

Zoogeography of the Irenidae (Aves: Passeres)

Daphne F. Dunn¹

Department of Zoology, University of California, Berkeley, California 94720 U.S.A.

ABSTRACT

The only family of birds endemic to the Oriental zoogeographical region is the Irenidae (genera *Irena*, *Chloropsis*, and *Aegithina*). The ranges of the 57 races (in 14 species) are described, and some taxonomic and distributional questions are raised. The southern Malay peninsula and Sumatra contain the largest number of species and subspecies, with numbers decreasing outward to their lowest values at the peripheries of the family's range. Several lines of evidence indicate that Malaya-Sumatra has served as the center of evolution of the Irenidae. Water gaps are important barriers to dispersal of birds of this family in which 28.6% of the species and 43.9% of the races are confined to a single island or island group. Mountains also impede dispersal, but ecological factors associated with altitude, latitude, and precipitation are probably more important than elevation *per se*. Much of the diversity of the Irenidae fauna in the Malaysian subregion may be attributable to Pleistocene sea-level oscillations. Some races and even species probably have evolved since the end of the last glaciation 11,000 years ago, making insular south-east Asia a natural laboratory for the study of bird evolution. Suggestions are made for ecological, ethological, zoogeographical, and taxonomic research to explain the restriction of this family.

AUTHORITIES DISAGREE about the precise number of families of birds in existence, but it is generally regarded as approximately 170. Of the 144 families of land birds considered by Barden (1941), 33 occur in all six zoogeographical regions. The Nearctic, Palearctic, and Oriental regions have only one indigenous family each, while the other three regions exhibit considerably more endemism (Pettingill 1970; Welty 1963), although because of taxonomic and distributional problems, even these generalizations are not accepted by all authorities (e.g. Darlington 1957; Van Tyne and Berger 1959).

The more recent treatments of the subject, however, recognize one family of Aves that includes the fairy bluebirds (*Irena*), the leafbirds (*Chloropsis*), and the ioras (*Aegithina*=*Aethorhynchus*) as being endemic to the Oriental zoogeographical region. Particularly in the early literature these genera were often classified within the family Pycnonotidae (bulbuls) (e.g. Caldwell and Caldwell 1931; Chasen 1935), which presumably accounts for Barden's (1941) listing of no family endemic to the Oriental region. When recognized as a separate family, this assemblage of three genera has been referred to as either Aegithinidae or Irenidae. Delacour used the former term in his books of 1946 (with Mayr) and 1947, but the latter in his contribution to Mayr and Greenway (1960), Ripley (1961), and Wildash (1968) also used Irenidae. Wetmore (1960) stated that the generic name *Chloropsis* antedates the others, hence should be used to designate the family, but he also placed *Irena* in the family Oriolidae (old world orioles) so that his family Chloropseidae in-

cluded only *Chloropsis* and *Aegithina*. Other arrangements include that of Henry (1971) in which *Irena* is the sole genus of the Irenidae, the other two genera constituting the subfamily Liotrichinae of the Pycnonotidae, and that of Robinson (1927) in which the Irenidae comprise *Irena* and the now-synonymized genus *Irenella* while the Aegithinidae consist of *Aegithina* and *Chloropsis*. I shall follow the majority of recent authors in considering *Irena*, *Aegithina*, and *Chloropsis* as comprising the family Irenidae.

Aside from taxonomic studies and brief discussions of the species in bird guides, very little has been written about this group, although Ali and Ripley (1971) have recently enhanced our knowledge of the Indian forms. It is hoped that this review will raise questions that will prompt further research into the systematics of the Irenidae, as well as the ecology and ethology with a view toward explaining their distribution. Although the familial position of the genera may have been a subject of some dispute, the genera themselves and the species (with two possible exceptions) seem well-defined. Their geographic distributions are also quite well-known. However, systematics at the subspecific² level, often based on subtle and apparently variable plumage differences (Hall 1957; Hoogerwerf 1962; Marien 1952; Robinson 1927), are to some extent not yet clear, particularly for *Aegithina*. The most general consensus of opinion is on races confined to islands or island groups. In this paper I shall, with a few exceptions, accept as valid those subspecies recognized as distinct by Delacour (1960),

¹ Present address: School of Biological Sciences, University of Malaya, Kuala Lumpur, Malaysia.

