevertheless be attributable in part to sexual differences, as in most rails the males are larger than the females.

Of the external characteristics of *A. elpenor* there is only Mundy's description to go on. From this we may assume the bird had a more variegated plumage than the drab-colored *A. rogersi*, although *A. rogersi* does retain some variegation. The red eye noted by Mundy corresponds well with the red eye of adult *A. rogersi*, although this is a character

TABLE 1.—Selected skeletal measurements of *Atlantisia elpenor* (shaft widths taken at the narrowest point; pelvic width taken across the antitrochanters)

Characters	n	min.	max.	mean
Cranial width	3	16.0	16.4	16.23
Length furcula	2	17.8	18.4	18.1
Length coracoid	34	15.2	16.3	15.58
Length scapula	6	21.4	26.2	24.53
Length humerus	36	24.0	28.0	26.34
Width head humerus	35	5.3	6.2	5.84
Width shaft humerus	35	1.3	1.7	1.51
Width distal humerus	29	3.6	4.9	3.95
Length ulna	13	17.8	22.0	20.13
Length radius	10	18.5	20.6	19.5
Length carpometacarpus	13	12.8	14.8	13.84
Length ilium	9	27.5	31.9	30.0
Width pelvis	8	13.5	14.7	14.16
Length femur	35	31.1	36.5	34.51
Width shaft femur	34	2.1	2.5	2.28
Width distal femur	33	5.3	6.2	5.80
Length tibia	28	51.2	58.5	55.29
Width shaft tibia	28	2.0	2.3	2.19
Width distal tibia	24	4.7	5.2	5.02
Length fibula	7	28.5	32.0	30.9
Length tarsus	32	33.0	38.0	35.48
Width head tarsus	25	5.0	5.7	5.31
Width shaft tarsus	29	2.2	2.5	2.32
Width distal tarsus	27	4.9	5.8	5.40

that appears at random throughout the Rallidae and is without taxonomic importance.

Environment and Extinction of the Ascension Rail

Ascension is a relatively small island (97 km²; 38 mi²), entirely volcanic in origin. Geological reports emphasize its extreme youth (e.g., Daly, 1925) and the oldest rocks have now been dated at only $1.5 \pm .2$ million years of age (Chace and Manning, 1972:5). Since the discovery of the island in 1501, there has been no volcanic activity reported there, which is considered odd in view of the very fresh appearance of some of the lava formations. The highest point on the island is the peak of Green Mountain (860 m; 2817 ft). The coastline consists mainly of steep rocky cliffs with a few scattered patches of beach composed of shell sand or pebbles. The climate is mild, temperatures ranging from about 26° to 29°C in the lowlands and 6° to 6.5°C lower on Green Mountain. Rainfall on Green Mountain, which is often enshrouded in mist and clouds, averages about 708.6 mm (27.9 in) annually, but in the lowlands, where near-desert conditions prevail, there is only about 127 mm (5 in) per year. Strong trade winds blow with great consistency from the southeast. There is very little seasonal variation in weather but at rare intervals heavy rainstorms occur which may destroy the nests and eggs of Sooty Terns (Huckle, 1924) and may have affected rails. These storms are usually followed by a marked burst in growth of vegetation. Unusually heavy rainfall preceded my second visit to Ascension by several weeks. When I arrived, most of the low areas of the island were covered with rippling waves of grass where before there had been only cinders. Within six weeks this grass had desiccated and turned yellow after having produced a prodigious amount of seeds to await the next rains.

Duffey (1964) summarized the history of the terrestrial fauna and flora of the island (although he failed to cite Mundy's journal (Temple and Anstey, ed., 1936), which contains several valuable points of information aside from the reference to the rail). Man has drastically altered the environment, probably from his first encounter with the island. In Mundy's account, which is earlier than any cited by Duffey, the only vegetation described as present in 1656 was "rushes" and "grass" on the

higher mountains. Goats were already present and Mundy is probably correct in assuming that they were released years earlier by the Portuguese discoverers of the island. The impressions of the earliest botanists to visit the island largely confirm Mundy's report. Only two shrubs are known to be native to Ascension, both of which are endemic (*Euphorbia organoides* and *Hedyotis adscensionis*, the latter apparently extinct). A few other flowering plants and grasses, as well as a number of cryptogams, including several endemic ferns, are native to the island, most of these being confined to the Green Mountain area. The disproportion of cryptogams to phanerogams indicates an early stage of floral colonization of Ascension somewhat similar to that reported for the Pliocene of St. Helena (Muir and Baker, 1968). Osbeck (1771, II:98) described "several petrifications of branches of trees and pieces of wood" and was under the impression that the island had formerly been forested. Murphy (1936:154, 865) assumed that Ascension was forested at one time, mostly on the basis of Osbeck's testimony. There is no other evidence, however, that this was the case. Palynological studies by Duffey (1964) showed no evidence of pollen from indigenous trees and he discounts the idea that the island ever possessed forest cover. Very likely Osbeck mistook some of the deceptively woodlike lava formations about the island for actual remains of trees. There is very little area of suitable soil for forest growth on the island and much of what is now present resulted from the mulch of introduced plants and from direct importation of soil.

The impoverished flora of the island has been greatly augmented by man's introductions, most of which, after the establishment of a permanent British garrison in 1815, were intentional. The invertebrate fauna is likewise depauperate and the presence of many species may well be the result of having been unintentionally introduced along with plants. There are now no native terrestrial vertebrates (the only one known was *Atlantisia elpenor*). Of the several species of birds that were released on the island, only four have persisted, and these are dependent on the man-made vegetation landscape. They are a francolin (*Pternistes afer*), a myna (*Acridotheres tristis*), and two finches (*Estrilda astrild*, *Serinus flaviventris*).

Pelagic seabirds that used the island for nesting and roosting were once present in tremendous

numbers on the main island of Ascension as all the early accounts testify (Temple and Anstey, ed., 1936; La Caille, 1763). Huge colonies of boobies (*Sula* spp.), Sooty Terns (*Sterna fuscata*) and frigatebirds (*Fregata aquila*) were reported, mostly from the northwestern and southern portions of the island (for an account of the history of the seabird colonies of Ascension, see Stonehouse, 1962). Because of introduced predators, all but the Sooty Terns and a few *Gygis* abandoned the main island and retreated to Boatswainbird Islet, a 96-meter (315 ft) high trachytic monolith, roughly 4000 m² in area, lying about 250 meters off the eastern side of the main island. Most of the island's remaining populations of tropicbirds (*Phaethon aethereus*, *P. lepturus*), noddy terns (*Anous stolidus*, *A. tenuirostris*), Fairy Terns (*Gygis alba*), and petrels (*Oceanodroma castro*) are also found on this crowded refuge and adjacent cliffs. Only large deposits of guano and dung-whitewashed rocks, especially in the area between Sisters Peak and English Bay, remain as mute testimony of the former great abundance of the seafoal of Ascension. In the vicinity of the fumaroles may be found guano and numerous rocks whitened on their leeward side (Figure 3a), and in crevices in the rough lava, skeletons and even feather shafts of boobies (*Sula dactylatra*) are occasionally encountered.

How did *Atlantisia elpenor* survive in its seemingly hostile environment? What role did it play in the island's relatively simple ecosystem? Upon what did it feed? The island's poor flora could hardly have provided enough, if any, suitable seeds or fruit; nor, presumably, was there ever much of an invertebrate fauna associated with this flora to provide it with sustenance. It is possible that some birds may have been able to glean a little food from the few beaches available for foraging, but these very small areas could hardly sustain a viable population of any bird. Furthermore, the only indications of the bird have come from the interior of the island. Mundy's (Temple and Anstey, ed., 1936) account implies that their birds were taken up on the mountain. The fumaroles are about 3 km from the nearest beach, over rough country—a long trip for a flightless bird. The locality south of South Gannet Hill, where Ashmole (1963a) collected a tarsus of *A. elpenor*, is about 1 km from the very small beach at Mars Bay and well over 2 km from the nearest suitable beach at Southwest

Bay. The species must have been fairly numerous, as evidenced by the abundant remains in the fumaroles and the fact that Mundy's men could catch a half-dozen individuals in one afternoon's foray.

It is obvious that there must have been a good many rails in the neighborhood of the fumarole and that they were finding food in the vicinity. The most probable explanation is that *A. elpenor* was a scavenger in the large colonies of seabirds. During the process of feeding, the young and adults of boobies and terns often drop food. Thus, the rails would have had an ample supply of pelagic fish, squid, and crustacea available to be picked up, or perhaps even stolen directly, not to mention an abundance of seabird eggs, which were no doubt taken as well. In the carcasses of birds on Boatswainbird Islet, I found numerous dermestid beetles which are probably an original element in the fauna and these could well have provided an additional food source for the rails. With the bird remains in both fumaroles were numbers of dipterous pupae cases which would indicate that flies and maggots were abundant. The Laysan Island Rail (*Porzanula palmeri*), which lived in a situation somewhat similar to that of *A. elpenor*, was observed to eat the eggs of seabirds and maggots from carcasses (Rothschild, 1893). The Spotless Crake (*Porzana tabuensis*) has been seen to eat petrel eggs in the Kermadec Islands (Soper, 1969), so there is ample precedent among rails for using seabird colonies as food sources. In a different order, adults and young of sheathbills (*Chionis*) during the breeding season subsist almost entirely on krill regurgitated by penguins (Jones, 1963) and seem particularly well adapted to this semi-parasitic existence. As there is seabird nesting activity the year around on Ascension (Stonehouse, 1960:213), the rail would have been able to reap an abundant harvest throughout the year in its commensal role.

Judging from the old reports and the guano that still remains, the seabird population of Ascension was very large, and one might assume a correspondingly large population of rails. Predation would certainly not have been a limiting factor under natural circumstances. The only possible predator of *A. elpenor* would have been the frigatebird *Fregata aquila*, a species that does prey to a certain extent on the chicks of Sooty Terns. The agility and speed of rail chicks and adults,

plus their relative scarcity in comparison to more easily obtained food would certainly have precluded their capture by frigatebirds on any but the most exceptional of conditions.

Unfortunately, we know nothing of the nesting of *A. elpenor*. The only typically suitable nesting cover would have been on Green Mountain and adjacent vegetated areas. The birds perhaps could also have nested in small sheltered crannies in the lava flows of the lowlands, using the sparse grass and possibly feathers to construct a nest. Again, *Chionis* provides a fine example, as it nests in rocky holes and lines its nest with feathers, eggshells, and bones of penguins (Jones, 1963).

One factor that is more difficult of explanation is the seeming ability of the rails to cope with the almost complete lack of fresh water on the island. The only more or less permanent sources of water are on Green Mountain. The nearest of these to the fumaroles is a small seepage area (Dampier's Drip), the result of an accumulation of water above an impermeable, compact layer of iron oxide (Darwin, 1844), which is 3.2 km away. South Gannet Hill is even farther from a source of fresh water. Rain does not collect in any appreciable amounts in the porous rocks and soil, and rainfall in the area of the fumaroles, for instance, is very slight anyway. *Atlantisia elpenor* probably ingested regurgitated invertebrates such as squid, which are isotonic to seawater, making some mechanism of salt excretion a necessity. In the salt-marsh dwelling rail *Rallus longirostris*, the interorbital bridge is narrowed to accommodate hypertrophied supra-orbital glands which function in the excretion of salt. The much narrowed interorbital bridge of *A. elpenor* is a good indication that its supraorbital glands were equally well developed. The birds, therefore, probably derived their water solely from their food.

With the coming of man, *Atlantisia elpenor* was a doomed species. As mentioned, goats were an early introduction to the island, although they probably had little effect on the avifauna. At some unknown time, rats and mice made their appearance. They were present by 1754 (La Caille, 1763) and Osbeck (1771, II:84) felt that they came to the island with the wreck of William Dampier's ship *Roebuck* in 1701, although they may well have reached shore previously with vessels stopping for sea turtles or other supplies. The rats at least

must soon have made inroads on the population of ground-nesting rails and probably some of the seabirds as well. Kepler (1968) has documented the grisly effects of direct predation by *Rattus exulans* on seabirds in the Pacific.

Just how long after 1656 the Ascension rail survived is not known. If present, its numbers must have been considerably reduced by the 1700s as the species was never reported again. If any persisted into the 19th century they could never have survived the *coup de grace* administered by the British who introduced cats for rodent control soon after 1815. By 1823, feral cats were in abundance and by the 1860s this vicious scourge had eliminated all but the Sooty Terns from breeding in significant numbers on the main island (Stonehouse, 1962:111-113). Thus, the rail and its source of food were both destroyed.

Vagrant Rallids

In recent times, three species of rallids have found their way across hundreds of miles of open ocean to Ascension. The first of these to be reported was a gallinule "killed with a stick near the summit of the island" in July 1836 (Darwin, 1841:134) and which was made the type of a new species "*Porphyrio simplex*" (Gould, in Darwin, 1841). Sharpe (1894) synonymized this with *Porphyryula parva* (= *P. flavirostris*), an uncommon South American species, which has not otherwise been recorded as an ocean-crossing vagrant. Gould's description is of an immature bird and does not tally with the appearance of *P. flavirostris* while the measurements given are too small for *P. martinica*. Therefore, I think that it is highly likely that this specimen represents the African species *P. alleni*. An immature specimen of *Porphyryula alleni* was taken on Ascension on 27 May 1920 and reported by Lowe (1924). I have examined this specimen and confirmed its identity.

I have reported and discussed two unexpected instances of the occurrence of the American Purple Gallinule (*Porphyryula martinica*), both immatures, on Ascension in June in 1970 and 1971 (Olson, 1972).

Stonehouse (1960, 1962) records the capture of a juvenile Common Gallinule (*Gallinula chloropus*) at Mars Bay during the Bou expedition. Unfortunately, the bird was not made into a specimen

and later escaped, eliminating the possibility of a subspecific determination. In view of the fact that both American and African species of *Porphyryula* have occurred on Ascension, it would seem that *Gallinula chloropus*, which is native to both continents, could come from either direction. Stone-

house (1960:153) mentions a farmhand on Ascension who had seen other gallinules in previous years, and my own discussions with islanders imply that gallinules (probably of all three species) are of fairly regular occurrence there. The significance of these records is discussed later.

RAILS OF ST. HELENA

Beneath the upper and central green circle, the wild valleys are quite desolate and untenanted.

Darwin, 1846

Darwin's impression of St. Helena is as true today as it was in 1836, but at one time the desolate valleys were well tenanted with multitudes of birds. The island of St. Helena has undergone a drastic alteration of its fauna and flora since its discovery by man in 1502. At present there are only two species of landbirds (an endemic plover, *Charadrius sanctaehelenae*, and a gallinule) not introduced by man, and only a handful of seabird species remain. Such was not always the case.

The BOU Ascension expedition also visited St. Helena and while there collected a small series of bird fossils from several sites on the island. These and other collections, which were reported on by Ashmole (1963b), indicated that there were many other species of birds on the island in the past. The deposits from which these fossils came range in age from Pleistocene to recent. In 1971 I visited these same localities, discovered a few other sites, and collected thousands of fossil specimens, mostly of seabirds. All of these specimens are now in the National Museum of Natural History, Smithsonian Institution. These sites and most of the specimens will be described in detail in a later paper covering the entire former avifauna of the island. Here I will concern myself only with the rails. An assortment of fossils from Prosperous Bay and Dry Gut collected by Arthur Loveridge and forwarded to the Museum of Comparative Zoology also contains a few bones of rails and these are included in the following discussions.

Redescription and Relationships of *"Aphanocrex" podarces*

From the extensive sediment deposits at Prosperous Bay, the BOU expedition collected several

elements of a very large rail. These were subsequently examined by Wetmore (1963) and described as a new genus and species, *Aphanocrex podarces*. The material available to Wetmore consisted of a left tarsometatarsus (the type), one right and one left femur, a left tibiotarsus, a proximal right ulna, a distal left humerus, and a partial pelvis.

My own collections contain a number of specimens of this species from four localities in all parts of the island. From the same deposits on the east bank of the gorge at Prosperous Bay came a right and left tarsus, proximal and distal left tibiae, a right femur, a cervical vertebra, and a pedal phalanx. In addition, on the west bank I unearthed much of a skeleton of a single individual associated with the bones of a frigatebird (*Fregata* sp.). This specimen (USNM 175878) is represented by a right femur, right and left tibiae, the head of a fibula, right and left tarsi, seven pedal phalanges (including two claws), right and left humeri (both lacking distal ends), right ulna (lacking proximal end), right and left carpometacarpi, digit II phalanx I of the wing, right and left coracoids (both lacking the sternal ends), 3 cervical vertebrae, 2 fragments of pelvis, and a fragment that appears to be part of the posterolateral process of the sternum. In the MCZ collections are a right and a left femur, right ulna, proximal right tibia, and a fragmentary right tarsus. The Prosperous Bay specimens do not appear to be mineralized and are probably of no great age. Including the material examined by Wetmore, there are at least four, and very likely more, individuals represented from this site.

From the eroded washes of Dry Gut, near Bencoolen, I collected the following material of the large rail: two left femora and a proximal right femur, a proximal right tibia, three proximal right tarsi, a fragment of a distal left tarsus, a distal left humerus and a proximal left coracoid. There is a

distal right tibia in the MCZ collections. Some of these specimens are quite well mineralized and are of obviously greater age than those from Prosperous Bay. Not less than three individuals are represented from this site.

Near Sugarloaf Hill are aeolian deposits of calcareous sand that are much dissected by erosion. These are thought to be Pleistocene in age (Baker, 1970) and contain fairly abundant bird remains. Here I collected a single, well-mineralized and nearly complete right tarsus of *A. podarces*.

Ashmole (1963b) has described all of the above localities but listed remains of *A. podarces* only from Prosperous Bay. However, a worn proximal end of a right tibia (BMNH S/1963.25.24) from the Sugarloaf site which Ashmole (1963b:405)

thought "may represent another species of columbid," on examination proves to be from *A. podarces*, and in a lot of unidentified specimens collected from this site by the Bou, I found a distal left ulna of this species.

