A CLASSIFICATION OF THE RALLIDAE

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THE family Rallidae, containing over 150 living or recently extinct species and having one of the widest distributions of any family of terrestrial vertebrates, has, in proportion to its size and interest, received less study than perhaps any other major group of birds. The only two attempts at a classification of all of the recent rallid genera are those of Sharpe (1894) and Peters (1934). Although each of these lists has some merit, neither is satisfactory in reflecting relationships between the genera and both often separate closely related groups. In the past, no attempt has been made to identify the more primitive members of the Rallidae or to illuminate evolutionary trends in the family. Lists almost invariably begin with the genus *Rallus* which is actually one of the most specialized genera of the family and does not represent an ancestral or primitive stock.

One of the difficulties of rallid taxonomy arises from the relative homogeneity of the family, rails for the most part being rather generalized birds with few groups having morphological modifications that clearly define them. As a consequence, particularly well-marked genera have been elevated to subfamily rank on the basis of characters that in more diverse families would not be considered as significant.

Another weakness of former classifications of the family arose from what Mayr (1949:3) referred to as the "instability of the morphology of rails." This "instability of morphology," while seeming to belie what I have just said about homogeneity, refers only to the characteristics associated with flightlessness—a condition that appears with great regularity in island rails and which has evolved many times. I have elsewhere (Olson, 1973) argued that flightlessness in rails is a neotenic condition that is evolved very rapidly, involves little genetic modification, and is without major phylogenetic significance. Flightlessness and its associated morphology can be used as a taxonomic character in the Rallidae only at the specific or subspecific levels. When this is done, the result is the elimination of much fragmenting of genera that had previously obscured the origins and relationships of many species.

Whenever possible in determining relationships I have tried to examine skeletons of each genus, but in many cases anatomical material was not available and often I have had to rely solely on skins. Consequently the classification of certain groups remains tentative. The skeletal material examined for this study is the same as that used in Olson (1973).

Downy young of some primitive rails: top—*Himantornis haematopus;*
middle—*Canirallus kioloides;* bottom—*Canirallus (Rallicula) farbesi.*
Painting by Willam Zimmerman

THE SUBFAMILIES OF RALLIDAE

The family Rallidae has traditionally been divided into three subfamilies—the Rallinae, the Gallinulinae, and the Fulicinae (see Brodkorb, 1967, for original citations), but there has been little justification for such a treatment and the assignment of many genera to a particular subfamily was often purely arbitrary. Sharpe (1893a:26) pointed out that

"the popular division of the family into Rails, Gallinules, and Coots was an untenable one, the Coots alone having definite characters for their separation as a subfamily, and that even these characters were approached by those of the Gallinules. It seemed therefore, best to keep the whole of the Rails together as a family, and not recognize minor divisions such as those specified. The gradual transition from typical Rails to Crakes . . . and from Crakes to Gallinules . . . was so marked that it was impossible to say where the Rails ended and the Crakes began, or where the Crakes ended and the Gallinules began,"

A similar opinion was voiced by Ridgway and Friedmann (1941:41):

"Notwithstanding the great dissimilarity between the typical rails . . . and the coots . . . there is so complete a gradation from one extreme to the other in forms of intermediate characters that it is doubtful whether any subfamilies can be satisfactorily defined."

With these opinions I am in full accord. Certainly there can be no realistic separation of "rails" from "gallinules." There are no external or osteological characters that can be used to distinguish the two groups and genera such as *Amaurornis* can scarcely be separated on the one hand from some of the crakes included in the "Rallinae" or on the other from the more typical gallinules of the "Gallinulinae."

A better, but not convincing, case might be made for recognizing the Fulicinae. However, the lobed toes are not confined to *Fulica*. The toes of *Porphyriops* are narrowly but distinctly lobed and those of *Gallinula chloropus* are at least somewhat emarginated. Ridgway and Friedmann (1941:207) state that

"*Fulica ardesiaca* Tschudi, *F. armillata* Vieillot, and *F. rufifrons* Phillipi and Landbeck agree with one another and differ from all the species of *Fulica* proper in having the lateral membranes of the toes very narrow, with the segments very slightly if at all convex, indeed almost bridging the gap between coots and gallinules."

This statement is correct only as it applies to *rufifrons*, the toes of *ardesiaca* and *armillata* being as well lobed as those of other species of *Fulica*. Nevertheless, *F. rufifrons* and *Porphyriops melanops* do clearly bridge the gap between the coots and the gallinules in this respect and there is no external character of subfamilial importance by which *Fulica* may be distinguished from the "gallinules."

The skeleton of *Fulica* is with few exceptions very similar to that of *Gallinula*. The most marked difference is in the pelvis, which in *Fulica* is narrower and more elongate. This is an adaptation that is correlated with the diving habit (Raikow, 1973). The tarsus of *Fulica* is somewhat more compressed

than in *Gallinula* and the cnemial crest of the tibia is better developed, both also correlated with diving locomotion. In all other Rallidae, except the flightless species, the humerus length is about the same as that of the femur, but in *Fulica cristata, F. atra, F. americana, F. ardesiaca, F. caribaea, F. armillata,* and *F. leucoptera* the humerus averages from 27 percent to 34 percent longer than the femur. However, in *F. rufifrons* the humerus and femur are equal in length as in most other rails (it thus appears that in at least two respects—humerus length and lobing of the toes—*rufifrons* is the least specialized species of *Fulica,* although the pelvis is modified in typical coot fashion). The apparently longer humerus of most species of *Fulica* is probably correlated in part with a high wing loading, such as reported for *F. atra* (Jeikowski, 1971), but may also reflect a shortening of the femur which is another characteristic of diving birds.

Both the adult and juvenal plumages of *Fulica* are similar to *Gallinula.* Clearly, *Fulica* is a derivative of a *Gallinula*-like ancestor and differs from gallinules only in adaptations for diving which parallel those of most diving birds. This is not the sort of profound phylogenetic dichotomy that should characterize a subfamily. *Fulica* is a well-defined genus in a family where generic lines are often difficult to draw. It has, however, diverged only slightly, and along predictable lines, from its quite-evident ancestral stock. I cannot support subfamilial status for the genus.

The most recent assessment of the subgroupings of the Rallidae is that of Verheyen (1957) who divided the family into five subfamilies as follows: Fulicinae (containing two tribes, Fulicini for *Fulica* alone, and Gallinulini for *Gallinula, Amaurornis, Rougetius, Tribonyx, Megacrex, Gallicrex, Habroptila, Pareudiastes, Porphyriops,* and *Porphyriornis*), Porphyriinae [sic]* (containing *Porphyrio, Porphyrula,* and *Notornis*), Sarothrurinae (for *Sarothrura* alone), Himantornithinae (for *Himantornis* alone), and Rallinae (for the remaining genera). Verheyen's inability to provide rational classifications has been well documented (Sibley and Ahlquist, 1972) and I found but little of value in his classification of the Rallidae, many of his characters being inconsistent or insignificant. None of the characters he gives for his Fulicinae serve to differentiate that group from his Rallinae. The same is true of the "Sarothrurinae." *Sarothrura* is very closely related to genera he includes in his Rallinae (see below).

A somewhat better case for subfamilial status could be made for the Porphyrioninae but no stronger than that for the Fulicinae. Most of the characters of the group given by Verheyen are not diagnostic. Those that are, are adaptations for locomotion on floating vegetation (many paralleling those

* The correct rendering of the subfamily name should be "Porphyrioninae," a term, according to Gray (1871), first used by Reichenbach in 1850.

seen in the Jacanidae) and for rather specialized feeding methods. I have elsewhere discussed the nature of some of these modifications (Olson, 1973). They constitute a derived state that is of about the same significance as the diving adaptations of *Fulica*. The specializations of the "Porphyrioninae" are unduly conspicuous because of the lack of specialization of most of the rest of the family. It is hardly of value to taxonomy to erect a subfamily for each genus that evolves adaptations for some specialized mode of locomotion.

One subfamily recognized by Verheyen is quite valid, namely, the Himantornithinae, containing the single species *Himantornis haematopus*. Previous to Verheyen, only Gray (1871) had elevated *Himantornis* to subfamily rank—an action that was subsequently ignored by both Sharpe (1894) and Peters (1934) who placed the genus *in medias res*.

Himantornis is a forest-dwelling bird (apparently even nesting in trees, Chapin, 1939:24) confined to western and west-central Africa. The adult is a large rail with very long slender legs, a short decurved bill, and a singularly unrail-like appearance. The natal down is also highly unusual (Chapin, 1939:29). The downy plumage of most rails is black. In some species of *Aramides* it may be uniform brownish or brownish-black and in *Mentocrex kioloides* and *Rallicula* the down is patterned with black and reddish-brown (frontispiece). In *Himantornis*, however, the chick is distinctively patterned with light and dark markings totally unlike any other rail (frontispiece). This presumably cryptic plumage pattern more closely resembles that of precocial chicks of other orders, such as the Galliformes or Anseriformes, than it does the remainder of the Rallidae. The all-black natal down of most rails is a wide departure from that of typical downy precocial chicks while that of *Himantornis* is not. The natal down of *Himantornis* probably represents a relatively primitive state while the black down of typical rails is a specialized, derived condition.

