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A Contribution to Comparative Systematics

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The Number of Species and Genera of Recent Birds: A Contribution to Comparative Systematics¹

WALTER J. BOCK² AND JOHN FARRAND, JR.³

ABSTRACT

Counts are presented for the numbers of species and genera of birds by orders and families to provide the data base for a comparative systematic analysis of the structure of the avian genus. These counts are based on the classification presented in the "Reference List of Birds of the World" and subsequent corrections. A total of 9021 species of birds exist in 2045 genera of which 3747 species in 941 genera are nonpasserine and 5274 species in 1104 genera are passerine. The species/genus ratio is calculated for each taxon with the average for all birds being 4.411 s/g. The distribution of genera of different size categories is tabulated for all birds and for selected

subgroups. These distributions have the characteristic hollow-curve shape with a preponderance of small genera; 60.5 percent of all avian genera possess one or two species. The 39 largest genera are tabulated and analyzed; these comprise only 1.91 percent of all genera and contain 17.8 percent of all avian species or twice as many as in the one- and two-species genera. The possible reasons for the evolution of species-rich genera are outlined; the major ones are the ability of species in large genera to disperse and colonize new areas and the ability of these species to establish sympatry with congeneric species without divergence.

INTRODUCTION

The exact number of species of birds has always held a fascination for ornithologists, and a series of counts has been published over the last five decades. These counts not only reflect the status of our knowledge of the world's avifauna, but also document trends in the species concept and its appli-

cation by ornithologists. Counts of genera, although rarely attempted, indicate changes in the generic concept used in avian systematics and in its relationship to the species- and the family-level categories. Publication of Sharpe's "A Hand-list of the genera and species of birds" (1899–1909) represents the

¹ Dedicated to Ernst Mayr on his seventy-fifth birthday in recognition of his earlier analyses of the numbers of avian species and genera and of his pioneering work in comparative systematics.

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culmination of the application to birds of the monotypic species concept. Sharpe did not recognize subspecies and hence considered all distinct allopatric forms as full species. He recognized 2810 genera and 18,939 species of birds, including fossils (see discussions in Mayr, 1935, 1946). The number of species was reduced rapidly during the two decades following the publication of the final volume of Sharpe's "Hand-list," with growing acceptance and application of the polytypic species concept and the use of subspecies by ornithologists. Stresemann (1927-1934, p. 6) estimated that approximately 8000 species of birds exist and that these are subdivided into approximately 30,000 subspecies. Later in his handbook under the heading of "Species number," Stresemann (p. 634), in disagreement with the estimate of 20,000 avian species given earlier by Reichenow (1913, p. 37), doubted that more than 10,000 species of birds exist. Unfortunately, Stresemann gave no further breakdown of species numbers by family in his section on classification. Thus a figure between 8000 and 10,000 can be taken as an estimate of the number of avian species at the start of the modern period of species systematics in ornithology (e.g., the work of Stresemann and his students, see Mayr, ms.), with the lower figure being closer to Stresemann's appraisal of the number of existing Recent species of birds. At the Eighth International Ornithological Congress in 1934 Meise summarized the number of new species and genera described from 1920 to 1933 in his report on progress in ornithological systematics, but did not provide figures for the known numbers of species and genera. Mayr (1935, 1946) and Mayr and Amadon (1951) provided counts of the number of avian species by families based largely on the ornithological collections in the American Museum of Natural History. These counts are the basis of the oft-quoted figure of 8600 ± 2 percent as the number of Recent species of birds. Further, Mayr (1935) estimated that 2600 genera of birds were recognized and later (Mayr, 1946, p. 68) suggested that approximately 1800 genera should be recognized for the estimated 8616 species. During the past quar-

ter-century most statements in ornithological texts on the number of avian species have been taken from the figures provided by Mayr and Amadon (1951), although Storer's (1960, 1971) counts appear to be independent. Of the several check-lists of birds published in recent years, only Edwards (1974) and Gruson (1976) gave the number of species in each family but these authors did not provide further analysis or the total number of genera or species. Comparison of these two lists shows disagreement in the counts for most families. Because neither author provided citations for the authorities followed for the classification of each family, it is not easy to compare their counts or to evaluate the differences between them. Morony, Bock, and Farrand (1975, p. vii) cited figures for the total number of genera and species of birds, but did not break them down into individual family counts, making comparison with Edwards and with Gruson difficult. Thus, in spite of the advanced state of knowledge of the species of birds and their classification, neither an accurate up-to-date count nor an analysis of avian species and genera are available.

We decided, therefore, to use the "Reference List" (Morony, Bock, and Farrand, 1975) and its subsequent corrections and updatings as the foundation for a tabulation of the species and genera of Recent birds by families and for an analysis of these data as a comparative systematic study of the structure of the avian genus. The "Reference List" has an advantage over other recent check-lists of birds in that authorities are cited for the classification followed for each family and for all deviations from any classification. All modifications from the "Reference List," including citations to the authority for each change, are given in Appendix I. We maintain, with very few exceptions, the policy adopted for the "Reference List" of accepting only those changes for which a published authority, preferably with reasons, could be cited; we avoid biasing the classification with our own undocumented opinions. Thus, anyone wishing to inquire further into the tabulations presented herein can find the actual classification used

for each taxon and the reasons underlying any particular arrangement of genera and species.

The basic problem in providing counts of genera and species is, of course, the accuracy and consistency of the underlying classifications. One person's species is another's subspecies, and the limits of genera vary widely depending on the particular approach to classification and the "taste" of each taxonomist. The empirical data on which taxonomic decisions are reached are constantly improving, leading to ever differing conclusions; the status of *Larus relictus* (see p. 25) is an excellent case in point. Each author presenting species counts has commented on these difficulties and we cannot offer any new insights or solutions. We are fully aware of the problems facing the compiler of species and genera counts and of the shortcomings of the reported figures, but we believe that the counts and the analyses presented herein have validity in spite of the inadequacies of the classifications on which they are based.

The major goals of the present paper are:

(a) To present counts of the number of genera and species of birds in each order and family (and in some cases, subfamilies and tribes) and to give the species/genus ratio for each taxon;

(b) To analyze the distribution of genera in different size classes (number of species per genus) for all birds and for selected samples;

(c) To list the 39 genera containing the largest number of species with a brief analysis of these genera;

(d) To show how these data may be used to test various evolutionary theories and different approaches to classification.

COUNTS OF GENERA AND SPECIES

The number of genera and species of Recent birds for all orders and families and the species/genus ratio for each taxon are given in table 1. To facilitate comparisons, we include subfamilies and, in some cases, tribes for those groups in which the classification adopted herein may differ radically from that used in other counts. The "Ratites" are

grouped together into a single "order" rather than the five orders used in most classifications; this arrangement is for convenience only and should not obscure comparisons. These counts are based on the "Reference List . . ." (Morony, Bock, and Farrand, 1975)⁴ with corrections and datings given in Appendix I; the cut-off date for new species was December 31, 1978. Revision of the families in the recently published volumes VIII (Traylor, 1979) and revised volume I (Mayr and Cottrell, 1979) of "Peters's Check-list" are not included because they were published after we had completed our analysis.

Recent birds are considered as those species observed alive by Western ornithologists and explorers — "known from at least a fragment of the skin and feathers" (Peters, 1931) — and include extinct species. Thus, the dodos and their allies (Raphidae) are included, but the moas (Dinornithidae), elephant birds (Aepyornithidae), and other subfossils are excluded. A few borderline species, notably among the parrots, are included because they were listed in the basic classification we followed.

The total number of species of birds is 9021, arranged in 2045 genera. These are subdivided into 3747 nonpasserine species in 941 genera and 5274 passerine species in 1104 genera. The average number of species per genus is 4.411 for all birds with the nonpasserine ratio of 3.983 being markedly lower than the passerine ratio of 4.776; the difference being over 15 percent.

The number of species for each avian family may be compared directly with those given by Mayr (1946), Mayr and Amadon (1951), Storer (1960, 1971), Edwards (1974), Gruson (1976), and Van Tyne and Berger (1976), taking into account some changes in the limits of family-level taxa and some shifts in the position of genera. Such comparisons cannot be made readily except with Edwards and Gruson because the authors of most of

⁴ The "Reference List of the Birds of the World" is published as looseleaf sheets and may be obtained from the Department of Ornithology, American Museum of Natural History.

TABLE 1
Totals of Species and Genera of Orders and Families of Birds

Taxon	Genera	Species	Ratio S/G
Ratites	15	58	3.87
Struthionidae	1	1	1.0
Rheidae	2	2	1.0
Casuariidae	1	3	3.0
Dromaiidae	1	2	2.0
Apterygidae	1	3	3.0
Tinamidae	9	47	5.22
Sphenisciformes	6	18	3.0
Spheniscidae	6	18	3.0
Gaviiformes	1	5	5.0
Gaviidae	1	5	5.0
Podicipediformes	5	20	4.0
Podicipedidae	5	20	4.0
Procellariiformes	23	104	4.52
Diomedidae	2	13	6.5
Procellariidae	12	66	5.5
Hydrobatidae	8	21	2.63
Pelecanoididae	1	4	4.0
Pelecaniformes	9	62	6.89
Phaethontidae	1	3	3.0
Pelecanidae	1	8	8.0
Sulidae	2	9	4.5
Phalacrocoracidae	3	33	11.0
Anhingidae	1	4	4.0
Fregatidae	1	5	5.0
Ciconiiformes	44	114	2.59
Ardeidae	16	62	3.86
Balaenicipitidae	1	1	1.0
Scopidae	1	1	1.0
Ciconiidae	6	17	2.83
Threskiornithidae	20	33	1.65
Phoenicopteriformes	3	6	2.0
Phoenicopteridae	3	6	2.0
Anseriformes	45	150	3.33
Anhimidae	2	3	1.5
Anatidae	43	147	3.42
Anseranatinae	1	1	1.0
Anserinae	7	30	4.29
Anatinae	35	116	3.31
Falconiformes	81	288	3.56
Cathartidae	5	7	1.4
Pandionidae	1	1	1.0
Accipitridae	64	217	3.39
Sagittariidae	1	1	1.0
Falconidae	10	62	6.2
Galliformes	79	269	3.41
Magapodiidae	7	12	1.71

TABLE 1—(Continued)