I found more bones of this species at one additional site that was discovered quite by accident. While walking along the well-used trail next to a small embankment immediately south of the old battery ruins in Sandy Bay Valley, I saw an avian tarsus which because of its size, location near houses, and new appearance, I assumed to be of a barnyard fowl or a pheasant. Picking it up out of force of habit, I was more than pleasantly surprised to find that it was a complete left tarsus of *A. podarces*. Further searching on this low hillside

TABLE 2.—Size comparison of the three species of *Atlantisia**

Characters	<i>A. podarces</i>	<i>A. elpenor</i>	<i>A. rogersi</i>
Cranial width	26.4 (1.96, 1.63)	16.2 (1.20)	13.5
Length mandible	— — —	40.5 (1.25)	32.3
Width interorbital bridge	10.7 (3.96, 3.60)	2.97 (1.10)	2.7
Length furcula	— — —	18.1 (1.20)	15.0
Length coracoid	27** (2.45, 1.73)	15.6 (1.42)	11.0
Length scapula	— — —	24.5 (1.22)	20.0
Length humerus	58** (2.93, 2.21)	26.3 (1.33)	19.8
Width head humerus	13.0 (3.25, 2.24)	5.8 (1.45)	4.0
Width shaft humerus	4.0** (4.00, 2.66)	1.5 (1.50)	1.0
Width distal humerus	9.1 (3.25, 2.33)	3.9 (1.39)	2.8
Length ulna	48.4 (3.56, 2.41)	20.1 (1.48)	13.6
Length carpometacarpus	35.5 (3.86, 2.57)	13.8 (1.50)	9.2
Length digit II phalanx 1	10.4 (2.81, 2.00)	5.2 (1.40)	3.7
Length ilium	— — —	30.0 (1.40)	21.5
Width pelvis	— — —	14.2 (1.22)	11.6
Length femur	66.3 (2.60), 1.92)	34.5 (1.35)	25.5
Width shaft femur	4.9 (3.06, 2.13)	2.3 (1.44)	1.6
Width distal femur	12.6 (3.07, 2.17)	5.8 (1.41)	4.1
Length tibia	108.5 (2.63, 1.96)	55.3 (1.34)	41.3
Width shaft tibia	5.3 (3.31, 2.41)	2.2 (1.38)	1.6
Width distal tibia	10.6 (2.94, 2.12)	5.0 (1.39)	3.6
Width head fibula	6.9 (3.14, 1.97)	3.5 (1.59)	2.2
Length tarsus	72.2 (2.97, 2.03)	35.5 (1.46)	24.3
Width head tarsus	11.1 (3.00, 2.09)	5.3 (1.43)	3.7
Width shaft tarsus	4.8 (3.00, 2.09)	2.3 (1.44)	1.6
Width distal tarsus	11.6 (2.90, 2.14)	5.4 (1.35)	4.0

*The numbers outside parentheses are the means for each measurement (except where there was only a single element available). The numbers in parentheses after *A. podarces* are the means of that species divided by the mean of *A. rogersi* and *A. elpenor* respectively; the number in parentheses after *A. elpenor* is the mean of that species divided by the mean of *A. rogersi*. Thus, for instance, we read that the cranial width of *A. podarces* is 26.4 mm, which is 1.96 times as large as *A. rogersi* and 1.63 times as large as *A. elpenor*, while the same measurement of *A. elpenor* is 16.2 mm, which is 1.20 times as large as *A. rogersi*. Shaft widths taken at the narrowest point. Pelvic widths measured across antitrochanters.

**Estimated.

disclosed the bones of other bird species and a left carpometacarpus, the shaft of a tibia, a right fibula, a cervical vertebra, a pedal phalanx, and a right quadrate of the large rail. By far the best find, however, was a complete cranium of this species. It unfortunately is fractured off at the naso-frontal hinge so that none of the bill or palate is present, but the remainder is nearly perfect, the parasphenoid rostrum, interorbital septum and ectethmoids being retained (Plate 1c). All of the specimens from this site appear very recent and are possibly from one individual.

With so much better material now available, it is possible to make more extensive comparisons. Wetmore (1963) in his analysis of the species compared it with *Aramides* and certain other large rails, for the purposes of description only. He did not suggest any relationships of the St. Helena bird other than to subfamily (Rallinae). A relative exists, however, but in all fairness one would hardly expect to look for the closest living relative of one of the largest species of the family in one of the smallest of the family that is also flightless and on an even more remote island over 1500 miles to the south. But with the perspective offered by the nearly intermediate-sized *A. elpenor*, the similarity of *A. podarces* to *A. rogersi* becomes apparent. These three species are so alike in most proportions (Table 3; Plate 10) and in most details of the skeletal structure and so recognizably different from related mainland genera, that in my opinion they must be regarded as congeners. *Aphanocrex* Wetmore then falls into synonymy with *Atlantisia* Lowe and its single species will hereafter be referred to as *Atlantisia podarces*.

The generic characters of *Atlantisia* I have set forth in Appendix 2. Here I will attempt to re-describe the species *A. podarces*, especially in relation to the other two members of the genus.

Atlantisia podarces is a large rail, among the largest of the family, but considerably more slender and less robust than is usual in the large flightless forms such as *Gallirallus* or *Nesotrochis*. In linear measurements it is double the size of *A. elpenor* and nearly thrice that of *A. rogersi* (Table 2) but is similar in proportions except that it appears to be slightly though consistently stouter, with somewhat longer wing elements (Table 3). The head, however, does not increase by the same proportion as body size, and, as in other birds, the

larger species has a proportionately smaller head. Inasmuch as volume increases as the cube of linear dimensions, the bulk of *A. podarces* must have been in the neighborhood of 8 times that of *A. elpenor* and 15–20 times that of *A. rogersi*.

The cranium (Plate 1c) of *A. podarces* is massive, about the size of *Aramides cajanea* and heavier than, though not as elongate as, *Gallirallus australis*. The interorbital bridge is wide (10.7 mm) and exceedingly thickened and inflated, being approached only by the ponderous *Tribonyx mortierii* in this respect. In comparison with *A. elpenor*, this wide bridge certainly indicates a much lesser development of the salt glands which reflects the abundant supply of fresh water on St. Helena. Apart from the interorbital bridge and the great disparity in size, the cranium of *A. podarces* is otherwise nearly duplicated on a smaller scale in that of *A. elpenor*. The great similarity in the shape of the scar for *M. pseudotemporalis superficialis* is especially striking. In *A. podarces* the cranium is more domed postorbitally than *A. elpenor*. The fossa for *M. adductor mandibulae* is deeper and the zygomatic area is enlarged, both, along with the reinforced interorbital bridge,

TABLE 3.—Comparative proportions of the three species of *Atlantisia**

Characters	<i>A. podarces</i>	<i>A. elpenor</i>	<i>A. rogersi</i>
Cranial width398	.470	.529
Length coracoid407**	.452	.431
Length humerus875**	.762	.776
Width head humerus196	.168	.157
Width shaft humerus060	.043	.039
Width distal humerus137	.113	.110
Length ulna730	.583	.533
Length carpometacarpus.....	.535	.400	.361
Length digit II phalanx I....	.157	.150	.145
Length femur	1.000	1.000	1.000
Width shaft femur074	.066	.063
Width distal femur190	.168	.161
Length tibia	1.637	1.603	1.620
Width shaft tibia080	.064	.063
Width distal tibia160	.145	.141
Length tarsus	1.089	1.029	.953
Width head tarsus167	.154	.145
Width shaft tarsus072	.066	.063
Width distal tarsus175	.157	.157

*Mean of each measurement from Table 2 for each species has been divided by the mean femur length of that species to obtain a proportion allowing the comparison of the relative size of each element.

**Estimated.

probably correlated with a heavier bill and more massive jaw musculature.

The quadrate of *A. podarces* is similar to that of *A. elpenor* save that the shaft of the otic process is wider.

The coracoid (Plate 6*d,e*) is quite large and heavy. Its head is much more massive than in *A. elpenor* or *A. rogersi* and the brachial tuberosity is turned internally and is not in a line with the shaft. The scapular facet is deep and cuplike in contrast to *A. elpenor* and *A. rogersi*. The stout shaft is bent and swollen at the midpoint, appearing almost pathological; but since both the right and the left coracoids of the same individual appear identical, this is probably the normal condition. From what remains, the sternocoracoidal impression seems to have been quite deep, more so than *A. rogersi* and unlike *A. elpenor* in which this impression is shallow.

The sternum of *A. podarces* is unknown except for most of a right posterior lateral process with an attached piece of sternal plate. This is wide and thickened and would seem to indicate a large, heavy sternum.

The head of the humerus (Plate 6*f,g*) is more bulbous, with the capital groove less transverse and closer to being parallel with the shaft than in *A. rogersi* and *A. elpenor*. The ligamental furrow is much deeper than in the latter two species. (See Wetmore [1963, pl. 9] for an illustration of the distal humerus). The ulna (Plates 6*h,i*; 10) of *A. podarces* is heavier than in *A. elpenor* or *A. rogersi*, with a larger internal condyle and deeper tendinal pit on the external condyle; the distal radial depression is not as deep as in *A. elpenor*. The carpometacarpus (Plates 6*j,k*; 10) is like that of *A. elpenor* but proportionately longer, with a longer, more tapered distal symphysis.

The femur (Plate 10; Wetmore, 1963, pl. 9) of *A. podarces* differs from *A. elpenor* and *A. rogersi* mainly in having the ligamental attachment above the fibular condyle rounder and deeper, with a prominent ridge around it. The fibula (Plate 6*c*) is essentially like that of *A. elpenor* but heavier and thicker. In *A. podarces*, the tibia (Plates 6*b,c*; 10) is very similar to *A. rogersi* and *A. elpenor* except that in dorsal view, the outer cnemial crest is thicker and curved more posteriorly, and the shaft is somewhat stouter. The tarsus (Plate 10; Wetmore, 1963, pl. 9) is of nearly identical pro-

portions to *A. elpenor*. It differs from that species and from *A. rogersi* in that the loop for the tendon of M. extensor digitorum longus is completely ossified, the posteriormost ridge of the hypotarsus is broad, flat, and more prominent, the scar for the attachment of the hallux is deeper but shorter and more rounded, and the internal trochlea is flared out farther medially.

The toes (Plate 6*a*) are long and strong (not as heavy as *Gallirallus*) with exceedingly long and sharp claws (longer than *Tribonyx mortierii*, *Gallirallus australis*, or any other rail I have seen). One claw core, which I assume by its size to be from the middle toe, is fairly straight and measures 18.5 mm in length. With its sheath it must have been well over 22 mm long. It composes 25.6 percent of the total length of the middle toe (with claw) whereas the claw of *A. rogersi* constitutes only 15.6 percent of the total length of the middle toe.

Of only the tarsus is there enough material to give some indication of individual size variation. These measurements are as follows: length 70.1, 72.4, 74.0; width of head 10.7, 10.7, 11.0, 11.4, 11.5, 11.6; width distal end 10.6, 11.4, 11.8, 12.2. Here, and in Tables 2 and 3, I have incorporated the measurements given by Wetmore (1963). Though there is little in these measurements to indicate the extent of variability in size, visual comparison of some of the elements (for instance the proximal tarsi from Dry Gut) shows a discernible difference in individual dimensions and this was likely correlated with sex.

A Second Species of Extinct Rail

From three of the four major collecting localities on St. Helena I uncovered numerous remains of a second species of flightless rail, much smaller than *A. podarces*. Considering the relative abundance of this species in these deposits, it is somewhat surprising that it had not been discovered before, but Ashmole (1963b) mentions no such bird.

Prosperous Bay (deposits on the east side of gorge): In addition to the nearly complete skeleton which I have designated as the type, the following elements were found: 3 right (one is a shaft only) and 1 left femora, 2 complete and 1 distal right tibiae, 1 distal left tibia, 3 right and 1

left tarsi, 1 left humerus, 1 distal mandible, 1 rostrum and the tip of another. Another individual, from the west bank of the gorge, is represented by a right humerus, distal mandible, and the left posterior lateral process of the sternum. In the MCZ collections are the proximal and distal ends of a left tibia and a distal right tibia. At least five individuals are included in the Prosperous Bay collections.

Dry Gut: One complete and 1 proximal right femur, 1 complete and 2 distal left femora, 2 distal and 2 proximal left tibiae, 2 distal and 2 proximal right tibiae, 1 complete and 2 distal left tarsi, 1 proximal right tarsus, 1 radius, 1 right carpometacarpus, and 1 left lower jaw articulation. In the MCZ collections is a complete right femur. A minimum of four individuals from this site.

Sandy Bay Valley: An articulated right tibia and tarsus, the latter with ossified tendons associated (later lost); 1 right and 1 left femur, 2 complete and 1 distal left tibiae, 1 proximal right tibia, 2 right and 1 left humeri (the latter from a juvenile). These remains represent not less than three and probably at least four individuals.

This small rail is a short-billed crane-like form. As the other landbirds of St. Helena of known derivation are African, and the prevailing winds on St. Helena are from the southeast, it is logical to expect the small rail also to be of African origin. However, the American species *Porphyryla martinica* has now been taken at least twice on St. Helena (see below). The small St. Helena rail does not agree with any of the species examined of the American genus *Laterallus*, as these all have markedly longer and more slender hindlimbs and pelvis. It in no way agrees with *Sarothrura*, being heavier throughout, longer billed, and having a different palatal structure among other things. It is much smaller than *Aenigmatolimnas*, *Crecopsis*, *Crex*, and *Limnocolax* and does not have the peculiar bill shape or long legs of *Aenigmatolimnas*, nor the narrow, twisted nasal bar of *Crecopsis* and *Crex*, nor any of the hindlimb modifications of *Limnocolax*. Of African "crakes," this leaves only the genus *Porzana*, with which it quite agrees in bill shape, palate, pelvis, and hindlimb structure. It represents an undescribed species.

Porzana astrictocarpus, new species

HOLOTYPE.—Nearly complete skeleton (Plates 7, 8, 9). Vertebrate paleontological collections of the National Museum of Natural History, Smithsonian Institution (USNM 175893). Collected from the bank of a dry wash on the east side of the lower portion of Prosperous Bay Valley, St. Helena Island, South Atlantic Ocean (approximately 15°56'18"S; 5°38'5"W), on 12 June 1971 by Storrs L. Olson. The specimen consists of a complete skull (braincase crushed) that includes the palate, sclerotic plates, hyoids, lacrimals, pterygoids, and right quadrate; complete mandible; pelvis (lacking pubic bones); both wings (lacking only digits I and III, radiales, and one ulnare); both scapulae; left coracoid; proximal two-thirds of left clavicle; complete right hind limb including all phalanges and ossified tendons; left femur lacking only the head. The bones are dark tan in color and are only slightly, if at all, mineralized. Unlike most of the specimens that were picked up from the surface or partially embedded in the fine silt in the upper layers of the Prosperous Bay deposits, the type was firmly embedded in an eroded embankment under nearly 2 meters of cindery sediment. In the skull and some of the other bones are minute holes or scars, the edges of which are reddish brown in color and appear almost as if burnt. Other specimens from Prosperous Bay bear these same sort of marks which may have been made by rootlets formerly growing around the bones. The type-specimen is remarkable in retaining almost all the important bones but totally lacking the ribs, vertebrae, and sternum. Since most of the toe bones were found in direct association with the skull, the specimen was probably buried doubled backwards on itself and the ribs, vertebrae and sternum later washed away. The left femur, the only element of that leg found, was discovered in two pieces washed out onto the bottom of the gully, a few inches directly below the rest of the skeleton.

PARATYPES.—The paratypal series consists of USNM 175894–175935, 175945–175949, and 175960.

RANGE.—St. Helena Island, South Atlantic Ocean.

STATUS.—Extinct, probably exterminated after the island's discovery in 1502.

ETYMOLOGY.—Latin, *arstrictus*, drawn together,

plus *carpus*, referring to the peculiar approximation of the metacarpals in this species. The specific name is considered a noun in apposition.

DIAGNOSIS.—A small, flightless *Porzana*; pelvis, and hindlimb intermediate in size and proportions between *Porzana pusilla* and "*Porzanula palmeri*" (I do not consider *Porzanula* separable from *Porzana*, see below); wings and pectoral girdle reduced to the same extent as *P. palmeri* (for comparisons see Table 4 and Plate 11); interorbital bridge with longitudinal furrow; proximal intermetacarpal space constricted; distal femur much expanded.

DESCRIPTION.—The only available skull, that of the type (Plate 7a,b) is slightly larger than *Porzana pusilla* and some specimens of *P. palmeri* and has the typical short bill of a *Porzana*. The nasal bar is wide and flat. In *P. palmeri* the bill is longer than *P. pusilla*, with a longer premaxilla and more elongate nostril. The St. Helena bird falls exactly between these two species in these respects and

is slightly more robust than either. A longitudinal furrow creases the interorbital bridge of *P. astrictocarpus*; only a hint of this may be seen in *P. palmeri* and it is not found elsewhere in *Porzana*. The postorbital process is blunt, ventrally directed and with a distinct depression above it. The palate is very similar to *P. palmeri*. Fortunately, the right lacrimal of the type is complete (Plate 7d). This is nearly identical to that of *P. palmeri* save that the descending process is longer. It is similar also to *P. pusilla* except that in that species the horizontal process is straighter and does not curve outward and downward posteriorly. These three species differ from *Porzana albicollis*, *P. porzana*, *P. carolina*, and *P. fusca*, in which the lacrimal is wider with a short, anteriorly curved descending process.

The mandible (Plate 7a,c) is a little heavier and more expanded in the articular regions, and in medial view is higher than in either *P. palmeri* or *P. pusilla*. The symphysis, which is rather long

TABLE 4.—Selected skeletal measurements of three related species of *Porzana* (shaft widths taken at narrowest point; pelvic widths across antitrochanters)

Characters	<i>P. astrictocarpus</i>			<i>P.</i>	<i>P.</i>
	<i>n</i>	<i>min.</i>	<i>max.</i>	<i>pusilla</i> (<i>n</i> =2) <i>mean</i>	<i>palmeri</i> (<i>n</i> =8) <i>mean</i>
Cranial width	1	—	—	14.9	13.3
Length skull	1	—	—	39.8	39.1
Width interorbital bridge	1	—	—	3.4	3.0
Length mandible	1	—	—	29.7	29.9
Length coracoid	1	—	—	12.4	10.8
Length scapula	1	—	—	20.0	19.4
Length humerus	4	19.8	20.9	20.2	20.0
Width head humerus	4	4.0	4.3	4.2	4.2
Width shaft humerus	4	1.2	1.3	1.3	1.2
Width distal humerus	4	3.0	3.2	3.1	3.0
Length ulna	1	—	—	14.8	14.9
Length radius	1	—	—	13.3	13.7
Length carpometacarpus	2	10.8	11.3	11.0	10.4
Length ilium	1	—	—	25.0	22.8
Width pelvis	1	—	—	12.2	12.0
Length femur	8	25.3	29.0	27.0	25.7
Width shaft femur	10	1.8	2.2	1.9	1.9
Width distal femur	10	4.3	5.1	4.6	4.1
Length tibia	5	42.4	44.5	43.3	38.5
Width shaft tibia	7	1.7	2.0	1.9	1.7
Width distal tibia	9	3.6	4.2	3.9	3.5
Length fibula	1	—	—	22.8	22.7
Length tarsus	7	26.2	27.9	27.0	23.5
Width head tarsus	7	3.9	4.1	4.0	3.6
Width shaft tarsus	5	1.9	2.1	2.0	1.8
Width distal tarsus	5	4.1	4.4	4.2	3.9

in *P. palmeri* and short in *P. pusilla* and other species of *Porzana*, is intermediate in *P. astrictocarpus*.

The coracoid (Plate 8*b,c*) is, of course, greatly reduced compared to flying forms such as *P. pusilla*, and is longer and more slender than in *P. palmeri*. In *P. palmeri* the procoracoid process is not as broad, and the fenestra is placed higher than in *P. astrictocarpus*. The head is narrow, in line with the shaft and not deflected internally in *P. astrictocarpus*. The sterno-coracoidal process is relatively high and blunt; sternal facet with a well-developed flange on internal side. Sterno-coracoidal impression not particularly deep but with a prominent thickened ridge on its antero-dorsal margin for the attachment of the sterno-coracoid ligament.

