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## A Revision of the Sub-Buteonine Hawks (Accipitridae, Aves)

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### ABSTRACT

This paper is a taxonomic review of the 25 species and approximately 10 genera of chiefly Neotropical hawks called sub-buteonines and allied to the more advanced genus *Buteo*. Generic diagnoses supported by logarithmic ratio diagrams of measurements are presented along with comments on intraspecific variation in a few of the

species. Changes from usual treatment include recognition of the genus *Asturina*, merger of the genus *Heterospizias* with *Buteogallus*, and transfer of the genus *Geranospiza* to the sub-buteonines. Finally, the broad systematics of the chief components of the family Accipitridae and the place of the sub-buteonine group within it are discussed.

### INTRODUCTION

The term “sub-buteonines” is here used for a group of hawks and eagles closely allied to the large and nearly cosmopolitan genus *Buteo*. As noted later, certain other genera or groups of genera may be regarded as sub-buteonines in a more general sense, but they are less closely allied to *Buteo* and beyond the main scope of the present paper. As the name implies and as defined below the sub-buteonines, though often specialized in various ways are on the whole more primitive than *Buteo*; they represent offshoots or continuations of the stock from which *Buteo* evolved. Indeed, the group merges more or less insensibly with the more primitive species of *Buteo* and some authors have included certain sub-buteonines, notably *Asturina* and *Parabuteo*, in that genus.

Eight of the 10 sub-buteonine genera here recognized are Neotropical. Three of the species in as many genera, cross the United States border. Two of them, *Asturina nitida* and *Buteogallus anthracinus*, have distributions that are primarily tropical and subtropical. The third, *Parabuteo unicinctus*, extends a little farther north to Kansas and farther south to central Chile. One of the two Old World genera, *Kaupifalco*, is African, the other, *Butastur*, African and Oriental, with one species ranging north in summer to Japan. By way of contrast, *Buteo* is well represented in the Holarctic, Neotropical, and Ethiopian regions, but virtually absent from the Oriental and entirely so from the Australian regions. The most primitive species of *Buteo*, such as *maguirostris*, are Neotropical.

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Unlike some species of sub-buteonines, none of the buteos is characteristic of lowland rain forest. The 10 genera of sub-buteonines have a total of 26 species; *Buteo* alone has almost the same number—24.

Of the 10 genera of sub-buteonines no fewer than six are monotypic and another two, *Harpyhaliaetus* and *Butastur*, may with more or less uncertainty, be termed what I (Amadon, 1968) have called “quasi-monotypic,” that is, comprised of a single super-species. While the number of genera seems excessive, the sub-buteonines are a rather diverse lot and additional information is needed before contemplating further changes. The principal changes made herein are to recognize *Asturina* (often regarded as a synonym of *Buteo*), to merge *Heterospizias* with *Buteogallus*, and to transfer *Geranospiza* to the sub-buteonines.

There has been relatively little recent discussion of the status and interrelationships of the genera of the family Accipitridae. Brown and Amadon (1968) outlined a classification for the Accipitridae and diagnosed the genera in somewhat general terms. This paper may be regarded as a more formal statement of part of that classification which is set forth with original citations and ranges for species and subspecies in a checklist of the order Falconiformes by the late Prof. E. Stresemann and the writer which forms part of volume 1, revised edition, of “Peters Check-List of Birds of the World” (Stresemann and Amadon, 1979). Original citations and other technical details may also be found in Peters (1931), Friedmann (1950), Hellmayr and Conover (1949), and Jollie (1976–1977).

Dropping back to a somewhat earlier era one must mention especially Ridgway (1873, 1876) who in his earlier years was particularly interested in raptorial birds. Since his papers have been largely forgotten and are scarce, I have quoted from them rather freely. Some of Ridgway’s conclusions were incorporated in Friedmann (1950), that volume being a continuation of Ridgway’s “Birds of North and Middle America” but the geographical limitations of this work and its general approach restricted the treatment of genera as such. Nevertheless, it is an important reference and, for the genera treated, includes line

figures of features usually used in generic diagnoses—beak, foot, wing, and tail. All the species of Accipitridae are illustrated in Brown and Amadon (1968). Even those familiar with all or most of the taxa involved may find these paintings useful in visualizing the characters of the genera and species.

Many of the genera and species of birds, especially large conspicuous ones such as hawks, were described by Linnaeus and by those who shortly followed him. At that time little was known of relationships and generic diagnoses were skimpy and often misleading. Still, the synonymies given in such relatively early works as Sharpe (1874) show that the conclusions of early students as to the affinities of various genera and species were sometimes sounder than those expressed decades later.

The phylogeny of the Accipitridae will in the course of time be increasingly dependent upon the fossil record. Birds of prey, because of their large size and because some were engulfed at sites such as the Rancho La Brea tarpits, are not so scarce as fossils. Nonetheless, fossils contribute relatively little as yet to our understanding of the sub-buteonines. Occasionally, in fact, faulty assignment of fossils has confused the issue (Amadon, 1963). A complete list of all known fossil hawks has been provided by Brodkorb (1964).

Genera of birds are difficult to define; one reason why one finds so few recent ornithological publications in which there is any attempt to do so. This state of affairs is in part the result of the well-known structural homogeneity of birds. On the other hand, to make a point that is seldom emphasized, a genus of birds may be comparable in geologic age, in degree of ecological uniqueness, and in every other respect except overt morphological characters, to genera of mammals, reptiles or other groups. The generic diagnoses indicate the size and proportions of each genus; a more detailed analysis of measurements follows in a separate section.

A general discussion of the sub-buteonines and of their place in the family Accipitridae is postponed until the genera have been dealt with individually. Inasmuch as *Buteo* is considered a later, more derived genus it would seem logical to define the sub-buteonines and

then compare *Buteo* with them. This is reversed here, first because the sub-buteonines are the main thrust of this paper, and second because they are a group of several genera, as against the single genus *Buteo*.

I am indebted to Drs. Wesley E. Lanyon and Lester L. Short for reading the entire manuscript and for numerous valuable suggestions. The late Dr. Eugene Eisenmann also read and criticized the entire paper. Many others provided useful assistance on one point or another, among them Dr. Tom J. Cade, Dr. and Mrs. Frederick N. Hamerstrom, Dr. Ned K. Johnson and Dr. Helmut Sick. I am grateful to all of them.

## COMPARISON OF BUTEO WITH SUB-BUTEONINES

GENUS *BUTEO* LACEPEDE, 1799

TYPE: *Falco buteo* Linnaeus.

DIAGNOSIS: Medium-sized to large hawks, usually of robust form. Bill of moderate size and normal shape. Head fully feathered. Wings rather long, longer than tail, broad and rounded. Outer three or four primaries notched on inner vane. Tail of moderate length, usually slightly rounded. Tarsus of variable length; feathered for at least one-third of its length on anterior surface. Tibial feathers usually long, forming "flags." Adults usually barred or monocolored below; immatures usually streaked. Melanistic and erythristic phases present in a high proportion of species. Habitat plains, semi-open or temperate woodlands, never the interior of tropical rain forest. The food of buteos is usually warm-blooded vertebrates, especially rodents, but some species consume reptiles and amphibians. For a list of the species and their ranges, see Stresemann and Amadon (1979).

DIAGNOSIS OF SUB-BUTEONINES: Small to eagle-sized hawks; form usually robust, occasionally slender. Wings typically broad, rounded, with long broad secondary quills. Tail variable in length; often rather short, usually with a conspicuous white cross band. Plumage color and pattern extremely variable; young usually different from adult and typically coarsely streaked on breast and abdomen. Face and sometimes forehead often sparsely feathered, bristly, or naked. Flank feathers usually short, not forming "flags."

Color phases rare. Outer primaries less sharply notched on inner vanes than in *Buteo*; often more than four outer primaries with emarginations on inner vanes thus suggesting that they are in general less skilled at soaring than the species of *Buteo*. Legs usually long, coarse, unfeathered; scalation usually as in *Buteo* but reticulate rather than scutellate in *Harpyhaliaetus* and partially so in *Butastur* and *Kaupifalco*. In general rather sluggish; several of the species feed primarily on cold-blooded vertebrates or upon crabs and large centipedes or other arthropods. Most sub-buteonines are tropical or subtropical in distribution, where, according to species, they are found in a variety of habitats, including lowland rain forest.

## THE SUB-BUTEONINE GENERA

GENUS *BUTEOGALLUS* LESSON, 1830

TYPE: *Falco aequinoctialis* Gmelin.

SYNONYMS: *Urubitinga* Lafresnaye, 1842; type, *Falco urubitinga* Linnaeus. *Hypomorphnus* Cabanis, 1844, same type. *Heterospizias* Sharpe, 1874, type *Falco meridionalis* Latham. There is dispute as to whether the generic name *Urubitinga* was properly introduced, so *Hypomorphnus* has been used by some authors; now considered a synonym of *Buteogallus*, the problem becomes academic.

RANGE: Southwestern United States (Texas to Utah and Arizona) south to central Argentina; also Cuba and the Lesser Antilles.

SPECIES: 1—*aequinoctialis*; 2—*subtilis*; 3—*anthracinus*; 4—*urubitinga*; 5—*meridionalis*.

