

Speciation in Amazonian Forest Birds

Most species probably originated in forest refuges during dry climatic periods.

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The richest forest fauna of the world is found in the tropical lowlands of central South America. This fauna inhabits the vast Amazonian forests from the base of the Andes in the west to the Atlantic coast in the east, and its range extends far to the north and south of the Amazon valley onto the Guianan and Brazilian shields, respectively (Fig. 1). Here I propose a historical explanation of the immense variety of the Amazonian forest bird fauna, postulating that, during several dry climatic periods of the Pleistocene and post-Pleistocene, the Amazonian forest was divided into a number of smaller forests which were isolated from each other by tracts of open, nonforest vegetation. The remaining forests served as "refuge areas" for numerous populations of forest animals, which deviated from one another during periods of geographic isolation. The isolated forests were again united during humid climatic periods when the intervening open country became once more forest-covered, permitting the refuge-area populations to extend their ranges. This rupturing and rejoining of the various forests in Amazonia probably was repeated several times during the Quaternary and led to a rapid differentiation of the Amazonian forest fauna in geologically very recent times.

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This interpretation should be considered merely a working model based on a number of inferences. It may, however, serve for testing the distribution pattern of various groups of organisms. Much more concrete information on the climatic and vegetational history of Amazonia, as well as on the population structure and species relationships of Amazonian birds and other animals, is needed if one is to reconstruct the actual course of species formation in particular areas or in certain families.

Climatic Fluctuations during the Quaternary

The worldwide climatic fluctuations of the Pleistocene and post-Pleistocene severely influenced environmental conditions in the tropics. In the mountains, altitudinal temperature zones and life zones were repeatedly compressed and expanded vertically during cold and warm periods, respectively (1). At the same time the lowlands probably remained "tropical," but humid and dry climatic periods caused vast changes in the distribution of forest and nonforest vegetation. The present continuity of the Amazonian forest seems to be a rather recent and temporary stage in the vegetational history of South America (2). Geomorphological observations in southern Venezuela (3), lower Amazonia (4), central Brazil (5), and eastern Peru (6) indicate that, during

the Quaternary, arid climatic conditions repeatedly prevailed over large parts of Amazonia. During these periods dense forests probably survived in a number of rather small, humid pockets (7). Palynological studies in northern South America (8) also revealed repeated vegetational changes over large areas during the Pleistocene and post-Pleistocene. The absolute ages of the various humid and arid climatic phases, in particular the age of the last severe arid period, are not yet known. Moreover, correlation of the warm-dry and cool-humid periods of the low-latitude lowlands with the glacial and interglacial periods of the temperate regions remains a matter of controversy.

The immense importance of the Quaternary climatic fluctuations for the latest differentiation of tropical faunas has been recognized for some time (9). Stresemann and Grote (10) long ago emphasized the significance of humid and dry periods for the history of the fauna of central Africa and the East Indies. The extent of vegetational changes in Africa has been amply demonstrated in recent years by detailed palynologic studies (11). Moreau (12) analyzed the differentiation of African bird faunas in the light of the geological and climatic history of the African continent, in a very convincing interpretation. Similar zoogeographic analyses have been published on the bird faunas of Australia (13), Tasmania (14), and parts of the Old World tropics (15). But the significance of Quaternary climatic fluctuations for the differentiation of the forest faunas of tropical South America has hitherto received little attention.

Reconstruction of Forest Refuges in Amazonia

On the basis of the theory of geographic speciation (16) let us assume that most or all Amazonian forest species originated from small populations which were isolated from their parent population and deviated by selection and chance. Most of this differentiation probably took place in re-

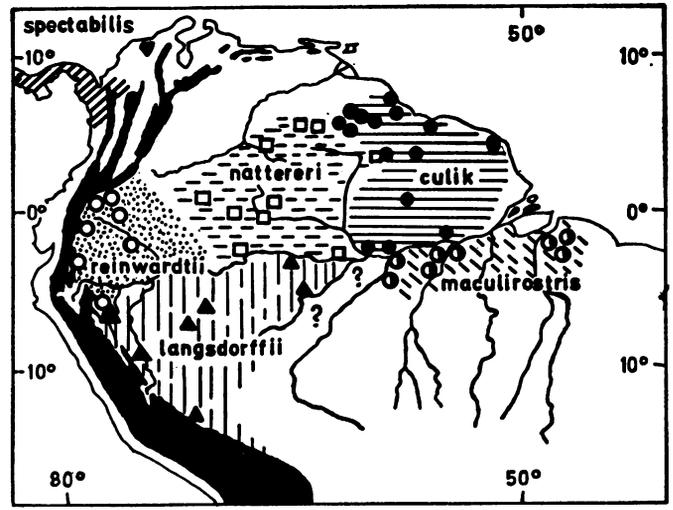
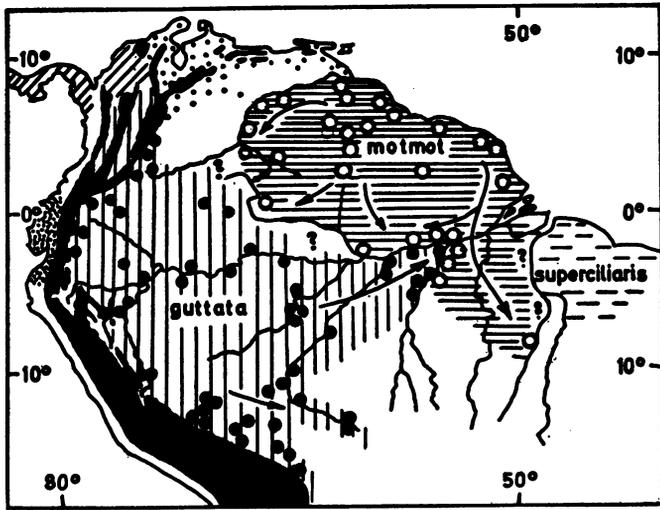