Of the furcula there is only part of the left clavicle (Plate 8*b*). This is a slender rod with a knob at the coracoidal extremity.

The scapula (Plate 8*a*) is smaller even than in *P. palmeri*, which it resembles in having the acromion rounded and blunt whereas this process is longer and pointed in other species of *Porzana*. *Porzana palmeri* differs from *P. astrictocarpus* in having the glenoid facet larger and more expanded. In *P. astrictocarpus* no vestige remains of the tubercle for the attachment of the *M. expansor secundariorum* tendon, although this tubercle is well-developed in volant species of *Porzana* and a small bump is still to be found in *P. palmeri*.

Of the sternum there is known only a left posterior lateral process with a small piece of the sternal plate attached. The anteriormost part of the sternal notch is indicated. The lateral process is very short and the notch shallow (Figure 5), much more so even than in *P. palmeri*. This abbreviated condition obtains in most flightless rails. I would estimate from this scrap, that the whole sternum of *P. astrictocarpus* was smaller than that of *P. palmeri*.

The humerus (Plate 8*d,e*) is identical to that of *P. palmeri* in size and proportions, although the distal end is slightly wider. In *P. astrictocarpus* there is a distinct longitudinal scar immediately below the median crest of the internal tuberosity; this is absent in *P. palmeri*. The olecranal fossa is wider and shallower and the distal condyles reduced in contrast to *P. palmeri* and *P. pusilla*. The brachial depression is much deeper than in the last-named species.

The ulna (Plate 8*f*) is nearly identical in size and details to *P. palmeri* but the shaft is not as stout, external condyle slightly larger and rounder, and brachialis impression deeper. The radius (Plate 8*f*) is very near in size to *P. palmeri* from which it does not otherwise differ.

The carpometacarpus (Plate 8*g,h,i*) is extremely similar to that of *P. palmeri* except in one singular detail. The proximal half of metacarpal III is expanded dorsally and from the opposite side, on metacarpal II, an excrescent ridge extends toward the expansion of metacarpal III, thus narrowing the proximal half of the intermetacarpal space to a small slit. In the more robust carpometacarpus from Dry Gut (Plate 8*i*), one of the projections of metacarpal II has succeeded in fusing with metacarpal III, leaving a small foramen proximally. This condition cannot be a pathological one, as it occurs identically on both sides of the type and in an entirely different specimen from a different locality. I have not seen a like condition in any other rail. On the dorso-medial surface of the left carpometacarpus of the type was a short portion of ossified tendon, doubtless of *M. flexor digitorum profundus* which is ossified in this area in other rails.

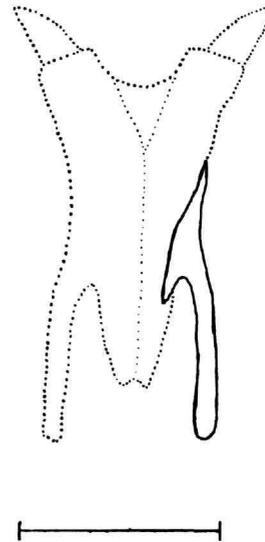


FIGURE 5.—Reconstructed sternum of *Porzana astrictocarpus*. Portion outlined in black is drawn from the specimen of posterior lateral process USNM 175907, Prosperous Bay, St. Helena. Dotted lines indicate the hypothetical shape of the rest of the sternum as extrapolated from the fragment. Scale=10 mm.

The pelvis (Plate 9a,b) is of interest for its intermediacy. It is neither as long and narrow as in *P. pusilla*, nor as short and broad as in *P. palmeri*. Other than in these general proportions, the pelvis of these three species do not differ appreciably.

The femur, also intermediate in proportions (Plate 9c,d), is not as long and slender as *P. pusilla* or as short and stocky as *P. palmeri*. However, it differs conspicuously from these and any other crakes in the much expanded distal articulation. This appearance is for the most part due to the greatly enlarged fibular condyle which projects farther laterally and posteriorly than in any related species. The trochanter is better developed also. The posterior intermuscular line is more prominent and displaced medially which may be correlated with the apparent lateral rotation of the entire distal end of the femur.

The fibula (Plate 9e) is the size of that of *P. palmeri* but the head is somewhat heavier, probably in accordance with the larger fibular area of the femur. Distally it is more attenuated than in *P. palmeri*.

The tibia (Plate 9e,f) presents intermediate proportions. It is shorter and stockier than *P. pusilla* but not as short and heavy as *P. palmeri*. The proximal end is broader than either. Associated with the tibia of the type were six ossified tendons. Three of these were ascertained to be the tendons of *M. peroneus brevis*, *M. tibialis anticus*, and *M. extensor digitorum longus*. On the tibial shank the following tendons may also be ossified in the Rallidae: *M. flexor perforans et perforatus digiti III*, *M. flexor perforatus digiti II*, *M. flexor hallucis longus*, and *M. flexor digitorum longus*. Any of these may have been ossified in *P. astrictocarpus*.

The tarsus (Plate 9g,h,i) is stout but not as short as in *P. palmeri* or as long and slender as in *P. pusilla*. The internal trochlea extends out farther medially and posteriorly in *P. astrictocarpus* and in *P. palmeri* than in *P. pusilla*, making the distal end wider. The medial side of the hypotarsus is strongly excavated in *P. astrictocarpus*, even more so in *P. palmeri*, and less so in *P. pusilla*. Of the seven ossified tendons associated with the type tarsus, five, from their location before removal, are known to represent the tendons of *M. extensor digitorum longus* (strongly ossified and triradiate distally), *M. flexor hallucis longus*, *M. flexor digitorum longus*, *M. flexor perforatus digiti II*, and

M. flexor perforatus digiti III. The other two are probably of *M. flexor perforans et perforatus digiti III*, and *M. flexor perforatus digiti IV*.

Extant Rails

THE RESIDENT *Gallinula*.—The presence of the Common Gallinule (*Gallinula chloropus*) on St. Helena was recorded as early as 1715 by Beekman (in Gosse, 1938:140). Melliss (1870) describes a bird, undoubtedly of this species, that was captured in Lemon Valley. Kinnear (1943) reported a specimen from Fisher's Valley and referred it to the African subspecies *G. c. meridionalis*. Benson (1950) mentions Kinnear's record but did not see the species himself. A single bird and a pair with young were seen by Haydock (1954:69) in Fisher's Valley and he mentions others seen in James Valley. The Fisher's Valley stock he says, "have, according to reports, only been there some eight years," but I am inclined to doubt this seriously. Under the name *Gallinula angulata* (a lapsus for *G. chloropus*) Loveridge (1964:430) relates that this species "is now known to nest in Sandy Bay and elsewhere," and informed me (in litt.) that the birds have been a constant feature of Fisher's Valley since his arrival on the island in 1957 and that he has seen a nest. Basilewsky (1970) noted the species at Bradley's Ruins (lower Fisher's Valley) and less frequently in James Valley.

I found this species abundant throughout the length of Fisher's Valley, the marshes and sodden yam patches of which I never traversed without seeing and hearing at least a dozen. I also heard them calling from the bottom of Lemon Valley. As a nesting bird it is well known to the islanders who call it "waterduck" or "waterhen" and I was told of its being common in Sandy Bay Valley and of an individual seen at Lemon Tree Gut. The species surely occurs throughout the island wherever there is suitable habitat. During my stay on the island I heard persistent and repeated rumors from a number of sources that another, similar species of bird with fully webbed feet also occurs on the island. Although skeptical I offered a substantial reward for a specimen, but I had no takers. I am quite satisfied that such a bird is imaginary. The legend may have arisen as a result of seeing the *Gallinula* swimming.

Four gallinules from Fisher's Valley that I col-

lected, in their small size and dark coloration, agree well with the African race *G. c. meridionalis*. There has been no decrease in flying ability, as the birds often took to flight readily and flew strongly. Considering the present populations of humans, dogs, and cats on the island, any trend towards flightlessness would no doubt be of great disadvantage. *Gallinula chloropus* on St. Helena is definitely a well-established, self-introduced, breeding bird.

ERRANT SPECIES OF *Porphyryula*.—Two species of purple gallinule have occurred on St. Helena as vagrants. The first record of the genus from the island is an immature specimen of the African species *Porphyryula alleni*, collected July 1938 and reported by Kinnear (1943). I have seen this specimen and can confirm that it was correctly identified. Loveridge (1964) mentions six occurrences of immature *Porphyryula* on St. Helena between 1959 and 1964. Two of these were identified from photographs by R. E. Moreau as *P. alleni*. Another individual (taken June 1964 in Jamestown), also identified as *P. alleni*, was preserved as a skeleton and is now in the collections of the Museum of Comparative Zoology (MCZ 5046). On measuring this specimen, however, I find it is too large for *P. alleni* (e.g., tarsus 60.2 mm) and it must therefore be referred to *P. martinica*. This is further corroborated by my collection of an immature individual of *P. martinica* on 10 June 1971 in Fisher's Valley (Olson, 1972).

As at Ascension, it is now certain that both species of *Porphyryula* occur at St. Helena. The records from both islands have nearly all been of subadult birds that appeared between May and September. Loveridge was under the impression that *P. alleni* might be breeding on St. Helena, but there is no evidence for this and I feel quite certain that no *Porphyryula* breed on any of the South Atlantic islands (see below).

Haydock (1954) discusses a bird that he saw on St. Helena that he thought to be *Porzana porzana*. Although possible, in the absence of a specimen the record is best considered questionable.

Environment and Lives of the Rails

St. Helena provided a much more equable environment for terrestrial birds than Ascension. It is larger (122 km²; 47 mi²) and displaced farther eastward and thus closer to West Africa than is

Ascension. The oldest rocks from the island have been dated at 14.3 ± 1.0 million years (Baker, 1970) so it is also considerably older than Ascension.

A rugged island, entirely volcanic in origin, St. Helena juts up abruptly out of the sea and is characterized by steep cliff faces and deeply dissected valleys. Access to the sea is limited to a few valley mouths. Melliss (1875:221) quotes the noted botanist Hooker as saying that the island "when discovered . . . was entirely covered with forests, the trees drooping over the tremendous precipices that overhang the sea." This must be to a certain extent an exaggeration of the facts. Today, much of St. Helena is barren and arid. The areas below 500 meters (1500 ft) receive little rainfall (Jamestown, near sea level, averages a little over 200 mm per year) and there is no reason to assume that they were much wetter in the immediate past. That there are a number of endemic invertebrates and one endemic species of bird that are adapted to these open, arid areas argues convincingly against the entire island having been covered with forest in the past. However, the areas above 500 meters, the "green belt," receive nearly four times as much precipitation and were once well vegetated with many endemic plants (Decelle, 1970). There are abundant clear streams of fresh water originating in this higher portion of the island.

After the discovery of St. Helena in 1502, man systematically set about his usual destruction. The forests were decimated by goats and by cutting for timber and fuel for lime burning. Hogs, rats, cats, and mice set upon the native avifauna, extirpating about 15 species. Today only two native landbirds (counting *Gallinula*) and six seabirds breed on the island and offlying rocks and the native vegetation is reduced to a small area on the central ridge, which is fast being encroached upon by introduced species of plants. With the destruction of the native vegetation, a number of species of endemic land snails also became extinct.

Unlike *Atlantisia elpenor*, there is no written record of either *A. podarces* or *Porzana astrictocarpus*. We can only guess at what their niches might have been. In contrast to the Ascension rail, the St. Helena rails shared their environment with other landbirds, for on the island there were at least a plover, a dove, and a large species of hoopoe present in addition to the rails (Olson, in prep. (b)).

St. Helena supports a much larger and richer fauna of terrestrial invertebrates than Ascension. This fauna was extensively collected by members of the Musée Royal de L'Afrique Central, Tervuren, Belgium, the first of several volumes of their results having already appeared (e.g., Basilewsky, 1970). In addition, the island once was a major breeding station for thousands of seabirds—almost all of which have now been extirpated. There were probably at least six species of shearwaters and petrels, two frigatebirds, boobies, and Sooty Terns breeding in large colonies on the mainland (Ashmole, 1963b; Olson, in prep. (b)). As on Ascension, these immense seabird colonies would have provided a veritable cornucopia for rails, and at least *Atlantisia podarces*, by virtue of its large size, would have been well equipped to turn this source to its advantage. The *Porzana*, like its counterpart on Laysan, also may well have taken sustenance from the seabird colonies. Another prime source of food would have been the diverse fauna of pulmonate snails formerly found on the island. Wollaston (1878) lists about 20 species of land snails in 5 genera, most of which are known only from subfossil remains. Snails are a favored food item of many continental rails and seem to be especially preferred by members of *Porzana*. They very likely were taken by *P. astrictocarpus*. Some of the St. Helena snails were far too large to be utilized by *P. astrictocarpus* but may well have been preyed upon by *A. podarces*. The great disparity in size of the two rails would have precluded much overlap in their respective food items.

Two morphological adaptations of *A. podarces* seem to be directly correlated with the nature of the island's terrain. St. Helena is possessed of many valleys that are exceptionally deep and precipitous. *A. podarces*, being a large and heavy flightless bird, would likely have had difficulty getting out of such steep-sided, rocky ravines. But as we have seen, compared to other large flightless rails from islands with more even terrain, *A. podarces* has proportionately better developed wings (Table 3) and much longer claws on the toes (Plate 6a). These I believe may have been adaptations for climbing and fluttering up the valley walls. In the National Zoological Park in Washington, I have seen the African rail, *Limnocolax flavirostris* (ordinarily a

very aquatic species), scale a nearly vertical rock face, accomplishing this feat with much fluttering of its wings, although never actually flying. Hagen (1952:197) observed that *Atlantisia rogersi* used its wings "as brakes when jumping down small declivities," and one in captivity climbed tussock stems "fluttering with the wings to aid the climbing." *Atlantisia podarces* probably used much the same technique. *Porzana astrictocarpus*, weighing approximately $\frac{1}{16}$ as much as *A. podarces*, would not have been in as much need of pronounced climbing adaptations.

The extinct rails of St. Helena would have had but very few natural enemies. Frigatebirds may have presented a possible, but not too likely, hazard to chicks of either species or even adults of the *Porzana*. On the other hand, *A. podarces*, being of such large size, very conceivably may have consumed both the young and eggs of *P. astrictocarpus* on occasion. Although there is no direct proof of the cause of the extinction of the two endemic rails of St. Helena, there can be little doubt that they survived up until man's arrival whereupon they succumbed to predation by man and his domestic animals and to their respective destruction of the habitat.

The establishment of *Gallinula chloropus* is an obviously recent event which probably did not occur until after man's coming. First of all, the nature of the marshy vegetation in the valleys it now occupies is the result of changes brought about by man and livestock. For instance, E. L. Jackson (1905:26) informs us that "shortly after the establishment of the colony [ca 1660] a species of yam had been introduced from Madagascar. Planted in the valleys it thrived wonderfully well, as it requires a constant soak of water . . ." Today this yam is one of the dominant plants of the marshy valley bottoms and its growths are the constant resort of gallinules. Secondly, had the gallinules attempted to colonize the island prior to the extinction of *A. podarces*, they most likely could not have competed successfully against such a well-established and adapted species. The recency of the arrival of *Gallinula chloropus* is testified to by the fact that it does not sensibly differ from the African mainland form and by its total absence from the fossil record.

RAILS OF THE TRISTAN DA CUNHA GROUP AND GOUGH ISLAND

In the remote Tristan group, consisting of the three associated islands of Tristan da Cunha, Inaccessible, and Nightingale, and on Gough Island, removed some 400 km SSE of Tristan, two vagrant and three endemic forms of rails are known. Although I have no new information concerning these birds, a short synopsis of them is included for the purposes of later discussion.

Easily the most interesting of the Tristan rails is the minute, flightless, *Atlantisia rogersi*, confined entirely to Inaccessible Island. A rail said to inhabit Inaccessible was described to members of the *Challenger* expedition in 1873 but they did not encounter it (Moseley, 1879). Nor was the Shackleton-Rowett expedition able to secure specimens of it in 1922 (Lowe, 1928:101). Not until 1923 did specimens collected by Rev. H. M. C. Rogers, then resident chaplain on Tristan, arrive at the British Museum where they were examined by Percy Lowe and briefly described as a new genus and species, *Atlantisia rogersi*, in honor of Rev. Rogers (Lowe, 1923). Lowe later (1928) gave a rather comprehensive treatise of the species, including anatomical notes and a color plate. The dark brown and black plumage of *A. rogersi* is fluffy and decomposed, appearing almost hairlike. The adults are variably barred with white or buffy on the flanks, thighs, wing coverts, scapulars, secondaries and even in the distal parts of the primaries, while the juveniles are entirely dark (Hagen, 1952). The iris is red in adults and dark brown in juveniles.

A fairly complete account of the life and habitat of this species has been given by Hagen (1952), and additional comments rendered by Elliott (1957). Uninhabited Inaccessible Island is small (12 km²) and is about 40 km removed from the main island of Tristan and 22 km from Nightingale. It is well vegetated, especially with dense fern and tussock-grass (*Spartina arundinacea*). In the past it has suffered somewhat at the hand of man and at one time was said to have been overrun with wild pigs and goats as well as being fired by sealers. By 1937, however, there were only seven sheep and one pig on the island, rats and mice apparently not having reached it (Hagen, 1952:210). The rails appear not to have been detrimentally affected. Hagen (1952:197) estimated the popula-

tion of *A. rogersi* at around 1200, but Elliott (1957:578) felt that this was much too low and that the figure would lie somewhere between 5000 and 10,000. The rails are found in small groups throughout the island in the dense fern and tussock growth, and communicate by various twittering trills. Three stomachs examined by Hagen contained seeds, berries, and insects. *Atlantisia rogersi* is not known to feed on the eggs or regurgita of seabirds even though Inaccessible is the breeding station for thousands of petrels and penguins. The rails are preyed upon, one being recovered by Hagen from the stomach of a Skua (*Catharacta*), but such predation is probably not significant.

The first railid described from the Tristan group was a gallinule "closely allied in general aspect to our Common Water-hen (*G. chloropus*), though readily distinguishable on accurate comparison" (P. L. Sclater, 1861:260). P. L. Sclater received specimens of this bird in 1861 "brought from the island of Tristan d'Acunha to Cape Town by a person formerly in the service of Sir George Grey" the then governor of Cape Colony who forwarded the birds (skins, specimens in spirits, and a living example) to London. The species was described as being slightly larger than *Gallinula chloropus*, with darker plumage, heavier legs and pelvis, reduced wings and sternum, and stouter bill, and was given the name *Gallinula nesiotis* by Sclater.

A similar bird was later collected on Gough Island, over 400 km from Tristan, by George Comer. This was described as a new species, *comeri*, by Allen (1892) who erected for it and *nesiotis* the genus *Porphyriornis*, based solely on the shape of the bill and the heaviness of the feet. Ripley (1954) quite justifiably sank *Porphyriornis* into *Gallinula* and considered *comeri* merely as a subspecies of *nesiotis*. Rand (1955), who saw no specimens, followed suit in the latter decision but was ambiguous about whether the species may have been derived from *Gallinula*, *Porphyryula*, or *Porphyrio* (let me emphatically interject here that the latter two genera have no close relationship to the Tristan-Gough birds) and he maintained the genus *Porphyriornis*. Voous (1961) and especially Eber (1961) have given comprehensive accounts of the Gough bird, *comeri*, both concluding that the spe-

cies was clearly derived from *Gallinula* stock and should be included in that genus. With this there can now be little dispute.