Taxon	Genera	Species	Ratio S/G
Cracidae	8	44	5.5
Phasianidae	63	212	3.37
Meleagridinae	2	2	1.0
Tetraoninae	6	16	2.67
Odontophorinae	10	33	3.3
Phasianinae	40	154	3.85
Perdicini	24	106	4.17
Phasianini	16	48	3.0
Numidinae	5	7	1.4
Opisthocomidae	1	1	1.0
Gruiformes	82	210	2.56
Mesitornithidae	2	3	1.5
Turnicidae	2	14	7.0
Pedionomidae	1	1	1.0
Gruidae	4	15	3.75
Aramidae	1	1	1.0
Psophiidae	1	3	3.0
Rallidae	53	142	2.68
Heliornithidae	3	3	1.0
Rhynchotidae	1	1	1.0
Eurypygidae	1	1	1.0
Cariamidae	2	2	1.0
Otidae	11	24	2.18
Charadriiformes	74	329	4.45
Jacanidae	6	8	1.33
Rostratulidae	2	2	1.0
Dromadidae	1	1	1.0
Haematopodidae	1	7	7.0
Ibidorhynchidae	1	1	1.0
Recurvirostridae	3	10	3.33
Burhinidae	2	9	4.5
Glareolidae	5	16	3.2
Charadriidae	8	64	8.0
Scolopacidae	23	86	3.74
Tringinae	9	31	3.44
Arenariinae	1	2	2.0
Phalaropodinae	1	3	3.0
Scolopacinae	1	6	6.0
Gallinagoninae	4	20	5.0
Calidridinae	7	24	3.43
Thinocoridae	2	4	2.0
Chionididae	1	2	2.0
Stercorariidae	1	5	5.0
Laridae	4	88	22.0
Larinae	1	45	45.0
Sterninae	3	43	14.33
Rynchopidae	1	3	3.0
Alcidae	13	23	1.77
Columbiformes	46	322	7.0
Pteroclididae	2	16	8.0

TABLE 1—(Continued)

Taxon	Genera	Species	Ratio S/G
Raphidae	2	3	1.5
Columbidae	42	303	7.21
Psittaciformes	81	340	4.2
Loriidae	11	54	4.91
Cactuidae	6	18	3.0
Psittacidae	64	268	4.18
Cuculiformes	43	147	3.42
Musophagidae	5	18	3.6
Cuculidae	38	129	3.39
Strigiformes	30	146	4.87
Tytonidae	2	11	5.5
Strigidae	28	135	4.82
Caprimulgiformes	24	105	4.38
Steatornithidae	1	1	1.0
Podargidae	2	13	6.5
Nyctibiidae	1	6	6.0
Aegothelidae	1	8	8.0
Caprimulgidae	19	77	4.1
Apodiformes	135	428	3.17
Apodidae	18	83	4.61
Hemiprocridae	1	4	4.0
Trochilidae	116	341	2.94
Coliiformes	1	6	6.0
Coliidae	1	6	6.0
Trogoniformes	8	37	4.63
Trogonidae	8	37	4.63
Coraciiformes	44	200	4.55
Alcedinidae	14	91	6.5
Todidae	1	5	5.0
Momotidae	6	9	1.5
Meropidae	3	24	8.0
Coraciidae	2	11	6.5
Brachypteraciidae	3	5	1.67
Leptosomatidae	1	1	1.0
Upupidae	1	1	1.0
Phoeniculidae	1	8	8.0
Bucerotidae	12	45	3.75
Piciformes	62	383	5.98
Galbulidae	5	17	3.4
Bucconidae	7	32	4.57
Capitonidae	13	81	6.23
Indicatoridae	4	16	4.0
Ramphastidae	6	33	5.5
Picidae	27	204	7.56
Jynginae	1	2	2.0
Picumninae	3	31	10.3
Picinae	23	171	7.4

TABLE 1—(Continued)

Taxon	Genera	Species	Ratio S/G
Passeriformes	1104	5273	4.78
Eurylaimidae	8	14	1.75
Dendrocolaptidae	13	52	4.0
Furnariidae	34	218	6.41
Formicariidae	51	230	4.51
Conopophagidae	2	11	6.5
Rhinocryptidae	12	30	2.5
Cotingidae	27	79	2.93
Pipridae	17	52	3.06
Tyrannidae	110	375	4.41
Oxyruncidae	1	1	1.0
Phytotomidae	1	3	3.0
Pittidae	1	24	24.0
Xenicidae	2	4	2.0
Philepittidae	2	4	2.0
Menuridae	1	2	2.0
Atrichornithidae	1	2	2.0
Alaudidae	15	78	5.2
Hirundinidae	20	80	4.0
Motacillidae	5	54	10.8
Campephagidae	9	70	7.78
Pycnonotidae	15	123	8.2
Irenidae	3	14	4.67
Laniidae	12	74	6.17
Prionopinae	2	9	4.5
Malaconotinae	7	39	5.57
Laniinae	2	25	12.57
Pityriasinae	1	1	1.0
Vangidae	9	13	1.44
Bombycillidae	5	8	1.6
Ptilogonatinae	3	4	1.3
Bombycillinae	1	3	3.0
Hypocoliinae	1	1	1.0
Dulidae	1	1	1.0
Cinclidae	1	5	5.0
Troglodytidae	14	60	4.24
Mimidae	13	31	2.38
Prunellidae	1	12	12.0
Muscicapidae	259	1427	5.51
Turdinae	48	309	6.44
Orthonychinae	9	19	2.11
Timaliinae	49	255	5.20
Panurinae	3	19	6.33
Picathartinae	1	2	2.0
Polioptilinae	3	12	4.0
Sylviinae	63	349	5.54
Malurinae	26	106	4.08
Muscicapinae	24	153	6.38
Platysteirinae	4	26	6.50
Monarchinae	17	91	5.35

TABLE 1—(Continued)

Taxon	Genera	Species	Ratio S/G
Rhipidurinae	2	40	20.0
Pachycephalinae	10	46	4.6
Aegithalidae	3	7	2.33
Remizidae	4	10	2.5
Paridae	3	47	15.67
Sittidae	4	26	6.5
Sittinae	1	22	22.0
Daphoenosittinae	2	3	1.5
Tichodromadinae	1	1	1.0
Certhiidae	2	6	3.0
Certhiinae	1	5	5.0
Salpornithinae	1	1	1.0
Rhabdornithidae	1	2	2.0
Climacteridae	1	6	6.0
Dicaeidae	7	58	8.29
Nectariniidae	5	117	23.4
Zosteropidae	11	83	7.55
Meliphagidae	39	172	4.41
Emberizidae	134	560	4.18
Emberizinae	65	279	4.29
Catamblyrhynchinae	1	1	1.0
Cardinalinae	9	39	4.33
Thraupinae	58	240	4.14
Tersininae	1	1	1.0
Parulidae	28	126	4.5
Drepanididae	10	23	2.3
Vireonidae	4	43	10.75
Cyclarhinae	1	2	2.0
Vireolaniinae	1	3	3.0
Vireoninae	2	38	19.0
Icteridae	23	95	4.13
Fringillidae	20	122	6.1
Fringillinae	1	3	3.0
Carduelinae	19	119	6.26
Estrildidae	28	127	4.54
Ploceidae	18	144	8.0
Bubalornithinae	2	2	1.0
Passerinae	8	37	4.63
Ploceinae	7	95	13.57
Viduinae	1	10	10.0
Sturnidae	26	111	4.27
Sturninae	25	109	4.36
Buphaginae	1	2	2.0
Oriolidae	2	25	12.5
Dicruridae	2	20	10.0
Callaeidae	3	3	1.0
Grallinidae	3	4	1.33
Artamidae	1	10	10.0
Cracticidae	3	10	3.33
Ptilonorhynchidae	8	18	2.25

TABLE 1—(Continued)

Taxon	Genera	Species	Ratio S/G
Paradisaeidae	20	42	2.1
Corvidae	26	106	4.08
Totals			
Nonpasserines	941	3747	3.982
Passerines	1104	5274	4.777
All Birds	2045	9021	4.411

these counts do not cite references to the classification on which their tabulations are based. A comparison of the number of genera per family can be made with Edwards (1974), Gruson (1976), and Storer (1971) the only authors to include this information; again difficulties exist because Storer did not cite the classification on which his generic figures were based.

A most interesting analysis of the changes in the number of species and genera covered in volume I of "Peters's Check-list" (orders Ratites to Falconiformes of table 1) was presented by Mayr and Cottrell (1979) in their introduction of revised volume I. We compared their figures with our counts, which are based on a mixture of classifications ranging from those in Peters's original volume I (1931), to those proposed in the 1950s and 1960s. The three sets are as follows: Genera—281 (Peters, 1931), 232 (this count) 218 (Mayr and Cottrell, 1979); species—853 (Peters, 1931), 825 (this count), 799 (Mayr and Cottrell, 1979). They demonstrate the general trend of recognizing polytypic species and broader genera over the past five decades since Peters completed work on the original volume of his "Check-list."

A comparison of recent counts, arranged in chronological order, for nonpasserine, passerine, and all species of birds is given in table 2. These counts are too few and the time span too short to permit meaningful discussion of any trends. With the exception of Storer's figures, the three counts based on published classifications (Edwards, Gruson, and the present one) are the largest and far

exceed the counts published by Mayr (1946) and Mayr and Amadon (1951) which were the first published. If extinct Recent birds are added to Edwards's figure, then his total of 8987 is scarcely different from ours; the difference is only 34 species or 0.38 percent. However, the difference between the total given by Mayr and Amadon and the present one is 500 species or 5.5 percent—a sizable difference.

It is not reasonable to suggest that newly discovered species of birds can account for the increase of 5 percent since 1951 in the number of recognized species of Recent birds. A more plausible conclusion is that increase in the number of species in this count over that presented by Mayr and Amadon in 1951 reflects a trend of changing concepts in current taxonomic revisions in which distinct allopatric forms are recognized as species rather than as subspecies of a broad polytypic species. Mayr (ms.) discussed the history of the polytypic species concept and its application to birds. He showed that since 1920, largely under the leadership of Stresemann and his students, the predominant trend had been to merge allopatric forms into broad polytypic species. This reduced the number of avian species from 20,000 or more to just above 8600. Further, he showed that a reversal has occurred during the past decade possibly as a reaction to the belief that the application of the polytypic species concept had been too extreme. More and more allopatric forms, especially those with disjunct ranges, are being recognized as biological (taxonomic) species even when the ob-

TABLE 2
Comparison of Recent Counts of Avian Species

Authority	Non- pas- serine	Pas- serine	Total
Mayr (1946)	3523	5093	8616
Mayr and Amadon (1951) ^a	3518	5001	8519
Storer (1960) ^a	3596	4982	8578
Storer (1971) ^a	3591	5048	8739
Edwards (1974) ^a	3665	5252	8917 ^b
Gruson (1976) ^a	3558	5146	8704 ^b
Van Tyne and Berger (1976) ^a	3546	5152	8698
Morony, Bock, and Farrand (1975)	3750	5266	9016
Bock and Farrand (this count)	3747	5274	9021

^a Totals based on tabulations of the figures given for individual families of birds.

^b Excludes extinct species of Recent birds; 70 species should be added to make the totals comparable to Morony, Bock, and Farrand (1975) or to this count.

served morphological differences are no greater than those found between integrating subspecies. Herein one must remember that the biological species concept is nondimensional (Mayr, 1963, pp. 17–19) and becomes less and less applicable to populations replacing one another over increasing geographical distances. Arguments about the specific status of allopatric populations found over a broad geographic range, especially when distinct geographic gaps separate them, have limited biological relevance. Yet the current trend in recognizing allopatric forms as biological species has a major disadvantage in that it distorts the picture of avian diversity whether it is viewed on a global scale or within more restricted geographic bounds. Recognition of several species of *Morus*, *Anhinga*, *Botaurus*, *Hematemopus*, *Himantopus*, and *Rynchops* suggests a greater diversity than exists in reality because the species in each of these genera replace one another geographically and form a single superspecies. To obtain a meaningful idea of diversity within a taxonomic group such as birds, it is necessary to have one measure of biological diversity in terms of reproductive units and a second measure of

diversity in terms of ecological units. A single species concept cannot provide both measures simultaneously (Mayr, 1963; Mayr and Short, 1970) because their causal evolutionary bases during the process of speciation are not closely correlated.