Fig. 3 (left). Distribution of the chachalaca, the *Ortalis motmot* superspecies, in Amazonia. Additional species occur north and south of the area shown. The trans-Andean forms are (stippled area) *O. erythroptera*, (hatched area) *O. garrula*, and (sparsely dotted area) *O. ruficauda*. [Adapted from Vaurie (42)] Fig. 4 (right). Distribution of a toucanet, the *Selenidera maculirostris* superspecies, in Amazonia. Additional isolated populations of *S. maculirostris* occur in eastern Brazil. Hybridization between *S. reinwardtii* and *S. langsdorffii* is known in northeastern Perú.

During arid periods the effective humidity in Amazonia was reduced by a reduction in rainfall or by a rise in temperature and an increase in evaporation, or by both. I assume that, during dry phases, rainfall in the areas of current rainfall maxima remained high enough to permit the continued growth of forests, while the forest probably disappeared from the intervening areas of lower rainfall. Since the major orographic features that cause the current inequalities in rainfall in Amazonia were present during most of the Pleistocene, possibly the basic rainfall pattern was fairly constant, though probably not entirely so, during the various climatic periods. For this reason I suggest that the main Amazonian forest refuges of arid climatic periods coincided with the present centers of high rainfall.

Current distribution patterns of Amazonian birds. Important indirect evidence concerning the possible geographic location of former forest refuges may also be obtained from the present distribution of localized Amazonian animal species, which apparently never extended their ranges far beyond their center of survival or area of origin. For Amazonian birds I distinguish the following "centers of distribution": (i) upper Amazonia from the base of the Andes east to the Río Negro and the Río Madeira; (ii) the Guianas west to the Río Negro and south to the Amazon; and (iii) lower Amazonia south of the Amazon from the lower Río Tapajós east to the Atlantic coast. Each of these areas is characterized by many distinct

and morphologically rather isolated bird species which do not range beyond the approximate limits indicated above. An additional "center of distribution" is the region between the Río Madeira and the upper Río Tapajós, where several endemic species occur. The foothills of the Peruvian Andes and the forests of the upper Río Negro-Río Orinoco region represent other such centers.

A number of Amazonian forest birds of particular zoogeographic interest form allopatric (that is, mutually excluding) species assemblages which are designated superspecies (16). Members of different superspecies often have similar distributions. Many are restricted to the Guianas and adjacent territories, to parts of upper Amazonia, or to various portions of the lowlands south of the Amazon. Numerous examples could be cited from the Cracidae (20), the toucans, the antbirds, the cotingas, the manakins, and others. The distribution of two superspecies is shown in Figs. 3 and 4. The component species of the Amazonian superspecies probably originated in forest refuges from a common ancestor whose range was split into a number of isolated portions during arid periods. By comparing the ranges of localized forms we may derive important clues concerning the former location of refuge areas.

Location of forest refuges. Using the above indirect evidence derived from rainfall inequalities and from patterns of avian distribution, I have reconstructed and named the probable geographic location of various Quaternary forest

refuges in the lowlands of tropical South America (Fig. 5). The postulated refuges west of the Andes are as follows.

Chocó refuge, which comprised the central Pacific lowlands of Colombia (21).

Nechí refuge, on the northern slope and the foreland of the central and western Andes of Colombia (21).

Catatumbo refuge, on the eastern slope and base of the Serranía de Perijá (21).

There are six postulated refuges east of the Andes, as follows.

Napo refuge, which comprised mainly the lowlands of eastern Ecuador from the Andes to the Marañón River. This may have been the largest and ecologically the most varied forest refuge for a great number of Amazonian forest animals. It is named after the Río Napo in eastern Ecuador (22).

East Peruvian refuges. Several isolated lowland forests probably existed along the eastern base of the Peruvian Andes and, farther east, on the low mountains between the Río Ucayali and the Juruá-Purús drainage (23).

Madeira-Tapajós refuge, which comprised the lowlands between the middle Río Madeira and the upper Río Tapajós (24).

Imerí refuge—a small area around the Sierra Imerí and Cerro Neblina between the headwaters of the Río Orinoco and the upper Río Negro (25).

Guiana refuge, on the northern slope and foreland of the mountains of Guyana, Surinam, and Cayenne (26).