Eber (1961:254), however, felt that it was wholly improbable that two such similar flightless species as *G. nesiotis* and *G. comeri* could develop on islands so distant from one another. Because no specimens were taken on Tristan after 1861 and because of the "round about way" (*Umweg*) that the original specimens reached Sclater, Eber concluded that the original specimens of *G. nesiotis* actually came from Gough Island and that the species never existed on Tristan (thereby making *comeri* a junior synonym of *nesiotis*). But, what Eber overlooked or disregarded were the several early accounts of the island of Tristan that mention a flightless gallinule.

Beintema (1972) has presented a thorough summary of the old accounts of gallinules on Tristan, and a review of the history of extant specimens attributed to *G. nesiotis*. A report of a gallinule on Tristan earlier than any cited by Beintema may be found in Pike (1873:34) who mentions the visit of a Captain Patten from the sealer *Industry* who stayed on Tristan from August 1790 to April 1791 and described there "a bird something like a partridge, only it is black, and cannot fly" as being "abundant." The accounts of Lambert (cf. Holdgate, 1958:19), Carmichael (1818), Earle (1832), Stirling (in Stoddart, 1971), and Gurney (1853) establish beyond doubt that a gallinule was resident on the island of Tristan da Cunha and was common enough to have played a fairly important role in the diet of the islanders.

In his study of the gallinule specimens allegedly from Tristan, Beintema (1972:112) concluded that only the skin of the type of *G. nesiotis* and two incomplete skeletons could be considered as definitely having been taken on Tristan rather than on Gough. He could find no external differences between *G. nesiotis* and *G. comeri* but reported that the smaller sterna and pelves of the two skeletons of *G. nesiotis* indicated a bird of "much less heavy build" than *G. comeri*. He felt that the two forms "obviously belong to the same species, *Gallinula nesiotis* Sclater (1861)" (Beintema, 1972:107).

What is known of the disappearance of *G. nesiotis*, late in the 19th century, is documented by Beintema (1972) and is presumed to have resulted from the combined depredations of cats, rats, man, and dogs. On the other hand, *G. comeri* on uninhabited Gough Island, still exists and in good numbers, despite a large population of introduced mice. Holdgate (1958) has given an account of this species in its native haunts. It is an inhabitant of the forest and tree-fern zones of the island but not the open mountain areas. Elliott (1957:579) also found the birds "very common in the boggy areas bordering the Glen" and observed them feeding on grass heads. Like *Atlantisia rogersi*, the Gough Island gallinule probably finds its only natural enemy in the skua.

The peregrine *Porphyrula martinica* once again is known as a regular vagrant to Tristan da Cunha. Rand (1955) has summarized numerous records of this bird, all apparently from the main island of Tristan. Voous (1962:110) adds another record, describing the species as a "regular visitor." As at Ascension and St. Helena, the birds are mainly immatures and occur during the northern spring and summer. The species is of such regular occurrence on Tristan that the natives even have a vernacular name ("guttersnake") for it (Hagen, 1952:201). There is no evidence of its breeding on the island, however.

W. L. Sclater (1911:94) discusses a specimen of what he describes as a quite young coot "very closely allied to *Fulica armillata* and *F. ardesiaca* from South America, though it presented some differences from those species," as having been obtained by a "Mr. Keytil" [sic] and forwarded to him by the director of the South African Museum. It is this same specimen that is referred to by Winterbottom (1958) as *Fulica armillata* and said to have been collected on Tristan and received from Keytel by the South African Museum in 1910. Winterbottom (in litt., to G. E. Watson, 21 Feb. 1972) reports that this specimen is currently under study by Beintema and "that it is an immature of one of the South American coots (definitely not *F. americana* . . . , though *armillata* is one of the possibilities)."

ORIGIN AND EVOLUTION OF THE SOUTH ATLANTIC RAILS

. . . imprison'd in the viewless winds,
And blown with restless violence round about
The pendent world.

Shakespeare
Measure for Measure
Act III, Sc. 1

The various facts previously outlined may be coordinated to arrive at a coherent explanation of the origins and relationships of the different groups of South Atlantic Rallidae. Each group contributes something different to this explanation and a fairly logical progression of ideas obtains. The distribution and status of the South Atlantic rails may be summarized as follows:

Ascension Island

Atlantisia elpenor (extinct endemic)
Gallinula chloropus (vagrant)
Porphyryla martinica (vagrant)
Porphyryla alleni (vagrant)

St. Helena Island

Atlantisia podarces (extinct endemic)
Porzana astrictocarpus (extinct endemic)
Gallinula chloropus (abundant breeding resident, recent colonizer)
Porphyryla martinica (vagrant)
Porphyryla alleni (vagrant)

Tristan da Cunha group

Atlantisia rogersi (resident endemic, Inaccessible Island)
Gallinula nesiotis (recently extinct endemic, Tristan)
Porphyryla martinica (regular vagrant, Tristan)
Fulica sp. (rare vagrant, Tristan)

Gough Island

Gallinula comeri (resident endemic)

Genus *Porphyryla*

The genus *Porphyryla* consists of three species. One of these, *P. flavirostris*, is a small form confined to South America. It does not assume the dark purple adult plumage of the other two species and does not seem to be given to oceanic wandering. *Porphyryla martinica* breeds from southern United States to northern Argentina and migrates out of the northern parts of its range in the winter. The species is a great wanderer. As we have seen, it is known as a more or less regular vagrant to Ascension, St. Helena, and Tristan da Cunha. It has also been recorded as a vagrant to Bermuda

(Bradlee and Mowbray, 1931), the island of South Georgia (Pereyra, 1944), the Falkland Islands (Bennett, 1935), the Azores (Bannerman and Bannerman, 1966), the Scilly Islands (Anonymous, 1960), the Galapagos (Lévêque, Bowman, and Billeb, 1966), the Pacific Ocean between the South American continent and the Galapagos (Castro and de Vries, 1970), and Clipperton Island in the Pacific (Ehrhardt, 1971:478). There have been no less than 12 records of this species from South Africa, all but two of which were immatures (for the most recent record and summary of references, see Broekhuysen, 1971). The similar but slightly smaller *P. alleni*, which might be considered as forming a superspecies with *P. martinica*, breeds in Africa south of the Sahara, and Madagascar, and is known to wander to southern Europe, islands in the western Indian Ocean and Gulf of Guinea (Peters, 1934), Denmark (Knudsen, 1930), the Azores and probably Madeira (Bannerman and Bannerman, 1965), as well as Ascension and St. Helena.

Porphyryla martinica and *P. alleni* illustrate excellently the propensity of rallids successfully to cross large stretches of open sea and arrive safely at remote oceanic islands and even different continents. Why rails should be so particularly predisposed to such peregrinations I cannot say. As a number of species are migratory and fly quite well, it seems improper to cite a weak flying ability being responsible as is usually done; yet it is probably true that most rails would be unable to overcome much of a headwind and would be carried along with little choice of direction once "imprison'd" in the wind until reaching land. The ability to land, rest on the water, and take off again would increase their chances of success over those of most purely terrestrial birds.

Now we have seen that two species of *Porphyryla* have arrived at a good many islands, often in sufficient numbers, one would think, to establish themselves as breeding residents. Yet nowhere on a remote oceanic island has *Porphyryla* established breeding populations nor given rise to endemic flightless forms. Quite in contrast, *Gallinula chloropus* has successfully colonized many oceanic islands; e.g., St. Helena, the Azores, Seychelles, Mariannas, and Hawaii to name some of the more

striking examples, and given rise to flightless forms on Tristan and Gough. What is responsible for this pronounced difference in adaptability?

Porphyryla normally inhabits bodies of water covered with floating vegetation. It is on this insecure substrate that the birds spend most of their lives, rarely swimming or traversing solid ground. To this specialized existence they are accordingly modified in morphology and behavior. Compared to *Gallinula*, *Porphyryla* has much longer toes and the elements of the hind limb are proportionately longer and more slender; the cnemial crests of the tibiae are reduced; the distal part of the fibula, to accommodate the enlarged *M. peroneus brevis*, is troughlike rather than a mere splint; the shaft and medial hypotarsus of the tarsus are greatly excavated to accommodate the better developed intrinsic muscles and the highly ossified flexor and extensor tendons; and the inner trochlea is markedly lower and in nearly the same plane as the outer. These modifications are all associated with support and locomotion on floating vegetation. In *Porphyryla* the ribs are pneumatic, whereas in *Gallinula* they are not; the significance of this is not clear. The skull of *Porphyryla* is strong, the bill short and heavy, the nostril small and the jaw muscles much better developed; all probably in accordance with such feeding habits as pecking open lotus pods (Olson, 1963) and birds' eggs (Beadel, 1946). In summary, *Porphyryla* (and the closely related but much larger *Porphyrio*, which has similar modifications) is much more specialized than *Gallinula*, which latter does not differ in any notable aspect from the basic rallid structure.

None of the species of *Porphyryla* appears to vary geographically either in size or coloration. On the other hand, *Gallinula chloropus*, throughout its nearly cosmopolitan range, varies considerably in size and to a lesser extent in coloration. In addition, *G. chloropus* appears to be more variable individually than *Porphyryla martinica*. To test this I measured the following elements of 13 *Gallinula chloropus* (5 males, 8 females) and 10 *Porphyryla martinica* (5 males, 5 females): cranial width; pelvic width; lengths of coracoid, scapula, humerus, ulna, carpometacarpus, femur, tibia, and tarsus. All of the specimens were from Florida and all but two of the former species and one of the latter were collected in the same locality on the same date. For each of these ten measurements,

the coefficient of variation was higher in *Gallinula* (average 4.99) than in *Porphyryla* (average 3.31). Although an inadequate sample size, the data seem to indicate less individual variability in size in *Porphyryla*.

My contention is, therefore, that *Porphyryla*, because of its lessened variability and specialized structure and habits, is not genetically plastic enough to adapt itself to the drastically different environments encountered on small oceanic islands, whereas the generalized and variable *Gallinula* is. The possibility remains that *Porphyryla* has not been able to establish itself because of competition with existing or incoming populations of *Gallinula*. This again, however, would be a reflection of the more specialized nature of the former. Of all the purple gallinule group, only the Takahē of New Zealand (usually placed in the genus *Notornis* but more realistically considered only a large flightless *Porphyrio*) has become flightless and cursorially adapted, but this occurred on a very large island with a much more diverse environment.

It is appropriate to suggest here that the generalized nature of the family Rallidae as a whole is quite likely one of the main factors for their adapting so well to so many different island situations. Only a few genera possess well-marked morphological specializations for feeding or locomotion and the family is basically a homogeneous one. In food habits, great variability is shown within most species. Unlike other groups which reach remote islands (e.g., herons or shorebirds), rails are better equipped to respond to new habitats and food sources. *Porphyryla* is a notable exception.

Another perplexing circumstance presented by *Porphyryla* in the South Atlantic is the matter of *P. martinica* turning up at St. Helena and Ascension. On both of these islands the tradewinds blow strongly from the southeast (Figure 1), so only the African *P. alleni* would be expected to occur. Other vagrants to Ascension and St. Helena have been of African or at least Old World origin and at least two of the endemic landbirds of St. Helena, the plover and the hoopoe, are definitely of African derivation, and the *Gallinula* is of the African race. On Ascension a number of observers, beginning with some of the island's commandants and including Lesson and Darwin (cf. Daly, 1925), have commented on the lack of symmetry of many of the island's volcanic cones. In every instance

the windward (southeast) slope of these cones is the steeper, indicating that the southeast trades, which caused the more rapid buildup of cinder and ash on the leeward side of the cones, have been in effect probably since the island's emergence. The same holds true for St. Helena where similar phenomena have been observed (Baker, 1970). If then, the trades are now and always have been blowing from the direction of Africa, how do we explain the occurrence of an American rail on these islands? I have already proposed two possible hypotheses (Olson, 1972): either *P. martinica* are wafted along on the westerly winds in the southern part of the South Atlantic until they approach the coast of Africa, where some are picked up on the southeast trades and blown back out to Ascension and St. Helena; or, the birds are arriving at these two islands on westerly winds above the shallow tradewind layer. Whatever the explanation, the case of *Porphyryla* demonstrates that the islands of the mid-South Atlantic could be colonized by rails arriving from either Africa or South America.

Genus *Gallinula*

Like *Porphyryla*, members of the genus *Gallinula* have also reached all the mid-South Atlantic islands. *Gallinula chloropus* is known only as a vagrant to Ascension and I imagine that this island is simply too austere and lacking in resources ever to have sustained a population of a rail species of this size. On St. Helena we find the African subspecies *G. c. meridionalis* an abundant breeding resident of the lush, moist, valley bottoms throughout the island. Its settlement of this island is probably quite recent, as it has not differentiated from the mainland stock. Lack of competition from the now extirpated *Atlantisia podarces*, and man's modification of habitat are probably the factors allowing it to colonize successfully where it could not have done so before.

On Tristan da Cunha, and 400 km away on Gough Island, are two forms of flightless gallinule. If, as by most current taxonomic practices, these are considered as subspecies of the one species, *Gallinula nesiotis*, then this implies that one form was derived from the other. Yet clearly both now are incapable of flying between islands. The difficulty of reconciling this situation is what tempted

Eber (1961) into trying to explain away the Tristan gallinule. On the other hand, Eber correctly contends that the differences between the flightless Gough Island gallinule and *Gallinula chloropus* are not much greater than exist between the various races of *G. chloropus*. The main structural differences are the heavy legs and pelvis, reduced wings and pectoral girdle, and stouter bill. Both adults and immatures of the flightless gallinules are darker than the corresponding plumage of typical *G. chloropus*. This, Eber attributes to higher humidity on the islands where the flightless forms are found, which may well be the case. Also, it may be observed that there is a tendency towards increased melanism of several of the races of *G. chloropus* and that *G. tenebrosa* of the Australian region—an obvious derivative of *G. chloropus* stock—is almost totally black.

It is, of course, possible that the population of one island became modified along the lines of present day *G. nesiotis* and colonized the other island before having become flightless, although the direction of the prevailing winds does not favor this hypothesis and there is no evidence among the other land birds of communication between Tristan and Gough. I suggest that the ancestors of both the Tristan and the Gough gallinules were volant *Gallinula chloropus* that probably arrived at their respective islands from South America. The prevailing winds in the Tristan-Gough area are from the west and all the vagrants there, and all the resident birds whose ancestry is apparent, are South American or New World in origin. I do not think it is necessary to invoke a "*Gallinula chloropus*-like ancestor" for either *G. nesiotis* or *G. comeri*. Both of these flightless populations could easily have been derived from the existing species *G. chloropus*. Flightlessness, and its correlated adaptations, is easily and quickly evolved and is in itself not a useful taxonomic criterion. I believe that *G. nesiotis* and *G. comeri* have evolved in parallel from separate colonizations of flying *G. chloropus* and are phylogenetically more closely related to that species than to each other. Plumage darkening and flightlessness probably involve a minimal amount of genetic change. The islands of Gough and Tristan present very similar ecological conditions, so it is not difficult to imagine that selection on a single stock would proceed much differently on one island

than on the other. Therefore, what we see is two forms on separate islands that have evolved features different from the parent stock but that are essentially identical to each other. This is similar to the rail *Dryolimnas cuvierii* which has a volant population on Madagascar with nearly identical subspecies on Assumption Island, Aldabra Island, and Astove Atoll at least one of which (Aldabra) is flightless.

Eber (1961) has shown that in captivity the Gough gallinules (*G. comeri*) are markedly aggressive towards *G. chloropus* and speculates that this would probably act as an isolating mechanism between the two forms. This being the case, the Gough bird would be a species separate from *G. chloropus* and should be known as *Gallinula comeri*, while the Tristan bird, having evolved independently of *G. comeri*, should be known as *Gallinula nesiotis*. Apart from the behavioral differences (if valid), it might be more realistic to consider *G. nesiotis* and *G. comeri* as well-defined flightless subspecies of *G. chloropus*.

Why other insular populations of *G. chloropus* have not become flightless is difficult to say; perhaps conditions of predation and habitat would not allow it. That there are no gallinule populations on either Nightingale or Inaccessible may possibly be correlated with the small size of these two islands.

Genus *Atlantisia*

With *Atlantisia* we come to the most interesting group of rails in the South Atlantic. The genus is confined to the islands of the southern mid-Atlantic ridge and is distinct from any genus found on either mainland. Up until now, *A. rogersi* was the only recognized member of the genus. Lowe (1928) theorized that rails were either primarily or secondarily flightless and considered *A. rogersi* as belonging to the first category (i.e., evolved from non-flying ancestors) and postulated that its ancestors arrived at Inaccessible Island on foot over extensions of continental land masses—an unnecessarily elaborate explanation and one that has nothing to support it. Stressmann (1932) has effectively shown that the emphasis Lowe placed on the degenerate plumage structure of *A. rogersi* is of little phylogenetic importance. Other major structural adaptations of *A. rogersi* are correlated

with flightlessness, do not differ greatly from other flightless rails, and are of no bearing on phylogeny (see below). There is no reason to believe that the ancestors of *A. rogersi* and the other species of *Atlantisia* did not arrive at their islands as wind-blown strays from continental areas, just as other species of rails still do.

Lowe suggested several possible relatives of *Atlantisia rogersi*, his choices being based entirely on their having dark plumage like *A. rogersi*. Hagen (1952:231, fig. 52) reiterated Lowe's suggestions, showing these species on a map captioned with unjustifiable certainty "geographical position of rails related to *Atlantisia*." The species shown are *Laterallus spilonotus*, *L. jamaicensis*, *Porzana spiloptera*, *P. tabuensis*, *Limnocorax flavirostra*, and fortuitously enough, "Ascension rail" based on Kinnear's 1935 paper. My comparisons of the species of *Atlantisia* with other rails have shown that this group has no affinities with the crane-like genera *Porzana*, *Laterallus*, and *Limnocorax*. Lowe himself did not think that *Limnocorax* was a very likely progenitor of *Atlantisia* and in a flash of perspicacity wrote (1928:105) that the former "may represent an early phase of the *Porphyrio* group." While *Limnocorax* does not represent an "early phase," it has acquired some similar structural adaptations in the hindlimb to the *Porphyrio-Porphyryula* group, probably through convergence as a result of its inhabiting floating vegetation.