² The terms "subspecies" and "race" (i.e. geographical race) are used synonymously (Mayr 1969b).

whose listing agrees with most recent literature on the subject.

Aegithina are black and yellow- or olive-green, mainly insectivorous birds; *Chloropsis*, bright green animals, are largely frugivorous, but feed on insects, nectar, and seeds as well; *Irena*, mainly blue in color, are almost exclusively fruit-eaters (Ali and Ripley 1971; Baker 1922, 1926; Hachisuka 1935; Robinson 1927; Smythies 1960; Whistler and Kinnear 1949). Thus all are tied to areas of abundant vegetation, occurring in forests, plains peripheral to forests, or areas of secondary growth, and most species are rarely resident much above about 1000 m elevation, although they may range higher (Ali and Ripley 1971; Baker 1922, 1926; Ripley 1961; Wait 1925). All are non-migratory although they may undergo altitudinal movements correlated with breeding season, so their ranges are strictly residential (Ali 1943; Ali and Ripley 1971; Deignan 1945; Whistler and Kinnear 1932).

Irenidae range from extreme northwestern Pakistan to the easternmost portion of the Philippine Islands, and from the latitude of the Himalayan foothills south to Wallace's line, an area almost precisely coincident with that generally recognized as the Oriental region. However, no one genus spans the entire distance east to west, although all three genera extend to the northern and southern extremes of the range. *Irena*, the most geographically restricted genus, has only two species. The other genera have about equally wide geographic spans, but *Aegithina* extends farther west and *Chloropsis* farther east. *Aegithina* consists of four species, *Chloropsis* of eight. Nothing can be deduced about the zoogeography of the Irenidae at the generic level for all three genera are found in lower peninsular India and Ceylon, from Bangladesh eastward through Burma, Thailand, Indochina, and into the Malaysian sub-region as far east as Palawan. *Aegithina* alone extends into Pakistan, while both *Chloropsis* and *Irena* are represented east of Palawan in the Philippines.

Irena

The two species of *Irena* are geographically disjunct, as illustrated in figure 1. There are four races of *I. cyanogaster*: *I. c. cyanogaster* in the north on Luzon and Polillo; *I. c. ellae* on Leyte and Samar in the central area of the range; *I. c. melanochlamys* on Basilan in the southwest; and on Mindanao in the southeast, *I. c. hoogstraali*.

Three races of *I. puella* are also autochthonous to islands or island groups: *I. p. turcosa* on Java; *I. p. tweeddalei* on Palawan, Balabac, and the Cal-

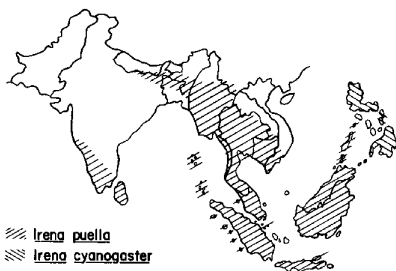


FIGURE 1. Distribution of the species of *Irena*.

mianes; and *I. p. criniger* on Sumatra, Borneo, and their satellite islands. Although Abdulali (1964) proposed a distinct race, *I. p. andamanica*, from the Andaman Islands, Ali and Ripley (1971) have determined that the island birds are not subspecifically different from those on the mainland to the north. *I. p. puella* was formerly considered by Ali (1953, 1962) and Ripley (1961) to be restricted to south India and Ceylon, with *I. p. sikkimensis* occupying northeast India, Bangladesh, much of Burma, Thailand, and southern Indochina, but they now (Ali and Ripley 1971) agree with Delacour (1960) in synonymizing the two subspecies as the nominate race. *I. p. puella* also extends into southwest Yunnan (de Schauensee pers. comm.). *I. p. malayensis* is endemic to Malaya (=Peninsular Malaysia) and extreme southern Thailand.