DIAGNOSIS: Heavily built rather sluggish hawks, with long coarse legs and relatively short, broad rounded wings, the secondaries unusually long; tail relatively short (the species *meridionalis* of somewhat different proportions). Face and even forehead often scantily feathered or with bristles only; four or five primaries weakly emarginate on inner vanes. Bill rather long and weak. Adults blackish or rufous barred with dusky, always with a white tail band. Immatures very different; coarsely streaked below; tail with numerous dusky bars. The species of *Buteogallus* are partial to wetlands, swampy woods or even seacoasts, and feed extensively on

crabs, cold-blooded vertebrates, or occasionally young birds or rodents.

REMARKS: In some early literature (e.g., Sharpe, 1874) *Buteogallus* was limited to the type species, *aequinoctialis*, whereas the two "black hawks" *anthracinus* (including *subtilis*) and *urubitinga* were placed in *Urubitinga*. In doing so Sharpe cited as the basis for such separation not the dissimilar coloration or denuded forehead and face of the Rufous Crab-hawk (*aequinoctialis*) but instead insignificant details of proportion. Ridgway (1876, p. 141) commented as follows:

*Buteogallus* [is] extremely similar to *Urubitinga*, the main difference being in the coloration; but differing somewhat also in the relative proportion of the lateral toes and the degree of development of the loreal bristles. The latter are almost entirely wanting . . .

It is extremely doubtful whether this form should be allowed more than subgeneric rank, the resemblance in most respects to *Urubitinga* being so exceedingly close. The points of difference pointed out above are indeed trifling, though characteristic; and although the adult plumage is strikingly different from that of any of the species of *Urubitinga*, the young stage is quite similar to that of *U. anthracina*.

Peters (1931, p. 244) did place *anthracinus* in *Buteogallus*, but left the Greater Black Hawk *urubitinga* in *Urubitinga* (= *Hypomorphnus*), thereby made monotypic. But although the Greater Black Hawk, as the name implies, is a somewhat larger species and one which has proportionately longer legs than the Lesser Black Hawk, *anthracinus*, the two are closely allied, so much so that they are often confused both in life and as specimens. Thus it was but a natural step when Amadon and Eckelberry (1955, p. 68), reverting to the classification adopted by some early authors, made *Urubitinga* a synonym of *Buteogallus*. This has subsequently been followed by Wetmore (1965, p. 229) and others.

Ridgway (1876, p. 167) regarded *Asturina schistacea* Sundevall, now placed in *Leucopternis*, as a "typical" member of the genus *Buteogallus*. In color and perhaps otherwise it and its allospecies, *plumbea*, do to some extent connect *Buteogallus* and *Leucopternis*, but are closer to the latter. The immature

plumage, though lightly barred, is quite unlike the coarsely streaked immature of all species of *Buteogallus*.

Turning now to "*Heterospizias*" *meridionalis*, the Savanna Hawk, here regarded as belonging to *Buteogallus*, the species has had a checkered taxonomic history. First described noncommittally as *Falco meridionalis* by Latham in 1790 it was placed in a monotypic genus *Heterospizias* by Sharpe (1874, p. 158), who merely separated it off in a key without giving generic characters of significance. As a genus it is related to *Buteogallus*, *Leucopternis*, *Asturina*, and *Parabuteo*. It agrees with *Buteogallus* in having a coarsely streaked immature plumage, in the rufous, finely barred color pattern, and in being primarily a bird of wetlands or low savanna. The resemblance is so great that I here place it in *Buteogallus*, even though *meridionalis* is a somewhat lankier, relatively longer winged bird than the other species of *Buteogallus* and has the face more fully feathered.

Peters (1931, p. 226), for reasons unknown, placed *Heterospizias* in his subfamily Accipitrinae, not Buteoninae. Plótnick (1956) corrected this error and demonstrated that the genus is a buteonine in the inclusive sense, not that *Accipiter* and *Buteo* are themselves as distantly related as Peters thought. Ridgway (1876, p. 139) was aware of the true position of *Heterospizias* and wrote: "Similar to *Urubitinga* but wings larger proportionately . . . Tibial plumes better developed and feathers of the pileum longer and more lanceolate . . . Five outer primaries with inner webs sinuated . . . Bill rather small, exactly as in *anthracina*. With a general correspondence to *Urubitinga* in most of the external features of form, this genus, or more properly subgenus, differs sufficiently in the greater development of the remiges and tibial plumes . . . the more lanceolate form of the feathers of the pileum, and the strikingly different coloration." When, however, the comparison is with *aequinoctialis* it is the other species of *Buteogallus* that differ in color. Friedmann (1950, p. 396) noted the similarity in color and pattern of *meridionalis* and *aequinoctialis*.

The lankier proportions of the Savanna Hawk (*meridionalis*) permit it to be a some-

what more active predator and "pirate," in the sense of Meinertzhagen (1959) than are the other buteogallines. I watched one as it pursued a stork (*Euxenura galeata*) in a long circling flight until the latter dropped its prey, probably a fish, which the hawk seized and ate. A pair of Savanna Hawks circling over a little valley in the uplands of western Argentina looked very buteonine; one of them had the tail of a snake dangling from its bill. The Savanna Hawk is also closely related to the Bay-winged Hawk, *Parabuteo unicinctus*. The question would seem to be whether *Parabuteo* should follow *Heterospizias* into *Buteogallus*. I am tentatively retaining it for reasons given later.

COMMENTS ON SPECIES: I now follow Monroe (1963, 1968) in treating *subtilis* as a species and not as a subspecies of *anthracinus*. Restricted to the coastal Pacific zone from southernmost Mexico to northwestern Peru (including the Pearl Islands, Panama) *subtilis* differs somewhat from *anthracinus* in bodily configuration and in habits (Dickey and van Rossem, 1938; Slud, 1964), and the two seem to be in contact without intergrading. I have elsewhere (Amadon, 1961) discussed the curious examples of *subtilis*, lacking melanin in the plumage, which occur in the southern part of the species' range.

The black hawks of the Atlantic coast of Honduras and the off-lying islands (*utilensis*) and of Cuba (*gundlachii*) differ from continental *anthracinus* in somewhat the same way as does *subtilis*, but the divergence is less and these taxa are probably still subspecies of *anthracinus*. On the other hand, the species *aequinoctialis*, which like *subtilis* is chiefly a coastal form of small size, ranging from the Orinoco Delta east and south well down the coast of Brazil, might be closer to *subtilis* than to *anthracinus*, though its dissimilar color and plumage pattern suggests that it is not particularly close to either. Alternatively, all three species may comprise a superspecies, and indeed the range of *anthracinus* terminates to the eastward on the north coast of South America about where that of *aequinoctialis* commences.

*Buteogallus (anthracinus) gundlachii* of Cuba, long considered a full species, may be written with the species name in parentheses to indicate some lingering doubt as to its sta-

tus. It is a "megasubspecies" in the usage of Amadon and Short (1976). It is of interest that *B. anthracinus*, unlike *urubitinga*, extends only to the northern coastal regions of South America. To the south its ecological niche may be filled by *Leucopternis schistacea* and *plumbea*.

#### GENUS *PARABUTEO* RIDGWAY, 1874

TYPE: *Buteo harrisi* Audubon = *Parabuteo unicinctus harrisi*.

SYNONYM: *Antenor*, Ridgway, 1874. Type, same as *Parabuteo*, name preoccupied.

RANGE: Southwestern United States, south to Chile and Argentina.

SPECIES: 1—*unicinctus*.

DIAGNOSIS: Medium-sized, robust hawk; wings and tail long, tail slightly rounded. Outer four primaries emarginate on inner vane. Lores with bristles only. Bill relatively longer than in *Buteo*. Legs long, robust; talons large, strongly curved, acute. Color pattern of adult, especially of the North American subspecies, *harrisi*, distinctive and contrasting. Immature very different: mottled dorsally, coarsely streaked ventrally as in *Buteogallus*. "The cranium is very similar to that of *Buteo [jamaicensis] borealis*, the details of structure being exactly the same . . . Its upper portion is more depressed, presenting in this respect, a closer resemblance to that of *Asturina*" (Ridgway, 1876, p. 161).

REMARKS: Elsewhere Ridgway (1874, p. 249) stated that his new genus *Parabuteo* finds its closest ally in *Buteogallus*. I would modify this only slightly to say that its very closest ally is the Savanna Hawk (*meridionalis*), then placed in a monotypic genus *Heterospizias*, but here in *Buteogallus*. Mr. William Mader (*in litt.*), who has studied both species intensively in the field, concurs with this opinion. Both species are somewhat lankier and longer winged than most species of *Buteogallus*. But *meridionalis* is close enough to be placed in that genus, whereas *Parabuteo*, in my opinion, may be retained. It is a bird of open chaco, savanna, and even desert rather than wetlands and is a more active powerful species than the buteogallines, preying primarily upon warm-blooded vertebrates: rabbits, wood rats, and the like, and also birds. Falconers find it a good subject: docile and easy to handle, but fearless

and rugged in hunting. Mader (1975) discovered a peculiarity in its mating: many nests have a trio of adults, two males and a female, and these trios produce more young than do pairs. A pair or trio has been known to start another brood while still feeding the young of an earlier one in the nest.

To summarize, *Parabuteo* is close to *Buteogallus*, especially to *meridionalis*. Its resemblances to *Buteo*, in which genus some would place it, are partly convergence, not that any of the sub-buteonines are far from that genus.

#### GENUS *ASTURINA* VIEILLOT, 1816

TYPE: *Asturina cinerea* Vieillot = *Falco nitidus* Latham.