Examination of the osteology of *Atlantisia* reveals that this genus is related to the "*Rallus* assemblage" which includes *Rallus*, *Hypotaenidia*, and a few other forms derived mostly from *Hypotaenidia*. The relationships of this assemblage will be dealt with in more detail elsewhere (Olson, in prep. (c)). *Hypotaenidia* consists of generalized species with rather stout heavy bills, pelves, and hindlimbs, and is confined to Australo-Malaya and southern Asia. *Rallus*, in the strict sense, is a group highly specialized to a habitat of reedy marshes and its species have much more slender and delicate bills, hindlimbs, pelves, and sterna. *Atlantisia* falls between these two extremes and belongs with what I have designated as a pro-*Rallus* group that has as its only other known members *Dryolimnas cuvieri* and "*Rallus*" *pectoralis*. The present distribution of this pro-*Rallus* group is quite evidently relictual, with its species found only on the South Atlantic islands, Madagascar and its offlying islands,

and on islands in the Australian region.

The ancestors of *Atlantisia* undoubtedly were flying species that came as wind-blown vagrants from a mainland area. With *pro-Rallus* representatives on islands on both sides of Africa, it seems certain that this stock must also have occupied the continent at one time. From the African continent probably came the ancestors of at least *A. elpenor* and *A. podarces*. *Pro-Rallus* may also have been in the New World where it possibly was replaced by true *Rallus*. The specialized true *Rallus* then invaded the Old World, replacing *pro-Rallus* on the mainland and leaving *pro-Rallus* derivatives isolated as insular relicts. *Atlantisia rogersi* may have been derived from the New World *pro-Rallus* or possibly from the same African stock that gave rise to *A. elpenor* and *A. podarces* and that somehow got to Tristan "against the wind" as *Porphyryula martinica* is still seen to do on Ascension and St. Helena.

It is conceivable that *Atlantisia* was derived from a single species as given to wandering as the gallinules are today. If I am correct in assuming that *Gallinula chloropus* twice independently gave rise to flightless populations that are virtually indistinguishable, then why may not the ancestral *Atlantisia* have done so thrice, the population of each island responding to different ecological conditions by changes in body size? It is also possible that *Atlantisia* may have been derived from two closely related species from different continents that arrived from different directions as *Porphyryula martinica* and *P. alleni* do today; or from a single species that inhabited both continents as we see in *Gallinula chloropus*, which has also reached all three of the islands inhabited by *Atlantisia*.

The size range in *Atlantisia* is extreme (Plate 10; Table 2). No other genus of rails varies as much in this respect. I would guess that *A. elpenor* is closest in size to the original stock. Ascension probably could not have sustained a larger species and a smaller species might have had difficulty utilizing the available food. The geographical distribution of size classes in *Atlantisia* does not follow Bergman's ecogeographic rule. If it did, one would expect to find the largest species in the coldest climate (i.e., the nearly subantarctic Inaccessible Island) where instead we find the smallest. The small size of *A. rogersi* may be a factor of the very small size of the island which it inhabits and possibly may have

been affected by the dense vegetation there which might impede the progress of a larger bird. On nearby Nightingale Island, which is still smaller (4 km²), we find no species of rail, which suggests that island area may at times be a limiting factor in establishing rail populations. The great size of *A. podarces* on St. Helena may possibly be explained by several factors. Of the islands inhabited by *Atlantisia*, St. Helena is the largest, was ecologically the most diverse, and had the most abundant sources of food and water, all of which would have allowed an increase in size. There may also have been selection for increased size in *A. podarces* as a result of competition with another rail (*Porzana astrictocarpus*), as *A. podarces* is the only member of its genus definitely known to have shared its island with another resident member of the same family.

An object of speculation is the absence of an *Atlantisia* from other South Atlantic islands. None is known from the main island of Tristan. This may be because of competition from the *Gallinula* or there may have been a species of *Atlantisia* there that became extinct before it could be discovered. This, however, would not explain the absence of an *Atlantisia* on Gough, which presumably has not been exploited to the same extent as Tristan. Likewise, the islands of Trindade and Fernando de Noronha each may have harbored an *Atlantisia* or at least some species of rail that was exterminated by introduced mammals before specimens could be obtained. Search for subfossil remains on these islands should prove of considerable interest.

Genus *Porzana*

The species *Porzana astrictocarpus* is the lone member of its genus known from the South Atlantic islands, and, as mentioned, probably had its origins in Africa. It is smaller than *P. porzana*, *P. carolina*, *P. fluminea*, *P. fusca*, *P. bicolor*, *P. albicollis*, *P. olivieri*, and *P. paykulli* and is larger than *P. spiloptera* or *P. flaviventer*. The only species near in size to *P. astrictocarpus* are *P. tabuensis*, *P. parva*, and *P. pusilla*. *Porzana tabuensis* is slightly smaller than *P. astrictocarpus* and is found in the Australo-Pacific region and thus is not likely to be related to *P. astrictocarpus*. *Porzana parva* is a rather uncommon migratory Palearctic species that is known in sub-Saharan Africa only

from Ethiopia, Somalia, and Uganda. The closely related and more abundant *P. pusilla*, on the other hand, has a much wider distribution (Figure 6), being found in Eurasia, Japan, Australia, and New Zealand, and is known both as a migrant and resident in much of sub-Saharan Africa and Madagascar. Because of its wide African distribution, migratory nature, similar size and structure, *P. pusilla* seems very likely to be the ancestor of *P. astrictocarpus*.

On nearly the opposite side of the world from St. Helena, on the island of Laysan in the Hawaiian chain, lived another small flightless crane, "*Porzanula palmeri*", that became extinct in the late 1940s. Fortunately there are numerous specimens of both skins and skeletons of *P. palmeri* available. This species has always been maintained in the monotypic genus *Porzanula* and no one has conjectured on its origins or relationships. Once again, however, *Porzana pusilla* is a very probable

ancestor. *P. palmeri* differs externally from *P. pusilla* in being slightly smaller, with shorter heavier legs, much reduced wings, and in having only eight primaries—all characters which are correlated with its flightlessness. The bill is longer in *P. palmeri*, this probably being an adaptation to different food.

The plumage patterns and color of *P. pusilla* and *P. palmeri* are extremely similar. *P. palmeri* always appears faded, probably as a result of nearly continual exposure to the sun, but it is gray below and brownish olive above with the centers of the dorsal feathers black, just as in *P. pusilla*. The plumage pattern on the heads of these two species is practically identical. The flanks and thighs of *P. pusilla* are barred with white and this barring, although reduced, is present in *P. palmeri* as well. The dorsal feathers of *P. pusilla* are streaked with white and although this does not at first appear to be the case in *P. palmeri*, there is yet a fair



FIGURE 6.—Breeding distribution of *Porzana pusilla* (shaded areas) and its two apparent derivatives. (After Voous, 1960.)

amount of white streaking to be found concealed amid the dorsal plumage of this species as well. There is less white streaking in immatures of *P. pusilla* than in the adults (Bauer, 1960) and the reduction of white in *P. palmeri* could possibly be a result of retention of this immature condition. The juvenal plumage of *P. palmeri* is a pale buff below, as is also found in *P. pusilla*.

The range of *P. pusilla*, extends along almost all the western Pacific, from Japan to New Zealand (Figure 6) and it is migratory in parts of this range. With such evident ability for dispersal it would be a prominent candidate for settling Laysan. Vagrant birds of a number of species from both Asia and America have reached the Hawaiian Leewards (Clapp and Woodward, 1968) but the New World holds no rail as similar in size or appearance to *P. palmeri* as *P. pusilla*.

Thus we see that it is possible that one species, *Porzana pusilla*, gave rise to two flightless insular forms on opposite sides of the globe. I do not feel that any of the characteristics of the Laysan rail are of generic value and, therefore, the species *palmeri* should be placed in *Porzana*. It is most interesting that except for the wing elements, *P. astrictocarpus* of St. Helena is almost exactly intermediate between *P. pusilla* and *P. palmeri* (Plate 11). This indicates that the direction of evolution

of the two insular species from a common ancestor has been similar. That the Laysan rail has diverged more from the original stock probably reflects the increased selection pressure of its smaller and more rigorous environment rather than a longer period of adaptation.

I do not feel it is necessary to assume the caution normally used in speaking of ancestral forms by referring to a "pro-*Porzana pusilla*" or a "*Porzana pusilla*-like ancestor" for the progenitor of *P. astrictocarpus* or *P. palmeri*, because it is very possible that the existing species of *P. pusilla* gave rise to both. The time involved in achieving flightlessness and its correlated adaptations is probably short (see following section) and selection on small oceanic islands is doubtless rapid. We have seen how rapidly man can alter the morphology of domestic animals by selective breeding, and the selective pressures on small insular populations of rails must be nearly as severe. Thus we could have populations of *Porzana pusilla* on Laysan and St. Helena, and of *Gallinula chloropus* on Tristan and Gough, evolving into new flightless forms and diverging to the point that some taxonomists would erect separate "genera" for them, while the ancestral mainland populations are not appreciably changing at all.

EVOLUTION OF FLIGHTLESSNESS IN RAILS

I have heretofore asked the question concerning Mauritius henns and dodos, thatt seeing those could neither fly nor swymme, beeing cloven footed and withoutt wings on an iland far from any other land, and none to bee seence[sic] elce where, how they shold come thither? Soe now againe concerning the Ascention birds allsoe, thatt can neither fly nor swymme. The iland being aboutt 300 leagues from the coast of Guinnea . . . the question is, how they shold bee generated, whither created there from the beginning, or thatt the earth produceth them of is owne accord, as mice, serpents, flies, wormes, etts. insects, or *whither the nature of the earth and climate have alltred the spape [shape] and nature of some other foule into this, I leave it to the learned to dispute of.*

from the journal of Peter Mundy
(Temple and Anstey, ed., 1936:83)

In the above passage, italics are mine, to remind the reader that Mundy's journal antedates Darwin by some 200 years.

The story of evolution in the class Aves as a

whole has, from its beginning, been one of adaptation for flight. Yet in a number of groups this capacity has secondarily been lost. Prominent among these is the Rallidae, roughly a quarter of which living or recently extinct members have lost the ability to fly. Why, and how, so many species of rails and other birds have on so many occasions so speedily renounced their heritage of millions of years of aerodynamic refinements is a subject of great interest. (Penguins and the non-volant alcids should not be included in discussions of flightlessness. Their outstanding adaptations are for flying through a medium many times denser than air and are much different from other flightless birds; in a sense, these birds are the best fliers of all.)

It need first be observed that all flightless rails occur on islands, although these may vary greatly

from tiny, austere islets like Laysan, to large, rich islands such as New Guinea and New Zealand. One often reads that flightlessness comes about as a result of the absence of predators, and while a number of islands where flightless rails occur do have avian predators, it is probably true that where one finds flightless rails one does not encounter native mammalian predators that are so destructive to ground-dwelling and nesting birds. Another factor of insular environments, as Holdgate (1965:370) has mentioned, is the reduced need for dispersal ability. Continental rails usually live in habitats that are discontinuous and widely spaced, necessitating some capacity to get from one area to another by flying, whereas most islands are relatively small in area with more homogeneous habitat. But it should be emphasized that these factors only *allow* flightlessness to occur and do not explain *why* flight should be done away with.

Darwin (1866), in discussing the flightless beetles of Madeira, suggested that selection for flightlessness occurred because flying beetles would be wafted out to sea by strong tradewinds and thus removed from the breeding population. This theory has been invoked by other writers to explain the flightlessness of birds as well, but as Darlington (1943:39) indicates, this is a gross oversimplification, and I will go a step further and say that it probably has had very little part in the evolution of flightlessness in birds. Two arguments may be made to dismiss the importance of the wind effect. First, flightless birds are found on islands that are large enough that winds could not be expected to affect adversely any but the most coastal of airborne birds—a prime example being New Zealand. Secondly, small land birds of various sorts which are *not* flightless have evolved and thrived on many small, remote, and wind-blown oceanic islands. Witness the example of a thrush and three finches in the Tristan and Gough group, and three small passerines on tiny Laysan. On both of these islands there are (or were) flightless rails. Some other explanation than wind effect must be put forth.

Holdgate (1965:371), in attempting to explain flightlessness in organisms from the Tristan group, stated that "flightlessness perhaps arises more for negative than 'positive' reasons: if strong selection pressure does not promote its retention, there is a tendency for it to disappear." Brace (1963:45), discussing structural reduction in evolution, con-

cluded that "if the structure controlled by the locus in question has no adaptive significance then it will be reduced in the course of time." This, he believed, was independent of selection and was a result of the generally deleterious effects of most mutations. These suggestions carry vague overtones of Lamarckian "disuse" and to me are not satisfying explanations.

Darlington (1943:44) probably comes as close as anyone to solving the enigma of flightlessness in remarking on carabids that "if flight becomes useless but not actually harmful, the advantage probably shifts directly to —winged [i.e. with reduced or vestigial wings] individuals, not because they are flightless, but because they are inherently better, more viable insects, with simpler structure, simpler metamorphosis, and lower energy requirements than +winged [flying] forms," the seminal consideration, I believe, being the latter, i.e., reduced energy requirements. Increased viability of flightless forms has been shown in weevils (D. J. Jackson, 1928) but would probably be difficult to demonstrate experimentally in birds. In their experimental studies of recolonization of defaunated islands by invertebrates, Simberloff and Wilson (1969) found that both weak and strong flying forms were early colonizers but that weak flyers were usually the first to produce large populations. These observations, coupled with the fact that flightlessness in rails has arisen time after time and at a rapid rate, suggest that there are very distinct advantages conferred by flightlessness and that it is not merely a gradual fortuitous phthisis of unused organs.

The most dramatic manifestation of flightlessness, of course, is the reduction of the whole pectoral apparatus, especially the large pectoralis muscles. In adults of flying rails, the flight musculature ranges from 12 to 17 percent of total body weight (Hartman, 1961:46). These figures are low compared to many other birds, but this is still a considerable proportion of the anatomy that is involved only in flight. In terms of energy consumption, active muscle utilizes more energy than any other tissue and the specialized and powerful avian pectoralis is in turn probably one of the most expensive of muscles to maintain. Any reduction in the flight muscles then, represents a potential energy savings relatively greater than a comparable reduction in almost any other organ.

Flight in birds has been attained through great changes in metabolism and at great energy cost. In an environment where a bird can get away with being flightless, and when its feeding methods will permit it, it is to the bird's advantage to become flightless. This is especially true where dispersal is not a problem, but where food resources are generally limited. Obviously, of two competing rails, the one with genetically reduced pectoral muscles would require less food and could spend more time engaged in reproductive activity, resulting in the perpetuation of its physiological advantage. The whole direction of organic evolution and adaptation has as its underlying force the more effective accumulation and budgeting of energy. What more direct way to get ahead evolutionarily can there be than the elimination of a costly energy drain when it is no longer needed for the preservation of the individual? Another factor that may be of importance is simply the loss of weight incurred with the reduction of the pectoral muscles. This would mean less mass to be propelled and sustained by the hindlimbs and would result in an advantageous shift of the center of gravity. In my opinion, the energy factor is the overriding consideration in the evolution of flightlessness and other factors are of secondary importance. This may well be true of many structural reductions in other organisms. (It would be of the greatest interest to compare the metabolic rates and energy requirements of a flying and a flightless rail, preferably congeners.)

It now remains to be seen *how* flightlessness arises. Let us first examine some of the characteristics of flightless rails. The elements of the wing and shoulder girdle and the sternum are reduced relative to the size of the body and hindlimbs. The depth of the carina sterni is reduced, often drastically. The angle formed by the coracoid and scapula is greater than 90 degrees. Correlated with the reduction of the pectoral girdle is the reduction of the flight musculature. These, at least, are the obvious distinctions. A more discrete manifestation of flightlessness in rails, is the reduction or loss of the scapular tubercle for the attachment of *M. expansor secundariorum*.

Now all this seems at first to be a rather complex set of characters that might involve a great deal of genetic modification to accomplish. But I think it can be fairly easily demonstrated that in-

stead, there is a relatively simple basic phenomenon responsible for these changes.

All rails are flightless during the beginning stages of their ontogeny, and as chicks, all exhibit the skeletal features that characterize adult flightless rails. In Figure 7 are shown two young individuals of the volant King Rail, *Rallus elegans*. The bird on the left is 17 days of age (posthatching), the one on the right is 47 days of age. The latter was nearly adult size but for the purposes of comparison the figure has been reduced so that the femur lengths of the two are equal. The differences in proportions are immediately apparent. In the younger bird, the bones of the wings and shoulder girdle are much smaller, the sternum is reduced and nearly keelless, and the coraco-scapular angle is obtuse (also, the head is larger, and the ischium has not fused posteriorly to the ilium; these differences will be discussed later).

It is obvious then, that if the proportions of the skeleton of the younger rail were maintained on into adulthood, the result would be a flightless rail. Thus, flightlessness would not be a result of numerous structural modifications, but a simple retention of a state already present in the young stages of every rail.

Lowe (1928:111) noted the "feeble development" of the wing of young rails relative to the body and legs, but did not exploit this observation to its more obvious conclusion and instead, in trying to justify his theory of "primary" versus "secondary" flightlessness, suggested that "rails, as a group, may in the past have been slow to acquire the power of full flight, . . . while some . . . may never have acquired it at all," and thus missed the point that flightless species were merely recently evolved neotenic forms. The condition of the feathers of the ostrich and of the palate of ratites in general, are discussed by de Beer (1958) as examples of neoteny in flightless birds, but that the characters involved in flightlessness itself are a result of neoteny seems to have escaped discussion. I shall confine my remarks to the Rallidae.

In the proportions of young versus adult, or flightless versus flying rails, we are dealing with differential growth rates of various structures (allometry). Because of the large size of the hindlimbs at hatching, these structures probably undergo positive allometry during the embryonic development of rails, while the pectoral apparatus,

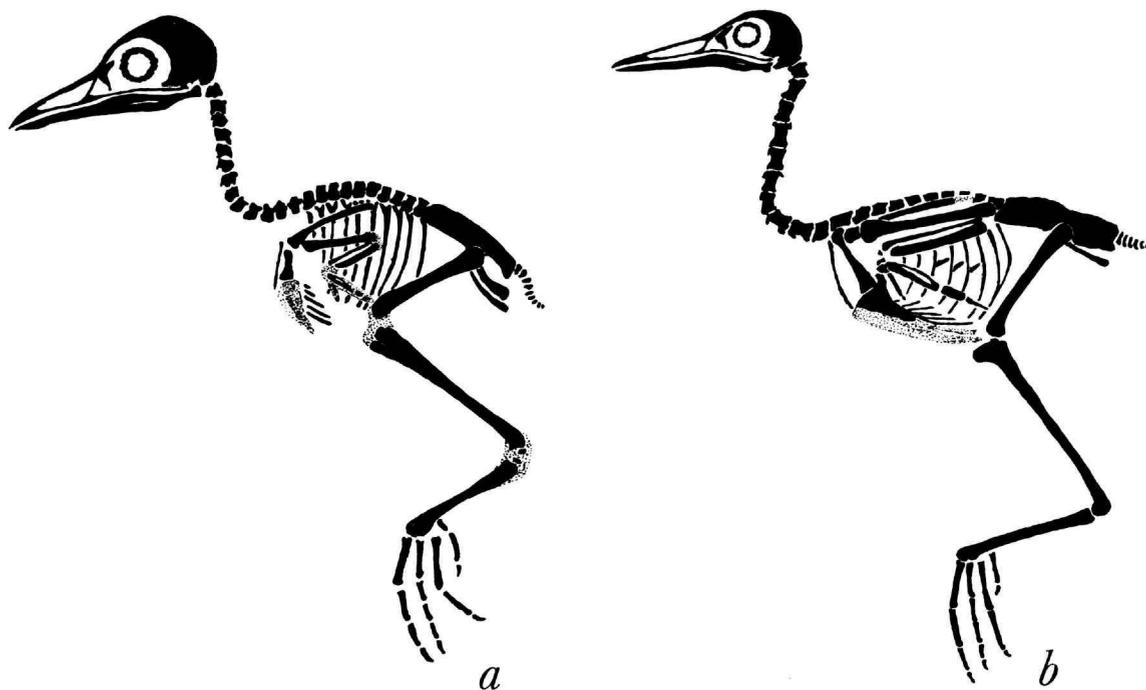


FIGURE 7.—Cleared and stained skeletons of *Rallus elegans*: *a*, 17 days of age (posthatching); *b*, 47 days of age (*b* is reduced so that the femur lengths of the two are equal). Stippled areas represent cartilage.

on the other hand, is negatively allometric or at least grows much slower than the hindlimb during this period, as has been shown to be the case in the domestic fowl (Romanoff, 1960, appendix tables II and III). In flying rails, at some point in their later development, these relative growth rates must reverse, so that the wings and pectoral girdle increase relative to body size (positive allometry) while the hindlimbs remain the same or possibly decrease. If this reversal in growth rates is arrested and not allowed to take place, yet all the other normal processes of maturation proceed, the result would be an adult rail that is as flightless as the young. Eber (1961) has attributed the skeletal differences between the flightless *Gallinula* of Gough Island and the flying *G. chloropus* to differences in allometry of the various parts.