The skeleton of *Himantornis* shows a number of peculiarities. The distinctive appearance of the skull cannot be matched by any rail (Fig. 1). *Himantornis* is the only rail in which the ectethmoid bone projects far outward and abuts firmly against the lacrimal. The very large, heavy lacrimal has a strong descending process with an expanded foot which comes in contact, or near contact, with the jugal. In these respects and in the general appearance of the skull, *Himantornis* is amazingly similar to the trumpeters (Psophiidae) and in fact comes closer to *Psophia* than to other rails (Fig. 1). *Psophia* differs in having the palatines, maxillopalatines, and the head of the lacrimal larger and more expanded and in its almost completely ossified interorbital septum. The greatly expanded orbital rims in *Himantornis* are asymmetrical in the specimen I examined and it appears as if they could very well have had their origins in something comparable to the accessory supraorbital bones found in
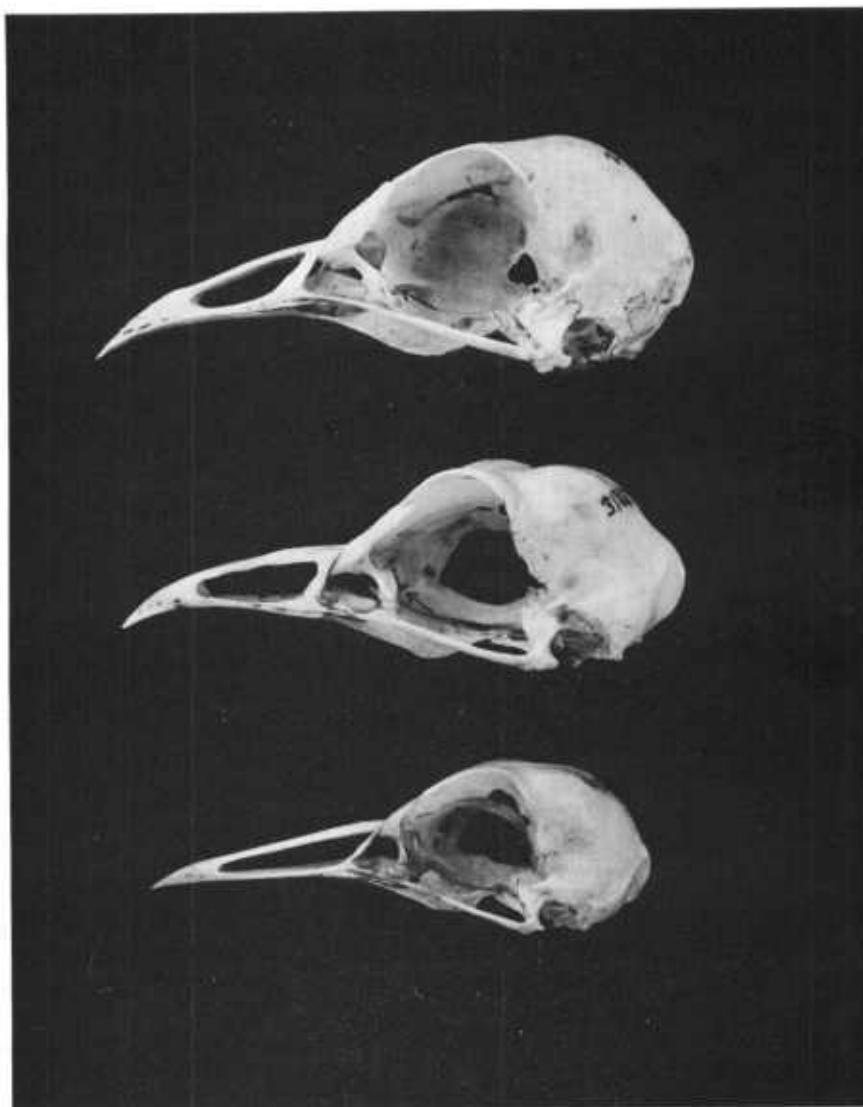
FIG. 1. Top to bottom: Skulls of *Psophia leucoptera*, *Himantornis haematopus*, and *Canirallus oculeus*. Note the lacrimal-ectethmoid contact (arrows) in *Psophia* and *Himantornis*, and the tenuous nasal bar in *Canirallus* versus the broad condition in the other two.
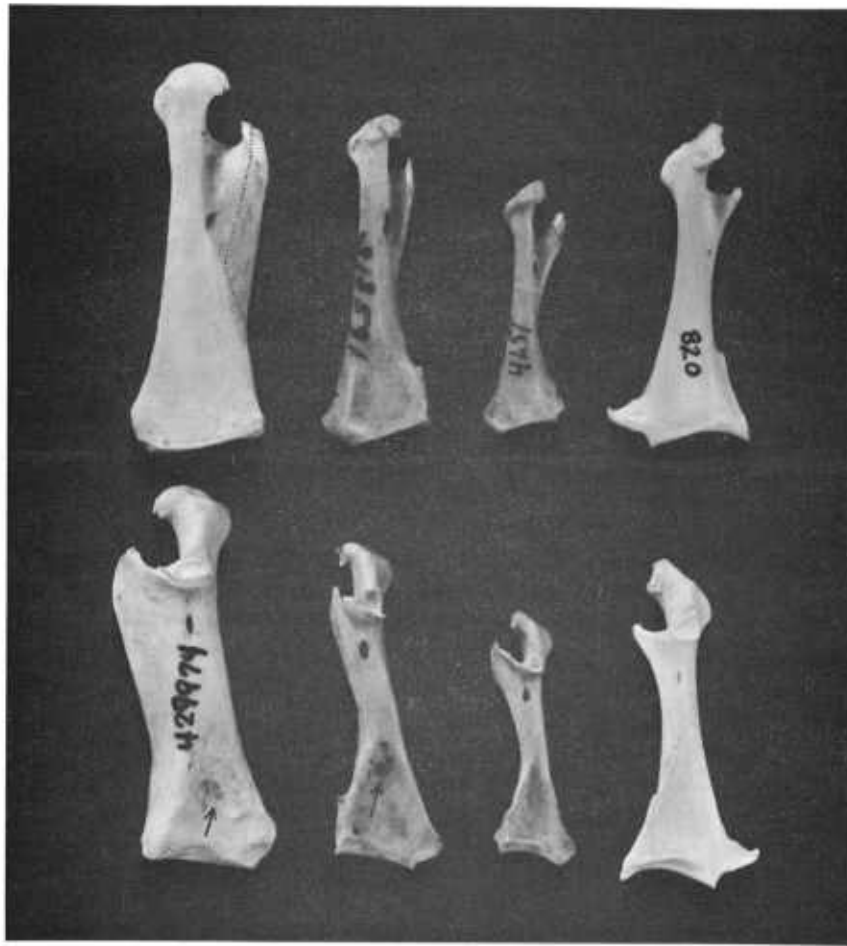
FIG. 2. Left to right: Coracoids of *Psophia crepitans*, *Himantornis haematopus*, *Canirallus oculeus*, and *Fulica americana* (ventral view above, dorsal view below). The dotted line on *Psophia* suggests that portion of the procoracoid that need be removed for the coracoid to approximate that of *Himantornis*. Arrows indicate pneumatic foramina.

Psophia. The distribution of nutrient foramina in the orbital rims of *Himantornis* and *Psophia* are similar.

Several elements of the postcranial skeleton of *Himantornis* are distinct from other rails and are closer to *Psophia*. The coracoid has a peculiar shape, with the head rather flat and oriented nearly perpendicular to the shaft, as seen in *Psophia*, and the procoracoid process is long and broad (Fig. 2). The head of the coracoid in typical rails is oriented in a line with the shaft and

the procoracoid process is usually smaller and more angular (Fig. 2). The procoracoid process of *Psophia* is extremely broad and expanded, more so than in any other family of birds, and thus exaggerates the condition seen in *Himantornis*. This process abuts against the dorsal portion of the clavicle, but why so much additional bracing is needed in *Psophia* is not known. If part of the procoracoid of *Psophia* were removed (as suggested by the dotted lines in Fig. 2) the result would be a coracoid almost identical to that of *Himantornis*. Of the other genera of rails examined, the coracoid of *Canirallus oculeus* (Fig. 2) comes closest to that of *Himantornis*, the procoracoid also being much expanded, but in a different manner. The sterno-coracoidal impression is very deep and pneumatic in *Psophia* and *Himantornis*. Although this cavity may be greatly excavated in other rails, such as *Canirallus*, in no other rail is the coracoid pneumatic. The shape of the pelvis in *Himantornis*, particularly in the more elongated postacetabular ilium and ischium, is more similar to *Psophia* than to the Rallidae. The very broad, pneumatic ribs of *Himantornis* are also more similar to *Psophia* than to the Rallidae.

The tibia of *Himantornis* is proportionately very long and more slender than in other rails. The medial face of the internal condyle is deeply excavated and the posterior rim of this condyle is a thin expanded flange, differing from other rails but closely resembling *Psophia*. The tarsus is likewise distinctive, being long and slender with a thin rectangular shaft and abruptly flaring articular surfaces. The inner trochlea is in nearly the same plane as the outer. In no other rail is the inner trochlea as low. In this respect also, *Himantornis* resembles *Psophia* (Fig. 3).

At this point the familial allocation of *Himantornis* might be questioned but a number of characters show that it indeed belongs to the Rallidae. It has the typical 2-notched sternum of the Rallidae, whereas the sternum of *Psophia* is long, narrow, entire, and rectangular like that of the Gruidae, Aramidae, and Rhynochetidae. *Psophia* lacks, and *Himantornis* has, the scapular tubercle for the dorsal branch of the tendon of M. expansor secundariorum—a rallid character (Olson, 1973). Vertebrae 19–21 are fused into one bone in *Psophia*, whereas the lumbar vertebrae are not fused in any rail, including *Himantornis*. Rails have either 14 or 15 cervical vertebrae, *Himantornis* has 15, but *Psophia* has 17. The humerus of *Himantornis* is rallid and unlike the peculiar knobby humerus of *Psophia*.

The external appearance, osteology, and natal down of *Himantornis* show it to be the most primitive and distinctive rail. It has no close relatives. The characters it shares with the Psophiidae suggest that it, of all rails, is closest to the stock that gave rise to both the Psophiidae and the Rallidae and it provides a definite link between the two families. No other species or group of living rails presents peculiarities of the magnitude of those of *Himantornis*.

FIG. 3. Left to right: Tarsi of *Aramides cajanea, Himantornis haematopus,* and *Psophia crepitans* (reduced for comparison). Note the lower inner trochlea in *Himantornis* and *Psophia.*

I therefore recommend that only two subfamilies of living Rallidae be recognized—the Himantornithinae and the Rallinae.

RELATIONSHIPS WITHIN THE RALLINAE

In attempting to determine relationships within the Rallinae, *Himantornis* at least gives us a few clues as to which species may be primitive. Forest-dwelling forms with long slender tarsi, broad procoracoid processes, and patterned natal down would provide good starting points.

Two other characters emerge as being of possible importance in grouping or separating certain genera. The presence of conspicuous white or buffy bars in the remiges ties in a number of genera that on other grounds as well seem closely related. This barring may be secondarily lost so that its absence in some species does not necessarily prove lack of relationship with bar-winged genera.

The second character of possible utility is the condition of the nasal bar. The nasal bar in the Rallidae may be broad and flat, contributing to a typically "holorhinal" nostril such as in *Himantornis* (Fig. 1), or it may be slender and twisted, forming the so-called "pseudoschizorhinal" nostril such as in

Canirallus (Fig. 1). The slender nasal bar and either schizorhinal or pseudo-
schizorhinal nostrils are found in most families of Gruiformes, but the broad,
flat nasal bar and holorhinal nostril are found in the Psophiidae and the
Heliornithidae, the two Gruiform families probably most closely related to
the Rallidae. It is difficult to say which condition is primitive and which
derived, although at least in some instances the broad condition of the nasal
bar appears to have been derived from the tenuous condition by a simple
ossification of the area between the nasal bar and the dorsal branch of the
nasal bone. Either condition may be found in both long-billed and short-
billed species, making a functional correlation difficult. (In a number of
species for which there was no skeletal material I was able to determine the
condition of the nasal bar by exposing it in skins.)