Several interconnected species concepts, based on the biological species concept, have been developed to provide the necessary measures of biological diversity among sexually reproducing organisms. We must exclude, for the purposes of this discussion, the question of species concepts and the recognition of biological diversity among nonsexually reproducing organisms because the biological species concept does not apply to them. The several species concepts of interest to us are the biological species, be it monotypic or polytypic, the superspecies, and the zoogeographical (or biogeographical) species (see Mayr, 1978 for a discussion of some of these terms). Definitions of these several species concepts vary somewhat and they are sometimes confused with one another (e.g., zoogeographical species was used in the sense of superspecies in volume VIII of Peters's Check-list). Because these concepts are central to our discussion we wish to define them and show their relationship to measures of biological diversity.

The biological species concept has as its essential criterion the lack of reproduction (or more precisely expressed, the lack of gene flow) between species—a biological species represents a single reproductive unit (Mayr, 1963). Yet the complete mechanism of speciation (the multiplication of species or splitting of a phyletic lineage—we need not restrict ourselves only to allopatric speciation but will do so for ease of discussion) consists of two separate evolutionary processes which are independent of each other and which may occur at different periods of the complete speciation event (Bock, 1979, pp. 30–36). The first process is the evolution of intrinsic isolating mechanisms which takes place during the allopatric phase of speciation. The intrinsic isolating mechanisms must be fully developed before the two species can coexist sympatrically without interbreeding—that is, to permit the two

species to maintain their status as separate reproductive units. The second process is the evolution of ecological differences (Lack, 1944; Mayr, 1963) which may take place during the allopatric phase or during the neosympatric phase of speciation or during both (Bock, 1979, pp. 32–35). These ecological differences permit the two species to coexist sympatrically—that is, they permit the two species to maintain their status as distinct, sympatric ecological units.

It is not possible to express the results of both of these processes contributing to speciation in one species concept and hence in a single taxonomic category. Historically, attention of evolutionary biologists was directed first to questions associated with reproductive isolation between species and with the evolution of intrinsic isolating mechanisms. Hence, the definition of the biological species was based on reproductive isolation and the taxonomic species category had been restricted to the biological species. The taxonomic species expresses the property of species as unique reproductive units, but not necessarily as unique ecological units. A list of biological (=taxonomic) species cannot represent the full range of all attributes resulting from the mechanism of speciation. It cannot provide a full measure of the ecological diversity of a group of organisms.

Species may be monotypic or polytypic depending upon whether they display geographic variation recognized as subspecies. Moreover, species may contain morphs which differ ecologically. In birds such ecological polymorphism is almost completely restricted to sexual polymorphism (Selander, 1971, pp. 97–98). Discussion of these infraspecific variations is outside the scope of this analysis except to note that the polytypic species with its geographic subspecies merges into the next concept to be discussed—the superspecies.

The concept of the superspecies was proposed in 1931 by Ernst Mayr for a group of closely related, still largely allopatric species (Mayr, 1978, p. 86; Selander, 1971, p. 120). Thus, the superspecies may be defined as a monophyletic (in the broad sense as used in

evolutionary systematics) group of biological species which still replace each other geographically. The amount of geographic overlap permitted between members of a superspecies is arbitrary. Members of a superspecies are biological species and have been called semispecies (Mayr, 1963), or allospecies (Mayr and Short, 1970); the latter is preferred because the term semispecies has been expanded to include all borderline cases of speciation (Mayr, 1978; Selander, 1971, pp. 120–121). Allospecies are biological species and may be monotypic or polytypic. The essential attribute of a superspecies is that its members (the allospecies) are so similar ecologically that they are unable to invade each other's geographical ranges and hence are unable to reestablish sympatry following the evolution of their intrinsic isolating mechanisms (see Lack, 1944). In some cases, members of a superspecies are kept apart by geographic barriers they are unable to cross and hence are unable to invade each other's range. Members of a superspecies have not completed the process of speciation in that the evolution of "full" ecological differences has not occurred. The allospecies of a superspecies have not been subjected to the evolutionary processes operating during the final neosympatric phase of geographical speciation (Bock, 1979, pp. 32–35).

Allospecies can be grouped into superspecies, but not all biological species are members of superspecies. For convenience of discussion, it is useful to have a single term for superspecies and those species not members of a superspecies. The term zoogeographical species has been used for this category of species.

A zoogeographical (or biogeographical) species is one that has completed the entire process of speciation, having evolved the necessary intrinsic isolating mechanisms and the necessary ecological differences to permit it to coexist sympatrically with other such species. Zoogeographical species include superspecies and biological species that are not members of a superspecies, or expressed somewhat differently, polytypic superspecies and monotypic superspecies. In an ecological sense, the zoogeographical

species represents a single unit—the ecological species—just as the biological species represents a single reproductive unit. A list of biological (=taxonomic) species provides a measure of reproductive diversity (the independent phyletic lineages), and a list of zoogeographical species provides a measure of ecological diversity. Both types of lists are required for a good estimate of total diversity within a group of organisms. The pattern of size distribution of genera (species per genus—table 3) depends upon whether one uses a list of biological species (as used in table 3) or a list of zoogeographical species. A list of zoogeographical species has been prepared by Mayr and Short (1970) for North American birds; however, one is not available for the world's avifauna.

The recent revisions of the Paradisaeidae by Diamond (1972), the Galbulidae and the Ramphastidae by Haffer (1974), and the Pipridae by Snow (1975) clearly illustrate the need to develop a list of zoogeographical species of birds. In each of these revisions the number of zoogeographical species is roughly half the number of recognized species (25 vs. 52 for the Pipridae; 8 vs. 17 for the Galbulidae; 14 vs. 33 for the Ramphastidae and 25 vs. 42 for the Paradisaeidae). Consequently, the species/genus ratio drops considerably (e.g., from 3.06 to 1.77 for the Pipridae) which supports the argument that the genera of birds are still oversplit. While it is possible that these four families do not constitute a fair sample of the ratio between biological species and zoogeographical species in all avian families, they do provide an approximation of the percentage of zoogeographical species. Based on this approximation it seems reasonable that the 9021 species of birds tabulated in the "Reference List" include only 5000 to 6000 zoogeographical species. Mayr (ms.) suggests that the number of zoogeographical species may be somewhat larger, perhaps 7000 to 7500.

A second problem lies in the generic limits accepted in most revisions followed in the "Reference List." The total of 2045 genera is less than Mayr's (1935) estimate of 2600, but more than his later (1946) calculation of

1800 and suggests that the genera of birds may still be oversplit. The number of genera recognized by Storer (1960, 1971) for non-passerine birds dropped from 1176 in 1960 to 1018 in 1971, but it is still larger than the 941 recognized in the "Reference List." It was not possible to obtain a count of the passerine genera in Storer's classification (1971) because he did not give exact figures for several families; yet his counts are higher than those in the "Reference List" (893 vs. 845 for all passerine families except for the large Muscicapidae). The trend toward large genera in most recent revisions is illustrated by Moynihan's (1959) treatment of the Laridae; he reduced the 20 genera recognized in the "Reference List" (based on Peters's "Checklist") to six, and raised the species/genus ratio from 4.8 to 16.0 which contrasts strongly to the average ratio of 4.4 for all birds. The contrasting trend is shown by Wolters's (1977) revision of the Nectariniidae in which he places the 117 species in 24 genera (46 genera and subgenera) giving a species/genus ratio of 4.43 as compared to the ratio of 23.4 reported herein. Wolters's classification is based on the cladistic approach to classification which must, by the basic tenets of this approach, result in small taxa (see below).

It is not clear what the consequences of future generic revisions would be as they will depend to a large extent on the accepted approach to classification and on the recognition of zoogeographical species. A few recent revisions have merged genera to the extent that the genus became equivalent to the lowest family-level taxon (tribe or subfamily), which is the essential consequence of Moynihan's (1959) revision of the Laridae and of Strauch's (1978) revision of the Charadriiformes. Such results reduce the usefulness of the genus, as much as does the recognition of very large numbers of monotypic genera. It seems clear that the present trend, under an evolutionary approach to classification, in generic revisions of birds will result in an increase in large genera and in the species/genus ratio, but it is not clear whether the percentage of monotypic and two-species genera (now 60.5% of all genera) will drop significantly compared to the in-

crease in large genera. If an average of six species per genus is accepted then the total number of genera would be approximately 1500; a larger ratio of eight species per genus would result in about 1100 genera. A more extensive use of the zoogeographical species concept as the unit on which to judge the size of genera may reduce the total number of genera even more, but it is doubtful that the number of recognized avian genera will drop below 1000 and it may not even approach that figure. It seems reasonable to us that the number of recognized avian genera may stabilize between 1000 and 1250 and quite likely the percentage of monotypic and two-species genera will remain about 40 percent of the total or between 400 and 500 genera.

DISTRIBUTION OF GENERA IN DIFFERENT SIZE CATEGORIES

The distribution of genera in different size categories (species/genus ratio) is given in table 3, showing the figures for nonpasserine, passerine, and all birds. The number of genera and the total number of species in these genera are given for each size category; the totals for genera and species correspond to the totals given in table 1. The most striking observation to be made of this table is the overwhelming preponderance of small genera and the rapid drop in the number of genera with increase in the species/genus ratio giving the characteristic hollow-curve distribution when plotted (fig. 1).

The concept of "hollow-curve" distribution of number of genera in different size categories for large taxonomic groups was introduced by Willis (1922, 1940) who established this as a general rule. Willis (1922) originally postulated the hollow-curve rule to describe the distribution of species in geographic areas and later generalized it (Willis, 1940, pp. 33–42, 173–175) to describe the distribution of species in genera in large families and other higher taxa. The "hollow-curve" frequency distribution of species in genera has been discussed by Mayr (1942, p. 288; 1969, pp. 236–237) who suggested that this characteristic curve results from the in-

dependence of branching and divergence in evolution.

The number of genera below the average species/genus ratio is 729, or 77.4 percent, for nonpasserine birds (mean = four species), 850 or 77.1 percent for passerine birds (mean = five species) and 1500, or 77.1 percent, for all birds (mean = 4.5 species). The number of genera with one or two species is 584 or 62 percent for nonpasserine, 654, or 59.2 percent, for passerine and 1238, or 60.5 percent for all birds. For nonpasserine birds, 50 percent, of all species are found in genera containing eight or fewer species, 75 percent are found in genera of 20 or fewer species and 90 percent are found in genera of 36 or fewer species. For passerine birds, 50 percent of all species are found in genera containing 10 (actually between 10 and 11) or fewer species, 75 percent in genera of 24 or fewer species and 90 percent in genera of 40 or fewer species. For all birds, 50 percent of all species are found in genera of nine (actually between 9 and 10) or fewer species, 75 percent in genera of 23 (actually between 23 and 24) or fewer species and 90 percent in genera of 39 or fewer species (actually between 39 and 40). Clearly the nonpasserine birds are more finely split than are the passerine birds on the generic level.