Flightlessness, then, does not involve the development of new structures, and the control of the relative growth of the limbs is likely determined by comparatively few genetic loci. It is easy to see how very little genetic modification could rapidly produce the seemingly drastic changes that mark

flightless rails. For this reason, flightlessness can have only limited phylogenetic or taxonomic significance and cannot, for instance, in itself be used as a generic character. Among other things, this helps explain how we can have flying and flightless races of a single species (as in *Dryolimnas cuvieri*), how a flightless bird can be present on an oceanic island less than a million and a half years old, how the three isolated species of *Atlantisia* can all be flightless and still retain so much similarity in the rest of their structure, and how two "identical" forms of flightless gallinules can evolve independently on islands over 400 km apart. The span of time needed to evolve flightlessness in rails can probably be measured in generations rather than in millennia.

The development of the sternum is of considerable interest in the evolution of flightlessness. In the ontogeny of the domestic fowl (*Gallus*), the major bones begin ossification between about the 8th and 12th day of incubation. The sternum, however, does not begin to ossify until the 17th day of incubation but is fairly well ossified at hatching.

Ossification of the sternum in the domestic pigeon *Columba livia*, and the grebe *Podiceps cristata*, does not take place until after hatching (Schinz and Zangerl, 1937). In rails, ossification of the sternum is also delayed. In *Rallus elegans* at hatching, ossification of all the major bones is well underway with the exception of the sternum. At 17 days posthatching, the sternum is still only a cartilaginous outline (Figure 7a), and at 47 days it is only beginning to ossify (Figure 7b). This postponement of sternal development may be one of the factors that predisposes certain birds to flightlessness. It is interesting to note that pigeons, grebes, and rails have each given rise to flightless forms, whereas the Galliformes, in nature, have not.

At least in rails, even after ossification of the sternum has begun, the cartilaginous outline of the carina has still not reached its fullest development. In its early stages, the developing sternum of flying rails goes through stages resembling the ossified sternum of various flightless forms (Figure 8). Flightlessness as I have stated, is a case of

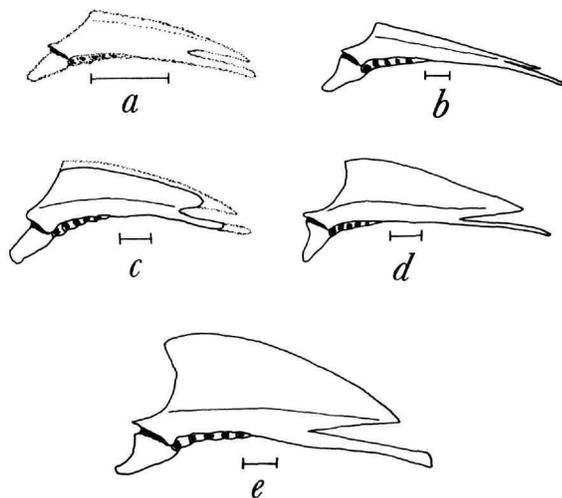


FIGURE 8.—Development of the sternum of a flying rail to show how the carina in its early stages corresponds to the shape of the carina in different species of flightless rails: a, *Porphyryla martinica*, downy chick about a week old; sternum entirely cartilaginous but has nearly the same conformation as b and as *Atlantisia elpenor*. b, *Gallirallus australis*, flightless rail, adult. c, *P. martinica*, immature fully feathered but not quite volant; sternum is still partly cartilaginous and now resembles d. d, *Hypotaenidia owstoni*, flightless rail, adult. e, *P. martinica*, adult. Scales=5 mm. Dotted lines indicate cartilage.

arrested development. Obviously, development could be arrested at any point between hatching and the flight-attaining stage, and the individual would still be flightless. Evidently this is what has happened throughout the Rallidae—different flightless species have had their development arrested at different points—for in some flightless forms the carina is greatly reduced and the remainder of the sternum markedly different from flying forms (e.g., *Atlantisia elpenor*, *Gallirallus*), and in others (e.g., *Hypotaenidia owstoni*, *H. wakensis*) the carina is moderately developed and the whole sternum, except for diminution in relative size, resembles flying species. This, in part, is what deluded Lowe into thinking that rails could be divided into primarily and secondarily flightless groups. This is also why the sterna of such closely related species as *Atlantisia rogersi* and *A. elpenor* can differ so greatly while the remainder of the skeleton does not. Therefore, the conformation of the sternum of flightless rails is not a useful taxonomic criterion above the species or subspecies level.

The obtuse angle formed by the coracoid and scapula was early recognized as a characteristic of flightless birds (Huxley, 1867; Parker, 1882). This too appears to be a neotenic condition as an examination of Figure 7a should disclose. Although I know of no published explanation for this condition, it appears that the decrease of this angle in flying birds is a function of increased size of the sternum and pectoral muscles and is a result of this mass being brought under the bird's center of gravity (Figure 7b) to aid balance and probably to confer mechanical advantage in flight.

As in most vertebrates, the skull is proportionately larger in the younger stages of rails (Figure 7) and is negatively allometric thereafter. There is no evidence that neoteny has affected this relationship in flightless rails; i.e., flightless rails do not appear to have larger heads than flying species. In fact, the postembryonic negative allometry of the skull is well illustrated by the comparative proportions of the skulls of the three species of *Atlantisia* (Table 3), where we see that while body size increases, the skull does not increase at the same rate.

Another condition of the skeleton of young rails deserves mention. This is the lack of a posterior fusion of the ischium and ilium (Figure 7a). This

juvenile condition does not persist into the adult stage of any known rail, even the neotenic flightless species. This condition of the pelvis, however, is very similar to that found in some of the ratites, especially the pelvises of kiwis and moas. The implications of this go beyond the scope of this paper.

One last skeletal feature that is correlated with flightlessness in rails is the reduction or loss of the scapular tubercle for the attachment of the dorsal ramification of the tendon of *M. expansor secundariorum*. The scapular tubercle appears to be unique to the Rallidae and I have been unable to find it in any other family. This tubercle is pres-

ent in all volant rails but is variously developed. In flightless species such as *Hypotaenidia wakensis*, *H. owstoni*, *Atlantisia rogersi*, *Gallirallus australis*, and *Porzana palmeri*, it is present but greatly reduced. In other flightless species, *Atlantisia elpenor*, *Porzana astrictocarpus*, and some specimens of *Tribonyx mortierii*, for example, it is lacking altogether. *M. expansor secundariorum* is most peculiar in that it is composed of smooth muscle fibers (Berger, 1956). Its function has never been determined. The reduction or loss of the scapular tubercle for its attachment in flightless rails implies that it is in some way used in the process of flight.

CONCLUDING REMARKS

We have seen in the case of *Atlantisia* that it is quite within reason to hypothesize that a single species could have given rise to three entirely new species, all flightless, and all on islands separated from each other and the nearest mainland by vast expanses of ocean. This is not without its implications to the origins of other species in other parts of the world. For instance, the three Mascarene islands of Mauritius, Rodrigues, and Reunion, in the Indian Ocean, were all apparently inhabited by very large flightless birds of columbiform ancestry (the Reunion bird is known only from old descriptions). Despite the fact that suggestions have been made to derive some or all of these birds from rails (Storer, 1970), there is no good evidence that the Dodo and Solitaire are anything but columbiform (Olson, 1971). It seems that what has happened here is that a single stock of pigeon colonized the three islands and that these populations then independently became flightless and achieved large size. If a single stock of rails can colonize islands as isolated as those of the mid-South Atlantic and give rise there to three flightless species, it seems only reasonable that the Mascarenes, which are much closer to each other and to the nearest mainland, could easily have been settled by a single stock of pigeon that also

gave rise to three flightless species, at least two of which subsequently evolved to the point of being generically distinct.

The adaptability of rails is nowhere as well exemplified as in *Atlantisia*, for this single stock successfully established itself on a barren, tropical desert island; a temperate, subtropical island of varied vegetation; and a cool, densely vegetated, temperate subantarctic island, all, of course, presenting very different environmental conditions.

The possibility that a single species (*Porzana pusilla*) may have given rise to two flightless species on islands on opposite sides of the globe is an example perhaps unparalleled in vertebrate zoogeography. With this group, as well as in *Gallinula*, I hope that the idea that existing flightless insular species may have been derived from other existing volant species will not be too difficult for some to digest, and I further hope that I have convincingly argued the ease and rapidity with which flightlessness may be attained.

The known rails of the South Atlantic islands illustrate more than their fair share of evolutionary and zoogeographical principles. It will be of no small interest to find out what the future holds in terms of paleornithological investigations of other islands in that ocean.

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Appendix 1

COMPARATIVE MATERIAL EXAMINED

In identifying and describing the fossil rails of Ascension and St. Helena, I used the skeletal material of the following species of living and recently extinct rails for comparison (all specimens except those indicated are in my collections or those of USNM): *Rallus elegans*, *R. longirostris*, *R. limicola*, *R. aquaticus*, *R. pectoralis* (NMV), *Hypotaenidia striata*, *H. philippensis* (AMNH), *H. torquata*, *H. owstoni*, *H. wakensis*, *Atlantisia rogersi*, *Tricholimnas silvestris* (MCZ), *Dryolimnas c. cuvieri* (UMMZ), *Gallirallus australis*, *Pardirallus maculatus* (UMMZ), *P. sanguinolentus*, *P. nigricans*, *Cyanolimnas cerverai* (AMNH), *Rallina eurizonoides*, *Canirallus oculus* (AMNH), *Himan-*

tornis haematopus, *Aramides cajanea*, *A. ypecaha*, *A. saracura*, *Limnocorax flavirostra*, *Porzana pusilla*, *P. carolina*, *P. albicollis*, *P. fusca*, *P. tabuensis*, *P. palmeri*, *Poliolimnas cinereus*, *P. flaviventer*, *Laterallus albigularis*, *L. viridis*, *L. leucopyrrhus*, *Coturnicops noveboracensis*, *Sarothrura pulchra*, *Porphyriops melanops*, *Tribonyx ventralis*, *T. mortierii*, *Amaurornis phoenicurus*, *Gallix rex cinerea*, *Gallinula chloropus*, *Porphyryula martinica*, *Porphyrio porphyrio*, *Fulica atra*, *F. americana*, *Nesotrochis debooyi*.

In the descriptions, the terminology of Howard (1929) is followed.

Appendix 2

CHARACTERIZATION OF THE GENUS *Atlantisia*

As the genus *Atlantisia* has taken on an entirely new scope, it is appropriate to discuss in what manner its three species are similar to one another and different from other related genera. The specific differences between the three have been indicated in the descriptions of *Atlantisia elpenor* and *A. podarces*. The generalizations to follow will, of course, pertain only to *A. rogersi* and *A. elpenor* when a certain element of *A. podarces* is unknown.

The bill of *Atlantisia* is of medium length, not short and stout as in "crakes" nor very elongate and slender as in "true" *Rallus*. It is not as wide and heavy as the species of *Hypotaenidia* but is quite similar to *Dryolimnas* and "*Rallus*" *pectoralis*. The nasal bar is twisted and narrow in *A. elpenor*, which is characteristic of the "*Rallus* assemblage," but in the one specimen of *A. rogersi* examined, it is broad and flat, a condition perhaps correlated with the reduced lacrimal of that spe-

cies. The cranium of *Atlantisia* is broader than *Rallus* and somewhat narrower than *Hypotaenidia*.

QUADRATE.—The orbital process is narrower than *Rallus* or *Hypotaenidia* and shorter than *Gallirallus*. On the internal side of the otic process is a foramen which is an open oval in *Atlantisia* and *Dryolimnas*, whereas in other genera it is partly closed over with bone and the opening is on a slant.

CORACOID.—Procoracoid process much broader than in related genera. Fenestra large, oval, set away from the shaft and well exposed, whereas in related genera it is more slitlike and may lie partially under the shaft. In ventral view the head joins the shaft to form a distinct narrow ridge, markedly different from other genera.

SCAPULA.—Furcular articulation not squared as in *Hypotaenidia* and *Gallirallus* nor as pointed as in *Rallus*.

HUMERUS.—Shaft very slender, straight; articulations enlarged. Distal end with internal side an-

gled much farther away from line of shaft than in other genera.

ULNA.—Shaft not greatly curved as in *Gallirallus*. Internal condyle larger and more prominent than in related genera. Impression of brachialis anticus short but steep. External cotyla reduced.

RADIUS.—Rather stocky; distal end not as widely expanded as in *Gallirallus*.

CARPOMETACARPUS.—Shorter and stouter than related forms except *Gallirallus* which is even stockier and more bowed. Proximal metacarpal symphysis long and wide; intermetacarpal space short. Pisiform process a blunt knob rather than a more bladelike process as in other rails. Metacarpal III thin and twisted distally (especially in *A. rogersi*).

PELVIS.—In dorsal view the synsacral area between the posterior ilia is convex and humplike in *Atlantisia*, unlike related genera in which this area is flat or concave. The portion of the posterior iliac crest above the antitrochanter is reduced. In ventral view, the preacetabular portion of the pelvis appears shorter and slightly wider in *Atlantisia* and the ischia are set farther apart and flare outwards more than in related genera.

FEMUR.—The markedly straight shaft of *Atlantisia* is distinctive; the antero-posterior and lateral-medial curvatures seen in other genera are almost completely straightened out. The shaft is narrow and the distal end greatly expanded. In medial view, the proximal end is narrower and less expanded posterior to the head than related genera. The trochanter does not extend as far anteriorly. Fibular groove of external condyle very deep with higher fibular condyle.

TIBIOTARSUS.—A bone with relatively slender shaft and expanded articulations; shaft narrower than *Gallirallus*, *Hypotaenidia*, and *Dryolimnas*, but stockier than *Rallus*. Distally, the internal side of shaft flares out into a very conspicuous internal ligamental prominence that is not as well developed in other genera. External condyle large and

bulbous. Anterior intercondylar fossa relatively wider than related genera.

TARSOMETATARSUS.—The slender shaft with much expanded articulations distinguishes all three species of *Atlantisia* from other rails on proportions alone. Similar to *Dryolimnas* but shaft narrower and articulations slightly more expanded; much heavier than *Rallus* throughout; proportionately longer and more slender than *Hypotaenidia* and *Gallirallus*. Proximal and distal ends wider relative to shaft. Scar for hallux deep. Inner trochlea expanded farther medially than in most other genera. Intercotylar knob low, flat and turned laterally, with cotylar surfaces more nearly in the same plane, unlike *Gallirallus*, *Hypotaenidia* and *Rallus* which have a more prominent intercotylar knob and a depressed external cotyla. *Dryolimnas*, however, is similar to *Atlantisia* in these respects. Distal foramen wide and rounded, not partially concealed and slitlike in anterior view as in related genera. Internal cotyla expanded well beyond line of shaft in *Atlantisia*, not as expanded in other genera. In internal view the ridge on the anterior proximal portion of the shaft is narrower and better defined in *Atlantisia*.

The ratios of the hindlimb elements of *Atlantisia* also differ from related forms. For example, in "*Rallus*" *pectoralis*, a species of about the same size as *A. elpenor*, the tibia is shorter than that of *A. elpenor* while the femur is longer.

In short, *Atlantisia* is intermediate in most respects between the generalized, heavy *Hypotaenidia* group and the slender, delicate, specialized *Rallus*. With *Dryolimnas* and "*Rallus*" *pectoralis* it forms a "pro-*Rallus*" group. *Atlantisia* differs from the rest of "pro-*Rallus*" (aside from flightless features, which are not considered of generic value) mainly in qualitative details of the coracoid and pelvis, in the straight shaft of the femur, and in the proportions of the hindlimb elements all of which have narrower shafts but wider articulations in *Atlantisia*.