One of the most primitive groups of the Rallinae is formed by the three
"genera" *Canirallus*, *Mentocrex*, and *Rallicula*, containing the species *C.
oculeus* of West Africa, *M. kioloides* of Madagascar, and the four species of
Rallicula in New Guinea. I have seen a skeleton of only *C. oculeus*. This
exhibited a very much expanded procoracoid process (Fig. 2) and very slender,
square-shafted tarsi with wide articulations as in *Himantornis*. All of these
forms are forest dwellers that are united by a combination of the following
characters: bill with similar shape (high flat-ridged culmen and large deep nasal
fossa) ; tenuous nasal bar; rich chestnut neck and breast; black or dark brown
lower belly, thighs, and crissum narrowly barred with buff; long, fluffy
red tail; black remiges and axillars barred with broad bands of white. Further-
more, the natal down of at least *Mentocrex* and *Rallicula* is distinctly patterned
(frontispiece), another indication of the primitiveness of the group. The
beautiful velvety down of *M. kioloides* is striped above and mottled with brown
and black below (Rand, 1936, gives a full description). The chick of *Rallicula
forbesi* is entirely mottled with black and brown and lacks the distinctive
dorsal pattern of *M. kioloides*. A chick of *Rallicula rubra* (AMNH 338622)
is similar to *R. forbesi* but darker, with black predominating over the brown.
Bannerman (1931:8) describes the chick of *C. oculeus* as "entirely covered
with blackish-brown velvety down" but does not mention any pattern. The
patterned natal down in this group is somewhat intermediate between the
primitive condition of *Himantornis* and the pure black down of typical rails.

The species *kioloides* was generally placed in *Canirallus*, along with *oculeus*,
until Peters (1932*a*) separated it in the genus *Mentocrex* because its im-
perforate nostrils differed from the perforate condition of *oculeus*. This
difference is not generically important, however, as Wetmore (1967) has
recently pointed out that two forms of *Neocrex*, previously considered con-
specific, differ in this same respect. As *kioloides* otherwise differs from
oculeus only in its smaller size, white versus gray throat, rufous versus green

scapulars, and absence of white barring on the upper coverts, I follow Rand
(1936) is not recognizing *Mentocrex*.

Peters (1932*a*) noted a similarity between *C. kioloides* and *Rallicula* but
later (1934) separated them widely in his checklist. *Rallicula* differs from
Canirallus only in its smaller size, sexual dichromatism (probably the result
of active speciation on New Guinea), presence of white markings and/or
black coloration instead of green in the dorsum, and absence of gray on the
head. In its intermediate size and presence of rufous in the dorsum, *kioloides*
bridges the gap between *oculeus* and *Rallicula*.

The great similarity in the structure, plumage, and natal down of *Rallicula*
and *Canirallus*, in my opinion, outweighs their comparatively minor dif-
ferences in plumage. It is more realistic and instructive to combine the two
genera, maintaining *Rallicula* Schlegel 1871 as a subgenus of *Canirallus*
Bonaparte 1856.

This has the zoogeographical effect of tying together West Africa, Mada-
gascar, and New Guinea. The relict nature of much of the Madagascan fauna
has long been recognized and this fauna has connections both with Africa
and Asia. The forests of West Africa have also acted as a refugium for relict
forms, many of which have their closest relatives in the Oriental realm.
Although the observant Chapin (1932) was well aware of the relationship
between the West African forest fauna and that of Asia, such was not apparent
to Moreau (1966:177) who gave it little consideration. A few examples
should suffice to establish the link: the African heron *Tigriornis* is apparently
closest to *Zonerodius* of New Guinea (Chapin, 1932); the relict Congo
eurylaimid *Pseudocalyptomena* has its closest apparent relatives in the Asian
genus *Calyptomena* which has its center of species abundance in Borneo;
the West African piculet *Verrauxia* is very close to, and probably should be
congeneric with *Sasia* of Asia; the Congo Peacock *Afropavo* has its
closest affinities with Asian peacocks; the most primitive living swallow,
Pseudochelidon eurystomina of the Congo, has as its closest relative the
recently discovered *Eurochelidon* (= *Pseudochelidon* auct.) *sirintarae* of
Thailand; the owl *Phodilus prigoginei*, known from a single specimen
taken in 1951 in the mountains northwest of Lake Tanganyika, has its only
relative in *Phodilus badius* of Asia; Ripley (1966) has noted that the West
African owl *Otus icterorhynchus* and its relict relative, *O. ireneae*, of Kenya,
seem to be most similar to *O. balli* of the Andaman Islands. Among mammals,
the chevrotains (Tragulidae) are known from West Africa, India, and
Malaysia, with fossil forms known in intervening areas and Europe (Anderson
and Jones, 1967). The presence of the most primitive living rail, *Himantornis*,
in the West African forests lends additional weight to the idea of their being
an important refugium. The list could no doubt be profitably expanded to

include other groups of organisms. It is clear that many forest-inhabiting taxa were once of much wider distribution and are now confined to disjunct refugia in West Africa and Asia because of the deterioration of the environment in the areas between. The fragmented distribution of *Canirallus* (sensu lato) is further testimony to the antiquity of the group.

Very closely related to *Canirallus* (especially *Rallicula*) is the African genus *Sarothrura* containing nine species of small "crakes" that appear to be a direct offshoot from a *Rallicula* stock (providing another link between Africa and New Guinea). Salvadori (1875) tentatively described *Rallicula leucospila* as a species of *Sarothrura* and the similarity of the two genera was also noted by Chapin (1932). This was not reflected by Peters (1934) who interposed 26 genera between them.

In *Sarothrura*, as in *Rallicula*, the sexes are strongly dichromatic, a condition found elsewhere in the Rallidae only in *Gallicrex cinerea* and *Porzana parva*. The male of *S. pulchra*, with its chestnut head, breast, and upper back, fluffy red tail, black mantle and wings with round white polka-dots, plush loreal feathering and nearly identically shaped bill, is an exact duplicate in miniature of the females of *Rallicula*. The black tail-barring of females of *S. pulchra* and *S. insularis* is found in some plumages of *Rallicula*, and the white streaking of males of *R. leucospila* is very reminiscent of males of the *Sarothrura rufa* group. The white barring on the flight feathers of *Rallicula* is present in *Sarothrura* only as spots on the outer webs of the remiges of *pulchra* and *elegans* and has apparently been lost in the other species of the genus. In *S. pulchra*, at least, the nasal bar is broader than in *Canirallus-Rallicula*.

Not only is *S. pulchra* the most similar in plumage to *Rallicula* but it also has by far the longest and most slender tarsi of the genus (Chapin, 1939), and with the exception of *S. elegans*, is the only truly forest-dwelling member of the genus. These features, as previously noted, appear to be primitive in the Rallidae. In this case, *pulchra* would be the most primitive species of *Sarothrura*, the others having secondarily adapted to more open grassland marshes. This is exactly the reverse of the phylogeny advanced by Keith et al. (1970). In the process of adapting to grassland habitat, *Sarothrura* has progressively lost many of the *Rallicula*-like characters such as the fluffy red tail and the wing-barring, while the tarsi have become shorter, and in the most advanced forms, the bill has become very short and deep.

Two other genera, *Coturnicops* and *Micropygia*, are possible relatives of *Sarothrura*. Both of these taxa consist of small species with very short, deep bills and which inhabit open grassland marshes. *Coturnicops* contains the species *notata* of South America and *exquisita* and *noveboracensis* which form a holarctic superspecies. All three have a large white patch in the

secondaries—a character that is found elsewhere only in *Sarothrura ayresi*, a relict species that has at times been placed in *Coturnicops*. As the white secondary patch is found nowhere else in the Rallidae and is shared by species of such similar build and ecological preference, a relationship between *Sarothrura* and *Coturnicops* is strongly implied. Furthermore, the plumage of *Coturnicops* is not unlike that of females of the more advanced grassland species of *Sarothrura*. *Coturnicops* is possibly a "hen-plumaged" derivative of *Sarothrura* stock that has lost its sexual dichromatism in isolation from related species.

In the South American species *Micropygia schomburgkii*, the ocellated dorsum, rufous crown, short bill, and grassland habits are also suggestive of *Sarothrura*, and in spite of its name it has a rather well-developed tail like *Sarothrura*. Dickerman (1968) has shown that there is a fairly consistent sexual difference in the crown color of *Micropygia*—perhaps a partial retention of the sexual dichromatism seen in *Sarothrura*.

There is nothing in the internal or external morphology of *Sarothrura* that supports the retention of Verheyen's "Sarothrurinae." The genus is obviously closely related to *Rallicula* and possibly to *Coturnicops* and *Micropygia* as well. The white, unmarked eggs of *Sarothrura* were believed by Verheyen (1957) to be distinctive, but unmarked eggs are also found in *Rallina*, and in *Laterallus viridis* and *L. leucopyrrhus* (Schoenwetter, 1961). I have been unable to find any reference to the eggs of *Rallicula*. A domed roosting nest, from which birds of both sexes were taken, has been reported by Mayr and Gilliard (1954) and is suggestive of the domed nests of *Sarothrura*.

Closely related to *Canirallus-Rallicula* are the four species of *Rallina*. They differ in possessing a broad, flat nasal bar and, in contrast to *Rallicula*, are not sexually dichromatic. They agree with *Canirallus-Rallicula* in their generally chestnut coloration, white-barred wings, and slender tarsi. *Rallina canningi*, found in dense forests on the Andaman Islands, is the only species of the genus with a long, fluffy, red tail. This is a definite link with *Canirallus-Rallicula* and *Sarothrura*, the only other genera in the family exhibiting this distinctive character. *Rallina tricolor* has a dark belly narrowly barred with buff as in *Canirallus-Rallicula* but the other three species of *Rallina* have the belly heavily barred with black and white—a pattern that also appears in some species of *Sarothrura*. *R. tricolor* occurs on New Guinea but inhabits swampy jungle and marshes and is thus ecologically isolated from *Rallicula*. *Rallina fasciata* and *R. euryzonoides* occupy both wet forested situations and marshes. *Rallina* appears to be a group that is in transition from the woodland habitat of the more primitive rails, to the wetland habitat usually thought of as typical for the family.

In the New World, the genera *Anurolimnas* and *Laterallus* appear to be

derivatives of *Rallina* stock. *Anurolimnas castaneiceps* is a forest rail with very similar structure and coloration to *Rallina* except that it lacks the wing barring and has a very abbreviated tail. Sharpe (1894) included the species *fasciatus* (= *Laterallus hauxwelli* auct.) in *Anurolimnas* but Peters (1934), ignoring its obvious similarity to *A. castaneiceps*, arbitrarily placed it in *Laterallus*. Stresemann and Stresemann (1966) were the only subsequent authors not to follow Peters' lead. They returned *fasciatus* to *Anurolimnas* because its pattern of primary molt was similar to that of *A. castaneiceps* and different from that of *Laterallus*. *A. fasciatus* differs from *castaneiceps* only in its smaller size and black-barred belly—the two are otherwise nearly identical. Another species, *Laterallus viridis*, also seems closer to *Anurolimnas* than to *Laterallus*. It is not as close to *castaneiceps* as *fasciatus* is, and the tail is slightly better developed than in those two species. Nevertheless, all three are larger than *Laterallus* and differ from that group in having proportionately longer tarsi, greenish backs, and bright chestnut crowns, and are best considered congeneric.