The distribution of genera of different size categories for six selected groups ranging from 419 to 1535 species is given in table 4. These groups, three nonpasserine and three passerine, were chosen because they almost certainly represent closely related, monophyletic assemblages of orders or families. The distributions of genera in different size categories parallel that shown in table 3 with a large majority of small genera; they represent hollow-curves similar to that shown in figure 1. One- and two-species genera comprise 61.3 percent, 53.5 percent, 57.5 percent, 58.6 percent, 58.7 percent and 63.0 percent of all genera in each group. The number of genera with fewer species than the average species/genus ratio is 79.0 percent, 72.4 percent, 74.6 percent, 74.6 percent, 75.3 percent and 76.3 percent of all genera in each group. In each group, 50 percent of the species are found in genera containing 6, 11,

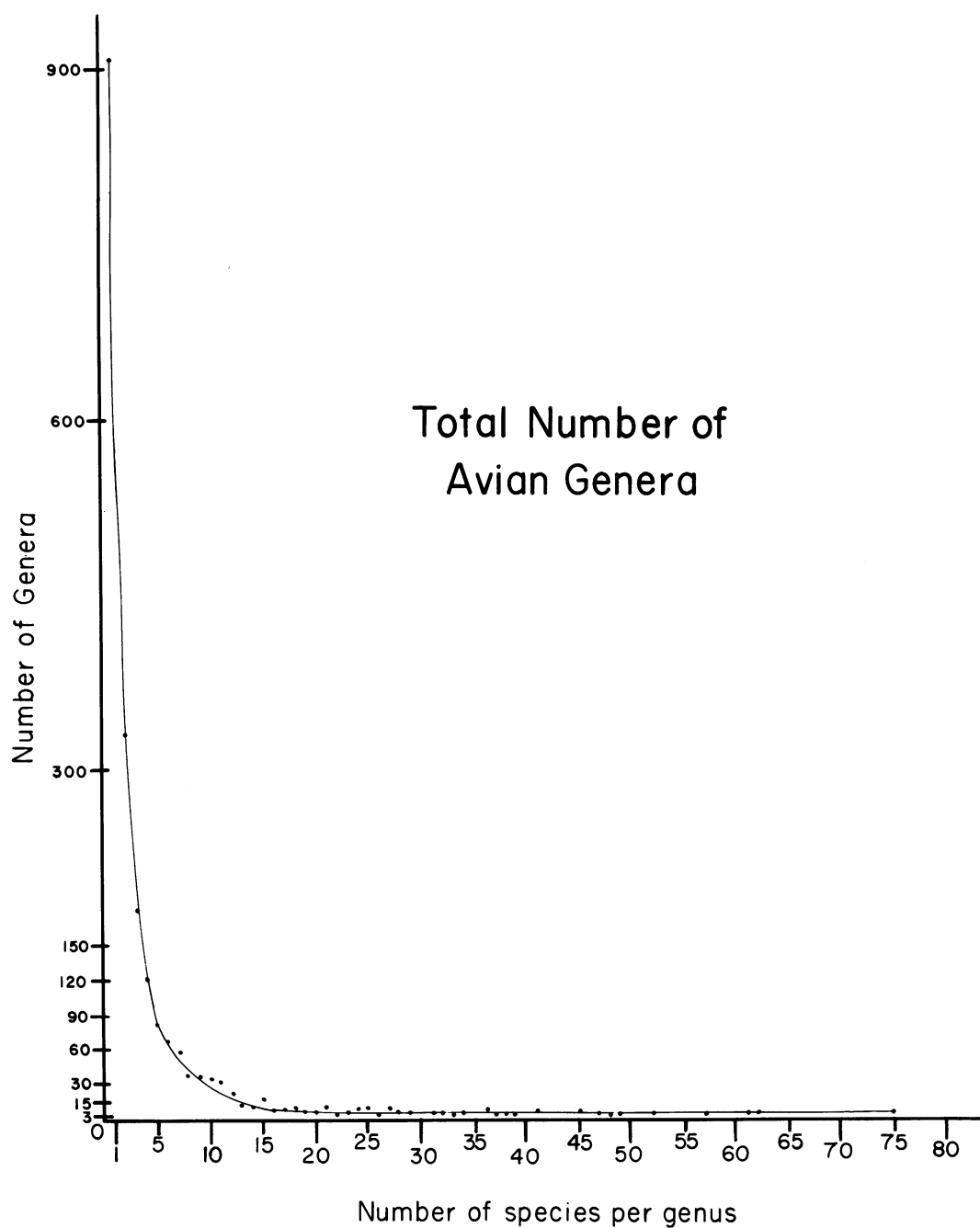


FIG. 1. Hollow-curve distribution of the number of avian genera in each size class (number of species per genus), plotted from the figures given in table 3. The long tail of the curve, above 15 species per genus, has been displaced slightly from the abscissa for clarity. The total number of avian genera is represented by the area below the curve.

TABLE 3
Distribution of Species in Genera of Different Size Classes

# Species per Genus	Nonpasserines		Passerines		All Birds	
	# Genera	Total Species	# Genera	Total Species	# Genera	Total Species
1	436	436	474	474	910	910
2	149	298	179	358	328	656
3	85	255	93	279	178	534
4	59	236	61	244	120	480
5	37	185	44	220	81	405
6	26	156	41	246	67	402
7	24	168	32	224	56	392
8	20	160	16	128	36	288
9	13	117	22	198	35	315
10	14	140	21	210	35	350
11	14	154	16	176	30	330
12	9	108	11	132	20	240
13	6	78	4	52	10	130
14	5	70	5	70	10	140
15	7	105	8	120	15	225
16	1	16	6	96	7	112
17	2	34	5	85	7	119
18	3	54	5	90	8	144
19	1	19	4	76	5	95
20	1	20	4	80	5	100
21	4	84	3	63	7	147
22	—	—	3	66	3	66
23	2	46	3	69	5	115
24	1	24	7	168	8	192
25	2	50	5	125	7	175
26	—	—	3	78	3	78
27	3	81	3	81	6	162
28	2	56	2	56	4	112
29	—	—	2	58	2	58
30	1	30	1	30	2	60
31	—	—	1	31	1	31
32	1	32	1	32	2	64
33	1	33	—	—	1	33
34	—	—	2	68	2	68
36	2	72	2	72	4	144
37	3	111	—	—	3	111
38	—	—	2	76	2	76
39	—	—	2	78	2	78
40	1	40	1	40	2	80
41	1	41	2	82	3	123
45	2	90	1	45	3	135
47	1	47	1	47	2	94
48	—	—	2	96	2	96
49	1	49	—	—	1	49
52	1	52	—	—	1	52
57	—	—	1	57	1	57
61	—	—	1	61	1	61
62	—	—	1	62	1	62
75	—	—	1	75	1	75
Totals	941	3747	1104	5274	2045	9021
S/G	3.983		4.777		4.411	

TABLE 4
Distribution of Species in Genera of Different Size Classes

S/G	A ^a		B ^b		C ^c		D ^d		E ^e		F ^f	
1	63	63	52	52	86	86	115	115	117	117	108	108
2	13	26	16	32	30	60	42	84	51	102	30	60
3	20	60	14	42	20	60	25	75	21	63	15	45
4	5	20	5	20	10	40	18	72	11	44	12	48
5	6	30	5	25	8	40	11	55	17	85	5	25
6	3	18	6	36	7	42	12	72	5	30	8	48
7	3	21	7	49	10	70	9	63	11	77	3	21
8	1	8	2	16	3	24	5	40	4	32	3	24
9	2	18	2	18	2	18	6	54	9	81	6	54
10	1	10	3	30	4	40	4	40	3	30	4	40
11	—	—	1	11	1	11	2	22	5	55	5	55
12	2	24	—	—	—	—	3	36	3	36	4	48
13	—	—	1	13	1	13	—	—	1	13	1	13
14	1	14	2	28	2	28	1	14	1	14	2	28
15	2	30	2	30	3	45	3	45	2	30	1	15
16	—	—	—	—	—	—	1	16	1	16	—	—
17	—	—	2	34	2	34	2	34	2	34	—	—
18	—	—	—	—	1	18	2	36	3	54	—	—
19	—	—	1	19	1	19	1	19	2	38	—	—
20	—	—	1	20	1	20	1	20	2	40	—	—
21	—	—	—	—	—	—	—	—	1	21	2	42
22	—	—	—	—	—	—	1	22	—	—	1	22
23	—	—	1	23	1	23	—	—	1	23	—	—
24	—	—	—	—	1	24	1	24	—	—	2	48
25	—	—	—	—	—	—	1	25	2	50	2	50
26	—	—	—	—	—	—	—	—	2	52	—	—
27	—	—	1	27	1	27	—	—	2	54	1	27
28	—	—	—	—	—	—	—	—	2	56	—	—
29	—	—	—	—	—	—	—	—	2	58	—	—
30	—	—	—	—	1	30	1	30	—	—	—	—
31	—	—	—	—	—	—	—	—	—	—	1	31
32	—	—	—	—	—	—	—	—	—	—	1	32
36	1	36	1	36	1	36	—	—	—	—	—	—
37	—	—	—	—	1	37	—	—	—	—	—	—
38	—	—	—	—	—	—	1	38	—	—	1	38
39	—	—	—	—	—	—	—	—	1	39	—	—
40	—	—	—	—	—	—	—	—	1	40	—	—
41	1	41	—	—	—	—	—	—	1	41	—	—
45	—	—	—	—	1	45	—	—	—	—	—	—
47	—	—	—	—	—	—	—	—	—	—	1	47
48	—	—	—	—	—	—	—	—	1	48	—	—
49	—	—	1	49	1	49	—	—	—	—	—	—
52	—	—	1	52	1	52	—	—	—	—	—	—
62	—	—	—	—	—	—	—	—	1	62	—	—
Gen.	124		127		201		268		288		219	
Sp.	419		662		991		1051		1535		969	
S/G	3.379		5.213		4.930		3.922		5.330		4.425	

^a The orders: Anseriformes, Galliformes.

^b The orders: Columbiformes, Psittaciformes.

^c The orders: Charadriiformes, Columbiformes, Psittaciformes.

^d The New World suboscines.—the families: Dendrocolaptidae, Furnariidae, Formicariidae, Conopophagidae, Rhinocryptidae, Cotingidae, Pipridae, Tyrannidae, Oxyruncidae, Phytotomidae.

^e The Old World insect-eaters—the families: Cinclidae, Troglodytidae, Mimidae, Prunellidae, Muscicapidae.

^f The New World nine-primaried oscines—the families: Emberizidae, Parulidae, Drepanididae, Vireonidae, Icteridae, Fringillidae.

11, 7, 13, and 10 or fewer species. These figures are remarkably uniform and similar to those obtained from table 3 for nonpasserine, passerine and all birds.