Aegithina

The ranges of the species of *Aegithina* are illustrated in figures 2 and 3. The validity of the species *A. nigrolutea* is still in some doubt. Its range is coincident with that of *A. tiphia* from Rajasthan east through much of northern India and south as far as the beginning of peninsular India. Whistler and Kinnear (1932) suggested that *A. nigrolutea* may be a subspecies of *A. tiphia*, but admitted that the two are apparently reproductively isolated, especially in the western part of their range. Marien (1952) declared the species easily distinguishable throughout their range, and Hall (1957), although more cautious, also accepted *A. nigrolutea* as valid. Five races of *A. tiphia* occur in the Indian subcontinent, three of them within the range of *A. nigrolutea*. *A. t. septentrionalis* is confined to the Northwest Fron-

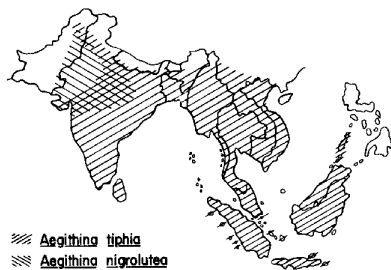


FIGURE 2. Distribution of some species of *Aegithina*.

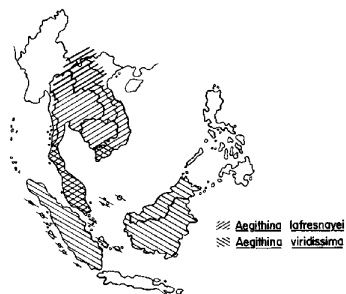


FIGURE 3. Distribution of some species of *Aegithina*.

tier Province and the Punjab. To the east, in northern India south to approximately the 20th parallel, *A. t. humei* occurs, intergrading in the region of Bihar with the nominate race which extends north and east into Assam, Burma, and parts of northern Thailand. *A. t. deignani* ranges south from about 20°N (excluding southern Kerala) and intergrades at the Palghat Gap with *A. t. multicolor* which occupies extreme southern India and Ceylon. Other races of *A. tiphia* recognized by Delacour (1960) are: *A. t. scapularis*, endemic to Java and Bali; *A. t. aequanimis*, inhabiting Palawan and northern Borneo; *A. t. viridis*, in southern Borneo (including Sarawak); *A. t. philipi*, occurring in Yunnan, north and central Indochina, and north and central Thailand, intergrading in the west with *A. t. tiphia*; *A. t. cambodiana*, resident in southern Indochina and

southeast Thailand; and *A. t. horizopectera*, occurring in extreme southern mainland Burma and Thailand, peninsular Burma and Thailand, Malaya, Sumatra and its islands. Hoogerwerf (1962) described a new subspecies, *A. t. djungkulamensis*, from far western Java, which, if valid, would be the 12th race of *A. tiphia*. *A. lafresnayei* contains three races: *A. l. lafresnayei* in Malaya and south peninsular Thailand; *A. l. innolata* in southern Burma, Thailand south to the Isthmus of Kra, north and central Indochina, and southern Yunnan (de Schauensee pers. comm.); and *A. l. xanthotis* in southern Indochina. The nominate race of *A. viridissima* is found in Malaya, peninsular Thailand, Borneo, Sumatra, and the islands off these areas except for the Anambas which have a distinct race, *A. v. thapsina*. Wildash (1968) listed *A. viridissima* as occurring in southern South Vietnam but did not specify the race.

Chloropsis

The ranges of the eight species of *Chloropsis* are illustrated in figures 4-6. Delacour's (1960) discussion of the ranges of *C. cyanopogon cyanopogon* and *C. c. septentrionalis* in Thailand is somewhat confusing, but reference to other sources (e.g. Baker 1922; Deignan 1963; Gibson-Hill 1949) makes it clear that the latter race extends from upper peninsular Thailand and Tenasserim south to northern Malaya where it intergrades with the nominate race which is found in the rest of Peninsular Malaysia as well as Borneo and Sumatra. *C. sonnerati* contains three subspecies: *C. s. sonnerati* on Java, *C. s. parvirostris* on Nias Island off the west coast of Sumatra, and *C. s. zosterops* in the Malay peninsula, Sumatra, Borneo, and all the islands between them including the Natunas. *C. palawanensis*, a monotypic species, occurs on Balabac, Palawan, and the Calamian Islands. Delacour (1960) lists two races of *C. flavipennis*, *C. f. flavipennis* on Cebu, and *C. f. mindanensis* on Mindanao. The subspecies were distinguished mainly by size, but Ripley and Rabor (1968), reporting the species on Leyte as well, believe it monotypic, with a cline of increasing size from Cebu to Leyte to Mindanao. *C. venusta* is monotypic and endemic to Sumatra.