With the removal of *fasciatus* and *viridis*, the genus *Laterallus* may prove to be more of a natural group than I was formerly inclined to believe (Olson, 1970). In the skeletons of the species I have examined (*leucopyrrhus*, *albigularis*, *jamaicensis*, and also *A. viridis*) the hindlimb elements are proportionately longer and more slender and the wing elements shorter than in any of the "crakes" in or near *Porzana*. They are more similar to *Rallina*. There are also some striking similarities in plumage between *Laterallus* and *Rallina*. *L. leucopyrrhus*, except for having the center of the throat and breast white instead of rufous and except for its discontinuous ventral barring, shows a marked likeness to *Rallina fasciata*. Both the adult and juvenal plumages of *L. albigularis* are near duplicates of the corresponding plumages of *Rallina euryzonoides*. The barring of the remiges characteristic of *Rallina* is generally lacking in *Laterallus*, however, the remiges of *L. jamaicensis* are spotted with white and those of occasional specimens of *L. albigularis* may be faintly mottled or barred with white. Except for *Sarothrura*, the only rails known to have white, unspotted eggs are *Rallina*, *A. viridis* and *L. leucopyrrhus*. I think it is highly likely that *Anurolimnas* and *Laterallus* were derived from an Old World *Rallina*-like ancestor and are not related to *Porzana*. Thus in Africa and South America there appears to have been a parallel radiation of diminutive "crakes"; one group being derived from a *Rallicula* woodland ancestor and the other from a *Rallina* stock.

Returning to the Old World, we encounter the two species of *Nesoclopeus* (*poeciloptera* of Fiji and *woodfordi* of the Solomons), both originally described as members of *Rallina*. Sharpe (1894) placed them in *Eulabeornis*, a quite unrelated genus, from which Peters (1932b) properly removed them,

creating the genus *Nesoclopeus* for their reception. Greenway (1958), with no explanation, returned them to *Rallina*, using *Nesoclopeus* as a subgenus. Both species have barred primaries and the broad white bars of *woodfordi* are indeed suggestive of *Rallina*. However, both species have the tenuous nasal bar, unlike *Rallina*, and both have relatively heavier, shorter tarsi. There is a faint but distinct outline of a facial pattern (better developed in *poeciloptera*) that is similar to that of the *philippensis* group of *Gallirallus* (sensu lato, see below) and the brown-barred wings of *poeciloptera* are more suggestive of that group than *Rallina*. Until more of their structure is known, it is preferable to maintain the genus *Nesoclopeus*. The genus may provide an intermediate between *Rallina* and the *Gallirallus* group.

We come next to a group of barred-wing rails the relationships of which have been greatly obfuscated by combining a number of the species with the more specialized species of *Rallus* (sensu stricto) and also by the creation of several unnecessary genera for flightless forms of the group. The species *philippensis, owstoni, wakensis, torquatus,* and *striatus* have either been combined with *Rallus* or segregated as a separate genus *Hypotaenidia*. Peters (1934) recognized *Hypotaenidia* as a subgenus of *Rallus* although he placed *striatus* in the subgenus *Rallus*. I recently revived the use of *Hypotaenidia* (Olson, 1973) but as we shall see below, this name must ultimately give way to *Gallirallus*.

The abovementioned species of "*Hypotaenidia*" differ from *Rallus* in being relatively unspecialized, with stouter bills, wider sterna, and heavier hindlimbs. They differ further in having the primaries barred conspicuously with white or reddish-brown, and most species are rather ornate with a bold pattern of stripes on the face and a chestnut or ochraceous band across the chest.

Within this group may be recognized subgroups, of which, that containing *philippensis* and its derivatives has the widest distribution and has given rise to the most flightless forms. The flightless species *owstoni* on Guam, although larger and longer-billed than *philippensis*, retains the same facial pattern and some individuals still show a faint ochraceous pectoral band and a pronounced reddish color on the nape recalling *philippensis*. Individuals of the small flightless species *wakensis*, of Wake Island, also retain traces of the pectoral band, rusty nape, and facial pattern of *philippensis*.

A confusing situation has existed concerning the *philippensis* derivatives of the Chatham Islands. This group of islands lies about 500 miles east of New Zealand and consists of the large main island of Chatham itself, smaller Pitt Island 14 miles to the southeast, and numerous other islets of which only Mangare, a satellite of Pitt, is of concern here (see map in Fleming, 1939). Two *philippensis* derivatives were described from this group, each of which eventually came to rest in its own genus. Erroneously, both of these species have commonly been regarded as occupying the whole Chatham group

(Rothschild, 1907; Peters, 1934; Greenway, 1958). Their rather complicated history runs as follows.

A single specimen of a distinctive rail was collected by Dieffenbach in 1842 on the main island of Chatham and was named *Rallus dieffenbachii* by Gray. The species is now extinct. A correspondent wrote Buller (1873:180) in 1863 that he knew this bird as a boy and that it disappeared in the third year of Maori occupation of the island.

In 1872 Hutton described a new species, *Rallus modestus*, from the islet of Mangare, which differed considerably in plumage from *dieffenbachii*. For this species Hutton (1874) quickly created a new genus, *Cabalus*, the basis for which lay in skeletal modifications correlated with flightlessness. Buller (1873) considered *modestus* to be merely the juvenal plumage of *dieffenbachii*, as at first did Forbes (1892) and Sharpe (1894—plate 6 shows an example of *modestus* encaptioned "*Cabalus dieffenbachii* juv."). Upon receipt of a series of skins from Mangare containing both young and adults of *modestus*, and upon the testimony of the collector Hawkins who stated that young and adult were alike, Forbes (1893*a*) rescinded his former opinion and maintained *modestus* distinct from *dieffenbachii*. Sharpe (1894:331) inserted an addendum to this effect in his catalogue.

The type of *dieffenbachii* came from Chatham Island. Forbes (1893*b*) reported bones of this species from Chatham. Andrews (1896) also discussed a collection of bones from Chatham that included this species and upon the basis of its better developed sternum, shorter bill, and different plumage, he removed *dieffenbachii* from *Cabalus* (where Sharpe had placed it) and created the genus *Nesolimnas* for it. Fleming (1939:492) mentions an adult of *modestus* in the Canterbury Museum labelled "Pitt Island" and a downy young in the Dominion Museum with the same locality. Apart from these two specimens, all known examples of *modestus* were taken on Mangare. Forbes (1893*b*:533) reported that "bones referable *apparently* [emphasis mine] to this species [*modestus*] have, however, been found among the subfossil remains in Wharekauri [= Chatham]." This single very doubtful statement seems to be the only evidence for the sympatry of *dieffenbachii* and *modestus* which is implied in later works. Andrews (1896) did not mention *modestus* in the extensive collections he examined from Chatham. It is more than likely that Forbes mistook bones of *dieffenbachii* for those of *modestus*. The range of *dieffenbachii* should therefore be restricted to Chatham Island proper and that of *modestus* to Mangare and possibly Pitt. Falla (1960) reported on bones of a small rail from Pitt Island that he tentatively referred to *dieffenbachii* on the basis of size. They were not compared to that species, however, and could easily have been of *modestus* or some other form.

Illustrations of *dieffenbachii* (Buller, 1873; Rothschild, 1907) show a bird that is extremely similar in plumage to *philippensis* except that the black and white ventral barring extends farther up the throat, the pectoral band is wider and barred with black, and the dorsum lacks white spots. All of these characters may be found in the juvenal plumage of *philippensis*. The bill in *dieffenbachii* is longer and more decurved than in *philippensis* and the flying apparatus is reduced. None of these characters is of generic value and the species is obviously a direct *philippensis* derivative as has already been observed by Delacour (in Mayr, 1949).

The plumage of *modestus* is more somber, being a uniform shade of brownish above and entirely barred below with brown and buff. The primaries

are barred with buff as in *philippensis*. The bill is longer and more slender
and decurved than in *dieffenbachii*. "Dr. Bowdler Sharpe [1893*b*] observed
that it was a singular fact that this little Rail [*modestus*] should possess in
its adult plumage the exact dress which might have been expected to char-
acterize the young of *C. dieffenbachii*." He later (1894:331) said that
"in this species the fully adult birds resemble the young of the species of
Hypotaenidia."

Flightlessness in rails is a result of a retention of juvenile skeletal characters
and proportions (Olson, 1973). It is evident that such a neotenic condition
is also responsible for the plumage characters of *dieffenbachii* and *modestus*.
The more reduced sternum and more somber plumage of *modestus* indicates
that the development of these characters was arrested at an earlier stage than
in *dieffenbachii*, in which the sternum is better developed and the plumage
more nearly like that of adult *philippensis*. Since *dieffenbachii* neatly bridges
the differences between *modestus* and *philippensis*, there is no need for
separate generic status for either of the Chatham Islands forms.

The large, flightless Weka (*Gallirallus australis*) of New Zealand, at first
sight seems to be a strange and distinctive rail. Early classifiers, deceived by
the neotenic characters associated with flightlessness, considered it as a
peculiar, primitive form without close relatives. However, Mayr (1949:4)
commented that "the currently adopted sequence [of rails] frequently separates
genera widely that appear related. For instance, it seems to me as if *Gallirallus*
were near *Rallus philippensis*." The plumage similarities are actually quite
striking, as noted by Delacour (in Mayr, 1949). The facial pattern is the
same—gray superciliary stripe, brown ocular stripe, gray throat. Some
individuals show the reddish nape of *philippensis*. The ochraceous pectoral
band is present in some birds, while in most the pectoral band is wider and
streaked with black as in the juveniles of *philippensis*. The dorsal plumage
is like that of juvenile *philippensis*. The flight feathers are strongly barred
with rufous and black, again a *philippensis* character. One of the most
striking features of the Weka is its large, well-developed tail, quite in contrast
to most large, flightless rails, in which the tail is usually almost obliterated.
But turning once more to *philippensis* we find that this species, too, has a
notably well-developed tail, longer and stronger than in any of the other species
of "*Hypotaenidia*."

In the skeleton the similarities are nearly as great. The skulls of *G. australis*
and *philippensis*, apart from the differences in size, are virtually identical.
Both have the tenuous nasal bar. The hindlimb elements of *G. australis* are
somewhat heavier than in *philippensis* but are otherwise similar and the
transition to the large size of *australis* appears to be bridged by the small,
extinct species *G. minor* and the still smaller and more slender *G. hartreei*

(Scarlett, 1970), both known from Quaternary deposits in New Zealand. The wings and pectoral girdle of *G. australis* are, of course, considerably different from those of *philippensis* but like the plumage, are simply recently derived neotenic characters. New Zealand must then have been colonized twice by *philippensis* stock. The first invasion gave rise to *Gallirallus australis*, *minor*, and *hartreei* and the second invasion was by *philippensis* itself. As even the species stock from which *australis* was derived is apparent, and since its flightless characters are without phylogenetic significance, I do not feel that generic segregation for the flightless New Zealand forms is warrented. Since *Gallirallus* Lafresnaye 1841 has priority over *Hypotaenidia* Reichenbach 1852, the entire *Hypotaenidia* group and its derivatives must now be placed in *Gallirallus*.