RANGE: Southern Texas to southern Arizona, thence south to Argentina, in lightly wooded or savanna country.

SPECIES: 1—*nitida* (includes *plagiata*), but see Johnson and Peeters (1963).

DIAGNOSIS: Rather small hawk. Wings relatively short, only four outer primaries sinuate on inner web. Tail long, almost square or slightly emarginate. "Feet large and robust . . . reaching almost to the end of the tail . . . tarsi very robust compared to the toes . . . the frontal and posterior rows of scutellae very distinct and regular . . . claws strong, well curved, but not very acute" (Ridgway, 1874, p. 244). Color pattern of adult distinctive: pale gray throughout more or less finely barred, according to subspecies, with darker gray, especially ventrally. Immature quite different: streaked or blotched ventrally. An open, often dry country species that prefers lizards as food.

Ridgway (*op. cit.*) wrote further: "The species of *Rupornis* [*magnirostris* and *leucorrhous*] have been associated with the species of the present genus [e.g., by Sharpe, 1874] but are very distinct. The genera (or more properly subgenera) most nearly allied to *Asturina* are *Leucopternis* Kaup of tropical America, and probably *Kaupifalco* Bonaparte of Africa. The former differs mainly in more or less rounded instead of emarginated tail and in having the old and young plumages similar; the latter in having the posterior face of the tarsus without a well defined row of transverse scutellae."

REMARKS: *Rupornis* is now considered a synonym of *Buteo*, properly in my opinion. Of the subgroups of that genus, it is probably the most primitive and hence nearest the sub-buteonines. Early authors, including even Ridgway, were impressed by the resemblance of *nitida* to the Northern Goshawk (*Astur* [= *Accipiter*] *gentilis*), and hence the name "*Asturina*" and the former vernacular "Mexican Goshawk." Everyone is now agreed that the resemblance is superficial.

Recent works treat *Asturina* as a synonym of *Buteo*. Its one species, *nitida*, is placed near the beginning of that genus, along with *leucorrhous*, *ridgwayi*, *lineatus*, and sometimes *brachyurus*. Johnson and Peeters (1963) set up an exclusively New World group they called "woodland buteos" for these species (except *leucorrhous*, which would presumably have to be added, though it does not have the color characteristics of the others). *Asturina* itself, however, is, I am sure, a sub-buteonine. Ridgway was correct in saying that its closest relative is *Leucopternis* and if the immature plumage were like that of the adult, it could be placed there. But it is not; rather it is coarsely streaked like that of *Buteogallus*. *Asturina* thus stands between these two genera. This may seem difficult to accept if it is compared with *B. urubitinga*, or even *B. anthracinus*, but if the comparison is with the small, extensively barred *B. aequinoctialis*, the relationship is more evident. *Asturina* is the oldest of the three names, and if any further reduction of genera were contemplated it would be necessary to combine *Leucopternis*, *Buteogallus* (and *Parabuteo*) with it. But one is hardly prepared to bring the smaller species of *Leucopternis* into the same genus with *Buteogallus anthracinus* and *B. urubitinga*. *Asturina* does have some characters of its own, as outlined above. The fact that only four outer primaries are emarginated suggests *Buteo*, and is probably correlated with the fact that in general it inhabits more open country than the species of *Buteogallus* and *Leucopternis* and is perhaps a more skilled flier and predator.

Ridgway noted the similarity of *Asturina* to the Lizard Buzzard (*Kaupifalco monogrammicus*) of Africa. It is of interest that Thiollay (1978) in a comparison of the raptors of the lowlands of southeastern Mexico

and of the Ivory Coast found a striking convergence in morphology and habits between the two genera (see also Niles, 1979). It may eventually seem possible to combine them, though *Leucopternis* will have to be considered also; it is more like *Kaupifalco* than is *Asturina* in one respect—the similarity of young to adult.

Johnson and Peeters (*op. cit.*) did not consider the number of emarginate primaries in defining their group of woodland buteos; indeed the group contains species with three (*lineatus*), four (*platypterus*), and even five (*magnirostris*) incised quills. The character was used extensively in the earlier literature to subdivide *Buteo*. It is one of those numerous characters which are sometimes useful, sometimes not. For example the subgroup of American buteos *swainsoni*, *albicaudatus*, *polyosoma*, and *galapagoensis* seems to be natural and all of them have three emarginate primaries. Yet one would not be inclined to associate *Buteo lineatus* with this group, even though it also is New World and has three notched primaries. It is possible that the similarities of the woodland buteos to one another are in part superficial and ecological, just as is the resemblance to them in plumages of *Accipiter striatus* and *A. cooperii*.

#### GENUS *LEUCOPTERNIS* KAUP, 1847

TYPE: *Falco melanops* Latham.

SYNONYM: *Morphnarchus* Ridgway, 1920, type *Leucopternis princeps* P. L. Sclater.

RANGE: Mexico to Argentina, usually in moist forest.

SPECIES: 1—*melanops*; 2—*kuhlii*; 3—*schistacea*; 4—*plumbea*; 5—*semitlumbea*; 6—*lacernulata*; 7—*albicollis* (including *ghiesbreghtii* and *occidentalis*); 8—*polionota*; 9—*princeps*.

*Leucopternis* has the following superspecies: (*melanops* + *kuhlii*); (*schistacea* + *plumbea*), (*albicollis* + *polionota*).

DIAGNOSIS: Small to medium-sized sub-buteonines. Immature plumage like that of adult in color and pattern; tail with prominent white band. Color variable from species to species; ranging from dull black throughout to almost entirely white. One species, *L. princeps*, finely barred on breast, recalling *Asturina* and *Geranoaetus*. Face sparsely

feathered but never as denuded as in some species of *Buteogallus*. Wings relatively short and broad.

Ridgway (1876, p. 174) added: *Leucopternis* is

similar to *Urubitinga* [= *Buteogallus*] but tarsus not more than twice as long as the middle toe; inner webs of only four or five outer primaries cut (the cutting being a distinct emargination); and nostrils more nearly circular, and rather vertical than horizontal. The genus is most similar to *Urubitinga*, but presents the above well marked differences, with the addition of another and equally important one, viz., the similarity of the young and adult stages in plumage . . . There is also a very close relationship to *Asturina*, but in the latter the old and young stages of plumage are exceedingly dissimilar, the nostril is very decidedly horizontal, and the emarginations of the primaries end abruptly with the fourth, on which it is very distinct.

The sternum of *L. semiplumbeus* most resembles that of *Asturina*. . . , from which it differs mainly in smaller size. That of *Rupornis (ruficauda)* [= *Buteo magnirostris ruficauda*] differs conspicuously in much greater posterior breadth and larger foramina, which in the other two are sometimes nearly or quite obsolete, and always small.

At the time Ridgway wrote he considered *schistacea* and *plumbea*, now placed in *Leucopternis* partly because their immature plumage is similar to that of the adult, as members of *Buteogallus*. This further emphasizes how closely interrelated these genera and *Asturina* are.

The species of *Leucopternis* are for the most part sluggish inhabitants of forest, where they catch cold-blooded invertebrates, large insects, and the like and only now and then a mammal or bird.

COMMENTS ON SPECIES: The genus *Leucopternis* offers several problems at the species level. *Plumbea* and *schistacea*, one west and one east of the Andes in lowland forest, form a superspecies; as do *melanops* and *kuhlii*, one north and one south of the Amazon. Whether the last two or *semitlumbea* of Middle America have any particular tie with the little known *lacernulata* of southeastern Brazil is more doubtful. Both *lacernulata* and *polionota*, discussed below, have been greatly reduced by the deforestation of southeastern

Brazil. The late E. Kaempfer, who collected in that part of Brazil during the 1920s never secured *polionota* and only two specimens of *lacernulata*. The former has long been a rare bird; the American Museum lacked it until we secured one from the Brazilian national collection.

In the *Leucopternis albigollis* complex there are three problems as to species limits. First, the whitest of the forms of the "White Hawk," *ghiesbreghtii* of Mexico to Costa Rica, was at one time considered specifically distinct from *albigollis*. When Meyer de Schauensee described an intermediate form, *williaminae*, from Venezuela, the question seemed answered; Wetmore (1965, p. 253), however, reverted to treatment of *ghiesbreghtii* as a species. I think this unjustified and see no reason even to express doubt by placing the name *albigollis* in parentheses.

The second doubtful member of the *albigollis* group was described as a species, *Leucopternis occidentalis*, by Salvin in 1876 from the Andean slopes of western Ecuador. Its entire back is uniform gray in contrast to the black markings of the other taxa in the group. It may be subtropical rather than tropical in zonal preference and is separated by the Andes from its nearest relatives. For this reason Brown and Amadon (1968) and others have listed it as a species, though subspecies status has been suggested by others. Stresemann in the manuscript, upon which Stresemann and Amadon (1979) is based listed it as *Leucopternis (albigollis) occidentalis*. I am now willing to follow this usage, which is an educated guess that the form has not yet crossed the species threshold.

This brings us to the third taxon, the one named from São Paulo, Brazil by Kaup in 1847 as *Asturina (Leucopternis) polionota*. Peters (1931, p. 242) wrote it *L. (albigollis?) polionota*; perhaps he was the first to suggest that it may be a subspecies of *albigollis*. Hellmayr and Conover (1949, p. 173, fn.) also pointed this out, but thought it best to leave *polionota* as a species until its relationships with *lacernulata* were clarified. The latter, however, is a considerably smaller bird, possibly allied to *L. melanops* and *kuhlii*. Dr. Helmut Sick, one of the few who has had field experience with *polionota*, wrote me that he prefers to keep it as a species, forming with

*albigollis* a superspecies. He states that it is usually found in the hills, whereas *L. lacernulata*, prefers the lowlands.