One subspecies of *C. hardwickii*, *C. b. melliana*, extends north from east-central Indochina into the Chinese provinces of Kwangtung, Fukien (the central part), and Yunnan; Hainan supports another race, *C. b. lazulina*; *C. b. malayana* occurs in Malaya; and the nominate subspecies is found from Simla in north-central India through eastern India, Nepal, Sikkim, Bhutan, Bangladesh, Burma, and at least into north Thailand and northwest Indochina, if not

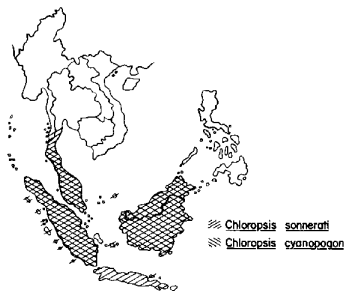


FIGURE 4. Distribution of some species of *Chloropsis*.

into southern Yunnan. The subspecific ranges of the other two species of *Chloropsis* are less well-defined. Subspecies of *C. aurifrons* follow a distribution in India similar to the races of *A. tiphia*: *C. a. insularis* in Ceylon and southwestern India north to the Palghat Gap; *C. a. frontalis* north of it along the west coast of the peninsula and along the east coast north to about the 20th parallel; and *C. a. aurifrons* east from Simla along the Himalayan foothills into Burma and south into Orissa. *C. a. priddii* occurs in Burma, northern Thailand, north and central Laos, and southwest Yunnan (de Schauensee pers. comm.); *C. a. inornata* ranges through central and southeast Thailand, eastern peninsular Burma, Cambodia, and southern South Vietnam (Cochinchina); *C. a. incompta* is found in the north of the same region, occupying northern South Vietnam, southern Laos, and eastern Cambodia; *C. a. media* is confined to Sumatra. The species is apparently absent from Peninsular Malaysia.

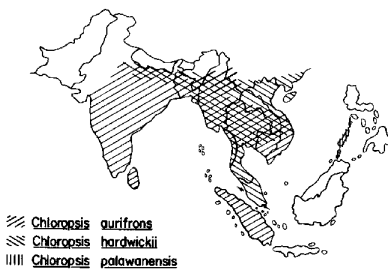


FIGURE 5. Distribution of some species of *Chloropsis*.

Five of the 10 races of *C. cochinchinensis* are restricted to islands or island groups: *C. c. billitonis* on Billiton Island; *C. c. icterocephala* on Sumatra; *C. c. natunenensis* on the Natuna Islands; *C. c. nigricollis* on Java; and *C. c. viridinucha* in Borneo. *C. c. jerdoni*, regarded in some of the earlier literature as a distinct species (e.g. Ali 1943, 1953; Baker 1922; Wait 1925), ranges from Ceylon through peninsular India into north-central India. Extending from the Isthmus of Kra to southernmost peninsular Thailand is *C. c. serithai*, Malaya is occupied by *C. c. moluccensis*, and *C. c. kinneari* occurs in northern Indochina and northeast Thailand. Distributional data on the nominate race have been confusing, for Delacour (1960) listed it as occurring only in south Indochina and southeast Thailand, but Deignan (1945, 1963) reported the race from much of Thailand, and Ripley (1961: 332) described it as extending from "Assam south of the Brahmaputra . . . , East Pakistan [Bangladesh], Burma, and parts of the Indochinese subregion. . . ." Ripley's (1961) much wider range includes that of *C. c. chlorocephala*, which he synonymized with the nominate race. Assuming this is valid, the range of *C. c. cochinchinensis* is from Assam in a belt east to Laos and south to the Isthmus of Kra.

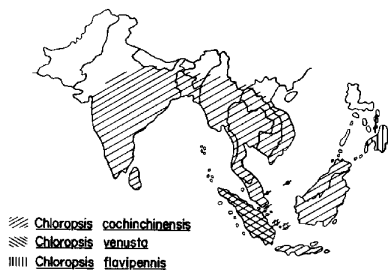


FIGURE 6. Distribution of some species of *Chloropsis*.