Two other insular rails are possible derivatives of *philippensis* stock. From Tahiti there is a rail known only from the Forsters' illustration and description (both reproduced in Rothschild, 1907). Rothschild lists this species as "*Hypotaenidia? pacifica*" based on *Rallus pacificus* Gmelin 1787, but "*Rallus ecaudata*" J. F. Miller 1783 is used by Peters (1934) and appears to have priority. The bird, as described and depicted, differs from "*Hypotaenidia*" in its black dorsum, unbarred belly, and blood-red bill and iris, but its ferruginous nape, white superciliary stripe, white spotted dorsum, and banded wings, as well as geographical probability, are all suggestive of *philippensis*.

The remaining possible derivative of *philippensis* stock is the species *sylvestris* of Lord Howe Island. This species has usually been placed in the genus *Tricholimnas* along with *lafresnayanus* of New Caledonia. Both species were originally described as members of *Gallirallus*. Sharpe (1893a: 28) erected the genus *Tricholimnas* for *lafresnayanus* only and felt that *sylvestris* should be congeneric with "*Cabalus*" of the Chatham Islands. Apparently Mathews (1912) was the first to place *sylvestris* in *Tricholimnas*, doing so merely in a list with no explanation. He later (1928) proposed the subgeneric name *Sylvestrornis* for *sylvestris*, still keeping it in *Tricholimnas*. Peters (1934) listed both species under *Tricholimnas*. Greenway (1958:225) did likewise and spoke of the two species as being "so similar that it is quite possible that they would breed freely if brought together." This is simply not so. The two species are so dissimilar that it may be rightly questioned if they evolved from the same ancestral stock.

In *sylvestris* the plumage is uniform olive-brown above and grayer below with a whitish chin. *Lafresnayanus* is much darker brown above with the plumage much more fluffy and decomposed than in *sylvestris*. The tail of *sylvestris* is better developed than that of *lafresnayanus* while the wings are more reduced. Most conspicuously, the remiges of *sylvestris* are barred with rufous and black as in *Gallirallus* while those of *lafresnayanus* are unpatterned.

Aside from their both being large, brown, flightless rails of some geographical proximity, there is nothing to indicate a relationship between *sylvestris* and *lafresnayanus*. Clearly they have been derived independently and each is more closely related to some volant ancestor than to the other. Whether this ancestor was the same for both species cannot now be discerned. If so, *lafresnayanus* has diverged to the point that any external resemblance to the ancestral stock has been obscured. I consider *lafresnayanus* as the only species of *Tricholimnas* and place the genus provisionally near *Gallirallus*.

Sylvestris has evidently evolved from some *philippensis* stock somewhat along the lines of *Gallirallus australis*. The skull of *sylvestris* is more slender with a longer more decurved bill than in *australis*. The lacrimal is much more tenuous and reduced than that of *australis* but this is not of generic importance (Olson, 1970; 1973). The wing and pectoral girdle are not as reduced as in *australis* and the leg elements are not as robust. The hindlimb elements, in fact, rather resemble those of *G. hartreei* shown in Scarlett (1970). The skeleton of *sylvestris*, except for the skull, has diverged less from its apparent ancestral stock than has *australis*, while the plumage has diverged more. I place it provisionally in *Gallirallus*. If generic distinction were desired, *Sylvestrornis* would apply.

The species *torquatus* and *insignis* form another subgroup within *Gallirallus*. *G. torquatus* is found throughout the Philippines and on Celebes and its off-lying islands. It inexplicably skips the Moluccas and reappears again in northwesternmost New Guinea on Salawatti and adjacent parts of the Vogelkop, but the species is not found elsewhere on that great island. It has a chestnut pectoral band which is reduced in the populations of the southern Philippines (Parkes, 1971) and lacking altogether in the Celebes and New Guinea populations. The species *insignis*, restricted to the island of New Britain and widely separated geographically from the nearest population of *torquatus*, is a somewhat larger bird with reduced wings, although it apparently is not completely flightless (Coultas, in Mayr, 1949). It is very similar to *torquatus*, being uniform olive-brown above, and black below finely barred with white from chin to abdomen, as in some of the Celebes individuals of *torquatus*. It differs from that species only in having the crown, cheeks, and nape dull reddish, and in lacking the white subocular stripe. Both have the flight feathers barred with white.

Sclater (1880a, 1880b), Salvadori (1882), Sharpe (1894), and Meyer and Wigglesworth (1898) all considered *insignis* to be a representative of *torquatus*. This obvious relationship was not altered until Stresemann (1932) created a new genus, *Habropteryx*, for *insignis*, based only on the characters associated with the apparent flightlessness of the bird. Peters (1934) recognized *Habropteryx* but Mayr (1949:11) felt it unwise to "camouflage its

obvious *Rallus*-nature by segregating it in a separate genus." There is nothing in the structure of *insignis* that merits retention of *Habropteryx*; its affinities are patently with *torquatus*. Just as *philippensis* stock gave rise to a large flightless form in *Gallirallus australis*, so did *torquatus* stock give rise to a large, nearly flightless form in *insignis*.

The only remaining species of *Gallirallus* (sensu lato) is *striatus*, which is the only member of the group found in continental Asia. It is superficially very similar to "*Rallus*" *pectoralis*, a species with a complementary range to the southward. Both have grayish breasts, barred flanks and belly, and a reddish nape and crown. That they are manifestly confusing is indicated by the fact that one form of *pectoralis* (*insulsus*) was originally described as a subspecies of *striatus*, and an aberrant individual of *striatus* was described as a new race (*deignani*) of *pectoralis* (cf. Ripley and Olson, 1973). Hartert (1927:21) even went so far as to say—"It is perhaps daring to treat *R. pectoralis, exsul,* and *alberti* [the latter two now considered subspecies of *pectoralis*] as subspecies of *striatus*, but I think it will be accepted. . ." Daring it was—accepted it was not.

Despite their superficial similarities, *striatus* and *pectoralis* are two quite different birds, as Parkes and Amadon (1959:306) have outlined. Although it lacks a breast band and distinct facial pattern, *striatus* agrees with "*Hypotaenidia*" (= *Gallirallus*) in being a larger, heavier bird with a stouter bill and heavier tarsi and toes than *pectoralis*. Also, the remiges are patterned with bold transverse white bars. This barring is reduced in one specimen (AMNH 545053) from Ceylon and is absent in one specimen from Celebes ("*deignani*"). Otherwise, the white-barred remiges are characteristic of *striatus* and serve to ally it with *Gallirallus*. The remiges of *pectoralis* are never barred, although in some specimens there may be vermiculations and irregular splotches of white. The skeletons of the two species are distinct. That of *striatus*, in all elements, is larger and heavier than *pectoralis*. The shafts of the long bones are stouter. The tarsi are markedly different—that of *striatus* while heavier in the shaft, has more constricted articulations and distally, both the inner and outer trochleae are turned toward the middle. The proximal end of the tarsus of *pectoralis* is noticeably more expanded than in *striatus*.

The skeleton of *striatus* is nearest that of other species of *Gallirallus* but the hindlimb, skull and bill, and pelvis are more slender. The sternum is very narrow, like *Rallus*. I interpret *striatus* as being an advanced form of *Gallirallus* that has *paralleled* the evolution of the true *Rallus* group in evolving towards their slender marsh-dwelling build.

The skeleton of *pectoralis* does not agree with true *Rallus* either; the hindlimb is not as elongate and slender, nor are the bill, skull, or pelvis as

long and slender as in *Rallus*. Yet it is not as heavy a bird as the species of *Gallirallus*. In contrast to *striatus*, *pectoralis* is a generalized, and in some ways more primitive species, forming part of a pro-*Rallus* stock. The plumage similarities of *striatus* and *pectoralis* are probably due purely to convergence.

From the island of Luzon, Amadon and Parkes (1959) described a new rail, *Rallus mirificus*, allied to *pectoralis* but differing mainly in its shorter bill, lack of dorsal streaking, and duller coloration. Paynter (1963), Ripley (1970), and Mayr (1971) considered *mirificus* as a subspecies of *pectoralis* but Amadon and duPont (1970:4) could not agree with Paynter that *mirificus* represented the termination of a "cline" and preferred "to reserve judgment" on the matter. Amadon and Parkes (1959:306) emphasized that *mirificus* and *striatus* were found "side by side" on Luzon. What was not indicated was that this is the *only* place where *striatus* and a form of *pectoralis* occur sympatrically. I suggest that the distinctive features of *mirificus* may have resulted from character displacement brought about by interaction with *striatus*, and that *mirificus* best be considered a well-marked form of *pectoralis*.

G. striatus appears to be a better adapted, more specialized species than *pectoralis*, that is expanding its range out of continental Asia and has already penetrated into the Australian realm as far as Celebes. If it were replacing *pectoralis* as it expanded, and entered the Philippines from the south *via* Malaya and Borneo, then *mirificus*, in the northern Philippines, might represent a relict population that has not yet been replaced or which has evolved mechanisms allowing it to compete successfully with *striatus*.

As I have indicated, *pectoralis* belongs to what I have designated as a pro-*Rallus* group (Olson, 1973) intermediate between the stocky generalized forms of *Gallirallus* and the slender specialized species of true *Rallus*. Closely related to *pectoralis* is the much larger species *Dryolimnas cuvieri* of Madagascar and the off-lying islands of Aldabra, Assumption, and Astove. The skeleton of *Dryolimnas*, except for the larger size and wider sternum, is virtually identical to that of *pectoralis*. The plumage is similar in that both species have the crown, cheeks, and nape rich rufous. It is a less conspicuous feature of *Dryolimnas* because the breast and belly of this species are also red. However, in *Dryolimnas* the crown and nape are a richer rufous than the red of the lower parts, which is washed with vinaceous. The barely visible line of demarcation between the two shades is at about the same place as the border of the red nape of *pectoralis*. The ancestor of *Dryolimnas* may first have had a red crown and nape like *pectoralis* and then later acquired the reddish underparts.

Another closely related group is the remarkable genus *Atlantisia* with its three flightless species on the remote South Atlantic islands of Inaccessible, St. Helena, and Ascension. *Atlantisia* differs from *pectoralis* and *Dryolimnas*

in proportions and several details of the skeleton (Olson, 1973) and also in
that in *A. rogersi* and apparently in *A. elpenor* as well, the red is lacking in
the nape and crown. Neither *pectoralis* nor *Dryolimnas cuvieri* can properly
be placed in *Rallus* and their lack of wing barring and less robust build
precludes their assignment to *Gallirallus*. Since they are more closely related
to each other than either is to any other species, *pectoralis* may be included
in *Dryolimnas*.