Belém refuge, in the region south of

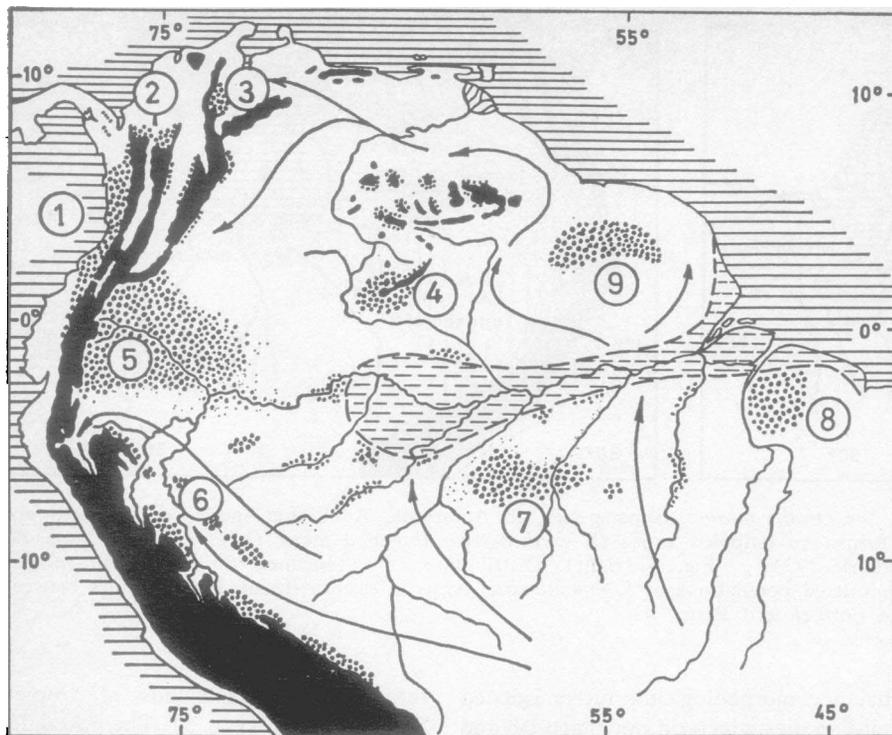


Fig. 5. Presumed forest refuges in central and northern South America during warm-dry climatic periods of the Pleistocene. The arrows indicate northward-advancing nonforest faunas of central Brazil. (1) Chocó refuge; (2) Nechí refuge; (3) Caturbo refuge; (4) Imerí refuge; (5) Napo refuge; (6) East Peruvian refuges; (7) Madeira-Tapajós refuge; (8) Belém refuge; (9) Guiana refuge; (hatched area) interglacial Amazonian embayment (sea level raised by about 50 meters); (black areas) elevations above 1000 meters.

the mouth of the Amazon and west to the lower Río Tocantins (27).

There were probably additional smaller forests along the major river courses of Amazonia, on the slopes of isolated mountains, and in the extensive lowlands between the upper Río Madeira and the Marañón River. Even when palynological field data from Amazonia become available it will remain difficult to map the distribution of forest and nonforest vegetation at any given time under the constantly changing climatic conditions of the Pleistocene. The table mountains of southern Venezuela are today located in the dry transverse zone of Amazonia and may have supported no tropical, but only subtropical, forests on the higher slopes during arid climatic phases. These may have served as refuges for the montane forest fauna of the highlands of Southern Venezuela.

Since climatic fluctuations were much more pronounced during the Pleistocene than in post-Pleistocene time, it seems possible that the rupturing of the Amazonian forest was most marked during the arid periods of the Pleistocene. During the post-Pleistocene merely a separation of an upper Amazonian forest from lower Amazonian forests

may have resulted from the disappearance of forest growth in the dry transverse zone through the Obidos-Santarém region.

During these arid periods many nonforest animals of central Brazil probably advanced across the lower Amazon to reach the upper Río Branco valley and the nonforest regions of central Venezuela and eastern Colombia (28). Many relict populations of nonforest bird species still inhabit the isolated remnants of savannas and campos found in the forests on both sides of the lower Amazon (29). Nonforest regions probably also extended during dry periods northwestward from central Brazil and eastern Bolivia, near the Andes, through the Ucayali-Huallaga valleys, to connect with the arid upper Marañón valley. A number of Brazilian bird species even crossed the Andes, probably in the area of the low Porculla Pass west of the upper Marañón River, to reach the arid Pacific lowlands of Peru and southwestern Ecuador (28). Without palynological data from eastern Peru we have no means of knowing during which dry phase (or phases) of the Quaternary the postulated connection of the upper Marañón fauna and the Brazilian

nonforest fauna may have been established.

During humid periods the Amazonian forest probably was repeatedly connected with the forests of southeastern Brazil over the now unforested tableland of central Brazil. The connecting forests may not have been very extensive, but they probably made possible the exchange of numerous plants and animals (30, 31). Remnants of these forests are still preserved in small humid pockets and are inhabited by isolated populations of Amazonian animals.

Secondary Contact Zones

Upon the return of humid climatic conditions many forest refuge populations followed the expanding forests and often came in contact with sister populations of neighboring or even far-distant refuges. Because of variation in the rate of differentiation of different animal species, the populations that came in contact reached many different levels in the speciation process. Basically, we may distinguish the following situations.

1) Geographic overlap. The speciation process was completed during the period of geographic isolation—that is, the allies had attained reproductive isolation as well as ecologic compatibility. This resulted in sympatry and a more or less extensive overlap of the ranges occupied.