The main conclusion that can be drawn from tables 3 and 4 is that the distribution of genera in different size categories is quite uniform for all birds. This suggests that the classifications on which the above species and genera counts were based are not extremely dissimilar. Extremes do exist for some monotypic families such as the Pittidae, for families with few genera such as the Nectariniidae or the Laridae with a high species/genus ratio, and for families such as the Threskiornithidae, Megapodiidae, Rallidae, or Trochilidae with a low species/genus ratio. Such extremes can always be expected. More important is that it is unlikely that large differences existed in the approaches of various avian taxonomists which would influence the distribution of genera in different size categories.

LARGEST AVIAN GENERA

Extremes in the size of genera are always of interest because of the question of why a genus may be very small or very large. The smallest, i.e., monotypic, genera are not important individually because they are so abundant; they should be examined collectively which is not feasible in this study. Mayr (1942, p. 288) discussed possible reasons for the large number of monotypic genera. The largest genera of birds possess unique interest because each represents a sizable radiation of species and in total they contain a considerable percentage of all avian species. Although some of these large genera may be artificial or even unnatural groups, their analysis would provide insights into prerequisite conditions for explosive adaptive radiation in birds.

The 39 largest genera of birds are listed in table 5; they range from 75 species down to 29 species. The lower cut-off figure was chosen arbitrarily with the major consideration being that below 29 species per genus, the number of genera in each size category increases rapidly. These 39 genera, 15 nonpasserine and 24 passerine, comprise 1.91 per-

TABLE 5
Genera with the Largest Number of Species

<i>Nectarinia</i>	75	<i>Synallaxis</i>	38
<i>Turdus</i>	62	<i>Emberiza</i>	38
<i>Zosterops</i>	61	<i>Sterna</i>	37
<i>Ploceus</i>	57	<i>Falco</i>	37
<i>Columba</i>	52	<i>Otus</i>	37
<i>Ptilinopus</i>	49	<i>Ducula</i>	36
<i>Pycnonotus</i>	48	<i>Dicaeum</i>	36
<i>Garrulax</i>	48	<i>Anas</i>	36
<i>Tangara</i>	47	<i>Meliphaga</i>	36
<i>Accipiter</i>	47	<i>Anthus</i>	34
<i>Larus</i>	45	<i>Lonchura</i>	34
<i>Parus</i>	45	<i>Picoides</i>	33
<i>Caprimulgus</i>	45	<i>Amazilia</i>	32
<i>Francolinus</i>	41	<i>Serinus</i>	32
<i>Coracina</i>	41	<i>Sporophila</i>	31
<i>Cisticola</i>	41	<i>Charadrius</i>	30
<i>Halcyon</i>	40	<i>Myrmotherula</i>	30
<i>Phylloscopus</i>	40	<i>Monarcha</i>	29
<i>Rhipidura</i>	39	<i>Zoothera</i>	29
<i>Corvus</i>	39		

39 genera = 1.91 percent of all genera
1607 species = 17.8 percent of all species

cent of all avian genera, but contain 1607 or 17.8 percent of all species of birds. These genera represent sizable radiations of species when compared with the size of avian families. Exactly 100 families contain fewer species each than the smallest of the large genera (29 species); these families have a total of only 819 or 9.08 percent of all avian species. Only 35 families contain more species each than the largest of these genera (75 species) but these families contain 6977 or 77.3 percent of all avian species. The large genera are distributed among 28 families and 34 subfamilies. The Muscicapidae have the largest number, seven genera, which are divided among five subfamilies. The Columbidae and the Emberizidae have three large genera each, and four families or subfamilies (Lariidae, Turdinae, Sylviinae, and Emberizinae) have two large genera each. Most of the families containing large genera are medium- to large-sized in terms of the number of species; only two (Motacillidae and Paridae) possess less than the mean number of species per family (56.4). Genera of some of the largest families (e.g., Muscicapidae,

1427; Emberizidae, 560; Trochilidae, 341 species) are included in this list, but a number of large families do not possess large genera (e.g., Tyrannidae, 375; Psittacidae, 268 or 340 species depending on the classification accepted). Half of these large genera contain at least 25 percent of the species in the family-level taxon and four of these genera contain almost all the species in the family-level taxon. Even in some of the largest families, the large genera account for a large percentage of the species (e.g., Columbidae, 45.2 percent; Muscicapidae, 20.2 percent; Emberizidae, 20.8 percent).

The basic attribute of large genera is that speciation and adaptive radiation have occurred with little accompanying phyletic evolution resulting in little divergence between the congeneric species. The radiation of species in many of the large genera may be compared directly with that of a higher level taxon (e.g., *Francoelinus* compared to the Tinamidae). The central question is whether the large genera have any special properties that permitted them to become species-rich without significant divergence between the species.

The geographical range of the large genera varies greatly. Only 15 have a worldwide or almost worldwide distribution (found in both the Old World and the New), five are restricted to the New World and 19 are restricted to the Old World. None of the large genera are restricted to a single continent, but some are limited to a single zoogeographical region (e.g., the Neotropics—*Tangara*, *Synallaxis*, and *Myrmotherula*, or the Australasian—*Meliphaga*). The geographical range of individual species in the large genera vary from small islands to almost worldwide (e.g., *Falco peregrinus*). Many species have broad continental ranges, whereas others have restricted distributions on large land masses. These ranges of the large genera and of the individual congeneric species do not differ from those of many small genera. Numerous small genera have a worldwide distribution with species of limited distribution and species of broad distribution.

The large avian genera include aquatic and

terrestrial birds with the majority being land birds. None of the large genera are primarily or solely marine although two (*Larus* and *Sterna*) possess a number of marine or coastal species. The large genera are composed of small- to medium-sized birds, yet the species of *Corvus* are the largest passerine birds. Ecologically, these large genera vary greatly, both in terms of habitat and feeding method, with the only possible generalization being that none of these large genera are highly specialized in their food, feeding methods, locomotion, or breeding system and habits. Many may be described as “generalists” compared to other members of the family or order.

Several reasons may be offered to explain the existence of these large avian genera, and it is quite likely that two or more may apply to a particular genus. These are:

(a) That the taxon is unnatural, i.e., polyphyletic in the broad sense. This does not appear to be the case of any genus in table 5.

(b) That the taxon is artificially large, but monophyletic, being composed of several monophyletic subgroups each of which are equivalent to other genera in the family or closely related families. Large genera can always be broken up into a number of smaller genera and most, if not all, of the genera in table 5 have been subdivided, some in the recent past. The question is not whether these genera can or cannot be subdivided but whether they comprise taxa equivalent to other closely related genera. Arguments have been raised by some recent workers that some of these large genera (e.g., *Nectarinia*, *Meliphaga*) should be divided because they are artificially large, but some other genera (e.g., *Turdus*, *Zosterops*, *Cisticola*) are very uniform and appear to resist all attempts at subdivision.

(c) That the taxon (genus) contains many insular species, be they on islands, mountaintops or other insular areas. These genera are characterized as being good colonizers because groups of individuals must be able to cross gaps to reach the insular areas. Species found on mountaintops are not necessarily good colonizers, but may be relicts associ-

ated with a particular habitat that was once more widespread and which became constricted to smaller areas at higher elevations with climatic changes. Genera having many insular species include *Nectarinia*, *Zosterops*, *Ploceus*, *Ducula*, *Ptilinopus*, *Coracina*, *Garrulax* (insular mountaintops), *Dicaeum*, *Lonchura*, and *Monarcha*.

(d) That the taxon (genus) speciated repeatedly in a series of refuges during climatically unfavorable periods with the species establishing sympatry during climatically favorable periods in a pattern described by Haffer (1974) for Amazonian birds. When this pattern of speciation is coupled with the ability of the newly evolved species to establish sympatry and to subdivide the ecological zone available to them without divergence, the result is a species-swarm in a restricted geographic area and possibly the evolution of a large genus. Genera showing this pattern include *Francolinus*, *Tangara*, *Cisticola*, *Ploceus*, *Synallaxis*, *Myrmotherula*, *Serinus*, and possibly *Amazilia*.

(e) That the genus has undergone adaptive radiations in several different parts of the world without divergence between the several subgroups. This pattern is seen in genera such as *Turdus*, *Parus*, *Columba*, *Anthus*, and probably in *Anas* and *Picoides*.

(f) That the genus has spread over a large part of the earth, subdividing the ecological zone available to it without significant divergence between the congeneric species, but without evolving a large number of sympatric species in any single area. The ranges of individual species are often broad continental ones, but still form a replacement pattern. This explanation grades into that of a pattern of adaptive radiations in several different parts of the world (e), but typical examples of each type are clearly distinct. Examples of the last type are seen in the genera *Accipiter*, *Larus*, *Corvus*, *Sterna*, *Falco*, *Otus*, and *Charadrius*.

It is clear that a number of the large genera do not fit exactly into one or another of these explanations or that several of these explanations apply to a particular genus.

Examination of this set of explanations for

the evolution of large genera suggests that the limitations preventing other genera from becoming large genera may arise from several factors; these are:

(a) That the species lack the ability to disperse and colonize a large part of the earth. This results in an absence of insular species and/or in the lack of the necessary area for species replacement.

(b) That the species possess an excellent ability to disperse and colonize new areas resulting in extremely wide-ranging species compared to the geographical distribution of the genus. This also results in the lack of the necessary area for species replacement and possibly in insular species if the rate of dispersal is large.

(c) That the species cannot become sympatric without diverging (i.e., evolving differences resulting from the mutual selection forces arising from species interactions during the neosympatric phase of speciation, see Bock, 1979). This results in greater differences between the species which would be reflected taxonomically by placing the species in different genera.

The explanation of why the taxa listed in table 5 are large genera and why other genera have not reached this size (remembering that the lower size limit was set arbitrarily) with the above set of reasons and any additional ones is a historical narrative as are all explanations of particular classifications or phylogenies. Because of the nature of a historical narrative explanation, it may not be possible to point to a particular set of causes as the definite reason for the evolution of a given large genus or as the reason why a given small genus had not evolved into a large genus.

DISCUSSION

Over the past decade, the advantages and disadvantages of different approaches to classification have been argued with most of the dispute being between advocates of evolutionary classification and of cladistics. One of the practical differences between these two approaches is the number of levels of

categories in the taxonomical hierarchy and hence of superspecific taxa needed to classify the group of organisms, in this case, the 9021 species of birds. Hennig (1966) is quite clear that one of the essential attributes of his approach to phylogenetic classification is that each node in the dichotomous branching system represents a categorical level and must be named as a taxonomic taxon. Evolutionary taxonomists have always accepted the idea that a number of phylogenetic branching points can exist between successive categorical levels and hence between named taxa. The practical consequences of this difference between these two approaches have been discussed in theory (e.g., Mayr, 1974; Hennig, 1974) but have not been examined in any detail for any sizable taxa. The counts provided here permit such a comparison.