DISCUSSION AND INTERPRETATION

Table 1 describes in quantitative terms what is seen in figures 1-6, and these data are summarized in figure 7. The southern part of the Malay peninsula and Sumatra contain the largest number of species and subspecies. Numbers decrease outward from there and are lowest at the extremes of the range of the

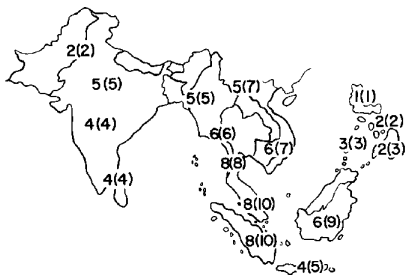


FIGURE 7. Number of species (and subspecies) of Irenidae in each area of the Oriental zoogeographical region.

family. Areas with more than one race of a species are areas of transition between two or more subspecies of a species, or areas that include islands where races have differentiated.

Based on presence of endemic species and/or absence of species present through much of the rest

of the Oriental region, the 17 areas in table 1 can be grouped into four larger subregions. These subregions, delimited by vertical lines in table 1, are: the Indian subcontinent (including Pakistan and Ceylon); mainland southeast Asia [Bangladesh, Assam, Bhutan, Burma, and Thailand (except their peninsular portions), Indochina and extreme southern China]; Malaysia (the Malay peninsula, Sumatra, Borneo, Java, and their neighboring islands north and west of Wallace's Line including Palawan); and the Philippines (the political entity excepting Palawan).

The faunas of Irenidae in the four subregions are compared in table 2 using the formula devised by Duellman (1966): $FRF = 2C / (N_1 + N_2)$, where FRF is the faunal resemblance factor, C is the number of species common to the two faunas being compared, and N_1 and N_2 are the number of species in each of the two faunas. The Philippines is the most faunistically distinct subregion, having an FRF of zero with each of the other three subregions, while mainland southeast Asia and the Indian subcontinent are most alike. Malaysia is more like mainland southeast Asia than like India.

Percentage endemicity may be used as another index of faunal difference. By this measure, too, the

TABLE 1. Distribution of species of Irenidae.

SPECIES	AREAS # races											No. of areas in which species occurs						
		S. pen. India, Ceylon	N. pen. India	NWFP, Punjab	N. cen. India	N.E. India, Assam, Bangladesh, N. Burma	S. Burma, Andaman, Nicobars, N. Thailand	S. China, N. Indochina	S. Indochina, E. Thailand	Pen. Burma, S. and Pen. Thailand	Malay pen. N. to Isthmus of Kra		Sumatra and islands	Borneo and islands, Natunas, Anambas	Java, Bali	Palawan and islands	Mindanao, Basilan	Cebu, Leyte, Samar
<i>I. cyanogaster</i>	4																	
<i>I. puella</i>	5	1	1			1	1	1	1	1	1	1	1	1	1	2	1	1
Subtotal		1	1	0	0	1	1	1	1	1	1	1	1	1	1	2	1	1
<i>A. lafresnayei</i>	3							1	1	1		1	1					
<i>A. nigrolutea</i>	1				1	1												
<i>A. tiphia</i>	12	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1		
<i>A. viridissima</i>	2										1	1	2					
Subtotal		1	1	2	2	1	2	2	2	2	2	3	2	4	2	1	0	0
<i>C. aurifrons</i>	7	1	1			1	1	1	2		1	1						
<i>C. cobincinensis</i>	10	1	1		1	1	1	1	1		1	2	2	2	1			
<i>C. cyanopogon</i>	2										1	2	1	1				
<i>C. flavipennis</i>	2																	
<i>C. hardwickii</i>	4				1	1	1	3	1		1	1				1	1	
<i>C. palawanensis</i>	1															1		
<i>C. sonnerati</i>	3										1	1	2	1	1			
<i>C. venusta</i>	1												1					
Subtotal		2	2	0	3	3	3	5	4		5	6	7	4	2	1	1	1
Total no. of races		4	4	2	5	5	6	8	7		8	10	10	9	5	3	3	2