The distribution of the pro-*Rallus* group (*Dryolimnas-Atlantisia*) is
essentially relictual, with the species being found on islands scattered around
both sides of Africa and in Australasia. The pro-*Rallus* line probably split off
from some *Gallirallus*-like stock and differentiated somewhat along the lines
taken by true *Rallus* later. The pro-*Rallus* stock then spread nearly worldwide,
including the South Atlantic islands and the Malagasy region. From it, the
specialized true *Rallus* line was derived in the New World. This group then
invaded the Old World, replacing pro-*Rallus* in continental Africa and leaving
representatives isolated on the islands around Africa. *Gallirallus striatus* may
possibly be responsible for the decline of pro-*Rallus* in Asia. It is interesting
that the specialized true *Rallus* has not colonized small, remote, oceanic
islands whereas the more generalized pro-*Rallus* group has been very successful
at doing so. This parallels the situation seen in the specialized genus *Porphyr-
ula* versus the generalized *Gallinula* on small oceanic islands (Olson, 1973).

Four problematical genera are perhaps best considered at this point. The
African genus *Crecopsis*, with its single species, *egregia*, has a "crake-like"
appearance which, combined with a superficial resemblance to *Porzana albi-
collis* of South America, has prompted Benson and Winterbottom (1968) to
suggest that the two form a superspecies. The plumage differences are rather
greater than Benson and Winterbottom allow and since *Crecopsis* has a slender
twisted nasal bar and *P. albicollis* has a broad, flat nasal bar as do other species
of *Porzana*, I am confident that they are unrelated. Actually *Crecopsis*,
although lacking the barred remiges, more closely resembles species in the
Gallirallus group. Its bill is not much shorter than short-billed examples of
G. philippensis and it has a white superciliary stripe of the same character
and position as *philippensis* which is lacking in *Porzana albicollis*.

The monotypic genus *Crex* also has a very tenuous nasal bar unlike most
other "crakes." Its bill and tarsi are proportionately shorter than in *Crecopsis*
and its rufous plumage is more similar to species of *Rallus* (e.g. *R. elegans* and
R. limicola) than to other rails. *Crecopsis* and *Crex* are probably not at all
related to other short-billed "crakes" and possibly fit somewhere between
Gallirallus and *Rallus*.

The large species *Aramidopsis plateni* of Celebes is superficially patterned
like the primitive South American genus *Aramides*, but the bill is shaped

entirely differently, the tarsi are not as slender, and the white ventral barring is quite unlike any species of *Aramides*. The remiges are unbarred. The bill shape, rufous nape, and the rest of the plumage is somewhat similar to the pro-*Rallus* group, near to which it may be provisionally placed.

Rougetius rougetii, an unpatterned, nondescript species restricted to the highlands of Ethiopia, was placed after *Amaurornis* by Sharpe (1894) and in the "Gallinulini" of Verheyen (1957). However, it has a tenuous nasal bar unlike *Amaurornis* or any of the gallinule line and may therefore possibly belong somewhere in the *Gallirallus-Rallus* lineage. It certainly cannot be placed in *Rallus* as was done in White (1965) and Urban and Brown (1971) and the monotypic genus *Rougetius* should be maintained for it until something more of its relationship is known.

The genus *Rallus* I restrict to the species *longirostris, wetmorei, elegans, semiplumbeus, antarcticus, limicola, aquaticus, caerulescens*, and *madagascariensis*. The Neotropical species *maculatus, nigricans*, and *sanguinolentus*, although often placed in *Rallus*, are completely unrelated and are treated later. The species of *Rallus* are much more specialized forms than *Gallirallus* and are highly adapted to a semi-aquatic existence in reedy marshes. Compared to the "*Hypotaenidia*" forms of *Gallirallus* the skull of *Rallus* is narrower and the nostril and premaxillary symphysis is longer; the sternum is narrower; the procoracoid process is less expanded, with a smaller foramen; the pelvis is narrower and the preacetabular portion longer; the femur is more slender with a narrower neck, smaller trochanter and straighter shaft; the whole tibia, particularly the shaft, is more slender; the tarsus is more slender, the proximal end more constricted and the intercotylar knob more delicate and more nearly vertical. Structurally, *Rallus* has gone much farther towards being "skinny as a rail" than has *Gallirallus*. The plumage of *Rallus* is much less conspicuously patterned and no species shows any evidence of a pectoral band or of barring in the remiges. With the exception of *caerulescens*, which is uniform above, all the species of *Rallus* look very much alike in dorsal view.

Rallus has its center of species abundance and diversity in the New World. Only three allopatric species are found in the Old World. *R. aquaticus*, which ranges widely through Eurasia, is one of few Palearctic rails that does not migrate to sub-Saharan Africa. There it is replaced by the species *caerulescens* which differs from *aquaticus* only in its longer, reddish-colored bill and uniform dorsum. Isolated on Madagascar is the distinctive species *madagascariensis*, differing from *aquaticus-caerulescens* in its extremely long, slender bill and in having the gray underparts replaced by an exquisite vinaceous color. Its chin, upper throat, cheeks, and postocular areas, however, are a clear gray, harking back to the *aquaticus* stock from which this species, too,

was likely derived. The three Old World species of *Rallus* appear to form a single superspecies which probably had its origins in a single invasion of *Rallus* from the New World.

We have traced a lineage from the primitive genus *Canirallus* through to the specialized genus *Rallus*. Included in this assemblage are all the forms with barred remiges and all those known to have a tenuous nasal bar. The genera remaining outside the *Canirallus-Rallus* line are mainly the relatively inornate crakes and gallinules centering around the genus *Amaurornis*.

The species of the Neotropical genus *Aramides* comprise an unspecialized group of forest birds with expanded procoracoid processes and long, slender tarsi. They seem to be primitive but have no apparent ties with the primitive genus *Canirallus*. Most species have the posterior culmen expanded into a rudimentary frontal shield such as seen in much of the *Amaurornis*-gallinule group. It is possible that *Aramides* may be close to the stock that gave rise to the *Amaurornis* assemblage but there is no real clear cut connection between them such as there seems to be between *Canirallus* and its derivatives.

Ripley (1964) has remarked on the similarity between *Aramides* and *Gymnocrex*. *Gymnocrex* consists of two species, *rosenbergii* of Celebes, and *plumbeiventris* ranging from the Moluccas through Papua to New Ireland. *G. plumbeiventris* has a rufous neck, olive dorsum, blue-gray breast, black tail, and white-barred underwing coverts and axillars, and is strikingly reminiscent of *Aramides*, particularly *A. calopterus*. It also has reddish primaries as in most species of *Aramides*. Both species of *Gymnocrex* are long-legged forest birds with expanded procoracoids. They differ from *Aramides* in the peculiarly shaped, sharply tapering bill, bare orbital skin, and much shorter toes. In a body skeleton of *G. rosenbergii* the pelvis was broader than in *Aramides* and had a convex rather than a concave dorsal surface of the posterior synsacrum. These differences are quite sufficient to separate *Gymnocrex* from *Aramides* at the generic level but the two quite possibly were derived from the same stock. Their disjunct distribution is a probable indication of their antiquity.

Another possible derivative of *Aramides* stock is the monotypic Neotropical genus *Amaurolimnas*. This bird, too, is a forest dweller with rufous underparts, brownish-olive dorsum and grayish juvenal plumage suggesting a diminutive *Aramides*. The structure of the bill is identical to that of the smaller species of *Aramides*. It lacks the barred underwing coverts and black venter of *Aramides* and I place it only provisionally near that genus.

One of the most difficult problems in rail taxonomy lies in the proper allocation of the species included in the genera *Porzana* and *Amaurornis*. The four species that Peters (1934) included in *Amaurornis* (*phoenicurus*, *akool*, *olivaceus*, and *isabellina*) form a rather basic stock from which both

the *Porzana* assemblage and the gallinules could have arisen. Baker (1929) placed *Porzana fusca* and *P. bicolor* in *Amaurornis*, as did Ali and Ripley (1969). The little known Madagascan species *olivieri* was originally described as a *Porzana* but later was listed under *Amaurornis* by Rand (1936). Benson and Wagstaffe (1972:163) have suggested that *olivieri* forms a superspecies with *Limnocorax flavirostris* of Africa and advocated putting *flavirostris, olivieri, bicolor,* and *Porzana tabuensis* in the same genus "perhaps most correctly [in] *Porzana.*"

Limnocorax on examination proves inseparable from *Amaurornis*. The skeleton is, except for size, virtually identical to that of *A. phoenicurus* and both have a relatively longer and more slender tarsus with the medial face of the hypotarsus more excavated than in the species of *Porzana* available for comparison (*P. carolina, fusca, pusilla, palmeri, albicollis, tabuensis*). The bill structure and plumage of *Limnocorax* is like that of *Amaurornis* and the grayish juvenal plumage is particularly similar to *A. akool.*

I note from Benson and Wagstaffe (1972) that the tarsus of *olivieri* and *bicolor* is proportionately shorter than in *Limnocorax*. They note as much similarity between *bicolor* and *olivieri* as between *olivieri* and *Limnocorax*. Until better anatomical material becomes available with which a more detailed study can be made, I prefer to place *flavirostris* and *olivieri* in *Amaurornis* and *fusca, bicolor,* and *tabuensis* in *Porzana*. I fully realize that *Porzana* may well be polyphyletic but if so it remains to be established what the different lines are and what their relationships are before most of the genus can be successfully divided.

A natural group within *Porzana* is formed by the species *pusilla, parva, carolina, porzana,* and *fluminea,* all of which have gray underparts, olive and black dorsum streaked with white, and a buffy juvenal plumage. The African species *Aenigmatolimnas marginalis,* often included in *Porzana,* basically agrees with these plumage characters but is larger, longer-legged, and has a distinctly broader, almost gallinule-like bill with a very broad, nearly vertical nasal bar and a smaller bony nostril than in any species of *Porzana*. It may prove quite distinct from *Porzana* and its merger with that genus should at least await comparison of skeletons.