The sequence in which the remaining genera of New World sub-buteonines are given is of little significance; all are offshoots of the preceding core group.

#### GENUS *BUSARELLUS* LAFRESNAYE, 1842

TYPE: *Falco nigrigollis* Latham.

RANGE: Mexico to central Argentina in lowlands near ponds, sluggish streams and lagoons.

SPECIES: 1—*nigrigollis*.

DIAGNOSIS: Medium-sized, stocky sub-buteonine, with very broad wings and short tail. In general like *Buteogallus* but adapted in various ways for catching fish and with a somewhat different color pattern. Soles of toes and feet covered by "rugose and thorny spicules" (Sharpe, 1874, p. 159); talons long, strongly curved, and acute. In both these respects it is like other fish-catching hawks and owls.

Ridgway (1876, p. 142) wrote of *Busarellus*:

General form and appearance of *Buteogallus aequinoctialis*. Bill, feet, and claws very strong; wings large (but primaries short), and outstretched feet reaching beyond the end of the rather short, nearly even tail . . . . Inferior surface of the toes with acute papillae . . . . Claws very strong . . . deeply grooved beneath. Head normally feathered . . . . Secondaries much developed and very broad. Plumage of the outer face of the tibiae short and close . . . . This strongly characterized and very remarkable genus exhibits a striking analogy to *Pandion* [Osprey] in the very strong and slightly graduated claws, the close feathering of the tibiae, the general form of the bill, and the sharp spicules of the toe pads.

REMARKS: This species often soars high in the blue, when its broad wings and short tail impart a distinct contour and make it appear larger than it is; it returns to earth in an impressive plunge, sometimes interrupted. It does not indulge in such dives when fishing, but seizes its prey in shallow stoops. Olson (in press) has recently come to a very different conclusion as to the affinities of *Busarellus*. He found that in six of seven specimens the



basal phalanges of the second toe are ankylosed, a feature found elsewhere only in the milvine kites (*Milvus*, *Ictinia*, and a few others) and in the true sea-eagles (*Haliaeetus*, *Ichthyophaga*, but not *Gypohierax*). On this basis and some general resemblances, Olson would place *Busarellus* with this group of kites. This I find difficult to believe, unless, perchance, such kites which I (Brown and Amadon, 1968, chap. 1) consider to be relatively primitive members of the Accipitridae, or their antecedents, gave rise to the subbuteonines, one of which, *Busarellus*, retains in most individuals this feature.

#### GENUS GERANOÆTUS KAUP, 1844

TYPE: *Falco aguai* Temminck = *Spizaetus melanoleucus* Vieillot.

RANGE: Southern South America, extending north at higher elevations in the Andes to Colombia.

SPECIES: 1—*melanoleucus* = *fuscescens* of some authors.

DIAGNOSIS: Size very large, female much larger than male; wings long and broad; tail short, wedge-shaped. Breast finely barred; feathers pointed and overlapping the white upper abdomen; feathers of nape and crown also lanceolate. Immature very different, streaked and splotched below as in *Buteogallus* or *Harpyhaliaetus*. Bill and head large. Legs long and coarse. Ridgway (1876, p. 131) added: "Form intermediate between that of *Buteo* and *Haliaetus*. Wings very long, the primaries rigid . . . five . . . with their inner webs deeply emarginated. Tail less than half the wing, graduated, the feathers very stiff. Feathers of the head and neck cuneate, approaching lanceolate, as are those of the lower breast; tibial plumes well developed; secondaries 17. Somewhat intermediate between *Buteo* and *Haliaetus*, this genus is nevertheless very distinct from either . . . . The feet . . . are much more like those of *Buteo*, there being a well developed web between the outer and middle toes, of which not a trace is seen in *Haliaetus*, while the scutellation is also that of the typical Buteones."

REMARKS: The Gray Eagle-buzzard inhabits open or lightly wooded country, both in plains and mountains. Like *Busarellus* it appears broad-winged and short-tailed when

soaring. As befits its aquiline size, it nests on ledges of lofty cliffs when they are available, but in low country builds in trees. The food includes medium-sized rodents but it is said to come to carrion. The slight resemblance of *Geranoaetus* to the sea-eagles (*Haliaeetus*) is, as will be evident from the above diagnosis, superficial.

In various respects *Geranoaetus* suggests *Buteogallus* and *Harpyhaliaetus*, whereas the barred breast recalls that of *Leucopternis princeps*. It also has some characters of its own, as listed above and certainly warrants generic status. In Hellmayr and Conover's (1949, p. 144) volume on the Falconiformes of the Americas, we find it well disguised as *Buteo fuscescens*, even the species name having been unnecessarily changed. I have elsewhere (Amadon, 1963) outlined the peculiar sequence of events whereby: (1) certain more or less fragmentary bones of fossils from North America were assigned to *Geranoaetus* because they were *Buteo*-like, but large; (2) other fossil or subfossil bones were assigned to the living *G. melanoleucus*; (3) Wetmore (1933), finding no difference between the fossil bones and those of *Buteo*, called them that; (4) thus the Recent *Geranoaetus melanoleucus* found itself in *Buteo* along with the fossils.

So far as the living species is concerned, it was all a mistake.

#### GENUS GERANOSPIZA KAUP, 1847

TYPE: *Falco gracilis* Temminck = *Geranospiza nigra gracilis*.

SYNONYM: *Ischnosceles* Strickland, 1844, same type species. Considered preoccupied by *Ischnoscelis* Burmeister, 1842 (Insecta) and for that reason renamed *Geranospiza* by Kaup. Wetmore (1965, p. 253) concluded that *Ischnosceles* is not preoccupied and used it, though it had never been in general usage and not at all for about 100 years. Thus the name *Geranospiza* may be retained on the grounds of usage, if for no other reason (Monroe, 1968, p. 85).

RANGE: Mexico to Argentina.

SPECIES: 1—*nigra*. The species varies in color from black in the north (Mexico) to finely barred with pale grayish in the south (Argentina) but there is a cline from the one

to the other and it is now evident that there is but one species.

DIAGNOSIS: "Form very slender, the wings and tail very long, the head small, bill weak and tarsi extremely elongated and slender. Outer toe very much shorter and weaker than the inner . . . its claw disproportionately small and weak. Tibio-tarsal joint flexible both backward and forward! Secondaries much developed, reaching nearly to the end of the primaries, and very broad. Bill much as in *Nisus* [= *Accipiter*]; nostril obliquely horizontal, oval. Tarsus . . . with frontal and posterior series of broad transverse scutellae, these often fused into continuous plates; claws normal. Tibial feathers short and close; not plume-like . . . fourth to the sixth quills longest, the first shortest and much bowed; outer six with inner webs sinuated. Tail long, nearly equal to the wing, rounded, the feathers very broad" (Ridgway, 1873, p. 82).

REMARKS: This small hawk probes with its long legs for frogs and the like in crevices, knotholes, the bases of bromeliads and among rocks (Brown and Amadon, 1968, p. 378). Called "Crane Hawk" presumably because of its long legs; they are not long enough to make the name more than fanciful.

*Geranospiza* has been thought to be related to the African Banded Harrier Hawk (*Polyboroides* = *Gymnogenys*) because both have "doubled-jointed" tarsi, and feed similarly by grappling in cavities for prey. There are also resemblances in color and proportions. Burton (1978) compared the limb bones of the two genera and has published an illustrated report. He found similar modifications in the two genera, but they do not involve fundamental changes. He summarized as follows:

The detailed resemblance between the two genera in the modifications of their tibiotarsi and tarsometatarsi appears to strengthen the assumption that they are related, particularly since the shared characters are derived ones. Nevertheless, convergence can by no means be ruled out. If such features as the orientation of the supratendinal bridge and the form and siting of the calcaneal ridges are simple consequences of the overall narrowing of the joint, they could perfectly well have arisen independently. In this connection, it is of some interest to note, as Brown and Amadon (1968) pointed out, that

the Asian Black Eagle *Ictinaetus malayensis* has a short outer toe as in *Polyboroides* and *Geranospiza*, and like them it often feeds on nestlings. *Ictinaetus* is not closely related to these genera, so in its case at least, some degree of convergence is indicated . . .

If similarities of the hind limb are discounted, the evidence for close relationship of *Polyboroides* and *Geranospiza* is much weakened. Other similarities are such features as general coloration, broad secondaries, weak bill, and some cranial resemblances. On the other hand, differences include facial feathering (a much larger bare zone in *Polyboroides*), tarsal covering (reticulate in *Polyboroides*, scutellate in *Geranospiza*), and totally different immature plumages. On balance I am inclined to doubt that the two genera are closely related.

Cooper (1980), after further comparisons, came to the same conclusion.

*Ictinaetus* has relatively short legs and does not share the modified tibiotarsal joint of the other two genera. The peculiar shortening of the outer toe, which is found in all three genera probably narrows the foot and makes it easier to withdraw it from narrow nests or crevices, especially when prey is clenched in the foot. In *Ictinaetus*, which feeds somewhat differently—slowly soaring above the forest and snatching nests or their contents from the treetops—there is a further modification: the talons are narrow, thin, and somewhat straightened, thus lessening the chance that the foot will become snagged when the bird snatches chicks from a nest. In *Geranospiza* and *Polyboroides*, which do not feed in flight and which frequently drag prey from crevices, the talons are normally curved.