TABLE 2. Resemblance of Irenidae faunas among subregions of the Oriental region.^a

	Indian subcont.	Mainland SE Asia	Malaysia	Philippines
Indian subcont.	N=6 (1 endemic =16.7%)	C=5	C=5	C=0
mainland SE Asia	FRF= 0.833	N=6 (0 endemic =0%)	C=6	C=0
Malaysia	FRF= 0.588	FRF= 0.706	N=11 (5 endemic =45.5%)	C=0
Philippines	FRF= 0.0	FRF= 0.0	FRF= 0.0	N=2 (2 endemic =100%)

^a See text for explanation of symbols.

Philippines is the most distinct of the subregions, and mainland southeast Asia is the least so, lacking endemic species altogether.

The large number of species and subspecies in the vicinity of Sumatra and Peninsular Malaysia suggests that this area has served as the center of evolution and subsequent dispersal of the Irenidae. The patterns seen in tables 1 and 2 and figure 7 support this working hypothesis. Darlington (1957: 31) cautions against reliance on such "numbers clues" alone, but other evidence also supports this theory.

Vigorous gene flow from Malaysia to mainland southeast Asia is reflected in the FRF of 0.706 between these two subregions. The diminution in the number of species to have dispersed with increasing distance is seen in numerical terms as an FRF of 0.588 between Malaysia and the Indian subcontinent. Thus mainland southeast Asia has occupied an intermediate geographical position, acting as a corridor between an area of some endemicity due to continual production of new species (Malaysia), and an area of lesser endemicism due to its peripheral location and the attenuation of gene flow (Indian subcontinent). Its greater similarity to the latter than to the former subregion can be attributed to the more rapid evolution of new species in Malaysia than in the Indian subregion, and because of this continual gene flow through mainland southeast Asia, no endemic species evolved there.

Within the Malaysian subregion itself, two factors in addition to distance *per se* contribute to the decreased number of species and races outward from the Malaya-Sumatra center. The stretches of open water to the east of the center evidently restrict the dispersal of the Irenidae, which appear to resemble "most tropical birds [in being] highly sedentary and respect[ing] water barriers to a high degree" (Mayr 1969a: 15). The other intimately related factor is

that the Irenidae in the eastern Malaysian subregion live on islands. The area-diversity relationship of island biota (MacArthur and Wilson 1967) almost certainly accounts in part for the greater number of species and subspecies of Irenidae on Borneo than on Java despite the shorter distance and narrower water gap from Malaya-Sumatra to the former than to the latter island. (It is also likely that Borneo is more ecologically diverse than Java.) Palawan, being even farther from Malaya-Sumatra and smaller, harbors a still more attenuated fauna of Irenidae.

The obstacle to dispersal presented by water is particularly obvious in the Philippines. Not only is the Irenidae fauna of that archipelago much reduced below the level of the fauna an equal distance to the west of the Malaya-Sumatra center, but, at the species level, it is wholly endemic. These facts indicate that propagules from the source gene pool to the west arrive in the Philippines very infrequently. Furthermore, the existence of only one species each of *Irena* and *Chloropsis* suggests that each species is the evolutionary result of a single major invasion by birds of the parent stocks. In these respects the Irenidae are typical of much of the Philippine avifauna which "... is in part that of a fringing archipelago type, the result of colonization and simple evolution of endemic forms in island isolation" (Rand 1970: 353). Although the species of Philippine Irenidae are endemic, neither has undergone adaptive radiation, but the existence of island-bound races of *I. cyanogaster*, if not *C. cyanopogon*, suggests that species may be evolving within the archipelago.

In light of the reluctance of Irenidae to cross even relatively narrow stretches of water, it is not surprising that four of the 14 species (28.6%) and 43.9% of the 57 races (seven of *Irena*, five of *Aegi-*

shina, and 13 of *Chloropsis*) are endemic to a single island or well-defined island group. This knowledge, however, may lead ornithologists to expect racially distinct birds on nearly every island, and to see differences where none of significance exists. Several races autochthonous to small islands have been proposed, later to be synonymized with previously described ones (e.g. Abdulali 1964; Chasen 1935; de Schauensee 1940). In fact, for birds, at least, it appears that speciation is more difficult on very small islands than on larger ones (Mayr 1965). The small population size on small islands makes it statistically likely that the birds will become extinct before evolving into distinct species. Thus the birds of very small islands are usually fairly recent immigrants from nearby sources.