2) Geographic exclusion. The speciation process was not fully completed. Although reproductively isolated (and therefore treated taxonomically as species) the allies remained ecologically incompatible. This situation led to mutual exclusion presumably as a result of ecologic competition without hybridization along the zone of contact (31a).

3) Hybridization. The speciation process was not completed and the allies hybridized along the zone of contact. Hybridization may occur along a rather narrow belt, indicating that a certain degree of incompatibility of the gene pools had been reached before contact was established in ecologically more or less uniform continuous forests (32). Hybridization over a broad zone may lead to the more or less complete fusion of the populations in contact.

The zones of presumably secondary contact of Amazonian forest birds are in areas between the postulated forest refuges—for example, north and south of the middle Amazon River and in the Huallaga-Ucayali region of eastern

Peru (Fig. 6). A number of representative bird species doubtless met along broad rivers, such as the Amazon or its large tributaries, which separate their ranges today. In these cases, expansion of the allies' range beyond the rivers appears to be inhibited by competition or by swamping of the occasional colonists which manage to get across the watercourse (33). A few forms were able to build up small populations on the opposite river bank. Most bird species eventually crossed the rivers in the course of extending their ranges, provided the opposite bank was not occupied by a close relative or, if it was, provided the two allies had acquired complete ecologic compatibility. Few species seem to be definitely halted solely by the river courses of Amazonia, especially a number of birds inhabiting the dark forest interior. However, many such bird species as well as arboreal and small terrestrial mammals probably surrounded the broad portions of the rivers by crossing the latter in the narrow middle and upper parts, in this way often extending their ranges far beyond the areas of origin or survival; again, provided they did not meet ecologically competing close relatives which extended their ranges from other refuge areas. Interspecific competition seems to be very important in limiting the range of numerous forest birds in tropical South America.

In summarizing, the rivers probably are not a causal factor of avian speciation in Amazonia (except perhaps in a few cases), but merely modified, or occasionally limited, the dispersal of forest bird species after the latter had originated in forest refuges during dry climatic periods.

Conclusion and Summary

The Tertiary forest fauna of central South America inhabited comparatively restricted forests along marginal portions of the Guianan and Brazilian shields. Although several species of the present Amazonian forest bird fauna may represent direct descendants of Tertiary forms, most or all species seem to have undergone considerable evolutionary change during the Pleistocene. Several factors, in combination, probably caused this rather recent faunal differentiation in Amazonia: (i) the great expansion of dense forests onto the fully emerging Amazonian basin and into the lowlands around the rising

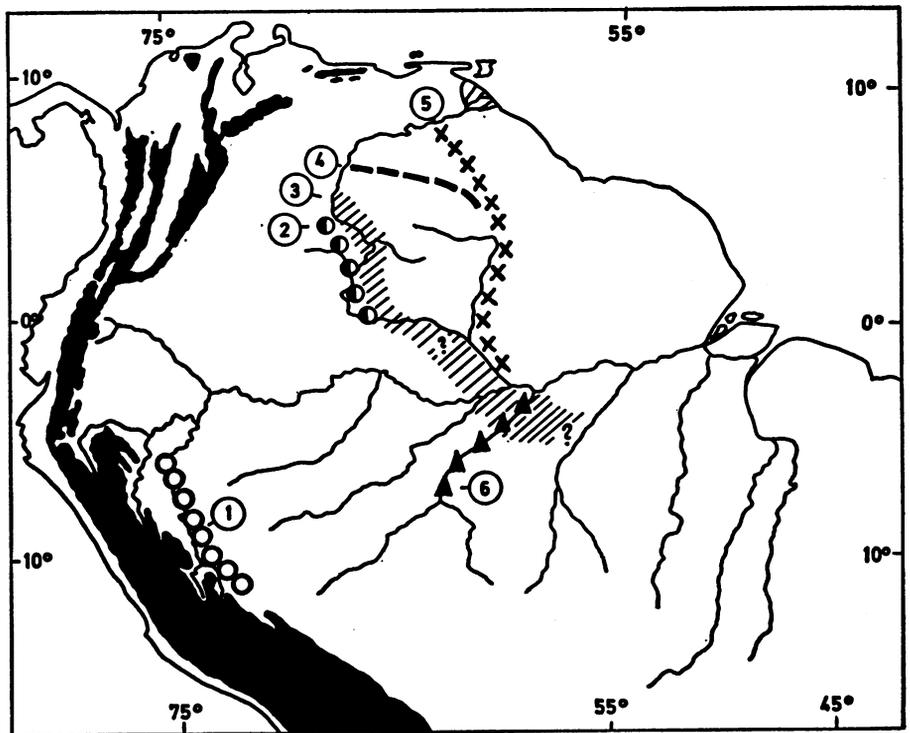


Fig. 6. Location of some secondary contact zones of Amazonian forest birds. (1, open circles) *Pipra chloromeros*-*P. rubrocapilla* and *Gymnopithys lunulata*-*G. salvini*; (2, half-solid circles) *Ortalis guttata*-*O. motmot* and *Gymnopithys leucaspis*-*G. rufigula*; (3, hatched area) *Ramphastos vitellinus culminatus*-*R. v. vitellinus*, north of the Amazon, and *R. v. culminatus*-*R. v. ariel*, south of the Amazon (this hybrid belt probably extends in a southeasterly direction beyond the Tapajós and Xingú rivers); (4, dashed line) *Pteroglossus pluricinctus*-*P. aracari*; (5, crosses) *Celeus grammicus*-*C. undatus* and *Tyrannetes stolzmanni*-*T. virescens*; (6, triangles) *Pteroglossus flavirostris mariae*-*P. bitorquatus*; (black areas) Andes mountains above 1000 meters.