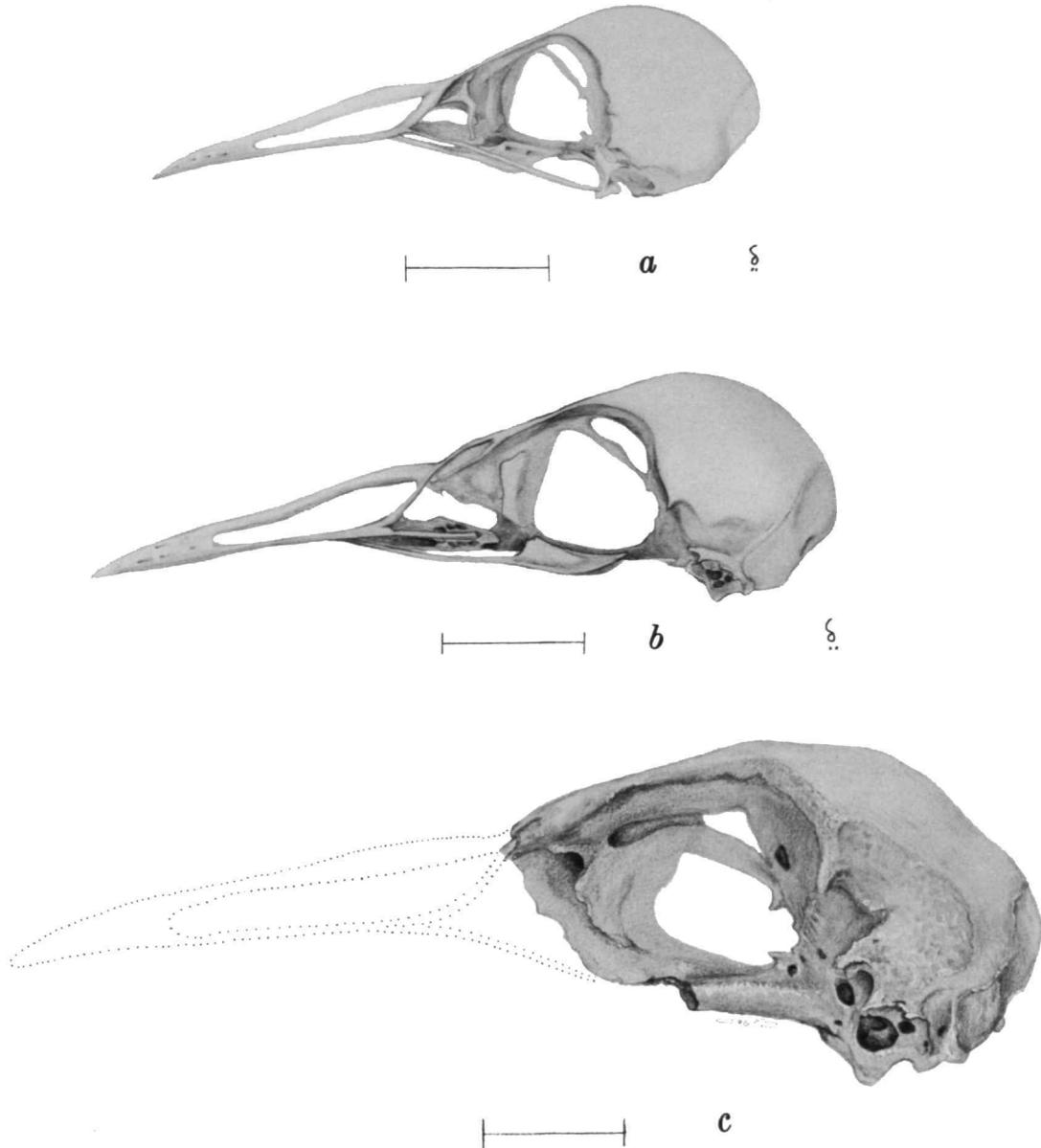


PLATE 1.—Skulls of the three species of *Atlantisia*: *a*, *A. rogersi*, female, USNM 319151, Inaccessible Island, Tristan da Cunha group. *b*, *A. elpenor*, Ascension Island. A composite drawing from USNM 170131, 170087, and 170088. Quadrate, pterygoid, lacrimal, and posterior portion of jugal bar lacking. *c*, *A. podarces*, USNM 175890, St. Helena. Cranium only, dotted lines indicate hypothetical bill shape. The drawing is actually of the right side of the specimen but the negative has been reversed to facilitate comparison. Scale=10 mm.

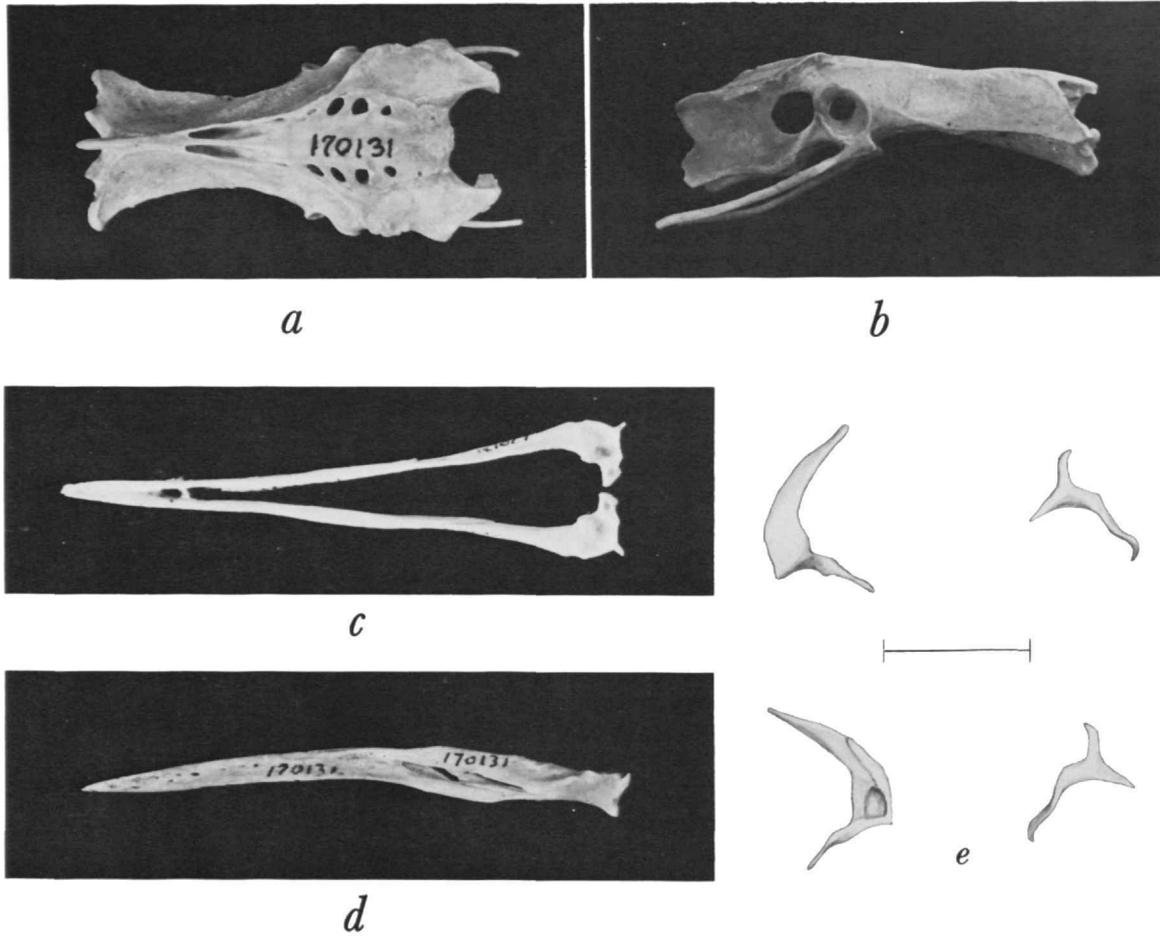


PLATE 2.—Pelvis and skull elements of *Atlantisia elpenor*: *a*, pelvis, USNM 170131, dorsal view; *b*, same, right lateral view; *c*, mandible, USNM 170131, dorsal view; *d*, same, left lateral view; *e*, lateral (upper) and medial (lower) views of the lacrimals of *A. elpenor*, USNM 170107 (left), and *A. rogersi* USNM 319151 (right). *a-d*, Twice natural size; *e*, scale=5 mm.

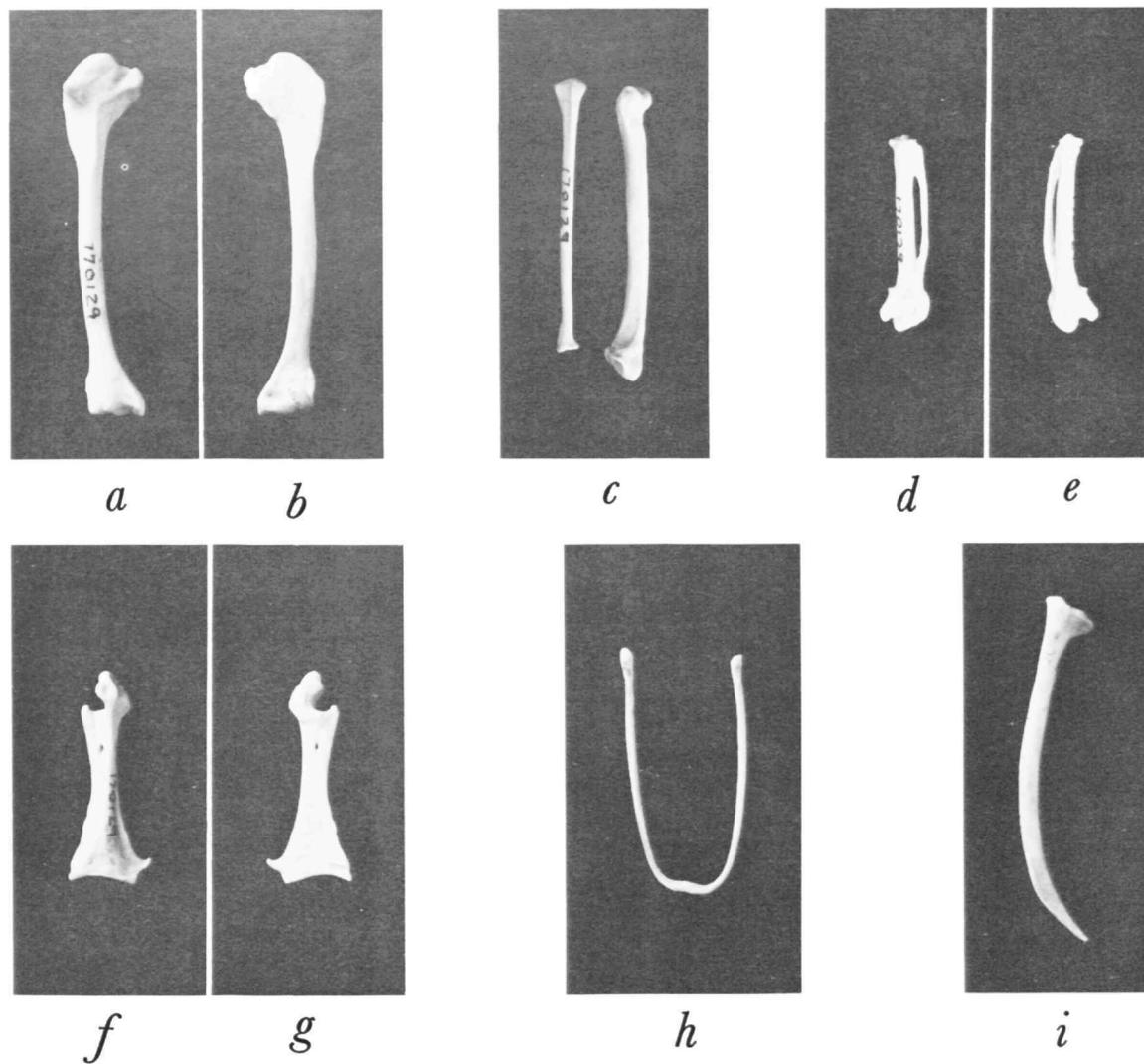


PLATE 3.—Wing and pectoral girdle elements of *Atlantisia elpenor*, USNM 170129: *a*, left humerus, anconal view; *b*, same, palmar view; *c*, left radius (anconal) and left ulna (palmar); *d*, left carpometacarpus, internal view; *e*, same, external view; *f*, left coracoid, external view; *g*, same, internal view; *h*, furcula; *i*, left scapula, ventral view. All twice natural size.

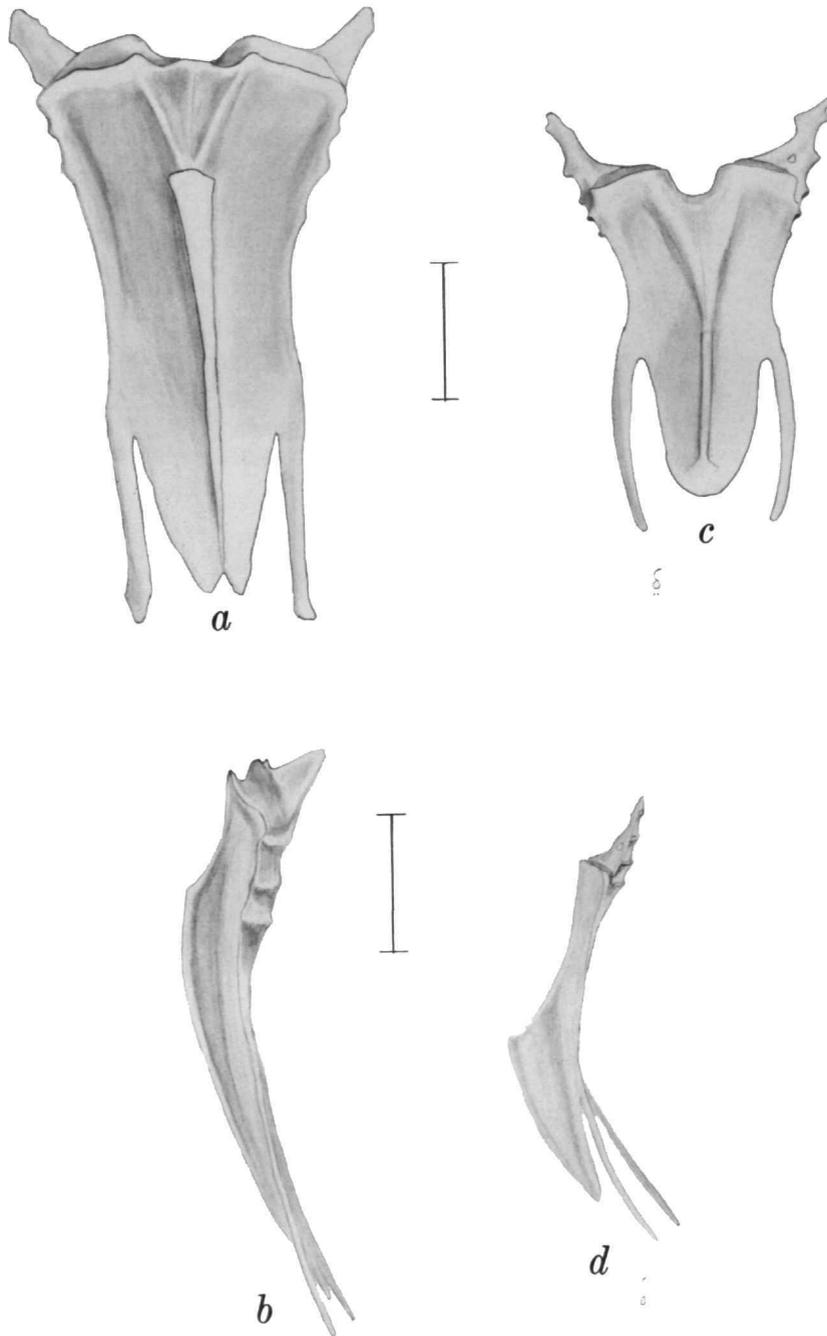


PLATE 4.—*Sterna* of *Atlantisia*. *A. elpenor*, composite drawing from USNM 170059 and 170129: *a*, ventral view; *b*, left lateral view. *A. rogersi*, USNM 319151: *c*, ventral view; *d*, left lateral view. Scale=5 mm.

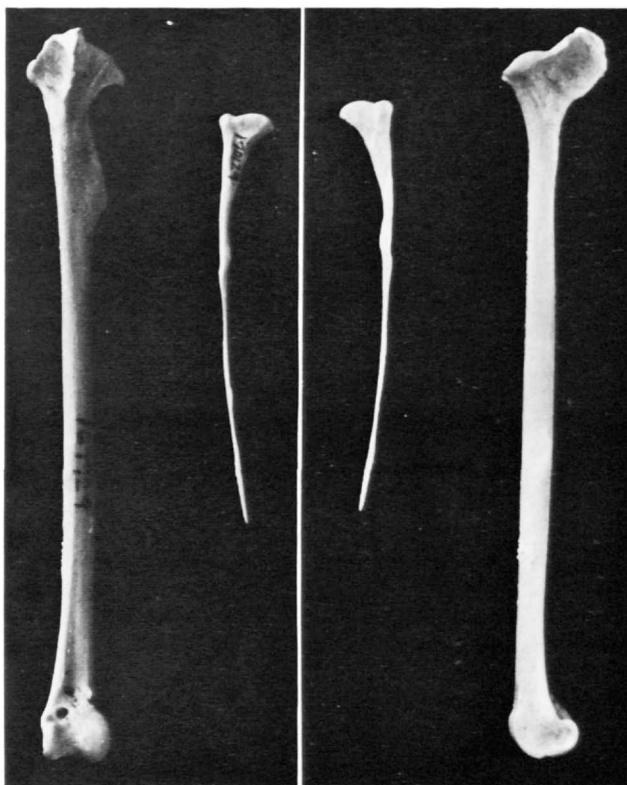
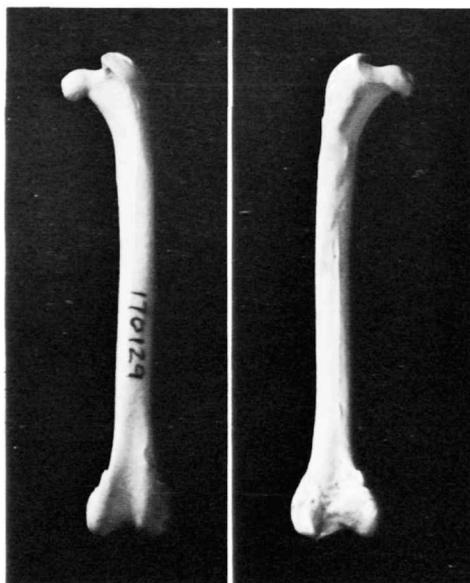


PLATE 5.—Hindlimb elements of *Atlantisia elpenor*: *a*, left tibia, USNM 169929, anterior view, and right fibula, USNM 170129, medial view; *b*, same, fibula in lateral view, tibia in medial view; *c*, left femur, USNM 170129, anterior view; *d*, same, posterior view; *e*, left tarsus, holotype, USNM 170129, anterior view; *f*, same, posterior view; *g*, same, medial view. All twice natural size.