The Malay peninsula appears geographically similar to an island, with only a narrow strip of land linking it to the rest of the continent of Asia. That it functions zoogeographically as an island is reflected in the fact that the upper peninsula (north from the Isthmus of Kra) represents the northernmost extent of three species of Irenidae and the dividing line between races of four others. Only one race ranges on both sides of it.

Mountains, like open water, often act to limit avian dispersal (Mayr 1969a; Welty 1963). In southwestern India, hills separate races of two species of Irenidae, and the Himalayas clearly demarcate the northern extent of the family in the Indian subcontinent and western mainland southeast Asia. *C. bardwickii*, the highest-ranging species in the family, extends to somewhat over 2400 m in the Naga hills (Ali and Ripley 1971). *I. puella*, found to a maximum of about 1800 m (Ali and Ripley 1971; Smythies 1960), is described by Robinson (1927: 276) as a "fairly strong" flier. It is therefore as unlikely that these birds lack the physical ability to fly higher than they do as it is that they cannot fly across the water gap between Bali and Lombok. Mayr's (1969a: 11) statement that "of far greater importance in the tropics than either water barriers or altitudinal barriers are vegetational barriers" suggests that the ecological concomitants of high altitude are what usually restrict these birds, rather than altitude *per se*. Vegetation might be expected to be very important in governing the distribution of this family of birds which is so dependent on forest for its diet of insects, fruit, nectar, and seeds.

Factors other than altitude also affect vegetation and thereby the fauna. The extreme northwestern portion of the range of Irenidae is essentially a climatic island, with an indigenous race and probably

also a species. The arid land west of Pakistan acts as a barrier to the dispersal of this family which probably originated in the rain forest of Malaysia. The northeastern limit of the family's range is broadly coincident with the transition from tropical to subtropical and temperate rain forest (Fullard and Darby 1969). Rainfall in mainland southeast Asia and in northern India is far more monsoonal and the climate more seasonal than in insular southeast Asia and peninsular India, resulting in vegetational differences (Fullard and Darby 1969). Thus the diminution in number of species in mainland southeast Asia as compared with the presumed source area of Malaysia is due not only to distance, but also to the necessity for potential immigrants to be able to adapt to the altered ecological situation. Clearly only a fraction of them can do so. Such ecological differences presumably account for the existence of subspecies in contiguous areas lacking obvious physical barriers between them, but the degree of ecological difference necessary for the separation of races remains to be determined.

The literature gives only very broad clues to these sorts of ecological differences. Borneo provides an example at the species level, and also illustrates how much research remains to be done (from Delacour 1947; Smythies 1960). The diets of birds of the three genera differ, as described previously. *Irena puella* is restricted to primary forest, and may range up to 1500 m. *Aegibina viridissima* lives in secondary jungle and lowland forest, while *A. tiphia* occupies open woodlands and cultivated areas (no note is made of any ecological differences between the two Bornean races of this species). *Chloropsis cyanopogon* is confined to lowland forest and secondary growth; *C. somerati* is also a species of primary and secondary forest but is found particularly in coastal areas; and *C. cochinchinensis* occurs in open forest. The latter two species may inhabit highlands up to 1200 m. Thus, at this level of analysis, vegetation type and elevation appear to be important parameters of the niches of Irenidae.

Vegetational barriers are less permanent than water or altitude barriers, but even these are subject to change. As recently as the end of the last glaciation, about 11,000 years ago according to Frerichs (1968), the Malay peninsula was broadly connected to the rest of southeast Asia, as well as to Borneo and Sumatra, which were, in turn, linked to Java (Ho 1960). Racial differentiation of the Irenidae in this land (Sundaland) during each of the four periods of sea-level depression during the Pleistocene was probably similar to that in mainland

southeast Asia today, where vegetation is the principal barrier separating races. With each rise in sea level the Malaysian subregion was dissected into hundreds of islands on which evolution could proceed in various degrees of geographical isolation. With each subsequent fall in sea level, most of the previously isolated populations would rejoin. The majority of them would not have achieved reproductive isolation and would have resumed interbreeding, infusing new genes into the species gene pool while losing their racial identity. Only a small percentage of the isolates (the number being roughly proportional to the duration of sea-level elevation) would have become sufficiently differentiated to survive as new species (Mayr 1969a). Populations restricted to higher altitudes, however, would have been affected to a much lesser extent, if at all, by these oscillations, since even at times of maximum sea-level lowering the mountains would have remained isolated from one another as biogeographical islands.