northern Andes, at the end of the Tertiary; (ii) the repeated contraction and expansion of the forests as a result of climatic fluctuations during the Quaternary, leading to repeated isolation and rejoining of forest animal populations; (iii) the increased rate of extinction of animal forms. Because the populations of many tropical forest animals are small, a reduction in the size of their habitat must have drastically increased the chances of extinction of a number of forms, either within the forest refuges or through competition with newly evolved forms from other refuges upon the return of humid conditions.

Possibly the Amazonian forest fauna was not nearly so rich and diversified in the upper Tertiary as it is at present, mainly because of intensified speciation in the greatly enlarged forests and because of the fluctuating climate of the Pleistocene. This evolutionary boom may have been comparable to that of the montane fauna of the Andes during the Quaternary.

On the basis of evidence discussed by Moreau (12), it appears possible that, under favorable circumstances, the

speciation process in birds may be completed in 20,000 to 30,000 years or less, particularly in the tropics, where birds generally seem to occupy smaller niches than they do in cooler and less stable climates. This estimate refers mainly, though not exclusively, to passerine birds with a high reproductive rate and evolutionary potential. Under the same conditions speciation may take longer in larger birds, perhaps requiring on the order of a hundred thousand to several hundred thousand years. Factors such as the size of the refuge population and the degree of isolation of course influence the rate of speciation considerably. The above estimates are highly speculative, and the error involved may be very substantial. However, if the order of magnitude is at least approximately correct, it indicates that the Tertiary ancestors of present Amazonian birds may have speciated repeatedly during the Quaternary, and that many connecting links may have disappeared due to extinction. A similar assumption may also apply to the insect (34), amphibian, reptile (35), and mammal faunas (36) of Amazonia. Some of the

more strongly differentiated species probably originated in early Pleistocene refuges, while most other species and semi-species may date back to the late Pleistocene or, in the case of the latter, to the post-Pleistocene only. In view of the length of the Tertiary period (60 million years), during which the Amazonian fauna probably evolved rather slowly under quite uniform environmental conditions, the Quaternary faunal differentiation in tropical South America during the last 1 to 2 million years is, geologically speaking, very "recent" and occurred rather "rapidly."

It follows from the foregoing discussion that the Quaternary history of tropical faunas was basically quite similar to that of the faunas of higher latitudes (37). In the temperate regions, as well as in the tropics, climatic fluctuations caused pronounced changes in the vegetation cover and led to the isolation of comparatively small populations in refuge areas. The presumably smaller niche size (and lower population density) of tropical relative to temperate-zone forest animals and the correspondingly higher rate of speciation in the tropics under conditions of large-scale climatic fluctuations may explain the rapid differentiation of tropical forest faunas during the Pleistocene.

References and Notes

1. During cold and warm periods the vertical temperature gradient probably was increased and decreased, respectively, relative to the present gradient (a change of approximately 0.5°C per 100-meter difference in elevation); see J. Haffer [*Amer. Museum Novitates* No. 2294 (1967)] for details pertaining to South America. The repeated vertical displacement of the temperature zones led to frequent interruptions and rejoining of the animal populations along the mountain slopes, thereby causing a rapid differentiation of the montane faunas during the Pleistocene.
2. The main uplift of the Andes mountains did not take place until the upper Pliocene and lower Pleistocene [R. W. R. Rutland, J. E. Guest, R. L. Grasty, *Nature* 208, 677 (1965); J. Haffer, *J. Ornithol.* 109, 67 (1968)]. The rise of the Andes caused the climate to be very humid along the eastern base and foreland of the mountains. This was partly responsible for the vast expansion of dense forests onto the fully emerging Amazonian lowlands and northward and southward along the base of the rising Andes to Colombia and Bolivia, respectively. During the Tertiary, prior to the Andean uplift and the emergence of the Amazonian lowlands, forests probably had a rather restricted distribution along rivers and marginal lowlands of the elevated land areas north and south of the present Amazon valley.
3. H. F. Garner, *Rev. Geomorphol. Dynamique* 2, 54 (1966); *Sci. American* 216, 84 (1967).
4. A. N. Ab'Saber, *Bol. Soc. Brasileira Geol.* 6, 41 (1957); *Notic. Geomorfol.* 1, 24 (1958); A. Barbosa, *ibid.*, p. 87.
5. A. Cailleux and J. Tricart, *Compt. Rend. Soc. Biogeograph.* 293, 7 (1957); J. J. Bigarella and G. O. de Andrade, *Geol. Soc. Amer. Spec. Paper* 84 (1965), p. 433; M. M. Cole, *Geograph. J.* 126, 166 (1960).
6. H. F. Garner, *Bull. Geol. Soc. Amer.* 70, 1870 (1959).