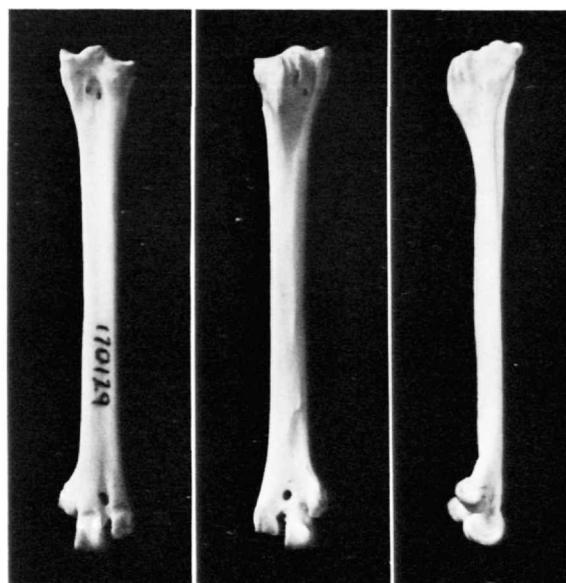
a

b



c

d

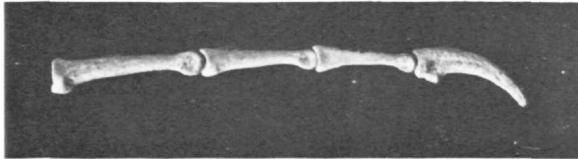
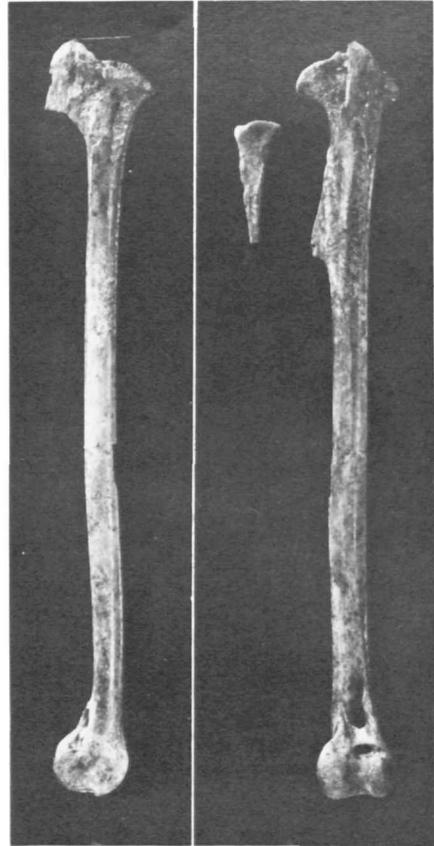
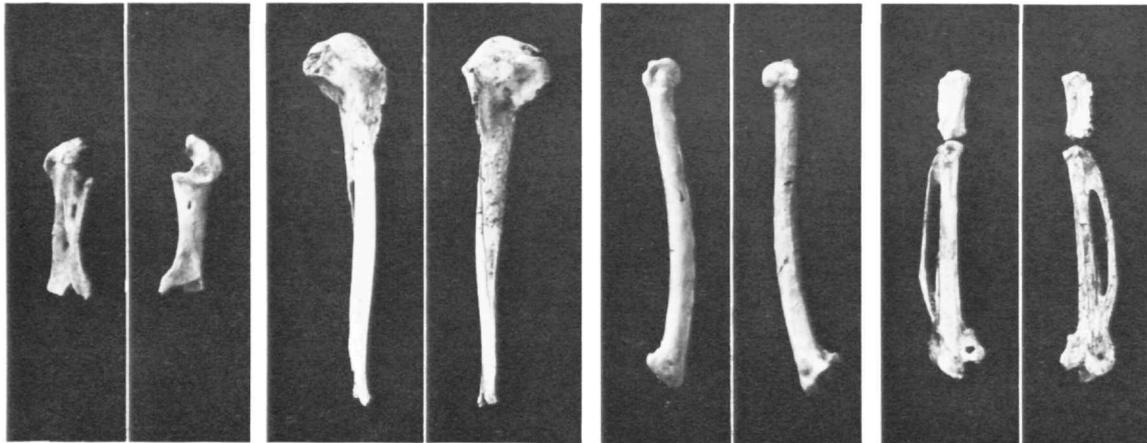


e

f

g

PLATE 6.—Skeletal elements of *Atlantisia podarces*: *a*, middle toe with claw; *b*, right tibia, medial view; *c*, head of fibula (internal view) and right tibia (anterior view); *d*, right coracoid (lacking sternal end), external view; *e*, same, internal view; *f*, right humerus (lacking distal end), anconal view; *g*, same, palmar view; *h*, right ulna, anconal view (MCZ 7197); *i*, same, palmar view; *j*, left carpometacarpus and digit II phalanx I, external view; *k*, same, internal view. All figures natural size from Prosperous Bay, St. Helena and all but *h* and *i* from USNM 175878.

*a**b**c**d**e**f**g**h**i**j**k*

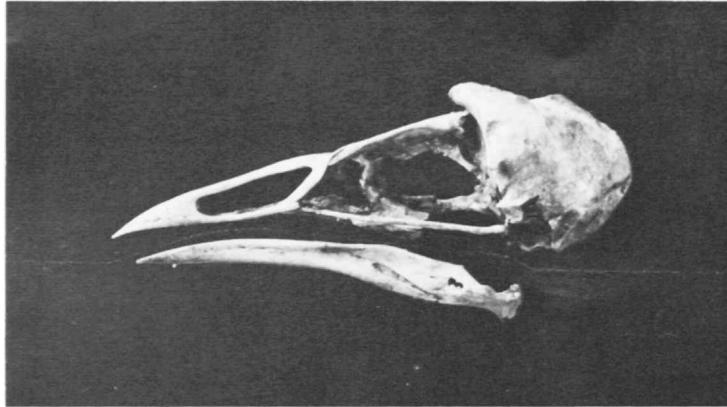
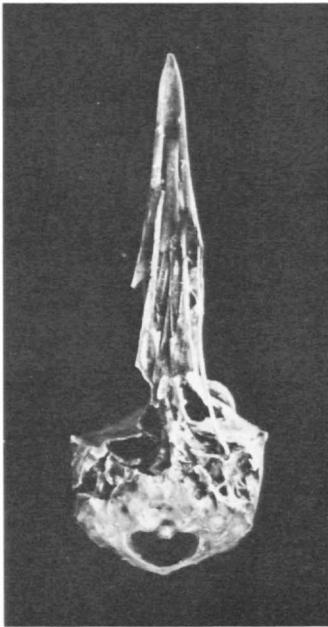
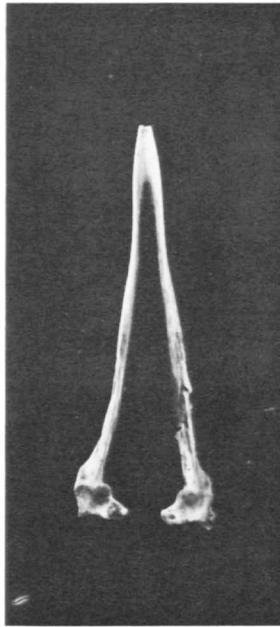
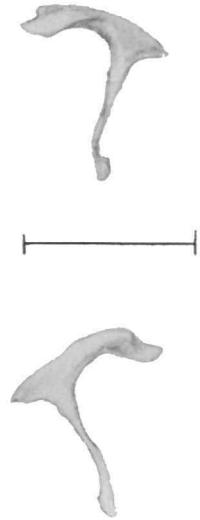
*a**b**c**d*

PLATE 7.—Skull elements of *Porzana astrictocarpus*, holotype, USNM 175893, Prosperous Bay, St. Helena: *a*, lateral view of skull and mandible (braincase crushed dorsoventrally); *b*, ventral view of skull; *c*, dorsal view of mandible; *d*, right lacrimal; external view above, internal view below. Scale=5 mm. All figures except *d* twice natural size.

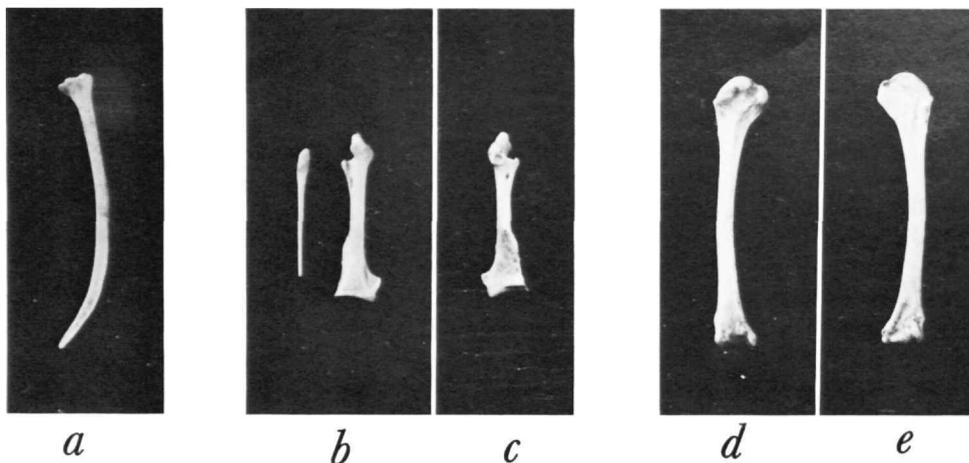
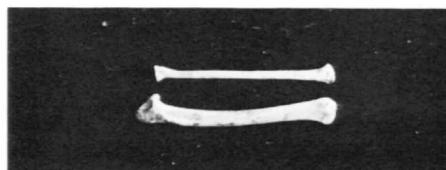
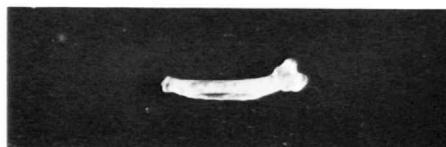


PLATE 8.—Pectoral girdle and wing elements of *Porzana astrictocarpus*: *a*, right scapula, ventral view; *b*, left coracoid, external view, with a portion of the left clavicle; *c*, same, internal view; *d*, left humerus, anconal view; *e*, same, palmar view; *f*, left radius (anconal view) and left ulna (palmar view); *g*, left carpometacarpus, external view; *h*, same, internal view, with ulnare and phalanges 1 and 2 of digit II; *i*, right carpometacarpus, internal view, USNM 175293, Dry Gut, St. Helena. Scale=approx. 5 mm. All but *i* are from the holotype, USNM 175893, and are twice natural size.



f



g



h



i

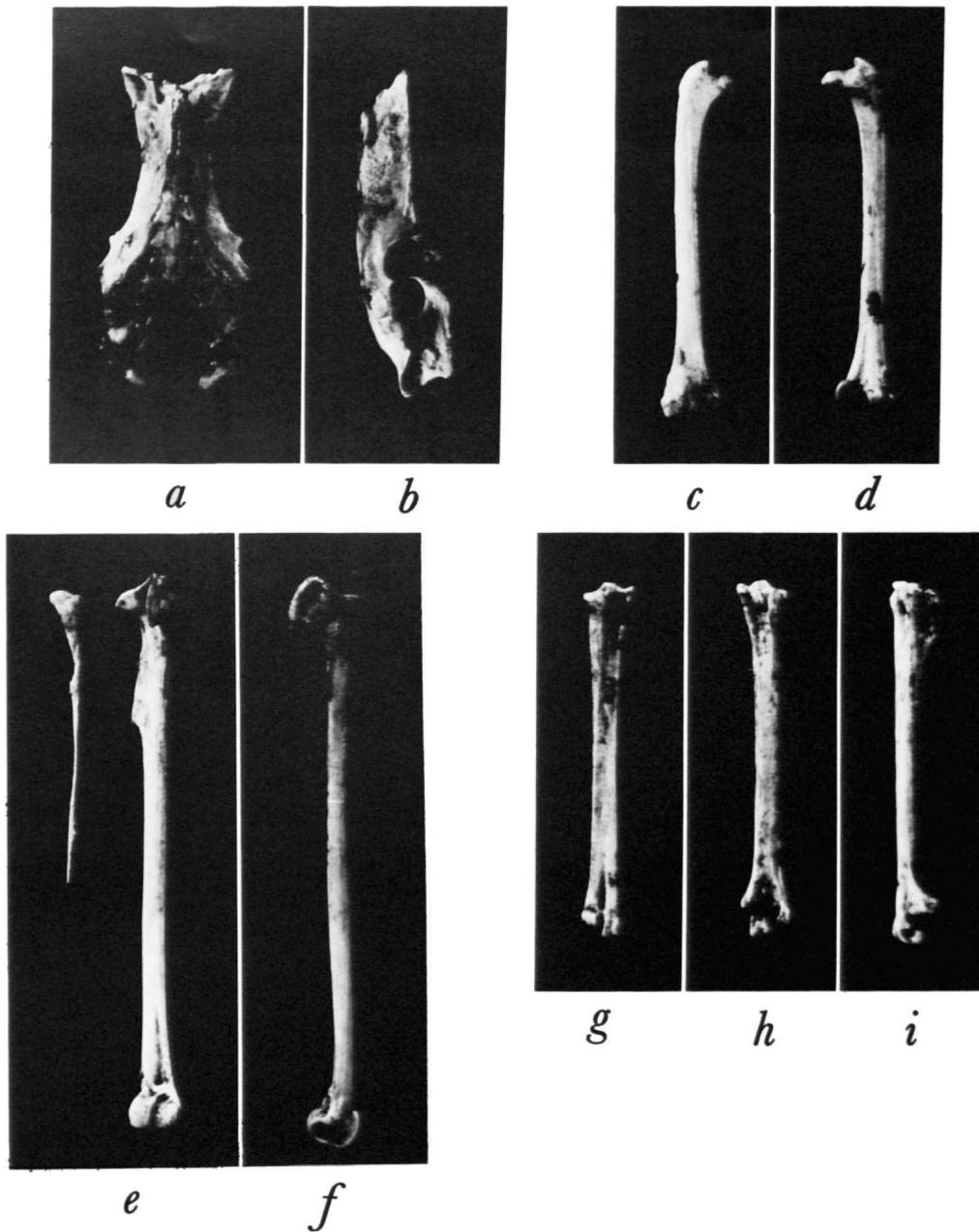


PLATE 9.—Pelvis and hindlimb elements of *Porzana astrictocarpus*, holotype, USNM 175893: *a*, pelvis, dorsal view; *b*, same, right lateral view; *c*, right femur, anterior view; *d*, same, posterior view; *e*, right fibula (external view) and right tibia (anterior view); *f*, right tibia, medial view; *g*, right tarsus, anterior view; *h*, same, posterior view; *i*, same, medial view. All are twice natural size.

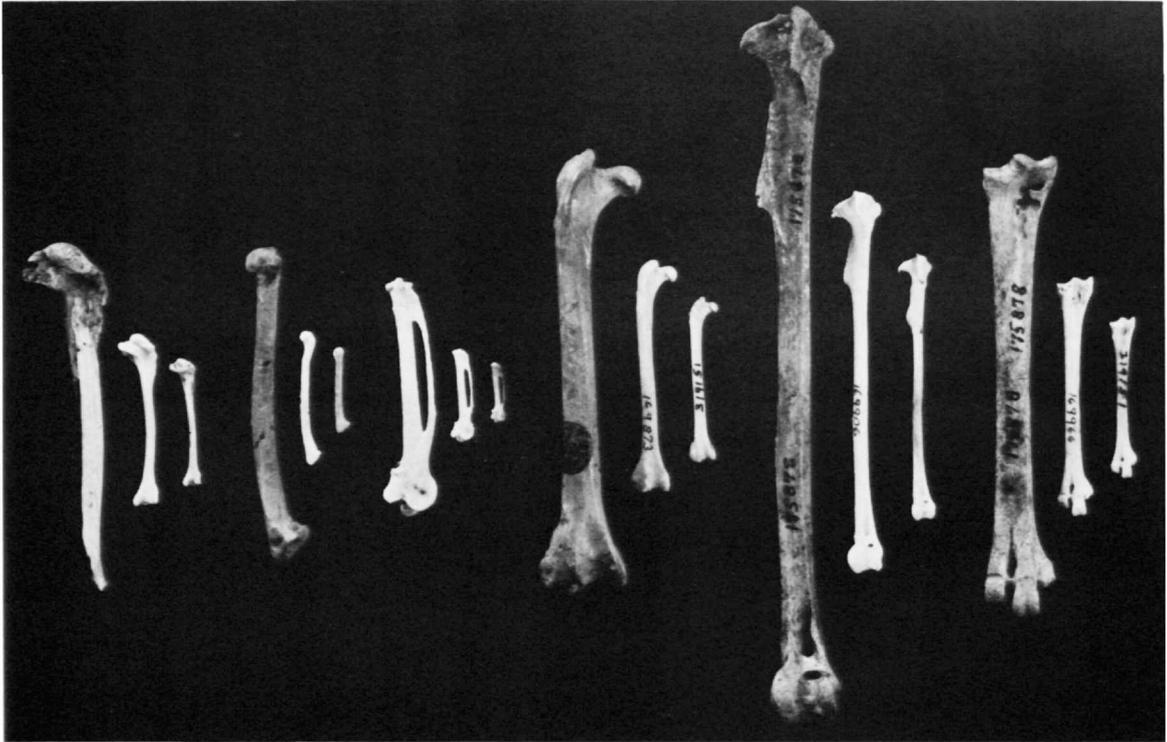


PLATE 10.—Leg and wing elements of the three species of *Atlantisia* compared: The elements shown (left to right) are humerus, ulna, carpometacarpus, femur, tibia, and tarsus. In each group, *A. podarces* is on the left, *A. elpenor* in the middle and *A. rogersi* on the right.

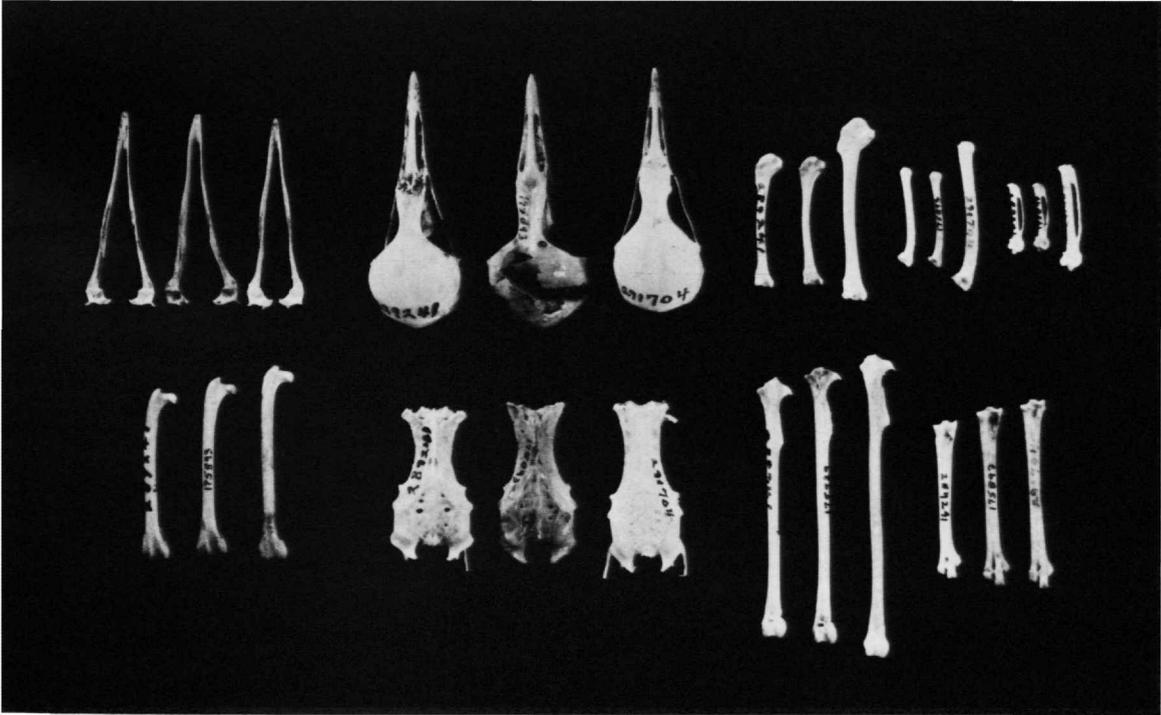


PLATE 11.—Skeletal elements of three species of *Porzana* compared: The elements shown (left to right, top to bottom) are mandible, skull, humerus, ulna, carpometacarpus, femur, pelvis, tibia, tarsus. In each group, *P. palmeri* is on the left, *P. astrictocarpus* is in the middle, and *P. pusilla* is on the right.

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