The position of *Polyboroides* is doubtful. Brown and Amadon (1968, p. 368) suggested relationship to the serpent-eagles, noting the reticulated tarsi and the resemblance of the immature plumage to that of *Spilornis*. I am still of that opinion, but Brown (1972) studied a nesting pair of *Polyboroides* and concluded that the genus is more closely related to the buteonines. Further studies are needed.

I here follow an earlier suggestion (Brown and Amadon, 1968, p. 21), placing *Geranospiza* with the sub-buteonines. Jollie (1976–1977, pt. 3, p. 119) also placed *Geranospiza* with the buteonine and sub-buteonine hawks. Apparently he does not discuss the genus in any detail in his compendious

work; it is not included in a list of genera which he dissected or which had been dissected by others; he mentions it in a short list of genera whose position in the family, even as he wrote, was still uncertain. I think he assigned it properly.

So far as general coloration and plumage are concerned, the southern (Argentina) gray, barred subspecies of *Geranospiza* is somewhat like *Polyboroides typus*, but equally like, for example, *Asturina nitida*. The black, northern race of *Geranospiza nigra*, from which the species takes its name, resembles some of the species of *Buteogallus* and *Leucopternis*; like them it has a white tail bar. Immatures of *Geranospiza nigra* or at least those of some of the subspecies, are similar to the adults; this may be a tie with *Leucopternis*. The same is not true of *Polyboroides*. The assumption is then that *Geranospiza* belongs to the Neotropical sub-buteonine assemblage and is only superficially like *Polyboroides*.

#### GENUS *HARPYHALIAETUS* LAFRESNAYE, 1842

TYPE: *Harpyia coronata* Vieillot.

SYNONYM: *Urubitornis* J. Verreaux, 1856.

Type, *Circaetus solitarius* Tschudi.

RANGE: Mexico to Argentina.

SPECIES: 1—*solitarius*; 2—*coronatus*.

DIAGNOSIS: Eagle-sized sub-buteonines. Primaries relatively short, secondaries long and broad, almost reaching tips of primaries in the folded wing. Adults monocolored blackish or dark brown according to species, with white tail bar. Immatures unlike adults: paler above, somewhat mottled; below dull white or buffy, coarsely streaked and blotched with dark or blackish brown. "Tarsi . . . without a continuous series of transverse scutella on either acrotarsium or planta tarsi . . . instead acrotarsium covered for the greater part with small, rough, hexagonal scales; about 6–8 large, broad transverse scutella on the middle portion" (Friedmann, 1950, pp. 67, 415–416; fig. 28, p. 418). Legs and feet large, extending to or beyond the tip of the rather short tail. Talons relatively small, not strongly curved. Friedmann's description of the tarsal scutellation of *Harpyhaliaetus* is based upon *solitarius*, but that of *coronatus* is similar, or if anything even more reticulated.

REMARKS: Friedmann and before him Peters (1931) recognized the genus *Urubitornis*; that is, they placed each of the two species under discussion in a monotypic genus. I (Amadon, 1949) set forth reasons why this seems to be unnecessary. *Coronatus* has a long pointed crest, *solitarius* does not; otherwise the two are similar. There are many birds of prey in which the crest varies enormously among closely related species or subspecies: e.g., *Spizaetus c. cirrhatus* vs. *S. (cirrhatus) limnaetus* or *Pernis ptilorhynchus orientalis* vs. *P. ptilorhynchus torquatus*. Hellmayr and Conover (1949, p. 197) swung to the other extreme and made *solitarius* a subspecies of *coronatus*. In this I am certain they were wrong, especially since *solitarius* is a bird of forest, often at subtropical elevations, whereas *coronatus* frequents semi-open savanna country.

Wetmore (1965, p. 239), who again recommended that *Urubitornis* be recognized, pointed out the extraordinary resemblance of *solitarius* to the Great Black Hawk (*Buteogallus urubitinga*). But if *coronatus* were black instead of dark brown and lacked a crest, it too would resemble *B. urubitinga*. He stated that the tarsal covering of *Buteogallus urubitinga*, "especially at its lower end" suggests that of *solitarius*, but I cannot see that it departs from the usual buteonine type. As Friedmann (1950, p. 389 and fig. 25) noted, the former has the "acrotarsium and planta tarsi with a continuous series of broad transverse scutella."

The Black Solitary Eagle was placed in the genus *Circaetus* by its describer, Tschudi, in 1844. Both species of *Harpyhaliaetus* do have some resemblance to this African genus of serpent-eagles and especially to *C. cinereus*. This is true not only in bodily size and configuration but in the reticulate covering of the tarsi. Nonetheless, it is virtually certain that this resemblance is superficial. Very little is known of the habits of either species of *Harpyhaliaetus* but at two nests of *solitarius* in Mexico, the only food observed was large snakes (Harrison and Kiff, 1977). The rough, reticulated tarsi may serve the same function in *Harpyhaliaetus* that they are assumed to in *Circaetus* and related genera, namely, to provide protection from the fangs of venomous reptiles. Hence the reticulation is con-

cluded to be a derived character in *Harpyhaliaetus*, not a primitive one.

I continue to regard the species *solitarius* and *coronatus* as forming a natural genus *Harpyhaliaetus*, derived from buteogalline stock, but not quite as close to *Buteogallus urubitinga* as might be thought at first glance. Its two species may form a superspecies, though probably not.

#### GENUS *BUTASTUR* HODGSON, 1843

TYPE: *Circus teesa* Franklin.

RANGE: Africa; Asia from India east to the larger islands of the East Indies, north in eastern Asia to southeast Siberia and Japan.

SPECIES: 1—*rufipennis*; 2—*teesa*; 3—*liverter*; 4—*indicus*. *Rufipennis* is African, *teesa* Indian, *liverter* southern Oriental and East Indian and *indicus* northern Oriental. The four may constitute a superspecies.

DIAGNOSIS: Rather small hawks; wings and tail long; body slight; flight buoyant. Color pattern brown to rufous with fine ventral streaking or wavy barring; immatures tending to be more streaked but much like adult. No white tail bar, but with a dark central throat streak. The typical buteonine row of large tarsal scutes, fore and aft, tend to be broken up and subdivided, especially the posterior one. Perhaps for this reason, or because Sharpe (1874) had *Butastur* and *Kaupifalco* associated with such genera as *Circus*, Hartert (1912–1921, p. 1186 and fig. 196) stated that *Butastur* finds its closest allies with the serpent-eagles, not with the buteonines. Everything else, however, points to the reverse.

REMARKS: *Butastur rufipennis* of Africa is quickly attracted to grass fires, where it flaps along without soaring but with buoyant flight, consuming insects wafted skyward by the heat and flames. *Butastur indicus* is a species of deciduous woodland, comparable perhaps with such a hawk as *Buteo platypterus* in eastern North America. It is the most migratory of all sub-buteonines, reaching Taiwan, the Philippines, and the East Indies. For the most part the species of this genus prefer savannas and semi-open woodland. Though rather sluggish, they have an accipiter or even falcon-like profile when perched.

Many large insects and sometimes small vertebrates are consumed, most of them seized from the ground or picked from foliage.

#### GENUS *KAUPIFALCO* BONAPARTE, 1854

TYPE: *Falco monogrammicus* Temminck.

SYNONYM: *Asturina* Finsch and Hartlaub, 1870, same type.

RANGE: Sub-Saharan Africa.

SPECIES: 1—*monogrammicus*.

DIAGNOSIS: Small, trim hawk, barred below, gray above, with prominent median throat stripe as in *Butastur*. Immature plumage very similar to that of adult. Wings of medium length; tail slightly rounded and with white bar. Bill small; nostrils rounded, with a bony tubercle. Posterior row of tarsal scutes tending to be somewhat subdivided (fig., Jackson and Sclater, 1938, p. 187).

REMARKS: The Lizard Buzzard is similar to some of the smaller species of *Leucopternis*, not least, as Ridgway noticed long ago, in that the immature plumage is like that of the adult. Yet *Kaupifalco* may be more closely allied to its Old World compatriot, *Butastur*, as indicated by the slightly unusual tarsal scutellation and other resemblances.

One hesitates to place the two Old World genera *Kaupifalco* and *Butastur* between some of the closely allied Neotropical ones, and since they are relatively unspecialized it is best to place them before that group, as for example in Stresemann and Amadon (1979, p. 349). In this paper, since the Neotropical group is larger and more diversified, it has been considered first.

The Lizard Buzzard inhabits semi-open and dry country, sometimes around villages. Rather sluggish, it spends much time perching, occasionally uttering a loud, melodious call. It drops to the ground to seize lizards, rodents and the like. Small birds do not seem to fear it.