7. The shrinkage of the humid lowland forests probably was more pronounced than it is shown to be on hypothetical vegetation maps by J. Hester [*Amer. Naturalist* 100, 383 (1966)] and T. C. Patterson and E. P. Lanning [*Bol. Soc. Geograf. Lima* 86, 8 (1967)]. The sweeping interpretation of Pleistocene vegetational changes in Amazonia by A. Aubréville [*Adansonia* 2, 16 (1962)] appears to be unacceptable in view of the fact that climatic changes occurred simultaneously in the Northern and Southern hemispheres.
8. T. van der Hammen and E. Gonzalez, *Leidse Geol. Mededel.* 25, 261 (1960); T. A. Wijmstra and T. van der Hammen, *ibid.* 38, 71 (1966); T. A. Wijmstra, *ibid.* 39, 261 (1967). Additional evidence of climatic fluctuations is available from currently arid western Peru; see E. P. Lanning, *Sci. Amer.* 213, 68 (1965); *Peru before the Incas* (Prentice-Hall, Englewood, N.J., 1967).
9. P. J. Darlington, *Zoogeography* (Wiley, New York, 1957), pp. 586-88; E. Mayr, *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, 1963), p. 372.
10. E. Stresemann and H. Grote, *Trans Intern. Congr. Ornithol.* 6th, Copenhagen, 1926 (1929), p. 358; E. Stresemann, *J. Ornithol.* 87, 409 (1939).
11. R. E. Moreau, *Proc. Zool. Soc. London* 141, 395 (1963); E. M. van Zinderen Bakker, Ed., *Palaeoecology of Africa and of the Surrounding Islands and Antarctica* (Balkema, Cape Town, 1967), vols. 2 and 3.
12. R. E. Moreau, *The Bird Faunas of Africa and Its Islands* (Academic Press, New York, 1966).
13. A. Keast, *Bull. Museum Comp. Zool.* 123, 305 (1961).
14. M. G. Ridpath and R. E. Moreau, *Ibis* 108, 348 (1966).
15. P. Hall, *Bull. Brit. Museum Zool.* 10, 105 (1963).
16. E. Mayr, *Systematics and the Origin of Species* (Columbia Univ. Press, New York, 1942); *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, 1963).
17. K. Knoch, in *Handbuch der Klimatologie*, H. Köppen and C. Geiger, Eds. (Borntraeger, Berlin, 1930), vol. 2, pp. 68-95; M. Velloso, in *Geografia do Brasil*, A. Teixeira, Ed. (Rio de Janeiro, 1959), vol. 1, pp. 61-111.
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19. J. A. Tosi, *Inst. Interamer. Cienc. Agr. OEA, Bol. Tec. No. 5* (1960), with ecological map of Peru.
20. C. Vaurie, *Bull. Amer. Museum Nat. Hist.* 138, 131 (1968).
21. J. Haffer [*Amer. Museum Novitates* No. 2294 (1967); *Auk* 84, 343 (1967)] has given details on this refuge as well as data on southern Central America.
22. Bird species which may have originated in this refuge include *Mitu salvini*, *Nothocercus urumutum*, *Gymnophis leucaspis*, *Grallaria (Thamnocharis) dignissima*, *Metopothrix aurantiacus*, *Ancistrops strigilatus*, *Porphyrolaema porphyrolaema*, *Heterocercus aurantivertex*, and *Todirostrum capitale*.
23. Bird species which may have originated in these refuges include *Pithys castanea*, *Gymnophis lunulata* and *G. salvini*, *Formicarius rufifrons*, *Grallaria (Thamnocharis) eludens*, *Contophtion mcilhennyi*, *Pipra chloromeros*, *Todirostrum albigacies*, and *Rhegmatorhina melanosticta*.
24. Bird species which may have originated in this refuge include *Neomorphus squamiger*, *Pyrrhura rhodogaster*, *Dendrocolaptes hoffmannsi*, *Myrmotherula sclateri*, *Rhegmatorhina hoffmannsi*, *Phlegopsis (Skutchia) borbae*, *?Heterocercus lineatus*, *Pipra nattereri*, *Pipra vilasboasi* (isolated forest east of the Tapajós river), *Todirostrum senex*, and *Idioptilon aenigma*.
25. Bird species which may have originated in this refuge include *Mitu tomentosum*, *Selenidera nattereri*, *Herpsilochmus dorsimaculatus*, *Myrmotherula ambigua*, *Myrmeciza disjuncta*, *Myrmeciza pelzelni*, *Percnostola caurensis*, *Rhegmatorhina cristata*, *Pipra cornuta*, *Heterocercus flavivertex*, and *Cyanocorax heilprini*.
26. Bird species which may have originated in this refuge include *Ortalis motmot*, *Brotogeris chrysopterus*, *Pionopsitta caica*, *Pteroglossus aracarí*, *Pteroglossus viridis*, *Selenidera culik*, *Ramphastos t. tucanus*, *R. v. vitellinus*, *Ceolus undatus*, *Hylaxetastes perrotii*, *Myrmotherula guttata*, *M. gutturalis*, *Gymnophis rufigula*, *Xipholaena punicea*, *Iodopleura fusca*, *Pachyrhamphus surinamensis*, *Haematoderus millitarsis*, *Perissocephalus tricolor*, *Pipra serena*, *Tyrannetes virescens*, *Microcochlearius josephinae*, *Phylloscartes virescens*, *Euphonia cayennensis*, and *Phaethornis malaris*.