I do not recognize the genus *Porzanula* for the species *palmeri* of Laysan but instead consider it a flightless derivative of *Porzana pusilla* (Olson, 1973). Mayr (1943:46) felt that the taxonomic position of the Hawaiian genus *Pennula* would "probably remain doubtful" as it "has lost all distinctive characters." However, in the two specimens I have seen, I note a likeness to *Porzana fusca* and can see no characters that would preclude its being considered a flightless *Porzana* derivative also. *P. fusca,* like *P. pusilla,* has a wide distribution along the western Pacific coast and is migratory in parts of

its range. It could have colonized Hawaii just as *P. pusilla* colonized Laysan. The extinct, flightless species *monasa*, in the monotypic genus *Aphanolimnas*, is known from two specimens from Kusaie Island, both of which are now in Leningrad. Mayr (1943) and Baker (1951) considered it related to *Porzana tabuensis* and "*Nesophylax*" *ater*. S. Dillon Ripley (pers. comm.), who has examined the specimens, considers *monasa* to be a *tabuensis* derivative that is referable to the genus *Porzana*. The characters used by Murphy (1924) to establish the genus *Nesophylax*, for the species *ater* of Henderson Island, are those associated with flightlessness and are not sufficient to distinguish it from *Porzana*. It too, is possibly derived from *P. tabuensis*. *Porzanula*, *Pennula*, *Aphanolimnas*, and *Nesophylax* are here considered synonyms of *Porzana*.

The genus *Poliolimnas* I have expanded to include *Porzana flaviventer* (Olson, 1970). I am still convinced that *P. flaviventer* and *Poliolimnas cinereus* are more closely related to each other than either is to any other species. In my previous note I neglected to point out that the white streaking in the dorsum of *flaviventer* is different from that found in the white-streaked species of *Porzana*. In the latter, each streaked feather has one or, more often, two streaks in the *outer* margins. In *flaviventer* each streaked feather has only a single streak down the *center*. The white streaks of *flaviventer*, therefore, must have evolved independently of those of *Porzana*.

In the New World is found another small assemblage consisting of the genera *Cyanolimnas*, *Neocrex*, and *Pardirallus*, that may have had its ancestry in an *Amaurornis*-like stock. *Cyanolimnas cerverai* is a nearly flightless relict species confined to Cuba (and formerly the Isle of Pines, Olson in prep.). *Pardirallus*, including the variegated species *maculatus* and the two uniformly-colored species *sanguinolentus* and *nigricans*, (= *Ortygonax* auct.) are long-billed Neotropical rails often mistakenly placed in *Rallus*. *P. maculatus* differs from the other two species mainly in its strikingly variegated plumage. Dickerman and Parkes (1969) and Dickerman and Haverschmidt (1971) have shown that there exists a dark phase of the juvenal plumage of *maculatus* that is similar to the plumages of *sanguinolentus* and *nigricans*. The plumage pattern of *maculatus* is evidently a recently evolved condition derived from an inornate plumage. As there are no structural differences of consequence between *maculatus* and the other two species, *sanguinolentus* and *nigricans* must be referred to *Pardirallus*. The two species *Neocrex erythrops* and *N. columbianus*, are rather small, short-billed Neotropical "crakes."

The three genera *Cyanolimnas*, *Neocrex*, and *Pardirallus* share a number of similarities. All (except *P. maculatus*) are drab olive-brown above and dark gray below, usually with light throats. All except *nigricans* have a paint-like red spot at the base of the bill. The loss of this spot in *nigricans*
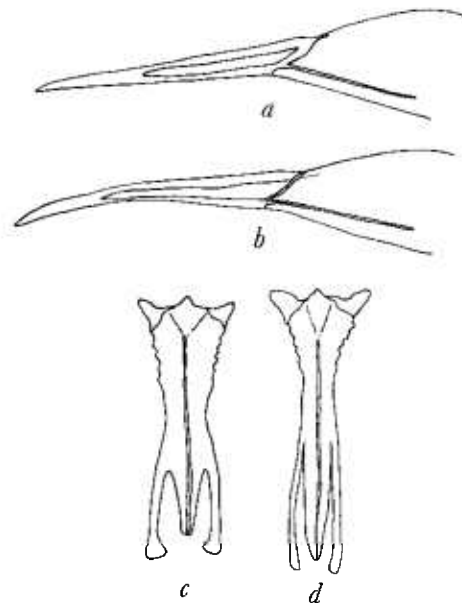
Fig. 4. *Rallus* and *Pardirallus* compared: a. bill of *P. sanguinolentus* b. bill of *R. longirostris* c. sternum of *P. sanguinolentus* d. sternum of *R. longirostris*.

may function in species discrimination, *nigricans* being broadly sympatric with *sanguinolentus*. The same phenomenon may be taking place in *Neocrex*, as the bill of *columbianus* is much less brightly colored than that of *erythrops*. *Cyanolimnas*, which a number of authors have noted as resembling *P. sanguinolentus* (Barbour and Peters, 1927; Bond, 1940, 1967, 1970; Green-way, 1958), forms a nearly perfect intermediate between that species and *Neocrex*. In fact, it may be closer to *Neocrex* than to *Pardirallus*. In its finely barred flanks and buffy crissum, *Cyanolimnas* combines characteristics of *N. erythrops* and *N. columbianus*, respectively, that are lacking in *Pardirallus*. Furthermore, the bill shape and the narrow, pointed frontal plate of *Cyano-limnas* is like that of *Neocrex* and differs from the broad, rounded frontal plate of *Pardirallus*.

The frontal plate of *Pardirallus* is also quite unlike that of *Rallus*. The skeletons of *Pardirallus* and *Rallus* exhibit a number of marked differences. In *Rallus* (Fig. 4), the nostril is longer; the premaxillary symphysis is shorter, broader, and slightly more decurved; the nasal bar is very slender and twisted; the brace from the jugal attaches on the anterior part of the maxillo-palatine process; and the cranium is narrowed. In *Pardirallus* (Fig. 4), the nostril is considerably more restricted in length and basal depth; the

premaxillary symphysis is longer, narrower, and straighter; the nasal bar is broad, flat, uniform in width, and not twisted; the jugal brace attaches nearer the middle of the maxillo-palatine process; and the cranium is broader than in *Rallus*.

In *Rallus*, the whole sternum (Fig. 4) is greatly narrowed throughout its length; the sternal notches extend anteriorly almost half the length of the sternum and terminate anteriorly in very narrow slits; the posterior lateral processes taper very gradually off the sternal plate and are closely adpressed to the xiphial area. In contrast, the sternum of *Pardirallus* (Fig. 4) is broader; the sternal notches extend only a little over a third the length of the sternum and are U-shaped anteriorly; the posterior lateral processes are farther away from the xiphial area and curve strongly into the sternal plate, giving the sternum somewhat of an hourglass shape like that of *Amaurornis* (Fig. 6). The coracoid of *Pardirallus* is heavier with a more expanded sternal end and a larger, more bladelike and recurved procoracoid process than in *Rallus*. The humerus is heavier with the distal end more expanded, the shaft more curved, and the brachial depression deeper than in *Rallus*. In *Rallus* the preacetabular portion of the pelvis is longer and straighter than in *Pardirallus* in which the median dorsal ridge is much more humped. The hindlimb elements of *Pardirallus* are proportionately shorter and stouter than those of *Rallus*.

It is quite evident that *Rallus* and *Pardirallus* are in no way related. I feel that *Cyanolimnas* is probably closest to an ancestral *Amaurornis*-like stock that has given rise both to long-billed species (*Pardirallus*) and to short-billed species (*Neocrex*) which are only convergently similar to *Rallus* and *Porzana*.

Another line apparently derived from *Amaurornis* is found in the three large Australasian species *Habroptila wallacei*, *Megacrex inepta*, and *Eulabeornis castaneoventris*. *Habroptila* and *Megacrex* are geographical counterparts, the first occuring on Halmahera and the other on New Guinea (Fig. 5). They differ only in plumage and bill color, *Habroptila* being all dark with a red bill and *Megacrex* brownish above, white below, with a yellowish-green bill. In the shape and size of the bill and frontal shield, the very large heavy legs, and abbreviated tails, *Habroptila* and *Megacrex* are so similar that it is difficult to see why they were ever placed in different genera. I can find no character of generic importance that will permit their separation; therefore *Megacrex* D'Albertis and Salvadori 1879 becomes a synonym of *Habroptila* Gray 1860.

Eulabeornis differs from *Habroptila* in having a well-developed tail and less heavy bill and legs, but these differences may possibly be attributable to the fact that *Eulabeornis* is not flightless, whereas both species of *Habroptila* reputedly are. Interestingly, *Eulabeornis* appears to be the exact geographical

Fig. 5. Allopatric distribution of *Eulabeornis castaneoventris* (dark shading), *Habroptila inepta* (light shading), *H. wallacei* (solid), and *Amaurornis isabellina* (hatched).

counterpart of *Habroptila*, as it occurs in northern Australia and even extends to the Aru Islands, but is not found in New Guinea and is thus nowhere sympatric with *Habroptila* (Fig. 5). *Eulabeornis* inhabits mangroves exclusively; *H. inepta* inhabits mangroves and to a lesser extent lowland forest and bamboo thickets, while *H. wallacei* is apparently more of a forest dweller than either. The similar choice of habitat and rather striking allopatry of *Eulabeornis* and *H. inepta* lends support to their affinity but in view of their external morphological differences it seems best to keep the two genera separate at least until skeletons can be compared. Although *Eulabeornis* and *Habroptila* have been likened to *Aramides*, they lack the barred underwing and the slender tarsi of that genus. They rather appear to be allied to *Amaurornis*, as already suggested by Mayr (1949). Ripley (1964:23) has said of *H. inepta* that it "closely resembles a giant rufous-tailed moorhen [*Amaurornis olivaceus*]." It also bears a resemblance to *Amaurornis isabellina* which is a heavy-legged species found on adjacent Celebes (Fig. 5).

The monotypic genus *Gallicrex* is quite distinctive and *G. cinerea* is one of few rails displaying marked sexual dichromatism. It has a superficial
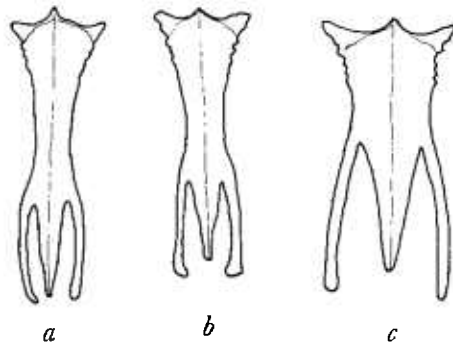
FIG. 6. Ventral view of sternum: a. *Gallicrex cinerea* b. *Amaurornis phoenicurus* c. *Gallinula chloropus*. The wide sternum of *Gallinula* is also characteristic of *Fulica*. The sternum of *Porphyrio* is intermediate between *Amaurornis* and *Gallinula*.

similarity to *Gallinula* and the female and immature plumages are even more reminiscent of the immature plumage of *Porphyrula*. It has some of the same structural modifications of the hindlimb as *Porphyrula* but the peculiar sternum is more similar to *Amaurornis* (Fig. 6). *Gallicrex* cannot be combined with any existing genus but it tends to bridge the differences between *Amaurornis* and the "gallinules."