We have based our counts on an evolutionary classification of birds, although the overall system and the classifications of the individual families were constructed by many different avian systematists with a diversity of opinions on species recognition, on the ideal limits of the genus, and on the arrangement of genera into family level groups. The 9021 species of birds are arranged (table 1) in 2045 genera, 36 tribes, 115 subfamilies, 159 families, and 28 orders. These counts do not include all the taxa recognized by ornithologists; some of the tribes and subfamilies were excluded. Not included are the superfamilies and suborders as, for example, given by Wetmore (1960) in his classification of birds. (The suprageneric taxa used in the "Reference List" and in "Peters's Check-list" but excluded from table 1 probably number between 200 and 250 which would cause only slight modifications to the figures presented below.) To be sure much disagreement exists on the limits, and hence the numbers, of families and orders of birds, but we doubt that many workers would recognize numbers of families and orders that exceed those given above by a factor of 2 in either direction (i.e., 80 to 318 families and 14 to 56 orders). Variation also exists in the number of categories needed to classify birds but most workers feel that sev-

en ranks suffice for Recent birds (i.e., genus, tribe, subfamily, family, suborder, order, and class). We omit the rank of subclass because all Recent birds and most fossil birds are currently placed in a single subclass, and we omit the subgenus because it is rarely used for birds. Not all of these categories are used in all cases, i.e., not all families are divided into subfamilies, as can be seen from the figures given above. Less than 2500 supraspecific taxa (exactly 2383) are needed to classify the 9021 species of birds. Thus, the number of supraspecific taxa is just over 25 percent of the number of species. Most workers agree that the class Aves is oversplit and that birds could be classified with half this number of supraspecific taxa.

No one has yet presented a complete cladistic classification for all birds or even an order, the closest being Wolters's (1977) revision of the Nectariniidae and his (1975-) still incomplete classification of the world's avifauna. Wolters was unable to resolve all relationships into proper sister group dichotomies and many of his taxa are not of equivalent rank. Even with the large number of generic names available for birds, Wolters was unable to find enough to name all the generic-level taxa recognized in his classification of birds and decided to leave these unnamed rather than coining many new names. And Wolters's classification is an incomplete cladistic one in which far less generic and higher level taxa are recognized than required under the strict rules of cladism. In a proper cladistic (dichotomous) classification of the 9021 species of birds, simple calculations show that a hierarchy with an absolutely minimum number of 14 categorical ranks and precisely 9020 supraspecific taxa would be required. The number of categorical ranks could be and probably would be far greater depending on the configuration of the cladogram; the minimum number of 14 ranks is based upon an absolutely symmetrical dichotomous branching throughout.

A dichotomous cladistic classification would require a total of 18,041 names to classify the 9021 species of birds, compared with the 11,424 names in the current, oversplit evolutionary classification as reported in this

count (table 1). The difference of 6617 names, all for supraspecific taxa, is 58 percent of the total number of names and 278 percent of the supraspecific names in the current evolutionary classification. Added to the large number of names is a larger and more complex hierarchy with a minimum of 14 ranks and probably many more (up to the theoretical maximum of 9020 categorical ranks) compared to the seven needed in the current evolutionary classification. A cladistic classification, compared with an evolutionary classification, would be difficult to learn and use because of its more complicated, cumbersome, larger hierarchy and many additional taxonomic names. It would require far more pages just to publish (an estimated 60–100 percent more pages for the "Reference List"). Thus, in any discussion of the merits of diverse approaches to classification, the practical disadvantages of cladistic systems stemming from their cumbersome hierarchy and larger number of supraspecific taxa must be considered in the balance of pros and cons.

The "hollow-curve" distribution of size classes of genera is clearly shown for all birds and for several selected samples (e.g., nonpasserine birds, passerine birds). A similar distribution would result if the size classes of families or of orders were plotted. The "hollow-curve" distribution of taxa size in a classification is a consequence of the theory underlying the evolutionary approach to classification. Such a distribution would not be found in a cladistic classification.

The pattern of diversity of organisms that is arranged in a classification is the result of three evolutionary processes, namely: (a) phyletic evolution (=modification in a single lineage); (b) speciation (=splitting of a phyletic lineage into two or more lineages); and (c) extinction (=the termination of a phyletic lineage). A basic assumption by most evolutionary biologists is that these processes and their underlying mechanisms are partly correlated with one another in a complex and possibly varying way. These processes are neither completely independent nor completely dependent with respect to one another. In the evolutionary approach to

classification, the known organisms are arranged according to some combination of the amount of shared similarity (the converse of the degree of phyletic evolutionary modification) and the pattern of phyletic branching (a reflection of speciation events). The size and pattern of gaps between supraspecific taxa (e.g., presence of relic genera) provides some information about the occurrence of extinctions. From a knowledge of the mechanisms underlying these basic evolutionary mechanisms, the biology of the organisms and the time-space distribution of available habitats, one would predict a hollow-curve distribution of size-classes of taxa of the same categorical rank in an evolutionary classification. The observed distribution (e.g., fig. 1) is consistent with the generally accepted evolutionary mechanisms underlying the diversity of organisms. However, it should be emphasized that the observed distribution of size-class of taxa can support other hypotheses about evolutionary mechanisms. Similar distributions may result if phyletic evolution, speciation, and extinction operate randomly as suggested by analysis of the phylogenies generated by computer simulations (see Raup and Gould, 1974).

The value of a classification and of any of its component parts depends to a large extent on its heuristic qualities. The overview of avian classification as gained during the preparation of these counts revealed several difficulties in sharp perspective. Development of the generic concept and its application with respect to both species and to the family-level categories had and still have numerous problems. It is clear that earlier workers used a narrow generic concept and seized upon almost any difference to separate genera with the result being that the genus became almost synonymous with the species. The consequences of this practice can still be seen, for example, in the *Threskiornithidae*, *Rallidae*, and *Trochilidae*. In recent years this trend has been reversed and workers have come to recognize very broad genera, frequently coupled with a narrower concept of family-level taxa. This results in the genus becoming almost synonymous

with the tribe, subfamily, or family as seen in Moynihan's (1959) analysis of the Laridae and Strauch's (1978) revision of the Charadriiformes. In both extremes, the generic category loses its usefulness with respect to the lower or higher category on which it has encroached.

A general tendency exists to view both small and large genera with suspicion and to seek to unite small genera and split large genera thereby achieving whatever size is believed to be proper, on average, for the genus. Although it may be true that in the current classification of birds some small genera are too indistinct to be recognized and some large genera are artificial conglomerates, efforts to have all genera of one single optimal size are in error. What is important is to maintain a consistent evolutionary meaning for the genus. This is best accomplished by setting the limits of the genus so that the members display approximately the same amount of diversity. This can be strengthened by adjusting the width of gaps between genera inversely to the size of the genus (see Mayr, 1969, pp. 92–94). It must be remembered that monotypic genera exist as well as those (e.g., *Nectarinia*, *Turdus*, and *Zosterops*) that are species-rich radiations having but little morphological variation. Some families contain many small genera and others (e.g., the Pittidae) contain a single large genus. Avian families vary from being monotypic to over 1000 species and orders from monotypic to over 5000 species. The existence of a wide diversity in the size of taxa at all levels in the taxonomic hierarchy has been recognized ever since the beginnings of classification, even before taxonomy was placed on a scientific footing. This diversity is not necessarily dependent on the theoretical foundation of classification as it was unaffected by the acceptance of Darwinian evolution as the basis of biological classification after 1859. Any attempt at artificially restricting the variation in the size of the genus or of other supraspecific taxa will result in a classification as valueless as that generated under the Quinary System for the same reasons given over a century ago

by Strickland (1840, 1841, 1845; see also the review by Newton, 1896, pp. 31–35) against that rigidly formal approach to classification.

On the surface, counting the numbers of avian species and genera may appear to be a harmless pastime resulting in interesting bits of information suitable mainly for textbooks and introductions to general reference works. Actually, these counts constitute the basic data needed for comparative systematic analyses of the generic and higher level taxa of the class Aves. Comparative systematics is a new area of inquiry within taxonomy, so recent that it has not been discussed in general texts on systematics and its major goals have not yet been clearly formulated. A preliminary statement of the goals of comparative systematics may be—the analysis of the structure and composition of taxa (i.e., the number of component subgroups in each taxon and their nature) and of their evolutionary history. These goals may change as more is learned about the comparative systematics of diverse groups of organisms. Few such studies have been published about birds and almost all of these deal with the structure of species taxa. Mayr and Short's (1970) analysis of the species taxa of North American birds is an outstanding example of a comparative study of the avian species found on a single continent. Some of the questions addressed in their study are: the numbers of monotypic, polytypic, and superspecies among North American birds, why avian species are so well-delimited, and the foundation of some recent trends in the application of the biological species concept in avian systematics. Mayr and Short (1970, pp. 105–107) also inquired briefly into changes in the generic concept in North American birds and showed that North American avian genera have an average of only 2.3 species. This is much lower than the average of 4.1 species per genus reported here, but the two figures are not directly comparable because of the restricted geographical limits used in Mayr and Short's study which would result in a lower species/genus ratio.

We know of no previous attempt to pro-

vide a detailed comparative systematic analysis of the higher level taxa (e.g., the genera) of the class Aves, nor are we aware of any similar study for other vertebrate classes. It was, therefore, necessary to formulate questions as the data were tabulated and to attempt to tabulate the data in the most meaningful way. Relatively little information about the structure of the genus could be gained by the counts of species and genera and by the species/genus ratio for each family-level taxon. The species/genus ratio is an average value which conceals too much important variation.

At this time, the best means of obtaining an overall picture of the structure of the avian genus appears to be the distribution of genera of different size-classes (i.e., number of species per genus) using the number of biological (taxonomic) species per genus. Such a tabulation was not feasible for each family because of the small number of genera in most families. It was presented for all birds, for passerine and nonpasserine birds, and for six selected subsamples. A comparison of these distributions suggested that the classifications of avian families are reasonably similar. The distribution of size-classes of avian genera is in agreement with the hollow-curve rule formulated by Willis (1922, 1940). Analysis of the largest genera revealed that a sizable fraction of all avian species (17.8 percent) is contained in these 39 genera (1.9 percent of all avian genera). Conversely, the smallest genera (those having one or two species) possessed almost the same number of species (17.4 percent), but these small genera number 1238 or 60 percent of all avian genera. The large genera generally contain 25 percent or more of the species in the family and each has more species than does over half (100) of the avian families. And only 35 families contain more species than the largest of these large genera. Analysis of these genera shows that they are mostly small- to medium-sized land birds that are not extreme feeding and reproductive specialists. Some suggestions were offered to explain how these groups were able to speciate with little phyletic divergence. Further study of these

large genera and comparison of their morphological-ecological properties with those of small genera may provide insights into the modes of adaptive radiations in birds.

It was not possible to inquire into the structure of the avian genus based on the distribution of genera of different size-classes using zoogeographical species because a list of the avian zoogeographical species of the world is not available. It is clear, however, that the results of such a tabulation would be a shift of the hollow-curve distribution, as shown in figure 1, to the left with a great increase in the number of small genera and decrease in larger genera.

The major conclusion that can be reached on the basis of the presented distribution of avian genera in size-classes based on biological species and on the projected results of such a distribution based on zoogeographical species is that a large majority (over 60 percent based on biological species, and probably over 70 percent based on zoogeographical species) of all avian genera contain only one or two ecological units. Thus, the genus, as currently used in avian classification, contains very little ecological and presumably little morphological diversity. This supports the oft-repeated statements that avian genera are too finely divided and that the genus as a taxonomic category has limited meaning in avian classification.