#### RELATIONSHIPS OF THE GENERA OF SUB-BUTEONINES

The interrelationships of the genera of sub-buteonine hawks are self-evident from the above diagnoses but may be summarized as follows. Four of them—*Buteogallus*, *Para-*

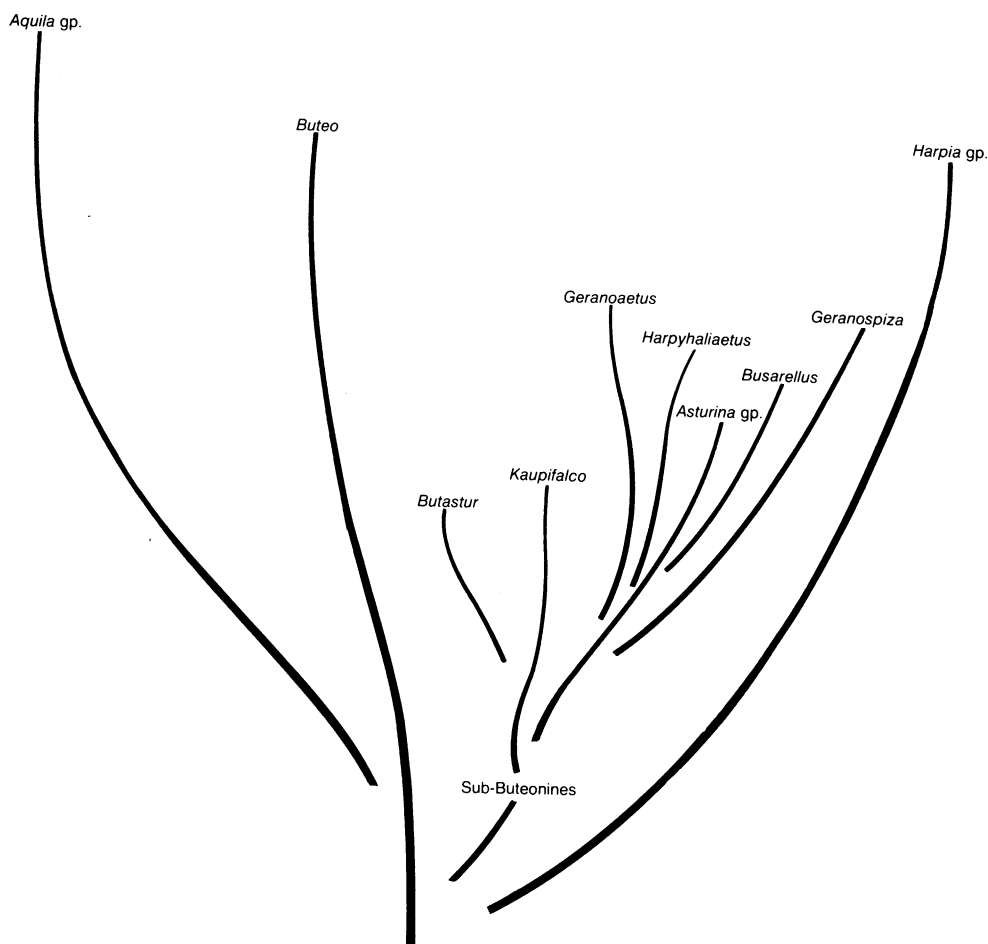


FIG. 1. Suggested phylogeny of sub-buteonines and close allies. The *Asturina* group includes *Asturina*, *Buteogallus*, *Leucopternis* and *Parabuteo*. For composition of *Aquila* group and *Harpia* group see caption for fig. 2.

*buteo*, *Asturina*, and *Leucopternis* form a closely knit group. They could all be subsumed under *Asturina*, the oldest name, without major distortion of the facts, yet to bring the smaller, more slender species of *Leucopternis* in the same genus with the large, coarse black hawks (*Buteogallus*) would scarcely be acceptable. Furthermore *Asturina* is usually placed in *Buteo* and it is advisable to await agreement that it is a sub-buteonine before consideration of combining other genera with it. Short of this, the only step that might be taken now that *Heterospizias* has been placed in *Buteogallus* would be to accord its close

relative *Parabuteo* the same treatment. Yet *Parabuteo* is ecologically and morphologically a step away from *Buteogallus* (including *Heterospizias*) and I prefer to maintain it.

The other New World genera of sub-buteonines—*Busarellus*, *Geranospiza*, *Geranoaetus*, and *Harpyhaliaetus*—are all to varying extents specialized offshoots of the above nuclear group. *Busarellus* is very close to *Buteogallus* but specialized for catching fish (but see Olson, in press). *Harpyhaliaetus* is *Buteogallus* converted to eagle-size, with appropriate changes in proportions. *Geranospiza* resembles various species of *Buteogal-*

*lus* and *Leucopternis* in many ways; the validity of the genus would not appear to be open to question. *Geranoaetus* as already noted has a mixture of characters of several of the other genera, plus some of its own.

As to the Old World genera *Butastur* and *Kaupifalco* the latter, if it were Neotropical, might be regarded as congeneric with *Leucopternis* or rather the other way around since *Kaupifalco* is the older name. In such spatially separated taxa, however, one suspects a degree of convergence and it is quite possible, as already noted, that *Kaupifalco* is closer to its Old World relative *Butastur* than to *Leucopternis*.

The genera of sub-buteonines will naturally be listed with the specialized offshoots last followed by *Buteo*. This means that the unspecialized sub-buteonines that are nearest *Buteo*, such as *Parabuteo* and *Leucopternis*, will be separated from it by genera less closely allied, but such dislocations are inevitable in any linear list. I prefer to place *Kaupifalco* and *Butastur* before the New World sub-buteonines as noted and hence near certain Old World genera such as *Melierax* to which they may conceivably be allied. In a linear classification one can only make such compromises as seem best and resort to diagrams or other devices to set forth details of the apparent phylogeny (figs. 1, 2).

Four genera of tropical eagles, all monotypic, may be thought of as descendants of an earlier offshoot of sub-buteonine stock. They are *Morphnus* and *Harpia* in the Neotropics; *Pithecophaga* in the Philippines, and *Harpyopsis* in New Guinea. The first two are closely related; *Morphnus* might be united with *Harpia*, but is much more slightly built. *Pithecophaga* and *Harpyopsis* are allied to each other also, but less obviously. These last two are insular relicts; there is nothing similar to them elsewhere in the Old World. Shufeldt (1919) mentioned some osteological similarities between *Harpia* and *Pithecophaga*.

Ridgway (1876, p. 167) set up a group "Morphni" for *Harpia* (his *Thrasaetus*) and *Morphnus*; to this could presumably be added *Harpyopsis* and *Pithecophaga*. He wrote: "The pterylosis of *Urubitinga* [= *Buteogallus*, in particular *B. urubitinga*] presents many points of resemblance to that of the Morphni . . . and it is likely that the genus

is in other respects intermediate between the latter group and the true *Buteones*; the resemblance is especially great in the wings, the secondaries having a similar excessive development, while the shallow sinuation of an indefinite number of primaries is another point of agreement." Whether the two groups are close enough to render such superficial similarities of significance is a moot question. Aside from the long bare tarsi, some of these eagles resemble the larger, shorter winged species of the "booted" eagles (with feathered tarsi) such as *Stephanoaetus coronatus* of Africa. It must be admitted that the whitish immatures of *Morphnus* and *Harpia* do resemble the similar plumage stages of *Stephanoaetus*, *Spizaetus*, and *Oroaetus*. Nonetheless, the coarsely scaled, long legs and other features of the *Morphni* suggest that they are an earlier offshoot of sub-buteonine stock, whereas the booted eagles are a more recent development from something very close to *Buteo*. The skeletons of *Buteo* and *Aquila* are extremely similar.

Finally a few words, which may be considered as supplementary to the discussion in Brown and Amadon (1968), about the classification of the family Accipitridae as a whole. I still regard the kites as the most primitive members of the family, though Stresemann (Stresemann and Amadon, 1979, p. 273) had them listed last, and hence presumably considered them advanced. The kites require study, in part to see whether their subdivision by Ridgway (1876) and later by Friedmann (1950) into three sections should be maintained and at what taxonomic level. The subgroup centered in *Milvus*, seems to lead naturally into the sea and fish eagles (*Haliaeetus* and *Ichthyophaga*). The latter in turn may be perhaps linked with the accipitrid ("Old World") vultures through the genus *Gypohierax*. Two problem genera, *Ictinaetus* and *Gypaetus*, may belong in this vicinity, though it is customary to leave the former with the booted eagles of the *Aquila* group.