The purple gallinules *Porphyrula*, *Porphyrio*, and *Notornis*, constitute an obviously monophyletic group and Mayr (1949) has already suggested their merger. *Porphyrula* differs from *Porphyrio* only in its smaller size, less massive bill, and more oval nostril, whereas the two genera share a number of specialized characters, particularly of the hindlimb (Olson, 1973). *Notornis* is but a large, flightless derivative of *Porphyrio*. It bears about the same relationship to *Porphyrio* as *Gallirallus australis* does to *G. philippensis*, and it is no more deserving of separate generic status than is *G. australis*. With the exception of *Porphyrula flavirostris*, the adults of *Porphyrula*, *Porphyrio*, and *Notornis* share a distinctive plumage of blue, green, and purple. *P. flavirostris* does not attain a purple-breasted adult plumage and looks more similar to the immatures of the other species. It is probably the most primitive species of the group. Because the three species of *Porphyrula* are more closely related to each other than to *Porphyrio* a case could be made for maintaining them as a subgenus. Nevertheless, *Porphyrula* and *Notornis* cannot be realistically separated from *Porphyrio* at the generic level and are here combined with that genus.

In the South Pacific are two distinctive gallinules, *Pareudiastes pacificus* of Samoa and *Edithornis silvestris* of the Solomons. The latter was described by Mayr (1933) just 17 days after the cutoff point for Volume 2 of Peters'

Check-list. *E. silvestris*, known only from the unique type, is a singular bird and differs from *P. pacificus* in the greater development of the legs and feet and in the monstrous development of the frontal shield. While recognizing the distinctiveness of *silvestris*, I propose that in view of the similarity of its coloration and the bare spot beneath the eye to that of *Pareudiastes*, it should be placed in that genus, as Mayr (1949) himself has already suggested.

The three very closely related genera *Tribonyx, Porphyriops,* and *Gallinula* share a generally dark plumage with a row or rows of prominent white spots down the flanks. Mayr (1949) felt that *Tribonyx* might be synonymized with *Gallinula.* The monotypic genus *Porphyriops* of South America is essentially similar in plumage and shape of the frontal shield to immatures of *Gallinula angulata.* It is intermediate in size between *G. chloropus* and *G. angulata* and there are absolutely no differences in its skeleton that can be construed to be of generic importance when compared to *Gallinula.* The skeleton of *Tribonyx* is equally similar to that of *Gallinula,* its short, heavy bill also being found in *Porphyriops* and *G. angulata.* I propose that both *Tribonyx* and *Porphyriops* be considered part of *Gallinula,* although the two species of *Tribonyx* by virtue of their decidedly shorter, heavier toes, lack of white in the under tail coverts, and longer tails, could be maintained in a separate subgenus. The gallinules of Tristan da Cunha and Gough Islands (*nesiotis* and *comeri*) were derived directly from *Gallinula chloropus* and the name *Porphyriornis* that has been used for them is not considered tenable (Olson, 1973).

As outlined previously, the coots of the genus *Fulica* are derived from a *Gallinula*-like stock that has become adapted for diving. Their center of species abundance and diversity is in South America and it seems likely that the genus may have originated there and later spread to the Old World.

CONCLUSIONS

Mayr (1949:3) lamented that of the 52 genera recognized by Peters (1934), 36 (70 percent) were monotypic and he felt that "such classification fails to recognize the function of the generic name in binomial nomenclature, namely, to indicate relationship." In the classification proposed here, the number of genera is reduced to 35, of which 11 (30 percent) are monotypic. Some of these may also prove untenable. I have perhaps been somewhat conservative in maintaining *Crecopsis* separate from *Crex,* and *Poliolimnas* and *Aenigmatolimnas* separate from *Porzana.* However, we have seen that "crakes" have evolved repeatedly from a number of lines and the possibility of convergence is great. Grouping all the "crakes" together, as Peters did in his arrangement of genera, can only result in an artificial assemblage. Most of the genera distinguished at first on flightless characters alone, have been combined with

volant genera. Of those remaining, (*Tricholimnas, Atlantisia, Cyanolimnas*, and *Habroptila*), only *Tricholimnas* is without obvious close volant relatives.

In Figure 7 I have diagrammed a theoretical phyletic tree of the Rallidae. A glance at this will show the absolute impossibility of listing the genera in a linear manner that reflects without interruption a primitive to derived sequence. Nevertheless, as a linear sequence is a necessary consequence of many methods of presentation, the following list will hopefully make the best of a difficult situation and will present a better understanding of relationships in the family than did the sequence of Peters (1934).

Himantornis, Canirallus, Sarothrura, Coturnicops, Micropygia, Rallina, Anuro-limnas*, Laterallus, Nesoclopeus, Gallirallus, Tricholimnas, Crecopsis, Crex, Rougetius, Aramidopsis, Dryolimnas*, Atlantisia, Rallus, Aramides, Amauro-limnas, Gymnocrex, Amaurornis, Porzana, Poliolimnas, Aenigmatolimnas, Cyanolimnas, Neocrex, Pardirallus, Eulabeornis, Habroptila, Gallicrex, Porphyrio, Pareudiastes, Gallinula, Fulica.

The Rallidae, and indeed the whole of the order Gruiformes, are usually thought of as being basically marsh and water birds. However, an aquatic or paludicoline origin for the Rallidae and most other gruiform families would appear to be a false impression.

The most primitive living rail, *Himantornis*, is a forest bird. Other primitive or unspecialized relict genera such as *Canirallus, Aramides*, and *Gymnocrex*, are also forest dwellers. On the other hand, the most specialized, derived genera of rails (e.g. *Fulica, Rallus, Porphyrio*) all contain marsh-dwelling or highly aquatic species. Thus the progression from generalization to speciali-zation in the Rallidae is from forest forms to aquatic forms, rather than the opposite being the case.

A brief review of other families included in the Gruiformes reveals a similar trend. The small, primitive, and largely relict families Rhynochetidae, Eurypygidae, and Psophiidae are all forest birds. The very primitive Mesoe-natidae are also inhabitants of forest or brushy areas. The Heliornithidae, although highly aquatic, are found mostly in forest streams and perch and nest in trees and bushes. The Limpkin (Aramidae) is also aquatic but is found mainly in wooded swamps. In the West Indies it normally occurs in forest and brush far from water. The Gruidae are as much inhabitants of dry uplands as of marshes and are probably precluded from strictly forest situ-ations by their large size, although some species, such as *Grus canadensis*, may

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* Placing *Laterallus viridis* in *Anurolimnas* and *R. pectoralis* in *Dryolimnas* makes the Bona-partian genera *Rufirallus* 1856 (type *Rallus cayanensis* Boddaert = *Rallus viridis* P. L. S. Müller) and *Lewinia* 1856 (type *Rallus brachypus* Swainson = *Rallus pectoralis* Lesson) available. *Rufirallus* has seen some use, even as recently as 1966 (Stresemann and Stresemann), but *Lewinia* has lain unused practically since it was proposed. In the interest of stability and to promote comprehension I have not used either name here.
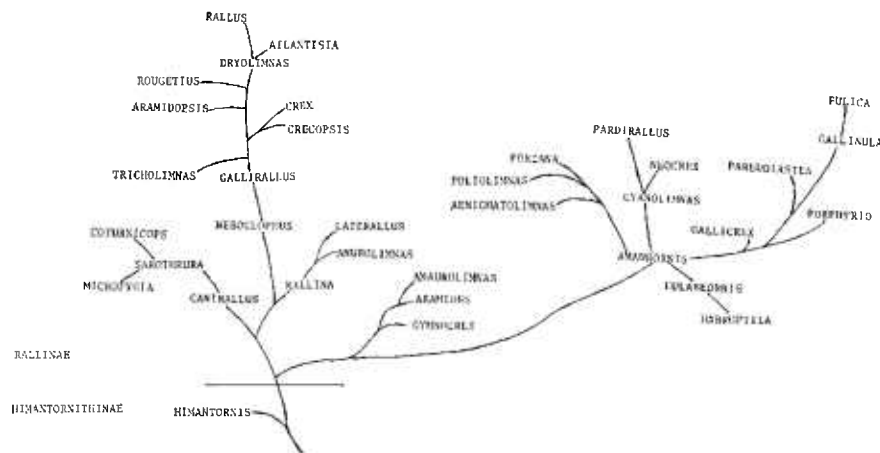
FIG. 7. Diagram of hypothetical phylogeny of the Rallidae. Distances reflect the dictates of space rather than phylogenetic distance. Several genera are placed only very provisionally (see text).

nest in open woodlands. In the Cariamidae, *Chunga* lives and nests in forests, and *Cariama*, although found in open savanna, still nests in trees. The Otididae, Turnicidae, and Pedionomidae are not at all aquatic and are for the most part open-country dwellers, although some turnicids live in forests. It seems likely that the primitive habitat for the whole order Gruiformes, as well as the Rallidae, was forest, and that certain groups have secondarily become adapted to aquatic situations or open grassland.

The geographic origins of the Rallidae have been obscured by the antiquity, cosmopolitan distribution, and inadequate taxonomy of the family. However, with the present and hopefully improved phylogeny, a familiar pattern emerges. The greatest number of species, the greatest number of peculiar genera, and the most primitive members of the Rallidae are found in the Old World tropics. The New World has relatively fewer groups, most of which are derived from Old World stem groups. A few genera appear to have specialized and radiated in the New World, some of which re-invaded the Old World.

SUMMARY

Himantornis is the most primitive and distinctive genus of the Rallidae, showing some characters in common with the Psophiidae. It is placed in a separate subfamily, the Himantornithinae. No subfamilial distinctions can be made among the remaining genera of rails and these are all placed in the Rallinae. A classification of the genera of Rallinae is advanced. The following generic changes have been made: *Mentocrex* and *Rallicula* into *Canirallus*; *Nesolimnas*, *Cabalus*, *Habropteryx*, and the subgenera *Sylvestrornis* and *Hypotaenidia* (including *striatus*) into *Gallirallus*; *Limnocorax* into *Amaurornis*; *Por-*

zanula, Pennula, Aphanolimnas, and *Nesophylax* into *Porzana; Ortygonax* into *Pardirallus; Megacrex* into *Habroptila; Porphyrula* and *Notornis* into *Porphyrio; Edithornis* into *Pareudiastes; Porphyriops, Porphyriornis,* and *Tribonyx* into *Gallinula.* The limits of the following genera have also been altered: *Sarothrura* to include *Coturnicops ayresi* (after Keith et al., 1970); *Anurolimnas* to include *Laterallus fasciatus* and *L. viridis; Tricholimnas* restricted to *lafresnayanus; Dryolimnas* to include *Rallus pectoralis; Rallus* to exclude *Pardirallus, R. pectoralis, R. striatus,* and *Hypotaenidia; Poliolimnas* to include *Porzana flaviventer.* Flightlessness and the crake-like build have each evolved several times from different parental stocks. The ancestral rails are believed to have been forest dwellers, the family having only secondarily adapted to aquatic environments. The Rallidae probably had its origins in the Old World tropics with secondary radiations in the New World.

ACKNOWLEDGMENTS

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