27. Bird species which may have originated in this refuge include *Ortalis superciliaris*, *Pyrrhura perlata*, *Xipholaena lamellipennis*, *Selenidera gouldi*, *Ramphastos vitellinus ariel*, *?Pteroglossus bioturgatus*, *Pipra iris*, and *Gymnstinops bifasciatus*.
28. J. Haffer, *Hornero (Buenos Aires)* 10, 315 (1967).
29. This historic interpretation of the occurrence of nonforest birds in lower Amazonia contrasts with the earlier explanation given by E. Sneath [*Bol. Museu Goeldi* 6, 226 (1910); *J. Ornithol.* 61, 469 (1913); *ibid.* 78, 58 (1930)], who assumed that the nonforest birds reached their present stations by following the river valleys. The following facts strongly support the interpretation of a natural rather than a secondary (man-made) origin of the isolated savannas of lower Amazonia. (i) The soil of the savannas is a bleached sand (podzol type) in contrast to the lateritic brown loamy soil of the forests. The forest soil could not have been replaced completely by podzol in the short period since the supposed artificial clearing by man [H. Sioli, *Erdkunde* 10, 100 (1956)]. (ii) The flora of the isolated campos is decidedly nonhylean and is similar to that of the *cerrado* of central Brazil [A. Ducke and G. A. Black, *Anais Acad. Brasil. Cienc.* 25, 1 (1953); *Bol. Tec. Inst. Agr. Norte Belém* 29, 50 (1955); K. Hueck, *Die Wälder Südamerikas* (Fischer, Stuttgart, 1966), pp. 18, 21, 23]. (iii) The fauna of the isolated campos must be comparatively old, as a number of endemic forms are present. Examples are the mockingbird, *Mimus s. saturninus*; the grassland finch, *Coryphospiza melanotis marajoara*; and the snakes *Bothrops marajoensis* and *Crotalus durissus marajoensis*, the latter being restricted to Isla Marajó [P. Müller, *Die Herpetofauna der Insel von São Sebastião (Brasilien)* (Saarbrücker Zeitung, Saarbrücken, 1968), pp. 60-61].
30. L. Smith, *U.S. Nat. Museum Contrib. U.S. Nat. Herbarium* 35, 222 (1962); P. Müller, *Die Herpetofauna der Insel von São Sebastião (Brasilien)* (Saarbrücker Zeitung, Saarbrücken, 1968), pp. 60-61.
31. P. E. Vanzolini, *Arquiv. Zool. (São Paulo)* 17, 105 (1968).
- 31a. Several examples of this interesting situation have been discussed by J. Haffer [*Amer. Museum Novitates* No. 2294 (1967); *Auk* 84, 343 (1967)] and by C. Vaurie (20).
32. This situation is probably much more common among Amazonian animals than is recognized. Examples are found among toucans and other forest birds.
33. According to this view the rivers merely keep the representative species (which originated in distant forest refuges) geographically separated. By contrast, H. Sick [*Atlas Simp. Biota Amazônica* (1967), vol. 5, p. 517] recently postulated that the ancestors of many Amazonian forest birds "must have lived at a time when the area was not yet divided by large rivers as it is today." He assumed that the rivers later acted as effective barriers and caused the differentiation of the representative species on opposite banks. The effect of the river barriers may be restricted to variation at the subspecies level.
34. M. G. Emsley, *Zoologica* 50, 244 (1965). Contrary to Emsley's views, I believe that the differentiation of the *Heliconius* butterfly species may be related to the Quaternary climatic history of tropical South America rather than to the Tertiary paleogeographic history of this region.
35. E. E. Williams and P. E. Vanzolini, *Papéis Avulsos Dept. Zool. (São Paulo)* 19, 203 (1963); —, in *Simp. sobre o Cerrado* (Univ. of São Paulo, São Paulo, 1963), p. 307; —, *Atlas Simp. Biota Amazônica* (1967), vol. 5, p. 85; P. Müller, *Die Herpetofauna der Insel von São Sebastião (Brasilien)* (Saarbrücker Zeitung, Saarbrücken, 1968). These authors emphasized the importance of vegetational changes in Amazonia for the most recent differentiation of the neotropical reptile fauna. Direct evidence of a rapid rate of speciation in Brazilian reptiles