The serpent-eagles (*Circaetus* and related genera) are probably derived from kite-like stock also, though no direct links remain. Two genera, *Polyboroides* and *Melierax*, may belong here. The advanced and widely distributed genera *Circus* and even *Accipiter*, if

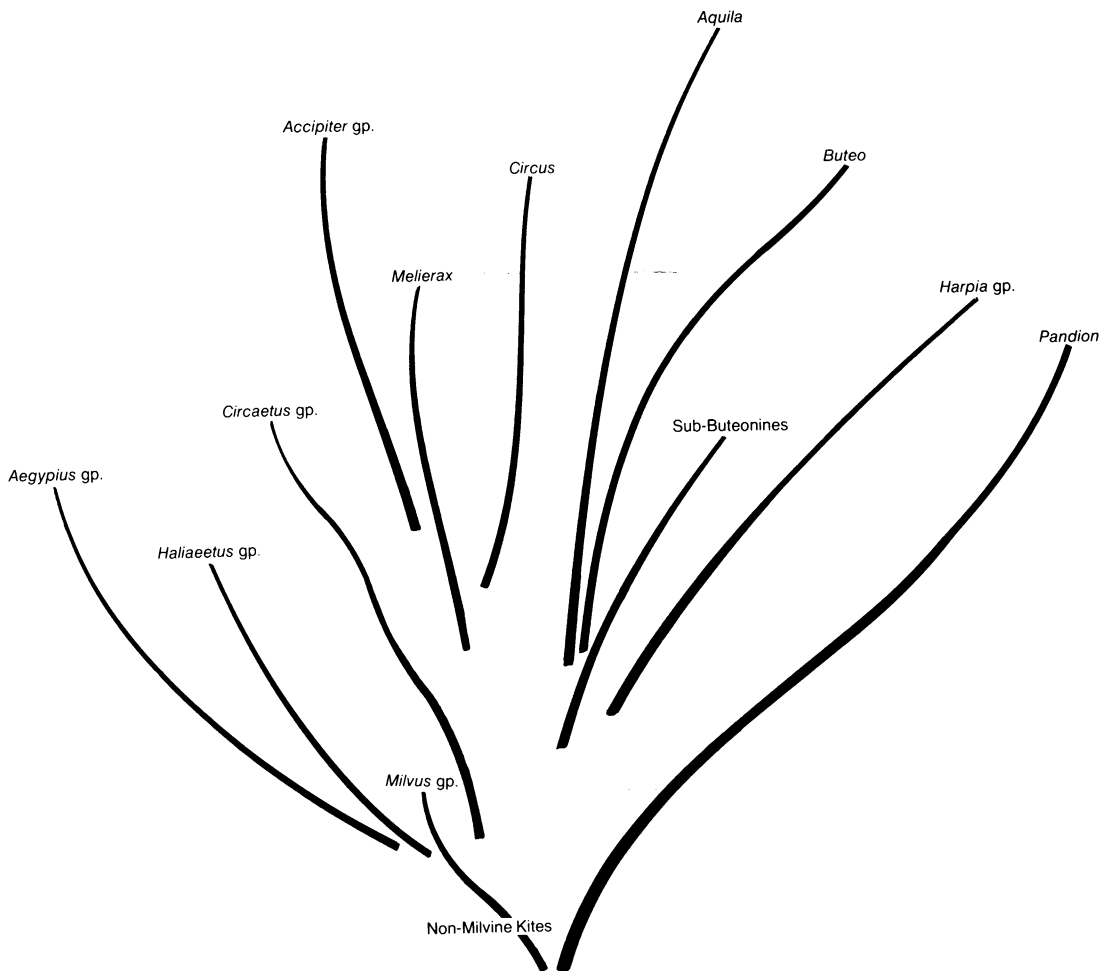


FIG. 2. Suggested phylogeny of family *Accipitridae*. This is a slightly amended version of the phylogenetic tree presented in Brown and Amadon (1968, p. 20). The contents of the groups (abbreviated "gp." on this figure and on fig. 1) are:

Non-Milvine Kites—13 genera—*Aviceda* through *Ictinia* in Stresemann and Amadon (1979, pp. xiii–xiv).

*Milvus* gp.—*Milvus*, *Haliaeetus*, *Lophoictinia*, *Hamirostra*.

*Haliaeetus* gp.—*Haliaeetus*, *Ichthyophaga*.

*Aegypius* gp.—All the accipitrid (=Old World) vultures, including doubtfully *Gypaetus* and very doubtfully *Gypohierax*.

*Circus* gp.—The five genera of serpent eagles and hawks, including doubtfully *Polyboroides*.

*Accipiter* gp.—Includes, after recent reduction (Amadon, 1978) only *Accipiter* and *Urotriorchis*.

Sub-buteonines—The 10 genera treated in detail in this paper; see figure 3.

*Harpia* gp.—*Harpia*, *Morphnus*, *Harpyopsis*, *Pithecopaga*.

*Aquila* gp.—All of the "booted" eagles, including very doubtfully *Ictinaetus*. Genera *Ictinaetus* through *Polemaetus* in Stresemann and Amadon (1979, p. xv).

the latter is as close to the subgenus *Micronisus* of *Melierax* as it appears to be, may be offshoots of similar stock. Next are the sub-

buteonines in the narrower sense used in this paper, and finally *Buteo* and the *Aquila* group. *Aquila* comprises eight genera and

TABLE 1  
Mean Measurements of Total Length, Wing, Tail, and Tarsus (in millimeters) and Weight (in grams)  
for Selected Species of Sub-buteonine and Buteonine Hawks<sup>a</sup>

	Weight	Total Length	Wing	Tail	Tarsus
<i>Kaupifalco monogrammicus meridionalis</i> ♀	311	180	235	148	54
<i>Butastur indicus</i> ♂	404	235	320	190	56
<i>Butastur rufipennis</i> ♀	360	205	317	177	56
<i>Buteogallus aequinoctialis</i>	725	295	312	160	78
<i>Buteogallus urubitinga ridgwayi</i> ♂	1160	342	376	243	116
<i>Buteogallus meridionalis</i>	935	315	407	203	101
<i>Asturina nitida plagiata</i>	485	265	251	160	71
<i>Leucopternis melanops</i> ♂	307	210	212	140	61
<i>Leucopternis albigollis ghiesbreghtii</i> ♂	652	288	354	225	83
<i>Parabuteo unicinctus harrisi</i> ♀	998	300	361	233	87
<i>Busarellus nigricollis</i> ♀	705	365	392	180	80
<i>Geranospiza nigra nigra</i> ♂	349	232	302	239	88
<i>Geranoaetus melanoleucus</i>	2420	414	506	228	109
<i>Harpyhaliaetus coronatus</i>	2950	450	542	290	130
<i>Harpyhaliaetus solitarius</i>	—	445	512	244	127
<i>Buteo jamaicensis borealis</i>	1126	315	380	223	85

<sup>a</sup> Sometimes, as indicated, the data are for one subspecies or one sex only, others represent the averages for the two sexes. The logarithms of these measurements, or of the cube root of the measurement, for weight, were used in plotting the ratio diagrams of figure 3 and figure 4.

a total of 30 species, all so close that only moderate havoc would be wreaked by placing them all in *Aquila*.

The cosmopolitan or nearly so genera *Circus*, *Accipiter*, *Buteo*, and *Aquila* appear on the one hand to be more advanced or derived than many related or putatively related tropical genera but at the same time to have as a rule simpler color patterns, and a lesser development of crests and similar features. This may reflect the fact that such genera, all of which have temperate or even subarctic zone nesting species, successfully coped with the glacial period and thus acquired certain characters and adaptations, such as migration, which contributed both to their dispersal and overall success. Parallels may be found in several other families, e.g., compare crows (*Corvus*) with some of the tropical magpies (*Kitta*, etc.) or *Sturnus* with some of the tropical starlings.

## MEASUREMENTS

The generic diagnoses presented above contain qualitative comparisons of mensural characters—general size and lengths of appendages, in particular wing, tail, and tarsus. The actual measurements of these features

in millimeters or for weight, in grams, may be found in various publications, e.g., Brown and Amadon (1968) and Friedmann (1950).

Wing, tail, and tarsus sometimes vary independently of general size, for example, *Buteogallus urubitinga* has relatively longer tarsi than the other species of that genus. It is useful to have a measure of general size when evaluating such variation. Total weight, despite its variability, is one such index (Amadon, 1943). In Brown and Amadon (1968) an effort was made to search the literature for weights, but even so none at all were found for some taxa and very few for many of the others. For present purposes I have been able to find at least one weight of a species from each of the 10 genera. For *Harpyhaliaetus* exactly one weight was available, that of an individual of *H. coronatus* in the zoo at Belem, Brazil, kindly sent to me by Dr. H. Sick. Only for *Parabuteo unicinctus* were the mean weights of long series of specimens available (Hamerstrom and Hamerstrom, 1978: birds trapped, processed, and released), and from others kindly sent to me by Prof. T. Cade. Weights for several species are from the contributions of Dr. F. Haverschmidt to the ornithology of Suriname. After figures 1 and 2 were completed, I found



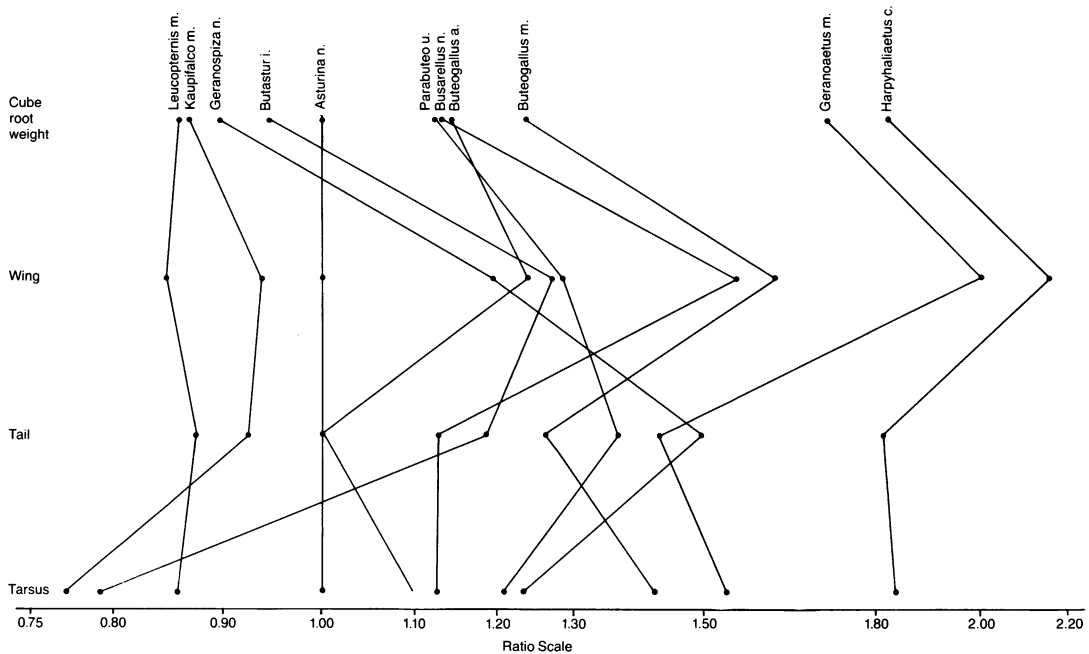


FIG. 3. Comparison by logarithmic ratio diagram of the proportions of wing, tail, tarsus and (cube root of) weight in the 10 genera of sub-buteonines. Usually the type species of the genera are presented, but see text. *Buteogallus meridionalis* is included because it is usually placed in a separate genus *Heterospizias*. The names correspond with those of table 1, which gives the mean measurements used in constructing figures 3 and 4.