Other problems concerning the structure of the avian genus as well as the structure of family-level groups became apparent during the course of this investigation, but further study did not seem warranted prior to the development of a list of zoogeographical species of birds and closer study of family-level groups. We regard the present study as a beginning in the comparative systematic analysis of the avian genus rather than a definitive investigation in that we have tabulated much of the basic data, provided some preliminary analyses of the structure of the avian genus, and outlined some of the problems to be addressed in future studies. Our hope is that other workers can build on the foundations we provide herein.

APPENDIX I

All changes from the classification followed in the Reference List are given here, arranged by family and with bibliographic citations. These changes include the addition of all newly described species and the correction of errors that have come to our attention. We also include reference to some recent revisions that we have not followed here, and a few additional comments to clarify our treatment of certain groups in the Reference List and in this analysis. Pages listed are to the Reference List.

PODICIPEDIDAE (p. 3). Add *Podiceps gallardoi*, new species, following *P. taczanowskii* (cf. Rumboll, 1974, Comunicaciones del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" 4(5):33).

ARDEIDAE (p. 8). Delete *Butorides virescens* and *B. sundevalli*, considered distinct species by Peters (Check-list, 1:102–107) and by Bock (1958, Amer. Mus. Novit. 1779), but shown to be conspecific with *B. striatus* by Payne (1974, Bull. Brit. Orn. Cl. 94:81–88).

We have made no attempt to integrate the generic revisions by Payne and Risley (1976, Univ. Mich. Mus. Zool. Misc. Publ. 150) and by Hancock and Elliott (1978, Herons of the world, New York, Harper and Row) because the latter arrived too late to be considered in this analysis. The latter differs from the treatment of species in the Reference List in the merger of the three species of *Butorides* (see above), and of genera in the recognition of *Pilherodius* and *Bubulcus*, and in the merger of *Hydranassa* with *Egretta*.

ACCIPITRIDAE. We have not followed the revision of *Circus* (p. 15) by Nieboer (1973, Geographical and ecological differentiation in the genus *Circus*, privately printed Ph.D. thesis, Univ. Amsterdam, 104 pp.), who includes *cinereus* in *cyaneus*; Amadon (1975, Auk 92:832–833) has reviewed this study.

We have not adopted the revision of *Accipiter* (pp. 15–16) by Wattell (1973, Publ. Nuttall Orn. Cl. 13), who includes *griseogularis* in *novaehollandiae*, *erythropus* in *minullus*, *gularis* in *virgatus*, and *rufiventris* in *nisus*, thus recognizing 43 rather than 47 species in this genus; Amadon (1975, Auk 92:822–832) has reviewed this study.

FALCONIDAE (p. 18). Add *Micrastur gilvicollis*, after *M. ruficollis*; formerly considered a race of *ruficollis* (cf. Schwartz, 1972, Condor 27:399–415).

PHASIANIDAE. Delete *Rheinartia nigrescens* (p. 22), conspecific with *R. ocellata* and listed in error (cf. Delacour, 1977, Pheasants of the world, 2nd ed., p. 346).

The revision of the Numidinae (p. 23) by Crowe (1978, Ann. South African Mus. 76:43–136) arrived too late to be included in this analysis.

RALLIDAE. Add *Fulica cristata* (p. 26), following *F. atra*; omitted in error.

We have not attempted to summarize the revisions of the Rallidae by Olson (1973, Wilson Bull. 83:381–416) and by Ripley (1977, Rails of the world, Boston, D. R. Godine). The treatments of these two workers differ and will require considerable study to combine.

CHARADRIIFORMES. The revision of this order by Strauch (1978, Trans. Zool. Soc. London 34:263–345) arrived too late to be considered in this analysis.

RECURVIROSTRIDAE (pp. 28–29). After reviewing the forms of *Himantopus* recognized as species by Mayr and Short (1972, Publ. Nuttall Orn. Cl. 9:47), whom we followed in the Reference List, we decided it unwise to include as species those allopatric populations that are not generally recognized even as subspecies. In the absence of a thorough review of the genus, we follow a course midway between the treatment of Mayr and Short and that of Peters (Check-list 2:289–290), who included all forms in a single species. We recognize five species, *himantopus*, *leucocephalus*, *novaezelandiae*, *mexicanus*, and *knudseni*, and include *melanurus* in *mexicanus*, *ceylonensis* and *meridionalis* in *himantopus*. All the forms in this genus constitute a single superspecies.

STERCORARIIDAE, LARIDAE, AND RYNCHOPIDAE (pp. 32–33). After reviewing these families, we decided to adopt the treatment of genera of Moynihan (1959, Amer. Mus. Novit. 1928), but not that author's treatment of species, which is incomplete, or his treatment of family-level taxa. We did not follow Moynihan in the Reference List because of his incomplete coverage of species. Moynihan divides the Laridae into two subfamilies, Stercorariinae and Larinae, and further divides the Larinae into three tribes, Larini, Rynchopini, and Sternini. The result is that his genera are very nearly equivalent to his lowest family-level taxa, an arrangement that reduces the usefulness of the genus. Thus, we advocate that the Laridae be recognized without subdivision above the level of the genus. In this analysis, for con-

sistency, we retain the same family-level taxa used in the Reference List. The following genera are recognized by Moynihan and accepted by us in this analysis: *Stercorarius* (including *Catharacta*) with five species; *Larus* (including *Gabianus*, *Pagophila*, *Rhodostethia*, *Rissa*, *Creagrus*, and *Xema*) with 45 species; *Rynchops* with three species; *Anous* (including *Procelsterna* and *Gygis*) with five species; *Larosterna* with one species; and *Sterna* (including *Chlidonias*, *Phaetusa*, *Gelochelidon*, *Hydroprogne* and *Thalas-seus*) with 37 species.

Delete *Larus cachinnans* (p. 32), conspecific with *L. argentatus* and listed in error (cf. Peters, Check-list 2:318).

Delete *Larus relictus* (p. 32), considered a subspecies of *L. melanocephalus* by Peters (Check-list 2:323) and listed by us in error. Vaurie (1962, Auk 79:303–309; 1965, Birds of the Palearctic fauna, Nonpasserines, p. 462) concluded that the unique specimen of *relictus* is a hybrid between *L. ichthyaetus* and *L. brunnicephalus*. We have recently learned that several large colonies of supposed *relictus* have been discovered (Auezov, 1971, Zool. Zh. 50:235–242), but we have not seen the published papers. For the purposes of this analysis, we follow Vaurie's conclusion, while noting that a definite decision cannot yet be made. (After this manuscript was accepted for publication, Bock examined specimens of *relictus* in Moscow. This taxon appears to be a distinct species closely related to *L. brunnicephalus*.)

PSITTACIFORMES. For the purposes of this analysis, we continue to follow Forshaw (1973, Parrots of the world, Melbourne, Lansdowne Press), but we have excluded those species that Forshaw recognized but believed to be based on aberrant specimens or hybrids.

LORIIDAE (p. 39). Delete *Lorius tibialis*, believed by Forshaw (p. 76) to be an aberrant individual of *L. domicellus*.

PSITTACIDAE. Delete *Tanygnathus heterurus* (p. 40), believed by Forshaw (p. 192) to be an aberrant specimen of *T. sumatrans*.

Delete *Platycercus adelaidae* (p. 41), regarded by Forshaw (pp. 228–229) as a population of hybrid origin.

Delete *Pyrrhura hypoxantha* (p. 42), believed by Forshaw (p. 428) to be an aberrant form of *P. molinae*.

MUSOPHAGIDAE (p. 44). Delete *Tauraco schuetti*, conspecific with *T. corythaix* and listed in error (cf. Moreau, 1958, Ibis 100, pp. 75, 101–102).

CUCULIDAE. Delete *Eudynamis cyanocephala* (p. 45), conspecific with *E. scolopacea* and listed in error (cf. Peters, Check-list 4:39).

Delete *Centropus grillii* (p. 46), conspecific with *C. toulou* (cf. White, 1965, Revised check list of African non-passerine birds, p. 188).

Add *Centropus cupreicaudus* (p. 46), following *C. monachus*, considered a race of *monachus* by Peters (Check-list 4:74) but separated by White (1965, Revised check list of African non-passerine birds, p. 189).

TYTONIDAE (p. 47). Delete *Tyto longimembris*, conspecific with *T. capensis* (cf. Ripley, 1961, Synopsis of the birds of India and Pakistan, p. 186).

STRIGIDAE. Add *Xenoglaux loweryi* (p. 48), new genus and species, following *Glaucidium* (cf. O'Neill and Graves, 1977, Auk 94:110).

NYCTIBIIDAE (p. 49). Add *Nyctibius jamaicensis*, following *N. grandis*, considered a race of *N. griseus* by Peters (Check-list 4:181), but regarded as a distinct species by Davis (1978, Pan-American Studies 1:4–21).

CAPRIMULGIDAE (p. 50). Add *Caprimulgus anthonyi*, following *C. maculicaudus*, considered a race of *C. parvulus* by Peters (Check-list 4:202), but regarded as a distinct species by Schwartz (1978, Condor 70:223–227).

APODIDAE. Add *Collocalia sawtelli* (p. 51), new species, following *C. leucophaea* (cf. Holyoak, 1974, Bull. Brit. Orn. Cl. 94:146).

TROCHILIDAE. Add *Threnetes grzimeki* (p. 53), new species, following *T. loehkeni* (cf. Ruschi, 1973, Bol. Mus. Biol. Mello Leitao, ser. Zool. 37:1).

Add *Threnetes cristinae* (p. 53), new species, following *Threnetes grzimeki* (cf. Ruschi, 1975, Bol. Mus. Biol. Mello Leitao, ser. Zool. 83:1).

Add *Phaethornis koepckeae* (p. 53), new species, following *P. philippii* (cf. Weske and Terborgh, 1977, Condor 79:143).

ALCEDINIDAE. Add *Halcyon senegaloides* (p. 59), following *H. senegalensis*; omitted in error.

Add *Halcyon ruficollaris* (p. 60), new species, following *H. tuta* (cf. Holyoak, 1974, Bull. Brit. Orn. Cl. 94:147).

PHONICULIDAE (p. 61). The treatment of this family in the Reference List was intended to follow that of White (1965, Revised check list of African nonpasserine birds, pp. 239–244), and not

that of Peters (Check-list 5:250–254) as stated in the Reference List (p. 162).

Delete *Rhinopomastus*, which is merged with *Phoeniculus* and was listed in error.

BUCEROTIDAE (p. 62). Add *Bycanistes brevis*, following *B. subcylindricus*; omitted in error.

GALBULIDAE (p. 63). A recent analysis of the speciation patterns and classification of this family was presented by Haffer (1974, Publ. Nuttall Orn. Cl. 14:313–344). Although his classification does not differ from that of the Reference List, Haffer shows that the 17 species constitute only eight zoogeographic species.

BUCCONIDAE (p. 63). For the purposes of this analysis, we follow the classification proposed by Cottrell (1968, Breviora 285:1–5), which we overlooked during the preparation of the Reference List. The following changes result:

The genera *Notharchus*, *Nystalus*, and *Hypnelus* are merged with *Bucco*.

Bucco (= *Hypnelus*) *bicinctus* is considered conspecific with *B. ruficollis*.