has been discussed recently by P. E. Van-zolini and A. N. Ab'Saber, *Papéis Avulsos Dept. Zool. (São Paulo)* **21**, 205 (1968).

36. P. Hershkovitz, *Proc. U.S. Nat. Museum* **98**, 323 (1949); *ibid.* **103**, 465 (1954); in *Ectoparasites of Panamá*, R. L. Wenzel and V. J. Tipton, Eds. (Field Museum of Natural History, Chicago, 1966), pp. 725-751; *Evolution* **22**, 556 (1968). The distributional history of the monkeys, tapirs, and rodents discussed in these articles may well be interpreted on the basis of Quaternary climatic and vegetational changes, many species probably having originated during the Pleistocene. B. Patterson and R. Pascual

[*Quart. Rev. Biol.* **43**, 440 (1968)] also assumed that a rapid differentiation at the species level, in some cases to the generic level, took place in South American mammals, particularly the rodents, during the Pleistocene.

37. G. de Lattin [*Grundriss der Zoogeographie* (Fischer, Stuttgart, 1967), pp. 327-329] summarized the Pleistocene history of the north temperate faunas.

38. K. Hueck, *Die Wälder Südamerikas* (Fischer, Stuttgart, 1966).

39. J. Haffer, *Amer. Museum Novitates No. 2294* (1967); *Auk* **84**, 343 (1967).

40. A. Aubréville, *Etude écologique des princi-*

pales formations végétales du Brasil et contribution à la connaissance des forêts de l'Amazonie brésilienne (Centre Technique Forestier Tropicale, Nogent-sur-Marne, France, 1961), pp. 1-265.

41. W. M. Denevan, *Ibero Americana* **48**, 7 (1966).

42. I am grateful to Professor Ernst Mayr, Harvard University, for many helpful suggestions concerning the manuscript of this article. I also thank Eugene Eisenmann, American Museum of Natural History, New York, and Dr. François Vuilleumier, University of Massachusetts, Boston, for critical remarks on an earlier version.

Biosynthesis of Oligosaccharides and Polysaccharides in Plants

Mechanisms of enzymic synthesis of complex plant carbohydrates are reviewed.

W. Z. Hassid

Plants are the chief producers of carbohydrates in nature by the process of photosynthesis. Most forms of life which are unable to photosynthesize depend either directly or indirectly on the assimilation of carbon dioxide by plants. All the organic substances which arise from photosynthetic processes serve the other forms of life as starting materials for diverse metabolic functions. While there are many ways in which organic substances are decomposed, there is only one reaction, photosynthesis, which for millions of years has counterbalanced death and decomposition.

Monosaccharides are synthesized by green plants, starting with a carboxylation reaction in which D-ribulose-1,5-diphosphate serves as the acceptor of CO₂ for the formation of phosphoglyceric acid (1). By a subsequent series of enzymic reactions, a number of phosphorylated monosaccharide derivatives are produced in the photosynthetic carbon dioxide cycle. Some of these phosphorylated sugars, such as D-glucose-6-phosphate and D-fructose-6-phosphate, are hydrolyzed to free sugars, causing in some cases the accumulation of large concentrations of D-glucose and D-fructose in plants.

The phosphorylated monosaccharides

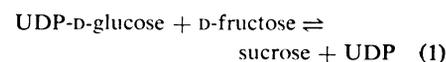
produced in the photosynthetic carbon dioxide cycle are partially consumed in respiration with the production of energy which is utilized for the numerous metabolic reactions of the plants. They are also converted by a series of enzymic reactions to sugar nucleotides, chiefly UDP-D-glucose (2), and to other sugar nucleotides, such as UDP-D-galactose, GDP-D-glucose, and ADP-D-glucose (3). The sugar moieties of these nucleotides are interconverted by various specific epimerases, and serve as donors for the formation of the numerous oligosaccharides and polysaccharides (4).

A monosaccharide must be activated to enable the enzyme to transfer it to an acceptor for the synthesis of an oligosaccharide or to lengthen the chain by subsequent transfers for the formation of a polymer. From the thermodynamic point of view, nucleoside diphosphate sugars are superior donors for complex saccharide formation, because they have the higher negative free energy of hydrolysis (ΔF°) than other glycosyl compounds (5). Uridine diphosphate-D-glucose has a relatively high negative ΔF° of hydrolysis of -7600 calories; although it has never been determined for other sugar nucleotides, it is assumed that the nucleoside

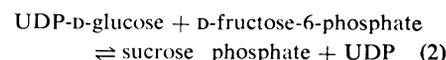
diphosphate sugars, containing bases other than uracil or sugars other than D-glucose, have approximately the same ΔF° values. The most important reaction for complex saccharide formation appears to involve sugar nucleotides.

Oligosaccharides

Sucrose, the most abundant oligosaccharide in higher plants, was first synthesized in vitro by a bacterial enzyme obtained from *Pseudomonas saccharophila* from α -D-glucose-1-phosphate and D-fructose (6). However, in this reaction the equilibrium favors the breakdown rather than the synthesis of sucrose. Various attempts by a number of investigators to synthesize sucrose by an enzyme from a plant source from α -D-glucose-1-phosphate and D-fructose failed. Leloir and his collaborators (7) later found that the donor of D-glucose for sucrose formation was not α -D-glucose-1-phosphate but the sugar nucleotide UDP-D-glucose. The synthesis takes place by two separate enzymes, one utilizing D-fructose and another D-fructose-6-phosphate as the acceptors according to the following two reactions



and



The sucrose phosphate formed in reaction 2 is hydrolyzed by a phosphatase, resulting in the formation of free sucrose.

Since ΔF° for hydrolysis of UDP-D-glucose is about -7500 calories per mole, formation of the glycosyl bond of sucrose is favored. For most glycosides, synthesis from a nucleotide sugar precursor would proceed with a favorable free-energy change of about

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