The ratios for the various measurements as compared with those of *Asturina nitida*, here selected as a typical sub-buteonine, may be read off directly from the ratio scale on the graph. Cube root of weight may be taken as indicative of general size. Thus from the graph one may conclude that *Leucopternis melanops* does not differ significantly in proportions from *Asturina*; that *Geranospiza* has long wings, tarsi and especially tail in proportion to its weight; that *Buteogallus meridionalis* has relatively longer wings than *B. aequinoctialis* (diverges more widely from cube root weight), etc.

Only the initial letters of species names are shown on this figure and on figure 4; these enable the species to be determined from table 1 in the instances where more than one species of a genus have been included.

that K. H. Voous (1969) had published weights of Suriname raptors based in part on Haverschmidt's work. Taxa by taxa comparison indicated that his figures did not differ sufficiently from those used here to warrant reworking the graphs.

When weights are compared with linear measurements such as wing length it is best to use the cube root of the weight (easily obtained from logarithms) to reduce it to a linear equivalent of the other measurements (Romer and Price, 1940; Amadon, 1943). Weight to be sure does not reveal that, for example, *Geranospiza nigra* is a much slenderer bird than *Buteogallus aequinoctialis*. Perhaps some index based on length, breadth, and depth of the body as taken from birds

in the flesh or from skeletons would better reflect some aspects of general size. Unfortunately such data are even scarcer than are weights.

Another measurement of general size of birds may be obtained from museum study skins. Although such specimens are empty skins stuffed with cotton or a similar substance, the preparator does endeavor to produce a skin that resembles as closely as possible a bird in the flesh as lying in a supine position. By selecting well made skins, "total length," as measured from the tip of the bill to the tip of the tail gives an approximation of the general size of the bird. When similar taxa are being compared, for example subspecies of the same species, such total lengths

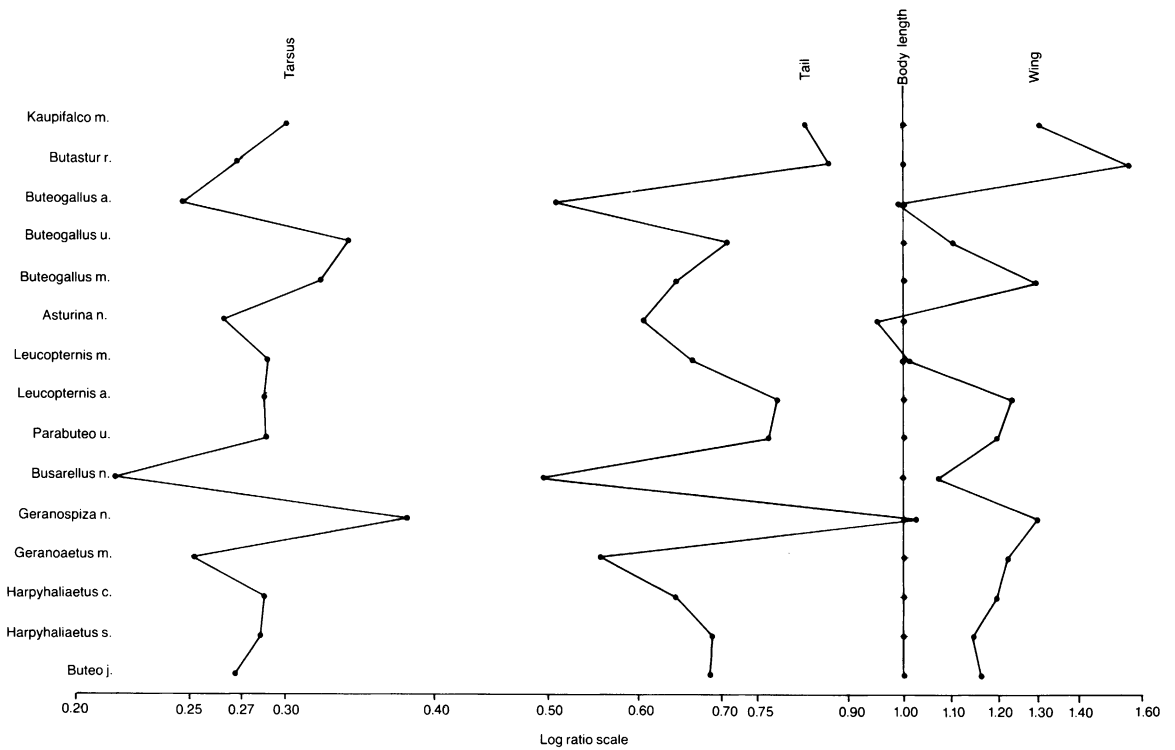


FIG. 4. Comparison by logarithmic ratio diagram of the proportions of wing, tail and tarsus in 14 species of sub-buteonines and of *Buteo jamaicensis*. In this figure body length, as defined in the text, has been used as the standard of comparison; hence differences in proportions as indicated on the graph should be independent of variation in general size. Major differences in proportions agree with those in figure 3; minor fluctuations are not statistically significant owing to inadequacies of material (see text). Additional species, as compared with figure 3, were included to show intrageneric variation in proportions, for example the relatively long tarsi of *Buteogallus urubitinga*. *Buteo jamaicensis* is similar or identical in proportions to *B. buteo*, the type species of the genus.

may be compared directly to show size differences as was done by Chapman (1940, p. 422) for *Zonotrichia capensis*. When the tail or bill vary independently of general size, these may be subtracted from the total length to give "body length" (Amadon, 1943, p. 165); the length of the neck as well should be subtracted from total length in long-necked species such as herons. In hawks it is sufficient to subtract the length of tail, which in birds is comprised of feathers only, from total length to give body length. This was done here (table 1).

In figure 3 (cube root of) weight is used as an index of general size and in figure 4 body length, taken from skins as just defined. If both are valid indexes to general size, the ratio of one to the other should be fairly constant from taxon to taxon. The following ra-

tios, calculated for six taxa at random, are sufficiently alike to indicate that such is the case, especially in view of the fact that total length is here based on measurements of only one to three specimens for each taxon, and the weights, also few in number, are not from the same specimens: *Kaupifalco monogrammicus* .368; *Butastur rufipennis* .369; *Leucopternis melanops* .357; *Geranoaetus melanoleucus* .440; *Parabuteo unicinctus* .400; and *Geranospiza nigra* .360.

Figures 3 and 4 are logarithmic ratio diagrams as devised by Simpson (1941) and later used by Amadon (1950) and others. In such diagrams a standard of comparison is first selected. In figure 3 it is *Asturina nitida*, chosen because it is a sub-buteonine of average size and proportions and the first named of a cluster of very closely allied genera, the

others being *Buteogallus*, *Parabuteo*, and *Leucopternis*. From the ratio scale on the graph one may read off directly the ratio of the other taxa on the graph to *Asturina* for each listed measurement. The figures for cube root of weight provide a basis point for comparing the differences in proportions per se. By copying off the scale and placing the reading 1.00 at any data point, the ratios of the measurements of all the others on that horizontal line to the point (species) selected may be read directly from the scale; a property of such logarithmic scales.

In figure 4 body length as defined above is used as the standard of comparison, thus eliminating size as a factor to be considered in comparing the proportions of the various taxa. Because of the scanty data and the fact that not all measurements are from the same specimens, only the more pronounced differences in proportions should be accepted as significant. For example, *Geranospiza* is characterized by relatively very long wing, tarsus, and especially tail. Supporting what was said above, the more significant intergeneric variation in proportions is in agreement on the two graphs even though the measurement of general size employed was, as noted, not the same. Many of the less pronounced variations in proportions, especially when they are in agreement on the two graphs will probably be demonstrated to be significant later when more adequate series of measurements are available.

The type species of each genus is included on the graphs except for *Butastur* where very poor material of the type, *B. teesa*, was at hand. When more than one species of a genus is included it is to illustrate some point, for example the relatively long legs of *Buteogallus urubitinga*. The actual measurements used are given in table 1. Usually an average of the two sexes (females are invariably larger) was used, but in a few instances where weights were of one sex only all the data are for that sex as indicated. Only means are given, complete measurements are in the works cited above supplemented by various sources, as noted, especially for weights. The body length measurements were taken from specimens in the American Museum of Natural History. Often only one or two specimens in a suite of a dozen or so were carefully

enough prepared for taking that measurement.

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