Nonnulla frontalis is considered conspecific with *N. ruficapillus*.

INDICATORIDAE (p. 65). Add *Prodotiscus zambeziae*, following *P. insignis*; treated as a race of *insignis* by Peters, but recognized as a distinct species by Friedmann (1970, Ostrich, suppl. 8:21–26).

Add *Indicator conirostris*, following *I. minor*; treated as a race of *minor* by White (1965, Revised check list of African nonpasserine birds, p. 276), but recognized as a distinct species by Friedmann (1970, Ostrich, suppl. 8:21–26; see also Friedmann, 1968, Proc. U.S. Nat. Mus. 125 3665:1–10).

RAMPHASTIDAE (p. 65). A recent analysis of the speciation patterns and classification of this family was presented by Haffer (1974, Publ. Nuttall Orn. Cl. 14:179–312). Although his classification does not differ from that of the Reference List, Haffer shows that the 33 species constitute only 14 zoogeographic species.

FORMICARIIDAE. Add *Grallaricula nana* (p. 76), following *G. ferrugineipectus*; omitted in error.

Add *Grallaricula cucullata* (p. 76), following *G. lineifrons*; omitted in error.

CONOPOPHAGIDAE (p. 77). We have retained this family for the purposes of the Reference List and of this analysis. Traylor (1977, Bull. Mus. Comp. Zool. 148:129–184) has discussed the placement of *Corythopsis* in the subfamily Elaeniinae of the Tyrannidae.

PIPRIDAE (p. 79). We follow here the recent revision of this family by Snow (1975, Bull. Brit. Orn. Cl. 95:20–27; see also Haffer, 1970, Jour. f. Ornith. 111:285–331). Snow reverses the sequence of genera, beginning with *Schiffornis* and ending with *Pipra*. The following other changes must also be made:

The genus *Teleonema* is merged with *Pipra*.

The genus *Allocotopterus* is merged with *Ma-chaeopterus*.

Manacus aurantiacus, *M. cerritus*, *M. vitellinus*, and *M. candei* are considered conspecific with *M. manacus*.

Pipra obscura is not listed by Snow or Haffer, and is probably a female of *P. vilasboasi*.

TYRANNIDAE. The recent generic revision of this family by Traylor (1977, Bull. Mus. Comp. Zool. 148:129–184) arrived too late to be considered in this analysis. Traylor's arrangement will serve as the basis for the treatment of the Tyrannidae in the forthcoming eighth volume of Peters's Check-list; only a summary of his many changes is possible here. Traylor recognizes three subfamilies (Elaeniinae, Fluvicolinae, and Tyranninae) and a total of 88 genera, compared with the seven subfamilies and 110 genera recognized in the Reference List and in this analysis. Thirty-five genera recognized by Hellmayr are synonymized by Traylor, and *Myiopagis* (p. 84), synonymized by Hellmayr is resurrected. One new genus (*Zimmerius*) is proposed for the species *vilissimus*, *bolivianus*, *cinereicapillus*, *gracilipes*, and *viridiflavus* formerly in *Tyranniscus*. Seven genera are transferred to the Tyrannidae from other families: *Attila*, *Pseudattila*, *Casiornis*, *Laniocera*, *Rhytipterna* (all p. 81) and *Xenopsaris* (p. 84) from the Cotingidae, and *Corythopsis* (p. 77) from the former family Conopophagidae (see above).

Other modifications of the treatment in the Reference List include the following.

Delete *Knipolegus subflammulatus* (p. 80), now regarded as the young of *K. cabanisi* (cf. Meyer de Schauensee, 1966, Species of birds of South America, p. 342; 1970, Guide to the birds of South America, p. 433).

Add *Empidonax wrightii* (p. 82), following *E. oberholseri*; omitted in error (cf. A.O.U. Check-list of North American birds, 5th ed., 1957, p. 346).

Delete the genera *Idioptilon*, *Microcochlearius*, and *Sneathlaga* (p. 83), synonymized with *Ceratotriccus* by Fitzpatrick (1976, Bull. Mus. Comp. Zool. 147:435–463; Fitzpatrick uses the name *Idioptilon* for his enlarged genus, but *Ceratotriccus* has priority).

Delete *Todirostrum albifacies* (p. 83), of which

the unique type has been attributed to *T. capitale tricolor* by Fitzpatrick.

Add *Todirostrum pictum* (p. 82), following *T. chrysocrotaphum*; often considered a subspecies of *chrysocrotaphum* but recognized as a distinct species by Fitzpatrick.

Delete *Todirostrum hypospodium* (p. 83), of which the unique type has been attributed to *T. sylvia* by Fitzpatrick.

Add *Ceratotriccus* (= *Idioptilon*) *kaempferi* (p. 83), following *C. mirandae*; often considered a race of *mirandae* but recognized as a distinct species by Fitzpatrick.

Delete *Oncostoma olivaceum* (p. 83), considered conspecific with *O. cinerigulare* by Meyer de Schauensee (1966, Species of birds of South America, p. 365) and presumably by Fitzpatrick, who does not mention *olivaceum* as a separate species.

Add *Euscarthmus rufomarginatus* (p. 83), following *E. meloryphus*; omitted in error (cf. Meyer de Schauensee, 1970, Guide to the birds of South America, p. 314).

Delete *Tyranniscus australis* (p. 84), of which the unique type has been attributed to *Xanthomyias sclateri* by Traylor (*in litt.*; see also Traylor, 1977, Bull. Mus. Comp. Zool. 148:146–147, where the species is not listed).

ALAUDIDAE. Delete *Mirafra candida* (p. 86), which is a rufous phase of *M. pulpa* (cf. Hall, 1961, Bull. Brit. Orn. Cl. 81:108–111).

Add *Mirafra degodiensis* (p. 86), new species, following *M. gilletti* (cf. Erard, 1975, L'Oiseau et R. F. O. 45:310).

Add *Heteromirafra sidamoensis* (p. 86), new species, following *H. ruddi* (cf. Erard, 1975, Alauda 43:123).

TROGLODYTIDAE. Add *Henicorhina leucoptera* (p. 94), new species, following *H. leucosticta* (cf. Fitzpatrick, Terborgh and Willard, 1977, Auk, 94:195).

TURDINAE. Add *Catharus frantzii* (p. 98), following *C. occidentalis*; considered a race of *occidentalis* by Peters (Check-list 10:168) but shown to be a distinct species by Phillips (1969, Auk 86:605–623; see also Raitt and Hardy, 1970, Auk 87:20–57).

ORTHONYCHINAE. Add *Sphenostoma occidentale* (p. 99), following *S. cristatum*; considered conspecific with *cristatum* by Peters (Check-list 10:231), but shown to be a distinct species by Ford and Parker (1973, Emu 73:113–118).

Add *Cinclosoma alisteri* (p. 99), following *C. castanotum*; considered a race of *C. cinnamo-*

meum by Peters (Check-list 10:234), but shown to be a distinct species by Ford (1976, Proc. XVth Int. Orn. Cong., Canberra, pp. 542–556).

The sequence of species of *Cinclosoma*, as arranged by Ford (*op. cit.*), is: *punctatum*, *ajax*, *castanotum*, *alisteri*, and *cinnamomeum*.

MUSCICAPINAE. Add *Eopsaltria georgiana* (p. 110), following *E. griseogularis*; omitted in error (cf. Schodde, 1975, Interim List of Australian Songbirds, p. 35).

PLATYSTEIRINAE. Add *Batis ituriensis* (p. 111), after *B. minima*; considered a race of *minima* by some workers but shown to be a distinct species by Erard (1975, L'Oiseau et R. F. O. 45:235–240).

MONARCHINAE. Delete *Monarcha muelleriana* (p. 111), confused with *Monachella muelleriana* and listed in error.

AEGITHALIDAE. Delete *Psaltriparus melanotis* (p. 114), now considered a morph of *P. minimus* (cf. Raitt, 1967, Auk 84:503–528).

SITTIDAE (p. 115). Add *Sitta ledanti*, new species, following *S. whiteheadi* (cf. Vieillard, 1976, Alauda 44:351).

NECTARINIIDAE. Add *Nectarinia hunteri* (p. 117), following *N. senegalensis*; considered a race of *senegalensis* in Peters (Check-list 12:235), but recognized as a distinct species by Hall and Moreau (1970, Atlas of speciation in African passerine birds, p. 258).

THRAUPINAE. Delete *Chlorospingus zeledoni* (p. 125), considered a distinct species in Peters (Check-list 13:259), but shown to be a morph of *C. pileatus* by Johnson and Brush (1972, Syst. Zool. 21:245–262).

Add *Hemispingus rufosupercilatus* (p. 125), new species, following *H. goeringi* (cf. Blake and Hocking, 1974, Wilson Bull. 84:321).

Add *Buthraupis aureodorsalis*, new species, following *B. eximia* (cf. Blake and Hocking, 1974, Wilson Bull. 84:323).

Add *Nephelornis onielli* (p. 128), new genus and species, before *Xenodacnis parina* in "Genera incertae sedis" (cf. Lowery and Tallman, 1976, Auk 95:415–428).

PLOCEIDAE. Bock and Morony (1978, Bonn. Zool. Beitr. 29:122–147) have suggested that the genera *Passer*, *Petronia*, and *Montifringilla* (p. 136) be removed from the Ploceidae and placed in a separate family, the Passeridae, and that the genera *Plocepasser*, *Histurgops*, *Pseudonigrita*, *Phileitairus*, and *Sporopipes* be retained in the Ploceidae with the subfamily name Plocepasserinae.

Ziswiler (1968, Bonn. Zool. Beitr. 19:269–279) has suggested that the genus *Sporopipes* be placed in a monotypic subfamily, the Sporopipinae. These changes have not been adopted in this analysis.

Add *Malimbus ballmanni* (p. 137), new species, following *Malimbus racheliae* (cf. Wolters, 1974, Bonn. Zool. Beitr. 25:290).

ORIOLIDAE (p. 140). Delete *Sphecotheres vieilloti*, *S. flaviventris*, and *S. hypoleucus* recognized as distinct species by Peters (Check-list 15:136–137), but considered races of *S. viridis* by Ford (1975, Emu 75:163–174).

CRATICIDAE (p. 142). Add *Cracticus cassicus* and *Cracticus lousiadensis*, following *C. nigrogularis*; omitted in error.

PTILONORHYNCHIDAE AND PARADISAEIDAE (pp. 142–143). Revisions of these families have been published by Diamond (1972, Publ. Nuttall Orn. Cl. 12:305–342) and by Schodde (1976, Proc. XVIth Int. Orn. Cong., Canberra, pp. 137–149). Schodde suggests that the two families be merged. Diamond reduces the number of genera from 20 to 10, and suggests that the 42 species constitute only 25 zoogeographic species. These revisions have not been adopted in this analysis.

CORVIDAE. Add *Corvus tasmanicus* (p. 144), following *C. mellori*; considered a subspecies of *C. coronoides* by Peters (Check-list 15:277), but shown to be a distinct species by Rowley (1970, CSIRO Wildlife Research 15:27–71). Rowley showed that *Corvus coronoides* is a complex of three sibling species, *C. coronoides*, *C. mellori*, and *C. tasmanicus*.

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