The sea-level elevation which divided a formerly extensive area into many much smaller ones can have resulted in diminution as well as enhancement of diversity. The apparent absence of *C. aurifrons* from Malaya may be a result of what Diamond (1973) termed "relaxation," and it is likely that other instances of the disappearance of species from islands within their presumed former range may be found as well. Conversely, the presence of *A. viridissima* in southern South Vietnam appears to be the result of the survival of a small relict area of typically Malayan fauna and flora after the intervening area was submerged (Delacour 1970).

In the Irenidae may lie the potential to determine the length of time necessary for the evolution of bird species and subspecies. It has probably been less than 11,000 years since the *A. viridissima* of South Vietnam was isolated from its parent population. The racial identity of that isolate, if it still exists, should be studied to determine if it has become subspecifically distinct. Many of the islands of the Malaysian subregion provide similar "natural laboratories." *C. palauensis* and *C. venusta* are endemic to islands which were part of Sundaland during the last glaciation. It is therefore possible that they have achieved specific status within the past 11,000 years. The degree of difference between these species and those most closely related to them should be studied to determine how recently speciation may have occurred. *C. cochinchinensis jerdoni* and *A. nigrolutea* appear to be promising forms in which to study evolution at the subspecies/species interface, for both have alternatively been called subspecies and full species. The degree of ecological and

ethological difference between each and its nearest relatives might help in understanding the nature of the transition from subspecific to species status.

Mayr (1954) specified the four criteria of geographical speciation as: geographic variation and polytypic species; geographical isolates with extrinsic barriers between; populations borderline between being species and subspecies; and the occurrence of superspecies. Only the last condition is not met in the Irenidae for the taxonomy is not sufficiently refined, but if Mayr's (1969a: 2) statement that in birds "all speciation is geographical" is true, superspecies of Irenidae must exist. The broad distribution of one species of *Aegithina* and two of *Chloropsis* suggests that these species are the evolutionary opposites of the type of species that would have been ancestral to a superspecies. That is, they are probably broadly adaptable stocks that did not diverge much during each period of isolation so that when sea level fell again, the isolates merged and spread even farther. Members of a superspecies, on the other hand, were probably derived from a rapidly evolving, highly specialized species. Each geographical isolate evolved rapidly in response to a very localized set of pressures so that by the time sea level fell again, it was reproductively isolated from the others. This would have resulted in many closely related species, each with a restricted range.

Darlington (1957: 32) states that "there should be greater differences between genera and between species, and more endemism, where a family has been for a long time than where it has just arrived." The genera of Irenidae are too few and widespread to be analyzed in this way, but the species should be. The degree of endemism among the Irenidae is highest for the Philippines, but that is a result of their isolation, a factor Darlington ignores in his very sweeping statement. The next highest degree of endemism, however, is in the Malaysian subregion, further evidence for its being the focus of the family.

Thus several lines of evidence point to the center of evolution and dispersal of the Irenidae being in present-day Malaya and Sumatra. The uniqueness of the Irenidae in its restriction to the Oriental zoogeographical region appears to be due to a combination of the low tendency of these birds to disperse, their fairly narrow ecological requirements, and possibly their relatively recent evolution (perhaps from the Pyconotidae or Oriolidae, the groups with which they are most frequently allied systematically) so that they simply have not had the time necessary to evolve mechanisms to overcome the physical, ecological, and behavioral barriers which seem to de-

termine the limits of their range. All of these parameters are in need of investigation. Comparison with similarly geographically circumscribed families of birds in other parts of the world, and with ecologically similar but more broadly distributed bird families in the Oriental region, might also aid in discovering the reasons for the restriction of the Irenidae.

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